



**Mating systems and sexual selection in ungulatesNew
insights from a territorial species with low sexual size
dimorphism:the European roe deer (Capreolus
capreolus)**

Cécile Vanpé

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UNIVERSITE PAUL SABATIER - TOULOUSE III
SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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MATING SYSTEMS AND SEXUAL SELECTION IN UNGULATES
New insights from a territorial species with low sexual size dimorphism:
the European roe deer (*Capreolus capreolus*)

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Jean-Michel Gaillard	CNRS Lyon	Invited

"Of the branches of biological science to which Charles Darwin's life-work has given us the key, few, if any, are as attractive as the subject of sexual selection"

(Fisher 1915)

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Note that figures from papers are not listed here.

ABSTRACT

The aim of this study was to use for the first time molecular techniques (microsatellite genotyping and paternity analyses), in combination with field ecology studies, to provide data on male breeding success and identify the main determinants of variation in male breeding success in two long-term monitored populations of European roe deer *Capreolus capreolus* (Bogesund in Sweden and Trois Fontaines in France). The results show that males can sire up to 6 fawns per year and 14 fawns during their entire lifetime. As expected from the low level of sexual size dimorphism and the territorial mating system of roe deer, variance in male lifetime breeding success, and so opportunity for sexual selection, are lower than in highly dimorphic species such as red deer *Cervus elaphus*, suggesting a low polygyny level in roe deer. Males can successfully breed as young as 2 years of age, but breeding success of sub-adults is lower than that of older males. Successful breeding among sub-adults may be restricted to those high quality males that are able to defend a territory. Breeding success also tends to decline after 8 years of age (senescence), probably in relation to the loss of dominance. Male body mass and antler size positively affect male breeding success. It is known that antlers are used by males as a weapon in combats to defend their territory. However, my results also show that antler size is a honest signal of male phenotypic quality and may be used as a cue for rival males and females to assess male fighting ability, sexual vigor and/or phenotypic quality. In addition, male access to females and male breeding success are positively related to territory size, but not to habitat quality within a male's territory. Hence, the territorial mating system of roe deer differs from the conventional resource defense polygyny system and seems rather to conform to a "low risk – low gain" strategy. Finally, using paternity analyses, I also provide evidence that multiple paternity is likely, but infrequent, in roe deer, suggesting that multiple mating among females may have evolved as a means to enhance fertilisation success. This study provides new insights into the evolution of mating systems and sexual selection in ungulates.

Keywords: antler size, *Capreolus capreolus*, lifetime breeding success, male, mating system, microsatellites, paternity analysis, roe deer, sexual selection, sexually selected traits, territoriality, ungulates.

RESUME

Le but de cette étude était d'utiliser les techniques moléculaires dans deux populations de chevreuil, pour estimer la variance du succès reproducteur des mâles et identifier les principaux déterminants de cette variance. Comme attendu du fait de son faible dimorphisme sexuel, la variance dans le succès reproducteur à vie des mâles, et donc l'opportunité pour la sélection sexuelle, sont faibles chez le chevreuil, suggérant un faible degré de polygynie. Les mâles peuvent se reproduire dès 2 ans, mais avec un succès reproducteur inférieur à celui des mâles plus âgés. Le succès reproducteur tend aussi à décroître après 8 ans. La masse corporelle, la taille des bois, de et la taille du territoire des mâles, affectent positivement leur succès reproducteur, mais pas la qualité de l'habitat dans leur territoire. Cette étude apporte de nouveaux éléments sur l'évolution de la territorialité et la sélection sexuelle chez les ongulés sauvages.

Mots clés: analyse de paternité, *Capreolus capreolus*, chevreuil, mâle, microsatellites, ongulés, sélection sexuelle, succès reproducteur à vie, système de reproduction, taille des bois, territorialité.

INTRODUCTION



Roe buck
(photograph by Olivier Villa)

I. GENERAL INTRODUCTION

CONTEXT OF THE STUDY

The European roe deer (*Capreolus capreolus*) is an economically and socially important game species which is widespread across Europe. It constitutes in Europe, with other wild ungulates, a resource of high economic (hunting), cultural (photography and other recreational activities) and ecological value (as part of biodiversity) (Cederlund *et al.* 1998). This interest, together with the quasi-disparition of large predators during most of the XXth century, the improvement of forest habitat, the mildness of weather during winter, the easy access to crop fields, the plasticity of this species with high reproductive and dispersal potentials, and the determination among hunters to increase game species populations, has favoured its geographical expansion with a demographic explosion of roe deer in Europe during the last decades (Gill 1990; Warren 1997; Cederlund *et al.* 1998; see Figure 1).

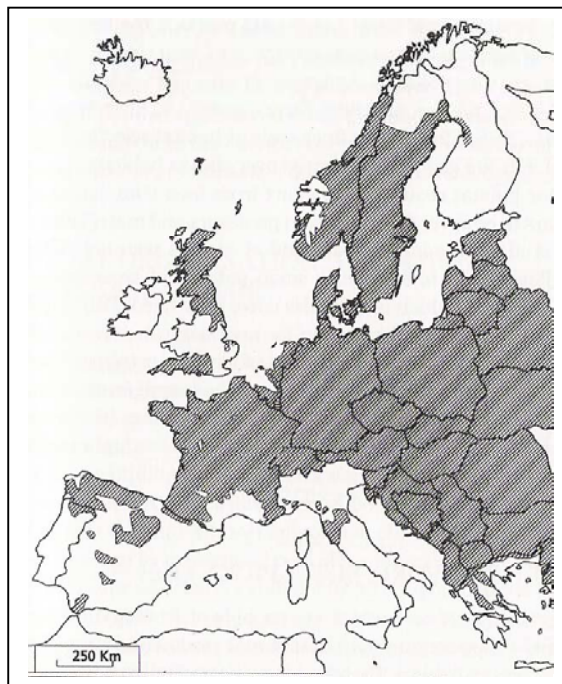


Figure 1. The present distribution of European roe deer in western Europe. In addition to the areas marked on the map, roe deer extend further in Russia to the Ural mountains and are found in scattered populations in Turkey. From Linnell *et al.* (1998a).

Roe deer is thus now the most widely distributed and abundant large herbivore in Europe (> 1.5 million in France; annual harvest x 6.1 over the last 20 years in France; data ONCFS; see Figure 2). In 1984, over 1.6 million roe deer were harvested in Europe (Gill 1990), a figure

which is probably over 2.5 million today (Linnell *et al.* 1998a). Although the roe deer is primarily a woodland species, adapted to exploit the early stages of forest succession where their preferred food is most abundant (Wahlström 1995), it occupies today a wide range of habitats, including deciduous, coniferous and Mediterranean forests, shrublands, moorlands and marshes and may even adapt to open agricultural areas (Zejda 1978; Danilkin & Hewison 1996).

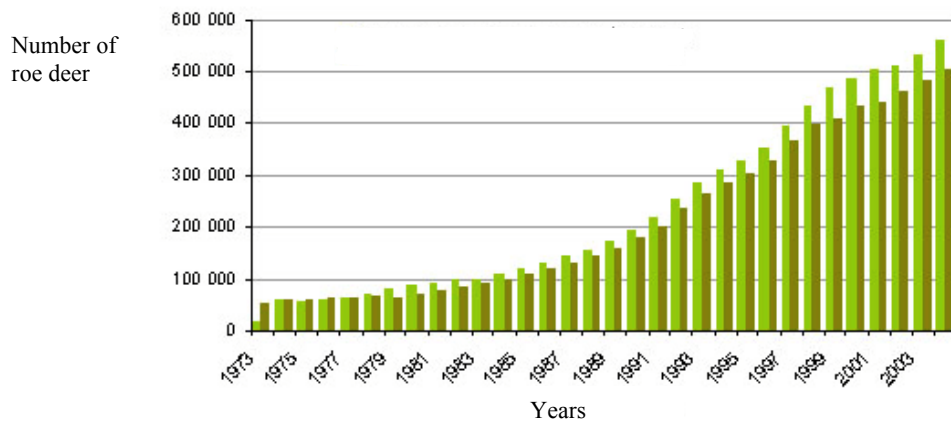


Figure 2. Variation of the number of roe deer allowed to be shot (in light) and actually shot (in dark) in France since 1973. Data ONCFS.

In parallel to this geographic and demographic expansion of roe deer, new problems have appeared, such as the increase in forest and agricultural damage (see Gill 1992; Cederlund *et al.* 1998 for more details), the growing number of collisions between animals and vehicles (> 20,000 / year in France; Bruinderink and Hazebrook 1996), and the expansion of diseases vectored by deer such as the Lyme borreliosis disease (Pichon *et al.* 1999; Gortázar *et al.* 2006). These new problems generate high costs to society (for example, in Germany, there are 50,000 - 100,000 reported accidents per year, costing perhaps 1 million \$US; Cederlund *et al.* 1998), which explains the urgent need to manage roe deer populations. The determination and the understanding of the factors governing population growth, especially in terms of individual survival and fecundity, have thus become a major challenge for ecologists and managers.

As a consequence, for three decades now, roe deer has been intensively studied. From long-term monitoring of marked populations, increasingly rich and accurate estimates of demographic parameters have been obtained, especially on survival (e.g., Gaillard *et al.* 1993a, 1997, 1998a; Loison *et al.* 1999a; Festa-Bianchet *et al.* 2003; Pettorelli *et al.* 2003a, 2003b, 2005). Female reproduction has also been widely investigated (e.g., Gaillard *et al.*

1992; Hewison & Gaillard 2001; Kjellander *et al.* 2004) and male territoriality broadly described (e.g., Bramley 1970; Strandgaard 1972; Putman 1988; Linnell & Andersen 1998). However, very few studies have analyzed the territorial behaviour of this species in the light of modern evolutionary theories of behavioural ecology (but see Johansson 1996; Börger 2006; and reviews by Hewison *et al.* 1998 and Liberg *et al.* 1998) and no reliable data are as yet available on male reproductive success. Such data are, however, necessary to better understand the evolution of the life history strategies and the demographic processes of this species in order to efficiently manage roe deer populations. A first reason for this lack of data on male reproductive success and male mating tactics is that population biologists have long under-estimated the role of males in population dynamics and so few efforts have been allocated to the estimation of male demographic parameters and male mating success. The majority of population dynamical models only view the population from the female point of view (Caswell 2001). Yet, males can affect the population dynamics by being a component of population density and also by affecting the demographic rates of females through their behaviour (e.g., mate searching behaviour, male harassment, male resource use; Mysterud *et al.* 2002; Rankin & Kokko 2007). Another reason is that the direct observation of territorial and mating behaviour is particularly difficult in roe deer because of the dense structure of its usual habitat (essentially forest and scrub areas), its solitary and wary behaviour. Hence, a reliable behavioural estimation of male reproductive success is virtually impossible, except maybe in open landscape areas (see Börger 2006).

Behavioural ecology is the study of the ecological and evolutionary basis for animal behaviour and of the role of behaviour in enabling an animal to adapt to its environment, enhancing its chances of survival and reproduction. Behavioural ecology draws its inspiration directly from Darwin's theory of evolution by means of natural selection, published in *On the origin of Species by Means of Natural Selection* in 1859. But when Darwin formulated his theory of natural selection, he had no knowledge of the mechanism of heredity, and the modern statement of the theory is now in terms of genes (e.g., Dawkins 1976). Behavioural ecology studies are thus based on three main principles directly derived from Darwin's theory of evolution (Krebs & Davies 1993). First, during evolution, natural selection favors individuals that adopt life history strategies which maximize their individual fitness (i.e., the genetic contribution to future generations; Endler 1986; Charlesworth 1994). Second, the way in which survival and reproductive output are best traded-off in life history depends critically on ecology, the physical environment an individual lives in, its food, competitors and

predators. Third, since an individual's success at surviving and reproducing depends on its behaviour, selection tends to design animals which are efficient in foraging, avoiding predators, mating, parental care, etc.

Mating systems were first discussed in evolutionary terms by Darwin (1871) and later by Fisher (1930) and Huxley (1938). But it is mainly over the last decades that the predictive framework provided by evolutionary theory, combined with field studies of increasing duration and sophistication (Clutton-Brock 1989) and major developments in genetic theory, has led to a rapid improvement in our understanding of the functional significance of social and reproductive behaviour, providing a better overall view of mating systems, sexual dimorphism, or patterns of parental care (e.g., Trivers 1972; Wilson 1975; Emlen & Oring 1977; Clutton-Brock & Harvey 1978). Despite this progress, studies which have used an evolutionary approach to investigate male mating systems in roe deer are rare (but see Johansson 1996; Börger 2006), since a reliable estimation of reproductive success is pivotal for behavioural ecology studies.

With the recent development of advanced molecular biology tools (particularly microsatellites) and sophisticated analytical methods in population genetics, an alternative and direct approach is now available for estimating male reproductive success by paternity analyses (e.g., McCracken & Bradbury 1977; Burke 1989; Pemberton *et al.* 1992; Marshall *et al.* 1998b). Molecular tools have thus recently allowed to document the social organisation and mating systems of many species in unprecedented detail, frequently challenging long-held beliefs on the subject (Birkhead *et al.* 1990; Hughes 1998). However, although this approach is especially useful for elusive species such as the roe deer for which a behavioural estimation of male reproductive success is very difficult, no study has yet used molecular tools to investigate male reproductive success and mating system in roe deer.

The purpose of my Ph.D. study was therefore to use, for the first time, molecular tools to provide data on male breeding success in roe deer and to explore the extent and causes of individual differences in breeding success among males. I investigated in detail the male mating system of roe deer within the framework of an evolutionary approach. In this context, I was interested in the theories of behavioural ecology on mating systems and sexual selection. As Gaillard *et al.* (1998b) pointed out, "*the mating system in relation to sexual selection are obvious gaps in our current knowledge of population processes in roe deer*". I examined the relationship between mating system and sexual selection in roe deer and, more widely, in ungulates, regarding the mating systems as one of the main factors that may influence the strength, form and consequences of sexual selection.

II. MATING SYSTEMS AND SEXUAL SELECTION WHAT THE THEORY TELLS US

In this chapter, I present the conceptual framework on which my study was based. More precisely, I introduce the theories of behavioural ecology on mating systems and sexual selection, and develop the theoretical predictions concerning the factors influencing variation in sexual selection among species, focussing on the role of mating systems.

II.1. DIVERSITY AND EVOLUTION OF MATING SYSTEMS

The term **mating system** is commonly defined as the general behavioural strategies adopted by individuals of both sexes in obtaining mates (Emlen & Oring 1977; Clutton-Brock 1989). It encompasses such features as the number of mates acquired, the manner of mate acquisition, the presence and characteristics of any pair bonds, and the patterns of parental care provided by each sex (Emlen & Oring 1977).

II.1.1. Parental care and party size

Although different mating systems have long been recognized in evolutionary biology, there is no strict agreement on their classification (Andersson 1994). The number of mating partners per male and female (also called party size) is one of the main criteria (Krebs & Davies 1993). It is linked to the ability of a portion of the population to control the access of others to potential mates, which depends in large part on the degree of **parental care** required for successful rearing of young (Emlen & Oring 1977). Four different mating systems have thus been distinguished in relation to the different patterns of parental care: (i) **Monogamy** (i.e. a male and a female form a pair bond) should be favored mainly when males and females share parental care for their young after birth and, in some cases, for the eggs. This is the case in the great majority of bird species (90% of birds: Lack 1968; e.g., in arctic skua *Stercorarius parasiticus*: O'Donald 1983), but in very few mammals (less than 3% of mammals, e.g., in several species of bats and foxes: Kleiman 1977). (ii) **Polygyny** (i.e. a male mates with several females, while each female mates with only one male) should be favored particularly when females are strongly predisposed to care for their young (for example, because of the constraints of a prolonged period of gestation and lactation). This is the case in most mammals for which males usually provide little parental care after birth and so females

take sole responsibility for the care of the young (e.g., in northern elephant seal *Mirounga angustirostris*: LeBoeuf 1974). (iii) **Polyandry** (i.e. a female mates with several males, while each male mates with only one female) is more infrequent and mainly appears when the male provides most parental care (e.g., in pipefishes and seahorses: Berglund *et al.* 1986; in spotted sandpipers *Actitis macularia*: Oring & Lank 1982). (iv) **Promiscuity** (i.e. both male and female mate several times with different individuals so that there is a mixture of polygyny and polyandry) should develop when either sex may care for the eggs or young (e.g., in Soay sheep *Ovis aries*: Coltman *et al.* 1999a).

II.1.2. Strategy of monopolization of mates and evolution of mating systems

In mammals, which are commonly polygynous since females commonly provide most of the parental care, the reproductive success of females is mainly limited by access to the resources necessary to breed and to meet the energy requirements of gestation and lactation (e.g., food, breeding sites), whereas the reproductive success of males is limited more by access to females (Trivers 1972). As a consequence, while the distribution of females should depend primarily on resource dispersion (modified by predation pressure and the costs and benefits of associating with other individuals), males should distribute themselves in relation to female dispersion (modified by male density) in order to gain access to as many mates as possible (Emlen & Oring 1977; see Figure 3).

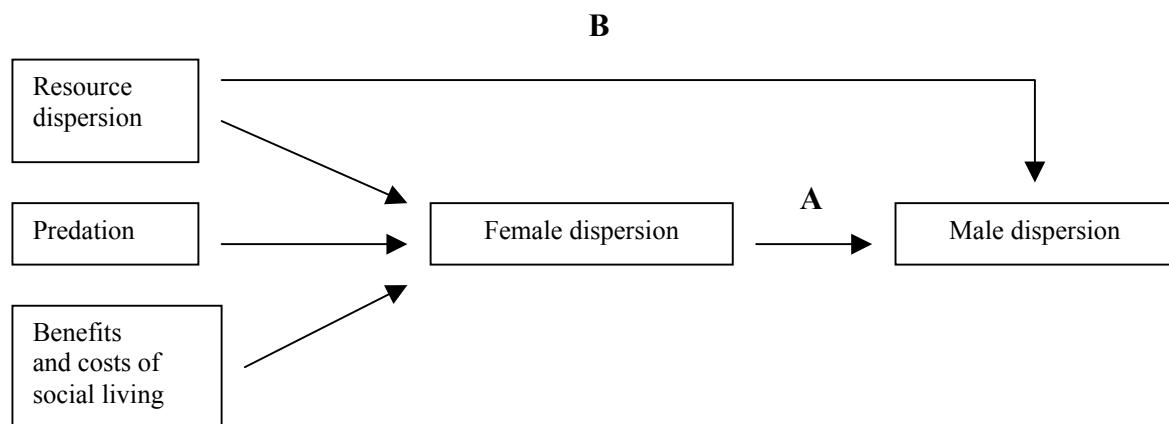


Figure 3. The two-step process influencing mating systems in cases where males do not provide parental care. Males thus have two main options to maximize the number of matings: they could either compete for females directly (A) or indirectly (B). Figure adapted from Krebs & Davies (1993).

Clutton-Brock (1989) concluded that variation in mating behaviour of male mammals depended mainly on the defensibility of females, and that this was directly related to the

density and distribution of females, female range size and female group size and stability, and indirectly to the distribution of resources. Hence, males may have two main options to gain access to females: they can either compete for females directly or they can compete indirectly, by anticipating how resources influence female dispersion and competing for resource-rich sites (see Figure 3).

Emlen & Oring (1977) have thus proposed the following classification of polygynous mating systems, based on the costs and benefits of defensibility or monopolization of mates (see Figure 4).

- In **female defence polygyny**, males gain access to females directly by following and defending one or a group of females against rivals.

- When females live in small groups, males move over large areas searching for, associating with, and trying to mate with females in estrous. This characterizes the « **roving/tending** » strategy (e.g., in bighorn sheep *Ovis canadensis*: Hogg & Forbes 1997; grey kangaroos *Macropus giganteus*: Jarman & Southwell 1986). This strategy should be favored when females are spatially and temporally unpredictable (e.g., at low population densities or when food is unpredictable and females range over large areas; Gosling 1986).

- When females live in large herds or groups, the most dominant males may attempt to defend and exclusively monopolize relatively stable groups of females. This characterizes the « **harem-defence** » strategy (e.g., in red deer *Cervus elaphus*: Clutton-Brock *et al.* 1982; northern elephant seal: LeBoeuf 1974, feral horses *Equus caballus* and Przewalski horses *Equus ferus przewalskii*: McDonnell & Haviland 1995).

- In **resource defence polygyny**, males gain access to females indirectly by defending a space against other males containing critical resources essential to females (e.g., food, birth sites) and where several females can occupy small ranges. This characterizes the « **territorial** » strategy (e.g., in roe deer: Liberg *et al.* 1998). This strategy is expected to be favored when females are spatially and temporally predictable (e.g., when females occupy small ranges containing clumped and high-quality food resources; Gosling 1986).

- In **male dominance polygyny or lekking polygyny**, males aggregate into groups during the breeding season on a communal display area where each male defends a tiny mating territory containing no resources at all and attempts to attract and court females which visit the communal display solely for mating. This mainly characterizes the « **lekking** » strategy (e.g., in fallow deer *Dama dama*: Langbein & Thirgood 1989). Males in this case

provide no material resources to females, only genes, and they compete directly for dominant status or position within stable assemblages. This strategy is expected to be favored when neither females nor their home range are economically defensible or monopolizable.

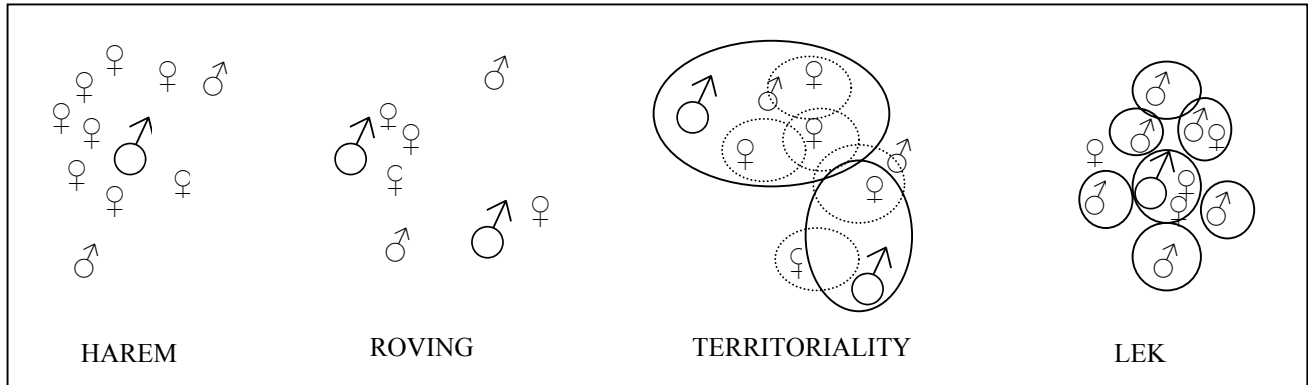


Figure 4. Schematic figure illustrating the various polygynous mating systems in mammals. Big ♂ signs represent dominant or territorial males. Small ♂ signs represent subordinates or non-territorial males. Dotted circles represent female home ranges. Solid circles represent male territories.

Hence, according to Emlen & Oring (1977), ecological factors determine the spatio-temporal distribution of mates, which determines the degree and the manner to which males can monopolize access to females, usually defined as the environmental potential for polygyny. This is formalized in the concept of **operational sex ratio** (i.e. the ratio of fertilizable females to sexually active males at a given time; Emlen & Oring 1977). The environmental potential for polygyny is expected to be maximal when the distribution of females (or the distribution of resources vital for them) is not homogeneous in space and time, and when the number of receptive females, at a given time, is higher than that of sexually mature males.

The three decades since the paper of Emlen & Oring (1977) was published have seen an explosion in empirical and theoretical studies of reproductive behaviour and, from these studies, mating systems have proven more complicated than originally thought (Reynolds 1996).

First, as Leuthold (1977) noticed, the classification of Emlen & Oring (1977) “*should not be viewed as final or comprehensive, but rather as an attempt to identify similarities and differences between social organizations on the basis of the information currently available*”. There is actually no discrete distinction between the 3 main types of polygynous mating systems described by Emlen & Oring, and the variability of polygynous mating systems should probably be more realistically described as a continuum. As Jarman (1974) pointed

out, “*any attempt to subdivide a continuum creates problems*”. Langbein & Thirgood (1989) have thus considered that the mating system can be regarded as a continuum depending on the type and degree of territoriality from lek to dominance and harem, via multiple stand, stand, temporary stand, and so on. Also, Maher & Lott (1995) suggested that territoriality could be viewed as one point along a continuum extending from exclusivity to a system based on completely overlapping ranges and dominance.

Second, it has long been thought that all individuals of one sex of a species display species-specific behaviour. However, as with other aspects of the phenotype, we know now that there is a wide variation in behaviour within a species (**behavioural plasticity**), especially in mating behaviour. Mating systems do not only vary between species, but also within species, depending on environmental factors such as population density, habitat, climate, food resources and predation pressure (e.g., Lott 1984, 1991; Thirgood *et al.* 1999). In fallow deer, for example, mating systems thus range from non-territorial males courting individual estrous females (roving), to both resource defence polygyny (territoriality), lek polygyny and female defence polygyny (harem-defence; see Langbein & Thirgood 1989). The mating systems used within a population thus depend mainly on food resource dispersion, which in turn affects female distribution. Also, variations in age distribution within a population can result in a mating system shift (see Byers & Kitchen 1988 on American pronghorn *Antilocapra americana*). On the National Bison Range, Byers (1988) observed in American pronghorn a mating system shift from territoriality to harem defence, following a winter in which most older males died resulting in a skewed age distribution of males towards young males. The decay of territoriality occurred gradually, over 5 years. Sometimes, mating behaviour can even vary between individuals within a population, for example, in relation to age class or body size. While the largest individuals usually tend to display and fight to attract mates, smaller individuals commonly tend to employ “sneaky strategies” which make the “best of a bad job”. One may then talk about alternative mating tactics. Rocky Mountain bighorn sheep are a good example. The rams use three different mating tactics: tending, blocking and coursing (Hogg & Forbes 1997). Tending males defend estrous ewes but do not prevent them from leaving. Blocking males also defend estrous females but try to prevent them from leaving for dominant males. Coursing males fight with other males to gain temporary access to copulations with females, instead of defending them. But bighorn rams are not stuck with one tactic, and mating tactics depend on social rank, with subordinates usually adopting a coursing strategy.

II.2. THE THEORY OF SEXUAL SELECTION

Mating systems, as defined by Emlen & Oring (1977), actually encompass both sexual selection (specifically the number of mates obtained and the manner in which they are acquired) and parental care (Reynolds 1996). Hence, if we want to better understand the evolution of mating systems, the study of sexual selection is pivotal (Emlen & Oring 1977).

II.2.1. Origin of the competition over mates

Sexual reproduction is commonly **anisogamous**: females produce a few large macrogametes rich in energy (eggs), whereas males produce a lot of small, highly mobile microgametes (sperm). As a consequence, while females need only one male to be fertilized and father a particular litter of young males, males have the capacity to fertilize a number of females (Bateman 1948). Trivers (1972) has expressed this difference in the size of gametes in terms of parental investment between the sexes: females usually allocate more energy to parental investment (including investment in the production of gametes, in the nourishing of the embryo and in the care of offspring) than males and so males can father more young than females. Hence, males usually have a much greater potential rate of reproduction than females. This has consequences in terms of optimal mating strategies for the two sexes. While males should attempt to mate with as many fecund females as possible, females should try to choose the highest quality males as mates. As a result, many sexually active males are searching at a given time for relatively few receptive females. As Bateman (1948) stated, “*the sex which invests the most in producing offspring becomes a limiting resource over which the other sex will compete*”. This sets up a competition among males for the scarce resource which is females and allows females to choose their partner, that is manifest as sexual selection. Notice however that in some cases (for example, when males provide nutrition for females, thus enhancing female fecundity), males can be the scarce resource too and then females compete between themselves for access to males (Gwynne & Simmons 1990; Gwynne 1991).

II.2.2. Darwin's theory of sexual selection

The observation of conspicuous traits (in appearance or behaviour) that defied explanation by ordinary natural selection for improved survival and which occur only in one sex, especially during the breeding season, lead Darwin to the conclusion that these traits may

be favored by competition over mates rather than by the struggle for existence (Darwin 1859). Classic examples of such elaborate traits are the train of peacocks (*Pavo* spp.), the ornaments of birds of paradise and the antlers of deer. These observations were at the origin of Darwin's theory of sexual selection, later developed in *The Descent of Man, and Selection in Relation to Sex* published in 1871. The objective of sexual selection theory is thus to explain the evolution of such differences.

Darwin (1859) drew a clear distinction between sexual selection and natural selection, because he saw them as forces which are often in opposition. As Darwin (1859) put it, sexual selection depends: "*not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex. The result is not death to the unsuccessful competitor, but few or no offspring.*" Sexual selection is nowadays often considered as a special case of natural selection (e.g., Mayr 1972). Natural and sexual selection would be part of an unitary process which can operate on variation in fitness generated for various reasons at several life-history stages (Clutton-Brock 2003).

Darwin (1859, 1871) defined **sexual selection** as selection acting on individual traits of one sex (usually males) that affects mating success or fertilization and which arises from competition over mates. If the differences in the traits are hereditary, sexual selection will lead to spread of those attributes that enhance reproductive success (named **sexually selected traits**). Sexual selection of a trait can then be viewed as differences in reproductive success, caused by competition over mates, and related to the expression of the trait (Andersson 1994).

Darwin (1871) recognized two main ways by which sexual selection can act. First, it could arise through **competition between males** to gain access to females. This form of competition for mates has been later called **intra-sexual selection** by Huxley (1938). Second, it could arise through **female mate choice**, which consists of competition between males to attract females and should lead to the elaboration of conspicuous structures or behavioural signals that attract females and that are reliable indicators of male phenotypic quality or sexual vigor (e.g., body condition, ornament, vocalizations, patch color). This form of competition for mates has been later called epigamic selection by Huxley (1938) and **inter-sexual selection** by others. In practice, these two mechanisms may occur together and may favor the same traits (e.g., the antlers of deer may be considered as weapons but also as epigamic ornamental traits).

II.2.3. The various forms of intra-sexual selection

Intra-sexual selection is not restricted to male-male combat. It can take several forms and favor a wide range of attributes (Andersson 1994):

- **contest competition**, which consists in direct interactions between males, such as display and/or fight, for access to females, or resources needed to attract mates, and is expected to favor the development of male traits that enhance their strength and their ability to fight and dominate (e.g., body mass or size, weapon size);
- **scramble competition**, which is linked to the rapidity of location of a mate, and is expected to favor sensory and locomotory organs, or protandry;
- **endurance rivalry competition**, which is linked to the ability of males to remain reproductively active and maintain a top rank during breeding season, the amount of time that a male can display without leaving for food or water;
- **sperm competition** (e.g., mate guarding, sequestering, ability of displacing rival sperm; see Eberhard 1985), which should favor production of abundant sperm and structures to store sperms. Male-male competition indeed does not stop when copulation is over. The true determinant of a male's mating success is not whether he copulates, but whether his sperm actually fertilize eggs. If a female mates with multiple males within a short period of time, there will be a race among the males to successfully fertilize her eggs.

II.2.4. Inter-sexual selection and evolution of female mate choice

As they are likely to play major roles in the evolution of conspicuous secondary sex traits, contest competition and mate choice have received by far the most attention (Andersson 1994). While contest competition has been rapidly and broadly accepted as a powerful selection pressure favoring an increase in male strength and the elaboration of structures used as weapons, female mate choice has been the subject of much discussion and criticism since Darwin first exposed his theory. Darwin simply assumed that females have preferences for certain types of males without suggesting how such preference might have arisen or how it might be maintained in a population by selection. But why do females choose mates, although such choice is likely to have costs? How did female preferences for male traits evolve?

- **Direct benefits**

It has been proposed that, by choosing mates, females may gain direct benefits. For example, the mate has higher fecundity and sexual vigor; or is a better provider of food to the

partner or care to the offspring; or defend a breeding place that is safer and/or richer in food; or offers better protection against predators or harassment by other males; than do other males (see reviews by Price *et al.* 1993 and Andersson 1994). However, this process cannot explain all sexually selected traits. In lekking species for example, females express a preference among males while males provide no resources nor parental care, and females only receive genes from the male they select.

- **Indirect benefits**

Attempts to resolve the paradox have postulated that females receive an indirect benefit in the form of increased genetic quality of their offspring. The preferred male may provide genes that increase the survivorship or mating success of the offspring as compared to the genes provided by less desirable males (reviewed in Kokko *et al.* 2003). Females would thus select mates on the basis of indicators of male genetic quality that predict higher offspring fitness. There are three main theories on how female preferences for male indicators of genetic quality may evolve. Notice that these alternative explanations of the evolution of female preference are all compatible and may apply in combinations (Andersson 1994).

- **Fisherian run-away process or sexy-son hypothesis**

Fisher (1930) suggested, in his book *The Genetical Theory of Natural Selection*, that male sexual ornaments could be driven to extremes because of female preferences. According to him, at the starting point, there is genetic variation for a male trait that gives males some advantage for surviving – to illustrate the thought of Fisher, I took here the example of a slightly longer tail makes the male a better flier, which allows him to better escape predators. In parallel, there is genetic variation among female preference for this male trait, with females preferring males with longer tails who tend to bear sons with higher survival. Both traits have thus a heritable genetic basis. Hence, male genes for an exaggerated tail and female genes for an exaggerated preference for the tail will spread among offspring and both genes will become linked together. Males with the preferred tail would then gain an additional advantage, because they would transmit their genes to more offspring and have higher mating success. Females preferring males with the longer tail would, in turn, gain an advantage because they would transmit the genes for that elongated structure to their sons, who would in turn survive better and so also be chosen by females with such a preference. A run-away process of selection would then ensue, favoring even stronger preference and more extreme trait. If the preference become strong enough, it can exaggerate the male trait enough to

reduce male survival. From generation to generation, the trait will be exaggerated still further until the disadvantage of the exaggerate trait in terms of survival outweighs its advantage in terms of female attraction. The Giant Irish elk (*Megalocerus giganteus*) is often quoted as a possible example of run-away sexual selection because of the extremely large antlers of the males (3 m antler span). But this has been criticized by Gould (1974) based on an allometric analysis of antler size which showed that the Irish elk is close to the predicted antlers for its body size. This theory is called the “**Fisherian self-reinforcing**” hypothesis after Fisher, and also the “**sexy-son**” hypothesis because the mothers gain in fitness by selecting fathers with heritable traits that make their sons attractive to females in the next generation.

- Good-genes hypothesis and handicap principle

While Fisherian run-away process is thought to be driven solely by the benefits of mating with “arbitrarily” attractive males to produce sexy sons, in the “**good-genes**” process, evolution of mate choice occurs because attractive males have higher breeding values for longevity or fecundity. Females should prefer precisely males displaying costly signals, because such traits are reliable indicators of genetic quality that can be passed on to their offspring (Pomiankowski 1988). Females which choose males with these indicators tend to have offspring with greater viability. Zahavi (1975) developed this hypothesis in the “**handicap principle**”, emphasizing the costliness of the honest signal. According to him, selection should favor female choice for conspicuous male traits which are costly to produce and maintain, and so confer a handicap on the male by decreasing its survival. Then, only good quality males would be able to develop such costly conspicuous traits and hence signal that they are able to survive despite their handicap. By mating with such males, females would thus ensure that their offspring survive well and are of good quality too. **Indicators mechanisms** can show a number of things, such as phenotypic condition, parasite resistance, age, heterozygosity, or fluctuating asymmetry (small random deviations from perfect bilateral symmetry in the development of a morphological trait, normally distributed around a mean of zero; VanValen 1962).

One example comes from a study on peacocks *Pavo cristatus* by Petrie (1994). In this experiment, peahens were mated to peacocks in a random mating design and the progeny were reared under uniform conditions. Petrie was thus able to eliminate “female choice”. The young birds were then released into a “semi-natural” population outside of Oxford, England. There was a strong positive relationship between offspring survival and peacock tail size. This indicates that by selecting males with longer tails, females indirectly produce higher quality

sons and daughters. This is evidence for the “good genes” hypothesis that the male tail is an true indicator trait.

- Sensory bias model

“Sensory bias” models predict finally that female preference for certain male traits may evolve prior to the appearance of the male trait. Males that happen by chance to produce that trait will thus be preferred by females. Female preference for a trait may thus be a by-product of the female sensory system that has adapted to be sensitive to a certain kinds of signals for reasons that are unrelated to mating (Ryan 1985). Females inherit sensory capabilities from ancestors that bias the traits that they select in males. For example, females incapable of hearing low-frequency sounds will not choose males that emit such sounds.

Evidence supporting the “sensory bias” model comes from phylogenetic studies. For example, in swordtails female (genus *Xiphophorus*) preference for the sworded tail of males appears in a phylogeny of the group prior to the appearance of the sword itself (Basolo 1990). This suggests that the sword evolved to take advantage of a pre-existing bias in females.

II.3. VARIATION IN SEXUAL SELECTION AMONG SPECIES: THE THEORETICAL POINT OF VIEW

II.3.1. How to measure sexual selection?

The question in sexual selection studies commonly concerns the strength, forms and consequences of competition over mates, or in other words, the intensity of sexual selection, mechanisms of competition over mates, and sexually selected traits. Since Darwin exposed his theory of sexual selection, many researchers have thus attempted to search for a suitable measure of the strength, or intensity, of sexual selection. Among others, the following measures have been proposed (see Andersson 1994 for more details), often originated from measures used in natural selection studies: relative parental investment of males and females (Trivers 1972), operational sex ratio (Emlen & Oring 1977), variance in male breeding success (Payne 1979, 1984), ratio of variance in breeding success between males and females (Ralls 1977; Payne 1979), ratio between relative variance in numbers of mates and relative variance in total breeding success (Wade & Arnold 1980), or variance in fitness divided by the square of the average fitness (Crow 1958). In addition, three “environmental” measures that are likely to affect the intensity of male-male competition are also sometimes used to estimate strength of sexual selection: the operational sex ratio (Elmen 1976), relative parental

investment by males and females (Trivers 1972), and the proportion of time males spend searching for mates (Sutherland 1985).

A major problem is that all these measures lack a link with the secondary sex traits that sexual selection theory seeks to explain (Andersson 1994). Sexual selection can indeed only occur if variation in mating success is correlated with phenotypic variation. Furthermore, the magnitude of change in the phenotype depends on the covariance with these measures (Wade & Shuster 2004). In addition, because not all of the variation in the measure is heritable, not all of this variance can lead to changes in the distribution of phenotypes in a population by natural selection. Thus, these measures set an upper bound not only to the change in mean fitness itself, but also to the standardized change in the mean of all other traits (Wade & Shuster 2004). Rather than quantifying the strength or intensity of selection of particular traits, they actually reflect the potentiality or the **opportunity for sexual selection** (Clutton-Brock 1988b). It is therefore important to use trait-related measures, in complement to these measures, to measure selection in progress, identify sexually selected traits or understand the adaptive significance of particular traits. Systematic relationships between mating success and trait variation are thus evidence of continued sexual selection on secondary trait variation. We can also use partial regression of relative fitness on phenotypic traits in a multiple regression analysis, the so called directional selection gradient (Lande & Arnold 1983; Arnold & Wade 1984), to measure only the direct selection of the traits (see Figure 5).

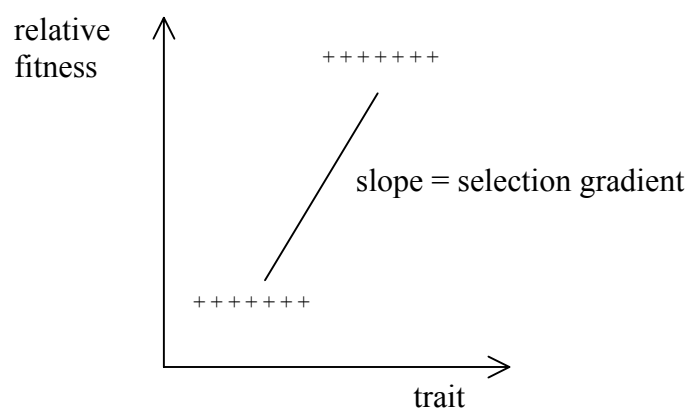


Figure 5. Method to estimate the intensity of sexual selection on a phenotypic trait. The slope of the multiple regression line of fitness on trait represents the selection gradient and is an indication of directional selection.

The gradient then indicates how much relative fitness will change with an increase in the size of the trait by a given unit, if other traits are held constant (Andersson 1994). The selection gradient should not be confused with the selection differential, which is defined as the difference between trait mean of the population before and after selection.

One major question concerning sexual selection is how the strength, forms and consequences of competition for mates vary among species, or in other words, how the opportunity for sexual selection, mechanisms of competition for mates and sexually selected traits vary among species.

II.3.2. Variation in the opportunity for sexual selection

Intuitively, it seems likely that the opportunity for sexual selection should increase with party size (Darwin 1871). Sexual selection theory indeed predicts that the opportunity for sexual selection is strong when males compete intensely for mates, creating the potential for reproductive success to vary widely among males (Emlen & Oring 1977), with a few males highly successful at mating and many others males failing to mate or siring only one (or a few) offspring (Darwin 1871). This has led to the general expectation of an association between strong opportunity for sexual selection, high mating polygyny, and high variance in male reproductive success (Huxley 1938; Wade 1979; Wade & Arnold 1980). Sexual selection, however, can only occur if variation in mating success is correlated with phenotypic variation. In polygynous species, variation in female reproductive success seems to be mainly linked to recruitment, and especially survival of young and so to environmental conditions and resources, whereas variation in male reproductive success should mainly be affected by the males' ability to defend females and so to win fights (Trivers 1972). Hence, phenotypic traits favoured by sexual selection should diverge between the two sexes and the differences in phenotypic traits between males and females should increase with the intensity of competition over mates between males. Many conspicuous male secondary sexual traits are thus thought to have arisen as a consequence of their advantage, either as weapons or as indicators of strength, fighting ability or quality, via sexual selection (Darwin 1871; Geist 1966), and there is wide acceptance of the idea that male-biased sexual dimorphism in body size and weaponry evolved principally as the result of intra-sexual competition over mates, given the scenario of high variance in male reproductive success (Darwin 1871; Andersson 1994). As a consequence, a close relationship is expected between party size, level of sexual dimorphism (particularly in size), variance in male reproductive success and the opportunity

for sexual selection (Clutton-Brock *et al.* 1977; Alexander *et al.* 1979; Harvey & Mace 1982; see Figure 6).

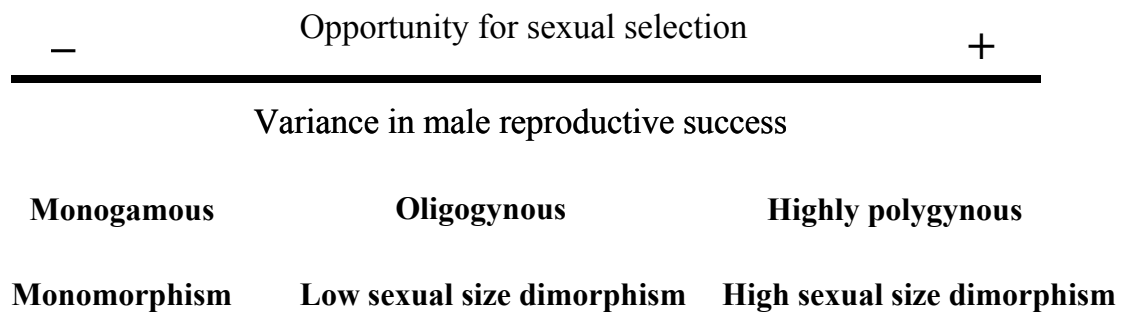


Figure 6. Illustration of the continuum of opportunity for sexual selection from monogamous and monomorphic species on the left-hand side to highly polygynous and highly dimorphic species on the right-hand side. Oligogynous = slightly polygynous.

Note that the opportunity for sexual selection is better estimated by the ratio of the standardized variance in lifetime reproductive success (LRS) between males and females than by the sole standardized variance in male LRS as shown in Figure 6. But mean LRS is expected to be equal in males and females. Hence, if female LRS has a Poisson distribution, the variance and the mean of females LRS should be equal and as a result, the ratio of the standardized variance in LRS between males and females should be equal to the standardized variance in male LRS.

II.3.3. Variation in sexually selected traits and mechanisms of competition over mates

The type of competition over mates favored by sexual selection and the expression of secondary sex traits are also expected to differ between the various forms of polygynous mating systems.

In lek polygyny, males establish dominance relationships among themselves and females then choose between them, largely on the basis of their status and probably independently of direct material benefits. Sexual selection should therefore be mainly intersexual, favoring the evolution of some very extreme male epigamic characters and elaborate male behaviours (Andersson 1994). However, male contest competition may also be involved, particularly in relation to the defence of the best lek positions (Andersson 1994). As females

are usually not synchronized in their periods of sexual activity, and only a small proportion of them will visit the male aggregation at any time, inter-male competition for mates is expected to be intense and mating success should vary greatly among the males on a lek (Andersson 1994). Sexual selection and sexual dimorphism may thus be stronger in lekking than in other related species (Darwin 1871).

In female defence polygyny, male aggressive behaviours should be directed mainly towards the defence of females. Since dominant males monopolize almost all matings within their harem, direct male-male interactions for the control of females are common. Sexual selection should be primarily intra-sexual, favoring the development of characters that enhance male strength and fighting ability, while female choice may not be so important.

Finally, in resource defence polygyny, male aggressive behaviours should be directed mainly towards the defence of the territory. As dominance commonly depends on location, with a reciprocity of dominance among neighbouring territory holders (Owen-Smith 1977), male-male fights between territorial males are quite infrequent, and intra-sexual selection may rather favor the enhancement of characters needed mainly for assessing male dominance, status and fighting ability, and for successfully defending the territory without resorting to fights (Halliday 1978). Moreover, female choice should be mainly directed not towards the males themselves, but towards the quantity or quality of the resources that the males are defending. However, selection could lead to the evolution of male indicator traits that facilitated mate choice by advertising the quality and quantity of a male's resources.

To sum up, the potential for mate choice by females is theoretically expected to be higher for lekking or territorial species compared with those that defend harems or tend females, because females have greater unimpeded opportunity to assess either the male and/or his territory (see Min 1997; and Figure 7). Conversely, the potential for competition between males is expected to be higher for species exhibiting tending or harem defence because only males that can defend females from competitors are commonly successful (Min 1997). Hence, while evolution should have mainly favored the development of weapons and strength in harem-holding and tending species (e.g., antlers in red deer, body mass in elephant seal, horns in bighorn sheep), it should have rather favored epigamic characters and complex display in lekking species (e.g., tail of sage grouse *Centrocercus urophasianus*, large palmate antlers in fallow deer). In territorial species, predictions are more complex, since both male-male competition and female mate choice, and also both male traits and male resources may be important in sexual selection.

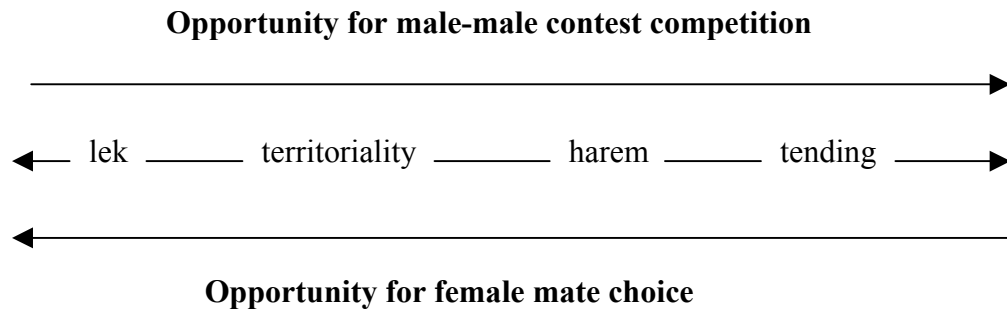


Figure 7. Relationship between the continuum of mating systems and the potential for the two modes of sexual selection. Adapted from the figure of Min (1997).

III. MATING SYSTEMS AND SEXUAL SELECTION NEW INSIGHTS FROM EMPIRICAL STUDIES

In this chapter, I confront the theory on patterns of variation in sexual selection among species with results of empirical studies, especially those based on molecular tools which have allowed major improvements in our understanding of patterns of sexual selection. I focus mainly on mammals, and especially on ungulates. I then review the main sexually selected traits reported in the literature in ungulates.

III.1. THE IMPORTANCE OF MAMMALS, AND ESPECIALLY UNGULATES, AS A STUDY MODEL

As Jarman (1983) noted, “*Darwin (1871), exploring the relationships between mating systems and sexual dimorphism, drew most of his examples and arguments from birds; and these have continued to contribute heavily to studies of mating systems and strategies, and to theories about sexual dimorphism. But while their numbers and observability make birds ideal animals from which to draw broad truths about behavioural ecology, they poorly illustrate complexities of social organisation.*” Few bird species approach the degrees of dimorphism or the complex forms of intra-sexual competition found in large mammals such as ungulates, primates or pinnipeds, with the possible exceptions of some grouse, bustards, and pheasants. It is therefore interesting to focus on large mammals to illustrate and attempt to better understand the complex links between polygyny level, sexual dimorphism, variance in male reproductive success and the opportunity for sexual selection.

In mammals, three groups of species have been the subject of great interest since Darwin (1871) developed his theory of sexual selection, as they represent some of the most spectacular examples of sexual dimorphism in vertebrates: primates, ungulates and pinnipeds (Alexander *et al.* 1979). In those groups, males of certain species can reach a body mass up to two (e.g., in Himalayan Tahr *Hemitragus jemlahicus*, ibex *Capra ibex*) or even five (e.g., in northern elephant seal) times higher than females. The males of these species also commonly differ from females in terms of some conspicuous secondary sexual traits such as highly developed antlers and horns (in Cervidae, Caprinae and Ovidae), or tusks and teeth (e.g., in walrus *Odobenus rosmarus*, Chinese water deer *Hydropotes inermis*, gelada baboon: *Theropithecus gelada*).

The **ungulate** group consists of medium sized and large herbivorous mammals. It is classified into two main orders: Artiodactyla (e.g., donkeys, camels, pigs, hippopotamus, peccaries, deer, musk deer, bovids, giraffes) and Perissodactyla (e.g., horses, zebras, tapirs, rhinoceroses). The ungulates show a wide variation in morphology, behaviour, mating system, mating tactics and social organization among species. Polygyny is most common in ungulates, but monogamy (Kleiman 1977) and promiscuity (Dasmann & Taber 1956) have also been reported. The ungulates also show a wide variation in sexual size dimorphism. While for a small number of ungulate species, females are larger than males (e.g., *Sylvicapra grimmia*, *Oreotragus oreotragus*, *Ourebia ourebi*; Loison *et al.* 1999b), for most ungulate species, males are larger than females. Dimorphism between males and females varies from 0.8 to 2.1 (Loison *et al.* 1999b). Ungulate males commonly have large antlers or horns, whereas females commonly have none (e.g., in roe deer, red deer, Buffon's kob *kobus kob*) or small ones (e.g., in reindeer *Rangifer tarandus*, ibex). As Darwin noted (1871), “*The ruminants are eminently polygamous, and they present sexual differences more frequently than any other group of mammals; this holds good especially in their weapons, but also in other characteristics*”. Finally, many different male mating systems to obtain mates are represented (Owen-Smith 1977): harem defence (e.g., in red deer, feral water buffalo *Bubalus bubalus*, reindeer), lekking (e.g., in fallow deer, topi *Damaliscus korrigum*, Uganda kob *Adenota kob thomasi*, white-eared kob *Kobus kob leucotis*, Kafue lechwe *kobus leche kafuensis*), roving/tending (e.g., in moose *Alces alces*, white-tailed deer *Odocoileus virginianus*, bighorn sheep, Soay sheep), and territoriality (e.g., in roe deer, Impala *Aepyceros melampus*, Chinese water deer, Kirk's dik dik *Madoqua kirki*, Reeves's muntjac *Muntiacus reevesi*). A lot of intra-specific variation in mating strategy has also been observed (Byers & Kitchen 1988; Apollonio 1989; Langbein & Thirgood 1989). It is therefore interesting to focus on ungulates, and especially ruminants (see Table 1), to further investigate the scope for development of sexual selection in relation to variation in breeding group size, sexual dimorphism and mating systems in mammals.

Table 1. Taxonomic organization of the world's ruminants (from Grubb 2005).

FAMILY	SUBFAMILY	TRIBE	GENUS	EXAMPLES OF SPECIES (common names)
Tragulidae			<i>Hyemoschus</i>	Water chevrotain
			<i>Moschiola</i>	Indian spotted chevrotain
			<i>Tragulus</i>	Java mouse-deer, Greater mouse-deer
Moschidae			<i>Moschus</i>	Forest musk deer, Black musk deer
Cervidae	Capreolinae	Alceini	<i>Alces</i>	Eurasian elk, Moose
		Capreolini	<i>Capreolus</i>	European roe deer, Siberian roe deer
		Odocoileini	<i>Blastocerus</i>	Marsh deer
			<i>Mazama</i>	South American red brocket, Dwarf brocket
			<i>Odocoileus</i>	Mule deer, White-tailed deer
			<i>Ozotoceros</i>	Pampas deer
			<i>Hippocamelus</i>	Taruca, Guemal
			<i>Pudu</i>	Northern pudu
		Rangiferini	<i>Rangifer</i>	Reindeer
	Cervinae	Cervini	<i>Axis</i>	Chital, Hog deer
			<i>Cervus</i>	Red deer, Sika deer
			<i>Dama</i>	Fallow deer
			<i>Elaphurus</i>	Père David's deer
			<i>Przewalskium</i>	White-lipped deer
			<i>Rucervus</i>	Eld's deer, Barasingha
			<i>Rusa</i>	Javan rusa, Sambar
		Muntiacini	<i>Elaphodus</i>	Tufted deer
			<i>Muntiacus</i>	Red muntjac, Reeves' muntjac
	Hydropotinae		<i>Hydropotes</i>	Chinese water deer
Antilocapridae			<i>Antilocapra</i>	American pronghorn
Giraffidae	Giraffinae	Giraffini	<i>Giraffa</i>	Giraffe
		Palaeotragini	<i>Okapia</i>	Okapi
Bovidae	Aepycerotinae		<i>Aepyceros</i>	Impala
	Alcelaphinae	Alcelaphini	<i>Alcephalus</i>	Hartebeest, Red hartebeest
			<i>Beatragus</i>	Hunter's hartebeest
			<i>Connochaetes</i>	Black wildebeest, Blue wildebeest
		Damaliscini	<i>Damaliscus</i>	Topi, Bontebok
	Antilopinae	Antilopini	<i>Ammodorcas</i>	Dibatag
			<i>Antidorcas</i>	Springbok
			<i>Antilope</i>	Blackbuck
			<i>Eudorcas</i>	Red-fronted gazelle, Thomson's gazelle
			<i>Gazella</i>	Arabian gazelle, Dorcas gazelle
			<i>Litocranius</i>	Gerebuck
			<i>Nanger</i>	Dama gazelle, Grant's gazelle
			<i>Procapra</i>	Mongolian gazelle, Tibetan gazelle
			<i>Saiga</i>	Mongolian saiga, Steppe saiga
		Neotragini	<i>Dorcatragus</i>	Beira
			<i>Madoqua</i>	Kirk's dikdik
			<i>Neotragus</i>	Bate's dwarf antelope, Royal antelope
			<i>Oreotragus</i>	Klipspringer
			<i>Ourebia</i>	Oribi
			<i>Raphicerus</i>	Steenbok, Cape grysbok
	Bovinae	Boselaphini	<i>Boselaphus</i>	Nilgai
			<i>Tetracerus</i>	Four-horned antelope
		Bovini	<i>Bison</i>	American bison, European bison
			<i>Bos</i>	Aurochs, Yak
			<i>Bubalus</i>	Water buffalo, Anoa
			<i>Pseudoryx</i>	Siola
			<i>Syncerus</i>	African buffalo
		Tragelaphini	<i>Taurotragus</i>	Derby eland, Common eland
			<i>Tragelaphus</i>	Bushbuck, Lesser kudu, Sitatunga
	Caprinae	Caprini	<i>Ammotragus</i>	Barbary sheep
			<i>Capra</i>	Tur, Markhor, goat, Alpine ibex
			<i>Hemitragus</i>	Himalayan tahr
			<i>Ovis</i>	Argali, Soay sheep, Bighorn sheep, Dall's sheep
			<i>Oreamnos</i>	Mountain goat
			<i>Pseudois</i>	Bharal, Dwarf bharal
			<i>Rupicapra</i>	Isard, Alpine chamois
		Naemorhedini	<i>Capricornis</i>	Chinese serow, Himalayan serow
			<i>Naemorhedus</i>	Himalayan goral, Chinese goral
		Ovibovini	<i>Budorcas</i>	Takin
		Pantholopini	<i>Ovibos</i>	Muskox
			<i>Pantholops</i>	Chiru
	Cephalophinae		<i>Cephalophus</i>	Brooke's duiker, Red duiker, black duiker
			<i>Philantomba</i>	Blue duiker
			<i>Sylvicapra</i>	Bush duiker
	Hippotraginae		<i>Addax</i>	Addax
			<i>Hippotragus</i>	Roan antelope, Sable antelope
			<i>Oryx</i>	Beisa, Gemsbok, Arabian oryx
	Reduncinae		<i>Kobus</i>	Waterbuck, Kob, Lechwe, Puku
			<i>Pelea</i>	Vaal rhebok
			<i>Redunca</i>	Common reedbuck

III.2. A NEW POWERFUL APPROACH BASED ON MOLECULAR TECHNIQUES

Studying male mating systems and sexual selection using an evolutionary approach necessitates good estimates of male reproductive success in order to be able to analyse the variance in success between males and to identify important correlates of this variance.

Historically, male mating systems and reproductive success have been investigated through intensive behavioural studies, often requiring long hours in the field (e.g., Byers 1997; Clutton-Brock 1988a). Parameters typically monitored are the number of copulations (rate at which each male mates) or the number of social associations during which time a male may have exclusive access to a female (see Brandt 1989; Clutton-Brock 1988a). However, the use of behavioural observations to quantify reproductive success has several limitations. First, behavioural observations may lead to incorrect assignments of offspring to particular individuals in cases where extra-pair fertilizations occur (see Gibbs *et al.* 1990; Westneat 1987), when males fail to guard females, when males do not constrain mate choice by females or when females mate with more than one partner. Furthermore, due to the logistical constraint of daily monitoring, behavioural studies often involve a small number of individuals and, as such, are inappropriate to evaluate variance in individual reproductive success. Finally, in species with cryptic and/or nocturnal mating behaviour or living in dense habitat, it is almost impossible to collect behavioural data on male mating success.

However, with the development of molecular tools (especially microsatellite markers) and sophisticated analytical advances in population genetics, an alternative and direct approach is now available for assessing information on male reproductive success and male mating systems by paternity analyses, based on the comparison of parental and offspring multilocus genotypes (e.g., McCracken & Bradbury 1977; Burke 1989; Pemberton *et al.* 1992; Marshall *et al.* 1998). Previous studies have shown the strong potentialities of this molecular approach, which has not only allowed us to access information on reproductive success and establish parentage or genetic relatedness with a high degree of confidence (Marshall *et al.* 1998), but has also revolutionized the understanding of mating systems of many species (Birkhead *et al.* 1990; Hughes 1998), by revealing some discrepancies between behavioural and genetic estimates of reproductive success (Pemberton *et al.* 1992; Amos *et al.* 1993; Coltman *et al.* 1999a). For example, extra-pair paternity was demonstrated in many bird species that were previously thought to be exclusively monogamous (Birkhead & Møller 1992). Likewise in mammals, a high proportion of offspring often have proved not to be sired

by the observed social partner or by the dominant males, revealing “sneaky” strategies (e.g., Gibbs *et al.* 1990; Coltman *et al.* 1999a). Finally, multiple paternities (result of insemination of a female by at least two males to produce a single litter or brood) have also been shown in several polytocous species (e.g., DeYoung *et al.* 2002; Carling *et al.* 2003). Molecular tools have thus allowed to document the mating systems of many species in unprecedented detail, leading to a rapid improvement in our understanding of the functional significance of mating systems. These new studies have begun to challenge long-held beliefs on patterns of variation in sexual selection among species.

III.3. PARTY SIZE, SEXUAL DIMORPHISM AND THE OPPORTUNITY FOR SEXUAL SELECTION: A COMPLEX LINK

Studies on primates (e.g., Clutton-Brock *et al.* 1977; Harvey *et al.* 1978; Clutton-Brock 1985; Albert *et al.* 2003), ungulates (e.g., Jarman 1974, 1983; Clutton-Brock *et al.* 1980; Loison *et al.* 1999b; Say *et al.* 2003) and pinnipeds (e.g., Lindenfors *et al.* 2002) have commonly shown that the level of sexual dimorphism (particularly in body size and weapon size) is linked to the level of polygyny (see Alexander *et al.* 1979 for a review). Jarman (1983), for instance, described a continuum of sexual selection intensity among African antelopes, with monogamous and monomorphic species at one extreme, exhibiting similar life-history traits in both sexes, and highly polygynous and dimorphic species at the other, with life-history traits that differ between the sexes. Among the Cervidae, species that are typically seen singly or in small groups during the breeding season and where males presumably cannot monopolise breeding access to large numbers of females (such as *Hydropotes*, *Mazama*, and *Muntiacus* spp.) commonly show little size dimorphism, while differences between the sexes are most pronounced in species where females congregate in large herds which males can defend (as in *Rangifer* and most *Cervus* spp.; Clutton-Brock 1987). The size of male antlers are also commonly greatest in species belonging to the latter group (Clutton-Brock 1987). Furthermore, these highly dimorphic and polygynous species have been shown to have a high variance in male mating success and so a strong opportunity for sexual selection (e.g., in primates: Clutton-Brock *et al.* 1977; elephant seal: LeBoeuf & Reiter 1988; red deer: Clutton-Brock *et al.* 1988). In contrast, monomorphic species seem commonly to be monogamous (e.g., Kleiman 1977) and sexual selection is relatively slight (Emlen & Oring 1977). Hence, in support of what is expected from sexual selection theory, there seems to be a close relationship between party size, level of sexual dimorphism,

variance in male reproductive success and the opportunity for sexual selection in these mammals.

But while dimorphism and polygyny are commonly associated, there are many exceptions to this general trend (Ralls 1977). Among the cervids, moose are more dimorphic than might be expected on the basis of their breeding system (Peterson 1955; Geist 1963). In other ungulate groups, there are polygynous species which show little sexual dimorphism, like Burchell's zebra *Equus quagga burchellii* (Klingel 1972). Finally, among African bovids, the extent of polygyny is not correlated with sexual size dimorphism (Owen-Smith 1993).

Furthermore, some recent papers have shown that the relationship between party size, level of sexual dimorphism, variance in male reproductive success and the opportunity for sexual selection may be more complicated than originally thought. First, male success in monogamous breeding systems may sometimes vary as widely as in polygynous ones, though this may not always be the case (see Clutton-Brock 1987; Andersson 1994). Indeed, under strict monogamy, no individual has more than one mate, but some males may actually have none in the case of skewed sex ratios (Andersson 1994). Also, mates can vary in fecundity or parental ability in relation to age, condition, and other aspects. The strength of sexual selection not only arises from selection on the number of mates or matings, but may also stem from differences in the properties (i.e. quality) of mating partners (Darwin-Fisher mate choice mechanism; see Andersson 1994). Furthermore, in many species, especially in birds, monogamy is not strict in the sense that some males achieve higher reproductive success through extra-pair copulations (Andersson 1994). Finally, while differences in mate number are probably the principal cause of variation in polygynous species, variation in male success in monogamous species may be caused principally by differences in mate or territory quality. Also, agility, implying a little body size, may be more important in male mating success, through scramble competition or courtship, than strength and fighting ability (agility-hypothesis; Andersson 1994). Monogamous males might thus be expected to compete as intensely for the best mates or territories as polygynous males do for the biggest harems (Clutton-Brock 1987). According to Clutton-Brock (1987), it is not the extent to which male success varies that will determine the development of sexual dimorphism, but the comparative effects of particular traits on breeding success in males and females. Dimorphism is probably related to polygyny because the factors affecting breeding success of the two sexes are more similar in monogamous species than in polygynous ones. But we have yet to demonstrate this and, hence, it could be interesting to focus new studies of sexual selection on monogamous species, or species with low sexual size dimorphism, for which we currently have little

information (Clutton-Brock 1987). To test current explanations of the adaptive significance of sexual dimorphism (see Clutton-Brock *et al.* 1977; Alexander *et al.* 1979), direct comparisons of the effects of size on reproductive success are needed in polygynous species where males are larger than females or where the sexes are similar in size.

Second, mating systems and environmental conditions may influence the relationship between sexual size dimorphism, party size, and variance in male reproductive success. Weckerly (1998) has thus found that, for ruminants and primates, the extent of sexual size dimorphism varies among species with different mating systems, even after correcting for the degree of polygyny. For antelopes, Jarman (1974) suggested that male mating tactics reflect the dispersion, grouping, and predictability of females, which in turn depends on habitat, food and risk of predation. Sexual monomorphism is associated with monogamy and dimorphism with polygyny in ways that depend on these ecological aspects (Clutton-Brock *et al.* 1982; Jarman 1974; 1983). Following Jarman (1974), Ralls (1977) suggested that the distribution of food and other resources affects the degree of clumping of females and hence, in part, determines the mating system and the strength of sexual selection in males (also see Emlen & Oring 1977). Hence, it is important to consider mating systems if we want to better understand patterns of variation in sexual selection among species. But whether variance in male breeding success is consistently higher in species where mate access depends on the individual's dominance rank than in species where males defend territories, or in lek-breeding animals compared with other polygynous species is not yet clear (Clutton-Brock 1988b).

III.4. MATING SYSTEMS, SEXUALLY SELECTED TRAITS AND MECHANISMS OF COMPETITION OVER MATES: THE CASE OF THE UNGULATES

Many aspects of morphology, physiology, and behaviour vary between breeding systems (Clutton-Brock & Harvey 1984) and studies of the determinants of fitness or sexually selected traits may provide important insights into the reasons underlying these associations, as well as into the evolution of the breeding systems themselves (Clutton-Brock 1988b). I thus attempted below to give a review of the main sexually selected traits that have been reported in male ungulates, with special reference to the Cervidae, Bovidae and Antilocapridae. To demonstrate sexual selection on a trait, we have to show that variation in the trait leads to variation in reproductive success due to competition between rivals through contests, mate choice, or any other mechanism of sexual selection (Andersson 1994). The

main criteria for the inclusion of a study in this review was therefore that it demonstrated a significant relationship between the quantitative variation in a character and mating or reproductive success. In some cases, however, despite the lack of such a demonstration, some studies for which results strongly suggested the role of a character in male contests or female mate choice have also been included.

III.4.1. Body size and mass

Larger male than female size, typical of most mammals, has usually been explained by a size advantage in contests over females (e.g., Darwin 1871; Andersson 1994). In mammal species in which fights are decided by contests involving pushing, larger male size has thus been shown to give an advantage in dominance contests and fights over females. However, few studies have clearly shown that dominance also leads to higher production of offspring in mammals and, so far, in ungulates (reviewed by Clutton-Brock 1988a). In fallow deer, McElligott *et al.* (2001) showed that male mating success was directly related to body size and that there was an indirect relationship between mating success and male body mass via pre-rut dominance rank. In Soay sheep too, body size was reported to be influential in determining access to females and should therefore be a significant predictor of siring success, regardless of the size of the testes and horns (Preston *et al.* 2003). In bighorn sheep, Coltman *et al.* (2001) demonstrated that mating success was positively correlated with body weight within and across years. Pelletier & Festa-Bianchet (2006) also recently found a positive effect of body mass on the social rank of bighorn rams. After 6 years of age, body mass was age independent and determines social rank in males. Finally, in red deer, body size and body weight may also affect reproductive success. Stags that were considerably lighter than their opponents usually lose contests. In addition, although not all large stags were good fighters, individuals that were consistently successful in fights and held large numbers of hinds in several seasons were almost always of more than average size (Clutton-Brock *et al.* 1982). Evidence for a relationship between body size and reproductive success was also provided by the fact that LRS among stags was well correlated with mean antler weight, which is known to be related to body size and weight in red deer (e.g., Clutton-Brock *et al.* 1979).

Large size may also give an advantage in endurance rivalry, permitting a male to spend a longer time at a given breeding site and compete for females (Andersson 1994). In Soay sheep, for instance, Preston *et al.* (2003) suggested that body condition is important in

determining mating success. Indeed, before gaining access to receptive females, males spent a lot of time roving, trying to locate females, and examining ewes for signs of estrous. This time was particularly costly in terms of energy: males were estimated to lose 30% of their body weight by the end of the rut. Thus, physical exhaustion may limit the success of males in poor condition to find receptive females. In red deer, stags in poor condition seldom rutted successfully since they often failed to secure harems, and Clutton-Brock *et al.* (1982) suggested that body condition determines male reproductive success. Furthermore, male body size has been reported to be related to mating success, via sequestering of females and forced copulation, or sperm competition if large size leads to higher sperm production (Wedell 1997). Sperm competition has been noted, for instance, in Soay sheep (Preston *et al.* 2003). The authors found that larger testes were independently associated with both higher copulation rates and increased siring success.

Finally, another advantage could be female preference for large males, for example because larger males may provide more resources than smaller males or because body size may be a honest signal of the genetic quality of the male (see Andersson 1994 for a review). A study of genetic variability in the major histocompatibility complex in white-tailed deer suggested that body size may provide an advertisement of heritable male quality and so females may act on this cue to select mates (Ditchkoff *et al.* 2001a).

III.4.2. Antler and horn size

A widespread idea is that horns and antlers in ungulates are used as weapons against rival males during the mating season (e.g., Darwin 1871). Large horn and antler size (irrespective of age, body size, condition and testes size) are often associated with increased access to receptive females due to the advantage that they confer in intra-sexual combat. But horns and antlers could also function defensively, acting as a shield (e.g., Geist 1966; Clutton-Brock 1982). The behavioural advantage of large horns and antlers should translate into reproductive success, with larger-horned and larger-antlered males siring more offspring. Clutton-Brock (1982) thus demonstrated that antler weight in red deer was well correlated with male reproductive success. But this relation may be due to the effect of male body mass on male reproductive success, since a correlation occurred between antler weight and body size or body weight in red deer (Clutton-Brock *et al.* 1979). However, Kruuk *et al.* (2002) showed that the size of antlers, which were used by males as weapons in fights over access to females, was significantly correlated with male breeding success in red deer in a given year,

but also across an individual's lifetime, and both before and after correcting for body size. In addition, experimental removal of antlers was shown to reduce reproductive success in male red deer and reindeer via a reduction in their fighting ability and dominance status (Espmark 1964; Lincoln 1972; Clutton-Brock *et al.* 1982). This indicates that antlers were important in competition among males, even if other factors such as age, body size, and condition also played a role. It was also shown that the number of offspring sired in a given year increased with male horn size in bighorn sheep (Coltman *et al.* 2001) and in Soay sheep (Preston *et al.* 2003). In Reeves' muntjac, Barrette (1977) demonstrated that antlers clearly played a role as weapons in intra-sexual competition over female access, but he did not test the correlation between antler size and male reproductive success. In roe deer, finally, a positive correlation was found between antler size and yearling dispersal tendency due to male-male aggression, which was directed mainly against the most sexually mature yearlings as antler size was also correlated with testicle size (Wahlström 1994). Sub-adults with well developed antlers were more frequently harassed by territorial males than sub-adults with poorly developed antlers, presumably because the former were a bigger threat in terms of mating competition. But no study has yet demonstrated a relationship between antler size and buck reproductive success for this species.

While large horns and antlers are efficient weapons in fights between males, they may also be used in display for intimidating opponents (e.g., Geist 1966; Lincoln 1972), functioning as indicators of male strength and fighting ability for other males. Horn and antler size are correlated with body size and nutritional condition, and hence probably also with strength (e.g., Clutton-Brock *et al.* 1982). Males might therefore assess each other, in part, by the size of horns and antlers, avoiding fights with superior competitors which may lead to serious injuries or even death (e.g., Geist 1966; Clutton-Brock *et al.* 1982). There is however very little empirical evidence for this in ungulates. In caribou, Barrette & Vandal (1990) distinguished between fighting (which is very violent, occurs between matched males, can cause injury and death, and is quite rare) and sparring (which usually starts slowly and is restrained, with the animals carefully adjusting the position of their antlers before pushing and twisting). In sparring, the animals with the smaller antlers initiated about half of the matches, but withdrew in almost 90% of them. The authors suggested therefore that frequent sparring could be a form of tactile assessment of fighting ability which might later permit visual assessment of other males based on their antler size. So antlers in reindeer may play a role in male assessment of competitors. In roe deer, Hoem *et al.* (2007) showed that male-male fights escalated more and were more complex when the difference in antler size between combatants

was smaller. When the difference in antler size was large, male-male interactions often ended without involving dangerous fighting. This suggested that males probably assessed fighting ability of rival males through antler size.

Finally, large and/or symmetric weaponry in ungulates may be preferred by females as an indicator of male quality, sexual vigor or condition (e.g., Darwin 1871). Theoretically, choosing a male with large weapons that reflect good condition might lead to short-term direct benefits for females, such as access to good quality territories, paternal care or male sexual vigour, and a reduced risk of being courted by young, inexperienced males (Price *et al.* 1993), or long-term indirect benefits, such as high genetic quality of offspring, to the extent that these benefits are heritable (Fisher 1915; Møller & Alatalo 1999). But there is, however, very little strong evidence in mammals that females choose a mate in relation to the size or symmetry of his weapons (Clutton-Brock 1982). A study of genetic variability in the major histocompatibility complex in white-tailed deer suggested that antler development may provide an advertisement of heritable male quality (Ditchkoff *et al.* 2001a) and so females may act on this cue to select mates. Antler size in red deer stags has also been recently shown to be heritable (Kruuk *et al.* 2002), to be positively related to the probability of becoming a harem holder in stags (Bartoš & Bahbouh 2006) and to be positively related to relative testes size and sperm velocity (Malo *et al.* 2005). This suggested that antler size in red stags was an honest signal of male quality which may be used by females to choose mates. Finally, Geist (1966) and Clutton-Brock *et al.* (1989) suggested that horn size in bighorn sheep and antler size in fallow deer respectively may be used by females to choose mates.

III.4.3. Antler and horn asymmetry

Sexual selection is often associated with asymmetry, with symmetric individuals enjoying higher mating success (Møller & Thornhill 1998), and this effect may be even greater than that for the size of the same characters (Thornhill & Møller 1998). Fluctuating asymmetry (FA) refers to small random deviations from perfect bilateral symmetry in the development of a morphological trait (such as weapons and ornaments), normally distributed around a mean of zero (VanValen 1962). Under the hypothesis that the degree of FA in secondary sex traits reflects the ability of males to cope adequately with environmental stress or physical damage during the development of the character, FA should reflect male quality and so might be used by females in inter-sexual selection to select mates, or by males in intra-sexual selection to infer competitor quality. If the trait development reflects individual

quality, a negative relationship is expected between this trait development and the degree of FA (Møller 1992).

Several studies have thus found a negative relationship between FA and weapon size, showing thus that the degree of FA in antler or horn size may reflect individual quality, but few of them controlled for age and body mass (Kruuk *et al.* 2003). Examination of FA in moose antlers revealed that asymmetry was lower and the number of antler points was greater in large-antlered males which presumably did most of the breeding (Solberg & Saether 1993; Bowyer *et al.* 2001), but there was a negative relationship between FA and the carcass mass of an individual after correcting for antler size and this relationship changed with age. In reindeer too, the degree of FA of antlers was negatively related with antler size and was positively correlated with parasite burden, so antlers could be visual indicators of individual quality (Markusson & Folstad 1997). In roe deer, absolute FA significantly decreased with age. It also tended to decrease with antler size at constant carcass mass and within age classes. Antler symmetry could therefore represent a reliable signal of individual quality (Pélabon & VanBreukelen 1998). According to Ditchkoff *et al.* (2001b), FA of the antlers of white-tailed deer followed patterns predicted for sexually selected traits, so may be reliable signals of male quality and, as such, may be important in maintaining honesty in intra-sexual advertisements during breeding.

Yet some studies have reached opposite conclusions. For instance, in mountain goat *Oreamnos americanus* and bighorn sheep, asymmetry in horn size did not reflect individual quality in males (Côté & Festa-Bianchet 2001; Fitzsimmons *et al.* 1995). In addition, almost no study has tested for a direct association between FA in male weaponry and mating success in ungulates or has investigated whether females select mates based on FA (Kruuk *et al.* 2003). While Malyon & Healy (1994) reported a negative association between measures of FA and dominance rank in eight farmed fallow deer, Pélabon & Joly (2000) found no association between levels of asymmetry and dominance rank in a sample of 45 male fallow deer in a zoo population. Miura (1984) found that the rank of sika deer (*Cervus nippon*) males was directly related to the configuration of the antlers. In red deer, finally, it seems that FA in male antler size did not predict either annual or lifetime breeding success (Kruuk *et al.* 2003). More importantly finally, as more studies tested whether FA exceeded measurement error, fewer and fewer detected significant associations between individual FA and sexual selection (Simmons *et al.* 1999). Studies of fluctuating asymmetry actually face a number of serious challenges (Palmer & Strobeck 1986): (i) random phenotypic variation arises for reasons other than developmental instability, (ii) all descriptors of FA estimate a variance and

variances are estimated with much lower confidence than means (i.e. repeatability is lower), (iii) subtle departures from symmetry are typically so minute they are exceedingly difficult to measure reliably, (iv) measurement error and trait size interact in complex and mischievous ways, and (v) tests for departures from normality are uncomfortably weak for small to modest sample sizes. However, while the reputation of FA has been tarnished by these critiques, it is too early to dismiss it as a useful tool for inferring developmental instability.

III.4.4. Territory size, location, and habitat quality

Even though a territory is not *sensu stricto* a male trait, territory size, location, and habitat quality can be considered as sexually selected traits in males (see Andersson 1994). Indeed, these territory characteristics may determine the number of potential mates that a territorial male can monopolize within its area of dominance, and males usually compete strongly to establish and defend the best territories in term of access to females and resources. The importance of habitat quality and territory size for male reproductive success is well documented in birds (e.g., Verner & Wilson 1966; see also Andersson 1994). It has also been suggested to be the case in a few ungulates, but data on male yearly and LRS are lacking in most of these studies to demonstrate the relationship between territory size, location or habitat quality with male fitness. For American pronghorn, Kitchen (1974) demonstrated a positive correlation between forage quality in a territory and the mean number of females present and male mating success. In a lekking fallow deer population in Italy, females appeared to choose mates partly on the basis of location, and thus males should compete for ownership of territories preferred by females (Apollonio *et al.* 1990). In a population of red deer with harem mating system, male reproductive success was affected by the area where the stag rutted (Clutton-Brock *et al.* 1982). At Kilmory and Samhnán Insir, where large numbers of hinds gathered on the greens, the reproductive success and harem size of stags was higher than in the Intermediate Area or the Upper Glen, where there were fewer hinds. In a population of red deer showing resource defence polygyny, Carranza (1995) fenced territories so that the territorial males had to defend a new territory at a different site. He showed that females were attracted by the area rather than by the male, and therefore the success of a territorial male largely depended on the location of his territory. In puku *Kobus vardonii* and topi antelopes, Balmford *et al.* (1992) found that female distribution was independently positively correlated with male phenotype as well as with the quality of forage and the risk of predation on different territories. Brø-Jorgensen (2002) also reported in topi that several male

morphological traits were correlated with the male location on the lek: males on the center of the lek, were darker and larger and were preferred by females as mates. In the same way, the frequency with which a male had females on his territory was shown to be related to the amount of preferred habitat that his territory contained in impala and waterbuck *Kobus defassa* (Jarman 1974). In Ugandan kob, females preferentially mated on leks situated in an area which reduced their risk of predation (Deutsch & Weeks 1992). In bighorn sheep, food biomass and the number of females present within the males' home range was not correlated with male reproductive success (Pelletier & Festa-Bianchet 2006). In roe deer, finally, according to Liberg *et al.* (1996), the quality of the territory, but not territory size, may influence male mating success, with males with clover fields in their range having the highest success.

III.4.5. Chemical signals

It has long been known that scent is used for mate attraction in insects and for territorial marking in mammals (e.g., Gosling 1982). Many male mammals scent-mark their home range or defended territory, especially in ungulates (e.g., in roe deer: Johansson *et al.* 1995, moose: Bowyer *et al.* 1994; Roosevelt elk *Cervus canadensis roosevelti*: Bowyer & Kitchen 1987; white-tailed deer: Kile & Marchinton 1977; fallow deer: Chapman and Chapman 1975). Marks consists of secretions from specialised glands, faeces, or urine, and are often placed at conspicuous positions to make them more obvious. In deer, it has been suggested that scent marks may be used both in the communication between males and between males and females.

Territorial scent marking might play a role in attraction or physiological priming of mates, especially in some small mammals, which could then play important roles in reproductive competition and sexual selection. Females might discriminate among males in relation to their odors (for example between dominant and subordinate males). Deutsch & Nefdt (1992) have thus showed, in two lekking reedbuck antelope species, that females may be attracted to successful territories by olfactory cues in the soil. They reported that transferring the topsoil between successful and unsuccessful territories on leks caused the numbers of females and matings on the unsuccessful territories to increase tenfold. Females were probably attracted to the soil by smells that had accumulated from heavy use by other females. Odors from adult males may also accelerate puberty in juvenile females, induce estrous and ovulation, help to synchronise oestrus in females and facilitate pregnancy in adult

females, delay puberty in juvenile males, and perhaps reduce testosterone levels in other adult males (Andersson 1994). For the male, these effects on females should often increase his mating and fertilization success. In moose, males dig rutting pits where they deposit odorous urine and females are strongly attracted to and often wallow in these pits (Whittle *et al.* 2000). Moreover, mating and parturition are highly synchronized in this species. Whittle *et al.* (2000) suggested that male urine may play an important role in the mating system and in synchronizing reproduction. They analyzed male urine, and found potential pheromones. They suggested that these compounds were related to hypophagia and catabolism of body reserves by rutting males, and thereby provided an honest advertisement of body condition by male moose during the mating season. Miquelle (1991) also showed that cows aggressively compete for access to bull urine, suggesting that male urinary components may increase the probability of successful reproduction in cows. Mature bulls that scent urinate may increase their reproductive success by inducing ovulation before their body condition declines and attracting cows by their scent so that courtship is possible.

Several aspects suggests that male scent marking may also be related to contest competition over mates (Andersson 1994). Males mark more than females, dominant males and territory holders mark more than others, and males often mark conspicuously during contests with others (Ralls 1971). Scent marks may thus function in competitor assessment (e.g., Gosling 1982, 1990). According to the “scent matching” hypothesis of Gosling (1982), territory owners scent mark their territories to provide intruders with a means of assessment: intruders can compare the scent of animals they meet with the scent of marks in the vicinity, identify the territory holder, and withdraw. As a consequence, both territory owner and the intruder avoid costly combats. In white-tailed deer, Miller *et al.* (1998) found some differences in compound presence and concentration of volatiles in urine between dominant and subordinate males and suggested that these differences may produce a rank-specific odor and may serve in the identification of social status in this species.

III.4.6. Acoustic signals

Song and other acoustic signals are the traits most often shown to be sexually selected, especially in insects, frogs, and birds (see review in Andersson 1994), but also in some mammals. Acoustic signals may be used in contests between males, but also for attracting females (Darwin 1871). In red deer, male roaring rate reflected male condition and was positively correlated with fighting ability and reproductive success through contest

competition (Clutton-Brock & Albon 1979; Clutton-Brock *et al.* 1979) and also with female choice. In two-choice loudspeaker tests with farmed red deer, females were attracted to high roaring rates and to leading bouts of roars (McComb 1991). In another experiment, females exposed to playback of roaring ovulated earlier than control females (McComb 1987). This suggested that roaring may enhance male success, both by attracting hinds and by making them more likely to ovulate and mate before being taken over by another stag. Reby *et al.* (2001) have also shown, by conducting playback experiments, that red deer hinds were able to discriminate between roars of their current harem-holder stag and those of other neighbouring stags and suggested that this ability may be important in female mate choice. In roe deer finally, Reby *et al.* (1999) suggested that barking was linked in part to the expression of territoriality among bucks and may enable them to identify and locate each other, and perhaps to assess dominance status, particularly during barking / counter barking sessions involving several animals. It seemed indeed that individual differences in propensity to bark were related to dominance in this species.

III.4.7. Visual signals

Darwin (1871) claimed that female mate choice has generally been responsible for the evolution of sex-dimorphic colors and other sex-dimorphic visual ornaments (such as feathers in birds or enlarged fins in fishes). He pointed to patterns suggestive of sexual selection in the expression of visual display in relation to sex, age, season, and situation. For example, the trait is not acquired before sexual maturity, or females develop the trait less than males or not at all, or males develop the trait only during the mating season, or the trait is displayed mainly to potential mates or sexual rivals. Taken together, such patterns suggest sexual selection. Birds are the most thoroughly studied group as regards to conspicuous visual signals (Andersson 1994). Among mammals, the most conspicuous sex differences in coloration are found in primates (e.g., pink or red anogenital skin swellings, face color), which have more advanced color vision and probably poorer sense of smell than other mammals (Andersson 1994). In ungulates, visual signals may also occur, but are probably less developed. In ungulates which engage in threats from a lateral position, their dewlaps, manes, or hair crests along the neck and back enlarge the apparent size viewed from the side (Andersson 1994). In species which threaten head on, the face is often enlarged by conspicuous ruffs, whiskers, or other hair (Andersson 1994). There is, however, no strong evidence in ungulates that these conspicuous traits may enhance male mating success or may be used by females to choose

mates or by other males to assess male quality, although, in the territorial puku, neck patches of males have been proposed to function as badges of status, and access to mates was affected by neck-patch intensity (Rosser 1990).

In the above, I have identified several traits that may be subject to sexual selection in ungulates. At the light of this review, it is difficult to establish whether empirical studies support theoretical predictions. The difficulty in such an exercise is to isolate indirectly selected traits from directly selected traits: a trait correlated with mating success may indeed be indirectly selected through correlation with some other directly selected trait (Andersson 1994). It is also often difficult to separate the respective roles of female mate choice and contests over mates in the sexual selection of a trait (Andersson 1994). For example, antlers and horns in ungulates can be used both as weapons and/or as ornaments, and both roles can lead to the selection of their size and symmetry. Finally, previous studies have focused mainly on species with female-defence polygyny (e.g., red deer, bighorn sheep, Soay sheep, reindeer) and lekking (e.g., fallow deer) mating systems. The few studies that have investigated sexually selected traits in a species with a resource-defence polygyny mating system (e.g., in roe deer and American pronghorn) up to the present have lacked data on male reproductive success to really demonstrate sexual selection on male traits. Hence, more empirical studies are required on a whole variety of potentially selected traits, in different species over the range of mating systems, to better understand the influence of mating systems on the mechanisms of competition over mates favored by sexual selection and the expression of sexually selected traits in ungulates and, more widely, in mammals.

III.5. CONCLUSION: LACK OF DATA IN SPECIES WITH LOW SEXUAL SIZE DIMORPHISM AND/OR TERRITORIAL MATING SYSTEM IN UNGULATES

The relationship between party size, sexual dimorphism, mating systems, variation in male reproductive success and the opportunity for sexual selection remains unclear in mammals, especially in ungulates. Also, mechanisms of mating competition and sexually selected traits favored by the different mating systems are still poorly understood. These gaps are mainly due to the fact that the available information on variance in male reproductive success and its determinants concerns almost exclusively highly dimorphic and polygynous species with dominance-based mating systems among large mammals (e.g., red deer:

Marshall 1998; Pemberton *et al.* 1992; bighorn sheep: Coltman *et al.* 2002; Soay sheep: Coltman *et al.* 1999a; Pemberton *et al.* 1999; but see data for the weakly dimorphic harbor seal *Phoca vitulina*: Coltman *et al.* 1998). By comparison, little is known about the opportunity for sexual selection in large mammalian systems without high male-biased dimorphism, where the traits under sexual selection might be less obvious, and in territorial species, where predictions relying on sexual selection might be more difficult to express due to the location-dependent dominance and the potential role of both phenotypic traits and territory characteristics (Owen-Smith 1977). This precludes any meta-analysis to detect general patterns in the opportunity for sexual selection and sexually selected traits among large mammals, which is very useful to better understand the evolution of mating systems (Andersson 1994). Hence, there is a great need of studies on species with low sexual dimorphism or monomorphism (Clutton-Brock 1987) and/or species with territorial mating systems in large mammals, and so far in ungulates.

IV. THE STUDY

MALE REPRODUCTIVE SUCCESS, THE EVOLUTION OF TERRITORIALITY AND SEXUAL SELECTION IN ROE DEER

IV.1. THE STUDY SPECIES: THE EUROPEAN ROE DEER, A TERRITORIAL SPECIES WITH LOW SEXUAL SIZE DIMORPHISM

The choice of the study organism, more precisely the match of question to organism, is a critical decision in ecological and evolutionary research (Travis 2006). The roe deer is a small-sized cervid (adults weigh about 20-30 kg, with a body length of 95-135 cm) with low male-biased sexual size dimorphism (males are less than 10% heavier than females: Andersen *et al.* 1998) and strong territoriality of adult males (see Liberg *et al.* 1998). This makes the roe deer an ideal model to further investigate patterns of variation in sexual selection among species in ungulates, to improve our knowledge on territorial species and species with low sexual size dimorphism which have been poorly studied up to now.

Through various aspects of its breeding behaviour, roe deer is unique among ungulates. Females in roe deer are commonly considered as non-territorial. During summer, they live solitarily (alone or together with only their fawns) in overlapping home ranges (Bramley 1970; Strandgaard 1972). During winter, they form small matriarchal groups consisting of one or a few adults, their dependent offspring, and yearling daughters. These groups are often accompanied by one or two males (Kurt 1968; Hewison *et al.* 1998). The reproductive cycle of female roe deer, with embryonic implantation delayed by five months (Lambert 2002) and only one short ovulation each year, seems to be unique among ungulates (see Figure 8). Despite being monestrous, up to 98% of females in a population are fertilized (Hewison 1996; Gaillard *et al.* 1992). Females are polytocous: they give birth to 1-4 neonates in May-June, with twins being most common and four being extremely rare. The fawns conform to the hider strategy in the first three to four weeks of life (Linnell 1994). They usually stay with their mother before becoming independent when they reach approximately one year of age, when most dispersal takes place (Wahlström & Liberg 1995). Both sexes disperse, females as yearlings and males either as yearlings or as two-year-olds. Females normally attain sexual maturity as yearlings, but under favourable conditions they may become pregnant already as fawns (Hewison 1996), whereas under poor conditions first reproduction is often delayed one year until the age of 3 years old (Hewison 1996; Gaillard *et*

al. 1992). Females seem to range independently of males, so that female ranges often overlap several male territories (e.g., Bramley 1970).

Adult males in roe deer are considered strongly territorial (Bramley 1970; Strandgaard 1972). Although territoriality has been defined in many different ways in vertebrates depending on the study species and authors, three criteria have been commonly used: exclusion, defence and site-specific dominance (Owen-Smith 1977). Ranges of roe bucks are, to a large degree, exclusive. During the territorial period, the degree of overlap between adjacent adult male ranges is low, particularly at low male density (e.g., Danilkin & Hewison 1996), while the core areas of the territories are non-overlapping, even at high density (e.g., Vincent *et al.* 1995). Territorial males are aggressive and intolerant towards intruder males (adults and sub-adults). Aggressive behaviours can take the form of threat, advertisement and fighting. It is often ritualized in displays (e.g., parallel walk, rubbing, scraping, barking), chases and retreats, more rarely actual combat (Bramley 1970; Danilkin & Hewison 1996). Dominance appears mainly site-specific, with a reciprocity of dominance among neighbouring territory holders (territorial males are dominant within their own territory but subordinate when exploring a neighbouring territory; Danilkin & Hewison 1996). Male territoriality is seasonal (see Figure 8). In winter, male roe deer are non-territorial like females. Territories are established in early spring (March-April) and maintained until late August - early September (e.g. Bramley 1970; Strandgaard 1972). Hence, the territorial period begins several months before the rut, which occurs from mid-July to mid-August. Roe deer is thus unique among deer in the Holarctic region, with their long-term territorial defence extending over a period of 5-6 months (Johansson 1996). Male territoriality is closely linked to seasonal changes in testosterone secretion, which affect both the antler cycle and aggressive behaviour (e.g., Sempéré 1982). During winter, when testosterone levels are low, males are non territorial while their antlers, which are in velvet, grow. As the secretion of testosterone increases during spring, male tolerance towards other males decreases, their antlers finish maturing and finally males shed their velvet in late spring. The increasing aggressiveness explains the onset of territorial behaviour, which commonly occurs before males get hard antlers (Johansson 1996). Finally, in late autumn, when testosterone once again reaches low levels, antlers are cast and roe deer territoriality breaks down. Although males become sexually mature as yearlings (at about 15 months of age), males usually do not defend territories until three or four years of age, depending on population density (see Hewison *et al.* 1998; Liberg *et al.* 1998 for more details).

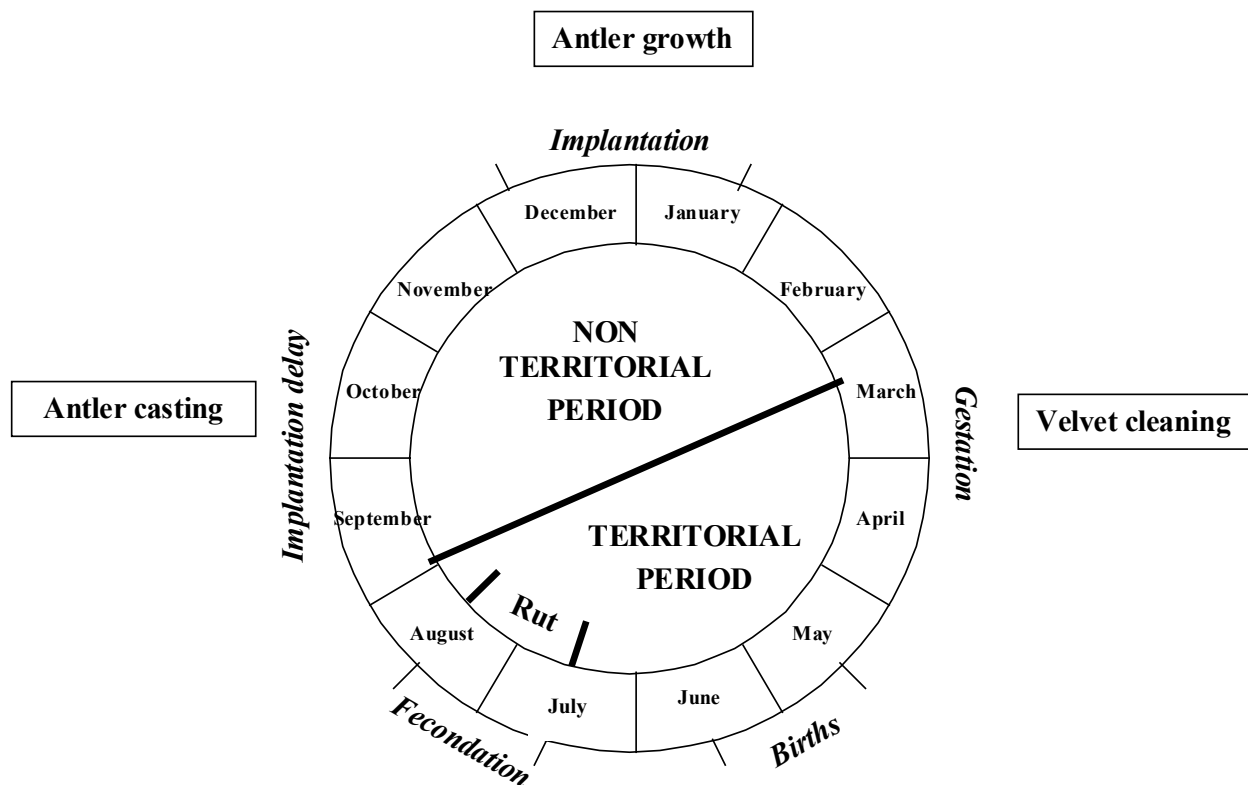


Figure 8. Reproductive cycle of male (not in italic) and female (in italic) roe deer.

IV.2. SUBJECT OF THE STUDY

Although territorial behaviours have been broadly described in roe deer (see above), very few studies have used an evolutionary approach to investigate the male mating system and sexual selection in this species (e.g., Johansson 1996; Börger 2006). Indeed, to investigate this issue, it is necessary to obtain good estimates of male reproductive success. Analysing the factors related to individual variation in yearly reproductive success, and identifying the characteristics of successful individuals, provides insight into the selective pressures affecting evolutionary processes, especially if summed over a lifetime. In roe deer, although it is possible to obtain accurate estimates of individual reproductive success of females from long-term monitoring of marked populations by observing females with their fawns just after they have given birth (Gaillard *et al.* 1998a, 2000a), similar information on male reproductive success is not available (but see Börger 2006, based on observations of courting and mating behaviours in an open landscape area). Male mating behaviours are difficult to observe in the wild due to the typical forest habitat of the species and its wary and solitary behaviour. In addition, females may mate with several males (see Liberg *et al.* 1998; Börger 2006). As a

result, it is very difficult to obtain reliable behavioural estimations of male reproductive success in roe deer. Yet, to date, the few studies on sexual selection in roe deer have assessed male breeding success from behavioural observations (see Johansson 1996; Börger 2006).

With the recent development of molecular techniques, and especially microsatellite genotyping and paternity analyses, an alternative approach is now available for estimating male reproductive success. When integrated with field studies molecular techniques provide a very powerful tool for understanding social systems (Hughes 1998). As yet, no study has yet used this approach in roe deer. My Ph.D. project therefore aimed to use genetic analyses in combination with long-term field data and field ecology studies to provide data on male reproductive success in roe deer and undertake the most detailed investigation on roe deer mating system using an evolutionary approach. More precisely, I attempted to answer to four fundamental questions about reproductive success (Clutton-Brock 1988a): (i) How widely does breeding success vary between males? (ii) How much of the variance in success is contributed by the different components of breeding success? (iii) To what extent does reproductive success change with age? (iv) And what factors affect breeding success in males? According to Clutton-Brock (1988a), these four questions are important in studies of population demography (Begon 1984), selection (Endler 1986) and adaptation (Williams 1966). From a theoretical point of view, this study aimed to provide new insights into sexual selection in ungulate species with territorial mating systems and low sexual size dimorphism, and thus, ultimately contribute to a better understanding of patterns of variation in the opportunity for sexual selection and sexually selected traits among species. This study also aimed to provide new insights into the evolution and adaptive function of male territoriality in roe deer and more widely in ungulates.

To investigate these issues, I studied three contrasting populations of roe deer in Europe (Bogesund in Sweden, Chizé and Trois Fontaines in France; see Materials and methods). The studies which have led to the greatest improvements in our understanding of mating systems and sexual selection in ungulates were all based on long-term monitored populations in which animals were individually marked. These populations indeed allow us to obtain data on longitudinal life-history of the individuals and, hence, to estimate LRS (see Clutton-Brock 1988a). The three populations of roe deer that I studied are exceptional in the sense that they have been subjected to long-term monitoring, with annual capture-mark-recapture sessions for more than 15 years (since 1977 at Chizé, 1975 at Trois Fontaines, and 1988 at Bogesund). There are few studied populations of ungulates with equivalent longitudinal data (see Table 2) and even less on individually marked animals.

Table 2. Main long-term monitored populations of ungulates in the world.

Species		Site name	Country	Study period
red deer	<i>Cervus elaphus</i>	Rum Island	Great-Britain	>30 years
Soay sheep	<i>Ovis aries</i>	St Kilda Island	Great-Britain	>30 years
roe deer	<i>Capreolus capreolus</i>	Trois Fontaines	France	>30 years
roe deer	<i>Capreolus capreolus</i>	Chizé	France	30 years
roe deer	<i>Capreolus capreolus</i>	Bogesund	Sweden	19 years
caribou	<i>Rangifer tarandus</i>	Rivière Georges et rivière aux feuilles	Canada	21 years
reindeer	<i>Rangifer tarandus</i>	Svalbard	Norvège	> 10 years
mountain goat	<i>Oreamnos americanus</i>	Caw Ridge	Canada	18 years
bighorn sheep	<i>Ovis canadensis</i>	Ram Mountain	Canada	35 years
bighorn sheep	<i>Ovis canadensis</i>	Sheep river	Canada	26 years
wild horse	<i>Equus caballus</i>	Great Basin Desert	USA	> 10 years
American pronghorn	<i>Antilocapra americana</i>	Bison range	USA	> 10 years
Alpine ibex	<i>Capra ibex</i>	Belledonne	France	> 20 years
chamois	<i>Rupicapra rupicapra</i>	Bauges	France	> 25 years
isard	<i>Rupicapra pyrenaica</i>	Orlu	France	> 20 years
isard	<i>Rupicapra pyrenaica</i>	Bazes	France	> 15 years
isard	<i>Rupicapra pyrenaica</i>	Pyrénées National Park	France	> 20 years
mouflon	<i>Ovis gnmelini</i>	Caroux	France	> 20 years
wild boar	<i>Sus scrofa</i>	Arc-en-Barrois	France	> 20 years
white-tailed deer	<i>Odocoileus virginianus</i>	Reserve Georges	USA	> 30 years
white-tailed deer	<i>Odocoileus virginianus</i>	Minnesota	USA	> 20 years
wapiti	<i>Cervus elaphus</i>	Yellowstone	USA	> 10 years
wapiti	<i>Cervus elaphus</i>	Grand Teton	USA	> 10 years
moose	<i>Alces alces</i>	Alaska	USA	> 25 years

IV.3. STRUCTURE OF THE STUDY

My study was divided into five parts, including 6 papers. The first part focussed on variation in male breeding success and the opportunity for sexual selection in roe deer and more widely in Ungulates (Paper 1). The second part analysed age-dependent variation in male breeding success (Paper 2). The third part concerned selection in progress and investigated phenotypic determinants of variation in male breeding success (i.e. body mass and antler size) and the adaptive significance of the tested traits (Papers 3 and 4). In the fourth

part, I questioned the role of territory in male access to mates and the evolution of territoriality, by investigating territory-related determinants of variation in male breeding success (i.e. territory size and habitat quality; Paper 5). Finally, in the fifth part, I addressed questions on the evolution of multiple mating in females and multiple paternity (Paper 6).

Notice that it has not been possible, unfortunately, to include data of all of the three studied populations in all the papers of my thesis. Indeed, because of lack of time and the high costs of DNA genotyping, we genotyped DNA samples and performed paternity analyses for the Bogesund and Trois Fontaines populations, but not for Chizé population. In addition, as genetic results for Trois Fontaines were obtained late (in February 2007), we could not include these results in the papers 1 and 4 of the thesis. Finally, paper 5, which necessitated intensive field-work (specifically, radio-tracking, vegetation sampling, and fawn captures) during the territorial period in 2004 and 2005 at Bogesund, concerned only this population. Below I outline the theoretical background and the major questions that were addressed and the approach that was adopted in each of these papers.

Variance in male breeding success and the opportunity for sexual selection

Understanding the extent and distribution of the differences in the number of offspring males produce during their life span is relevant both to studies of population dynamics (Lomnicki 1978) and to studies on selection (Wade & Arnold 1980). How widely does breeding success vary between males? Do a few males monopolize the major part of the reproduction, or are paternities equally shared between males within a population? How much of the variance in success is due to the different components of breeding success? These are the kind of questions which I attempted to answer in the Paper 1 of this thesis. Based on a panel of microsatellite markers and paternity analyses, I studied the distribution of paternities within a long-term monitored population of roe deer (Bogesund). I could thus provide the first data on male (both annual and lifetime) breeding success and estimate of the opportunity for sexual selection in roe deer, based on genetic analyses. I then investigated the extent to which annual breeding success and the reproductive life span contribute to fitness variation in males. In roe deer, males weigh less than 10% more than females and defend spatially stable territories. The variation in the number of female ranges partially overlapped by a male's territory is commonly low (usually < 5 females; Liberg *et al.* 1998), and roe deer have long been regarded as being weakly polygynous (Putman 1988; Kurt 1991; Hewison *et al.* 1998) or even monogamous (Prior 1968). As a result, I expected a low variance in lifetime breeding success between males, and so a weak opportunity for sexual selection (Hewison *et al.* 1998).

I finally compared my results with published data on various other ungulate species and thereby tested the hypothesis of a continuum of opportunity for sexual selection, from monomorphic monogamous species to highly polygynous et sexual size dimorphic species, in ungulates (e.g., Jarman 1974).

Age-specific variation in male breeding success and age of first reproduction

The LRS of an individual may be greatly affected by the age at which it first reproduces (Lewontin 1965; Caswell 1982) and the age-specific reproductive rate is one of the fundamental parameters for assessing population growth and viability (Caughley & Sinclair 1994). The study of variation in male breeding success in relation to age is therefore important for both population ecology (Caughley 1977) and life-history theory (Pianka 1978). In Paper 2, I therefore investigated age-specific variation in male breeding success in two populations of roe deer (Bogesund and Trois Fontaines). The main questions asked were: At which age do males begin to breed? To what extent does breeding success change with age? Does breeding success increase with experience? Does male breeding success decrease in very old males due to senescence? I discussed results within the framework of life-history theories (Roff 1992; Stearns 1992).

Phenotypic determinants of male breeding success and selection in progress

Sexual selection can only occur if variation in reproductive success is correlated with phenotypic trait variation (Andersson 1994). It is therefore important to use trait-related measures, in complement to the previous measure based on the standardized variance in male breeding success, to estimate selection in progress and not only the opportunity for sexual selection (Clutton-Brock 1988; Andersson 1994). In deer, male body mass and antler size are certainly the most likely candidates for sexually selected traits, since they could be favoured by both male contests (especially in species in which fights involve pushing) and female mate choice, as honest indicators of male quality (see Andersson 1994). I therefore focussed on these two phenotypic traits in my study to investigate sexual selection in progress in roe deer. But identifying factors shaping secondary sexual traits is essential to understand how their variation may influence male reproductive success and explore their adaptive function. To test whether male antler size could be considered as a honest signal of male quality for rival males and females in roe deer, I first identified the main determinants of variation in male antler size, exploring the effects of both phenotypic (i.e. age and body mass) and environmental (i.e. food resources, climatic condition and population density; see Paper 3) factors in three

contrasting populations of roe deer (Bogesund, Chizé and Trois Fontaines). I then investigated the effects of male body mass and antler size on variation in male breeding success and tested the occurrence of continued sexual selection on the variation of these secondary traits in one of these populations (Bogesund; see Paper 4). Notice that the Paper 4 includes only data from Bogesund in the thesis, but I will later add data from Trois Fontaines before submitting the manuscript to a journal.

The role of territory characteristics in male breeding success and the evolution of territoriality as a resource defence polygyny mating system

Some attempts have been previously made to identify the adaptive function of roe buck territoriality. One of the main hypothesis is that territoriality may have evolved as a mating tactic analogous to a resource defence polygyny (e.g., Putman 1988; Wahlström 1994; Johansson 1996). Males would defend resources (e.g., food, birth sites, shelter against predators) against other males to attract potential mates during the breeding season and assure mating success. However, several aspects of the territorial behaviour of roe bucks suggest that territoriality is not an optimal mating strategy in roe deer: the excursions of females outside of their normal home range during the rut (see Liberg *et al.* 1998); the independence of the spatial system of the two sexes and multiple mating of females (Liberg *et al.* 1998), the high fidelity of males to the same area where they establish their first territory and the stability of territories both in size and limits (e.g., Bramley 1970; Johansson 1996; Linnell & Andersen 1998). Hence, no consensus on the adaptive function of male territoriality in roe deer has been achieved and the understanding of the role of male territory in male mating success remains unclear. I therefore investigated this issue in Paper 5 and further explored the role of resource distribution on female distribution and the role of female distribution on male distribution and male breeding success in a population of roe deer (Bogesund). If territoriality has evolved as a resource defence polygyny mating tactic, as females are expected to distribute themselves in relation to resources, males should anticipate how resources will influence female distribution and compete for resource-rich sites to establish their zone of dominance. In addition, male territory size and habitat quality are expected to determine the abundance of females present within a male's territory, which should in turn influence male access to mates and male breeding success. This analyse allowed me to explore the role of territories in male breeding success.

Evolution of multiple mating and multiple paternity

Multiple paternity is a result of the insemination of a female by at least two males to produce a single litter or brood. In ungulates, this has been demonstrated in two enclosed populations of white-tailed deer (one captive: DeYoung *et al.* 2002 and one natural: Sorin 2004) and in a wild free-ranging population of American pronghorn (Carling *et al.* 2003). However, the occurrence of multiple paternity has never been explored in a fully territorial ungulate species. The discovery of multiple paternity in a strongly territorial species could have important consequences, since it would require us to revise our view of territoriality as a mating tactic, particularly regarding party size and the operational sex ratio (i.e. the ratio of fertilizable females to sexually active males; Emlen & Oring 1977), and hence the opportunity for sexual selection. In roe deer, females are polytocus and are courted and mated repeatedly and frequently during estrous. Hence, among ungulates, roe deer is a likely candidate for displaying multiple paternity. Based on the results of paternity analyses, I thus investigated this issue in two populations of roe deer, Bogesund and Trois Fontaines (see Paper 6). I also discussed the evolution of multiple mating in female roe deer.

MATERIALS AND METHODS



DNA prelevment on fawn
(photograph by Cécile Vanpé)

I. STUDY POPULATIONS

My thesis was based on the analysis of data from three contrasting populations of roe deer in Europe: Bogesund in Sweden and Chizé and Trois Fontaines in France (see Figure 9).

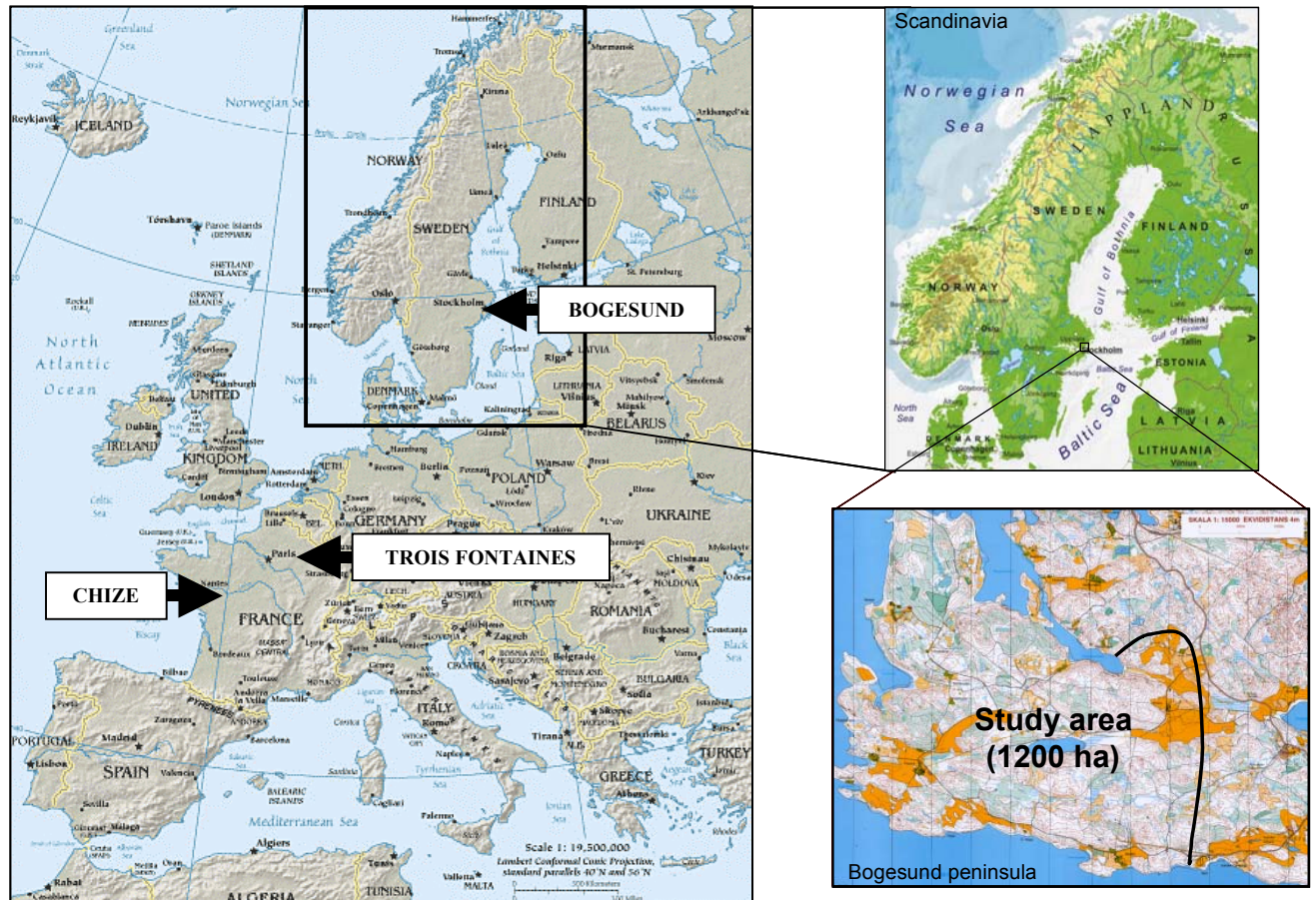


Figure 9. Situation of the 3 study sites: Bogesund, Chizé and Trois Fontaines and map of the Bogesund peninsula indicating the situation of the study area.

The population of Chizé is situated in the Chizé reserve, 2614 ha of enclosed forest in western France (46°06'N, 0°26'W), a reserve managed by the Office National de la Chasse et de la Faune Sauvage. The climate is oceanic under Mediterranean influences, with mild winters (mean temperature in January: 5°C, annual number of frozen days: 44) but with hot and dry summers (mean precipitation in May-June: 88 mm) (Gaillard *et al.* 1993a, 1997). Productivity of the forest is low, probably because summer droughts are common and soils are swallow, stony and not really fertile. The dominant trees are deciduous (oak *Quercus* spp., hornbeam *Carpinus betulus*, maple *Acer campestre*, beech *Fagus sylvatica*) and understories are dominated by hawthorn *Crataegus monogyna* and dogwood *Cornus* spp.

The northern area of the reserve is covered by 1397 ha of oak forest, in which the principal food plants for roe deer in spring and summer occur more frequently, and have a higher nitrogen content than in the southern part of the reserve covered by 1143 ha of a limestone beech forest (see Pettorelli *et al.* 2001 for more details; see Figure 10).

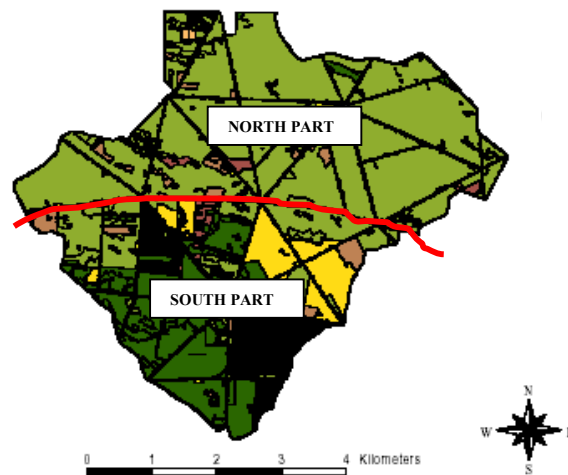


Figure 10. Map of the dominant trees in the Chizé reserve. In dark green: beech, in light green: oak, in yellow: hornbeam. The red line represents the limit between the two contrasting areas: the rich North part and the poor Southern part. From ONF and M. Pellerin.

The population of Trois Fontaines is situated in an experimental study enclosure (Territoire d'Etude et d'Expérimentation) of 1360 ha in eastern France (48°43'N, 4°55'E), a reserve managed by The Office National de la Chasse et de la Faune Sauvage. The climate is continental, with harsh wintering conditions (mean temperature in January: 2°C, annual number of days with frost: 70) and heavy precipitation during summer (mean precipitation in May-June: 150 mm) (Gaillard *et al.* 1993a, 1997). The habitat is quite homogeneous in this area and the spatial heterogeneity occurs only at a fine scale (see Figure 11). Forest is dominated by oak *Quercus* spp. and beech *Fagus sylvatica*, whereas coppice is composed primarily of hornbeam *Carpinus betulus* and understories are dominated by ivy *Hedera helix* and brambles *Rubus* sp. Productivity of the forest is quite high, due to fertile soils. This population is also managed by the Office National de la Chasse et de la Faune Sauvage.

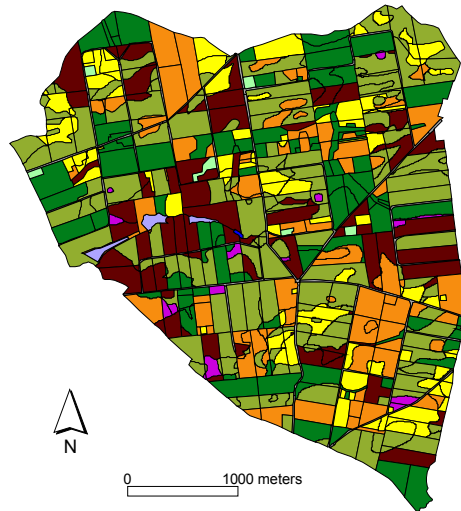


Figure 11. Map of the main habitat types in the Trois Fontaines enclosure (exemple of 2004). In yellow and orange: thickly-wooded areas, in brown: mature closed forest, in green: more open forest. From ONCFS.

The population of Bogesund is situated on a little peninsula, situated 10 kilometres Northeast of Stockholm, on the coast of the Baltic Sea on the inner portion of the Stockholm Archipelago, in the hemiboreal zone of east-central Sweden (59°23' N, 18°15' E). The study area (1,200 ha) was part of a 2,600 ha research area (see Kjellander 2000). A mosaic of forested (dominated by commercial coniferous and mixed forests) and field habitats characterises the area (about 65% of forest, 25% of agricultural areas, 10% of bed rock and bogs; see illustrations on Figure 12). The forests are dominated by two coniferous tree species, Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), whereas deciduous species, including birch (*Betula* spp.), aspen (*Populus tremulus*), oak (*Quercus robur*), ash (*Fraxinus excelsior*) and willow (*Salix* spp.), are also common in most forest types (Kjellander 2000). Dwarf shrubs, primarily bilberry (*Vaccinium myrtillus*), were patchily distributed as ground cover in mature forest stands, while numerous herbs were abundant in most habitats. Some agricultural fields were resown in early autumn, but most were ploughed after harvest, kept bare during winter and sown in spring. Common crops were rape (*Brassica napus*), oats (*Avena sativa*) and wheat (*Triticum* spp.). Pastures make up less than half of the agricultural land. Associated with the open areas are numerous small meadows and former fields that lay fallow or are replanted with birch or spruce (Kjellander 2000).

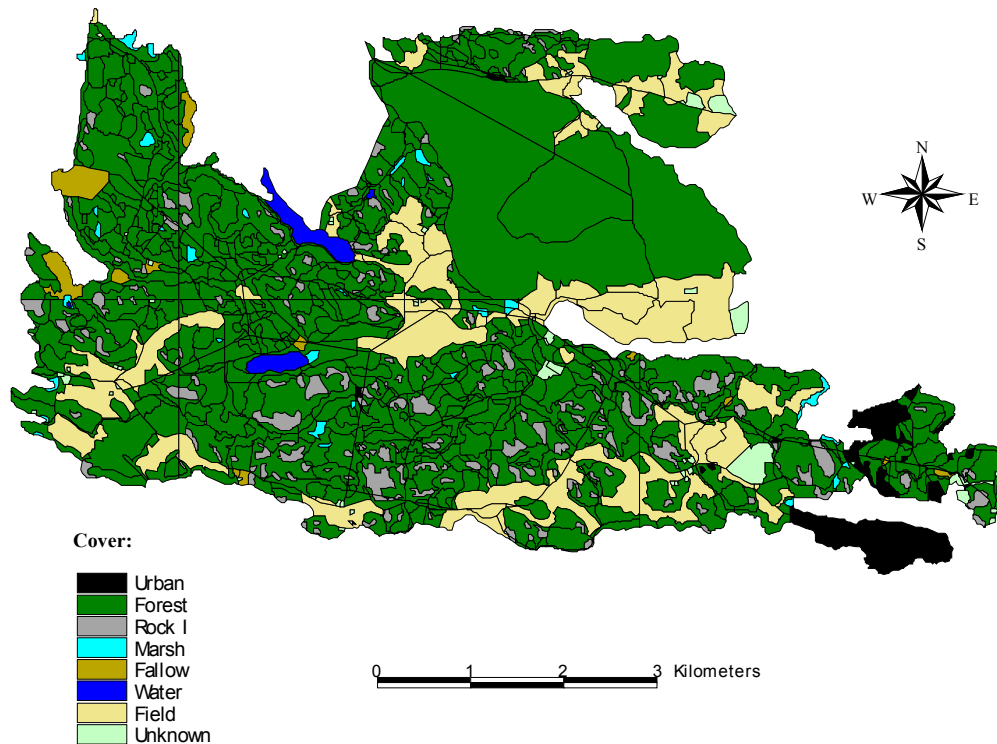


Figure 12. Map of the main habitat types at Bogesund.

The continental climate of Bogesund is influenced by the Baltic Sea. It is characterised by rude winters (mean temperature in January (the coldest month): -3.7°C ; mean length of snow cover: 80 days (usually from late December to early March); maximum snow depth: 13 cm in February) and relatively mild and dry summers (mean temperature in July (the warmest month): 16.7°C ; annual precipitation: 550 mm with most falling in July, and the least in February) (Kjellander 2000). Apart from roe deer, other larger mammalian herbivores included low density moose ($0.5\text{-}1/\text{km}^2$) and wild boar populations. Both mountain hare (*Lepus timidus*) and brown hare (*Lepus europaeus*) occurred and fluctuated in numbers between years. The only roe deer predator of importance (for fawns) is the red fox (*Vulpes vulpes*; see illustrations on Figure 15) which was almost absent during the first half of the study period due to an outbreak of sarcoptic mange in Scandinavia (Lindström *et al.* 1994). Human residents in the area are few and dispersed. A few people are living in small cottages or summer-houses, and there were three large farms in the area associated with the open agricultural areas. During weekends and vacations, the area was used extensively by the large nearby Stockholm population for recreation. Hunting on the research area was controlled by the research project.

Hence, these three sites differ mainly with respect to climatic conditions: while Chizé has a temperate oceanic climate, with mild winters and hot and dry summers, and Trois Fontaines has a continental climate characterised by moderately severe winters, with low temperatures and rainy summers, Bogesund has a continental climate under the influence of the Baltic sea, with relatively harsh snowy winters and mild and dry summers. But the three sites also differ with respect of habitat fragmentation: the two French (enclosed) populations are mainly forest, whereas the Swedish (free-ranging) population is more fragmented (25% of agricultural areas).

II. THE METHODS

A COMBINATION OF MOLECULAR TOOLS AND FIELD ECOLOGY STUDIES

I used a combination of molecular tools and field ecology studies to investigate sexual selection and mating system in roe deer. Specifically, my study was based on the analysis of longitudinal data (especially Capture-Mark-Recapture data) from the three study populations, laboratory work in molecular ecology to genotype DNA samples collected at Bogesund and Trois Fontaines during the long-term study, and intensive field-work (mainly radio-tracking, vegetation sampling, pellet-group counts, fawn capture and behavioural observations) at Bogesund from late March to late August (territorial period) in both 2004 and 2005. Below, I briefly present the long-term monitoring of individually marked animals in the three populations. I then describe in details the methods of molecular analyses and paternity analyses allowing me to estimate male breeding success. Methods of field ecology studies are finally described. Unless otherwise mentioned, all the statistical analyses were carried out in R 2.4.1 software (Ihaka & Gentleman 1996) and were detailed in the Materials and Methods part of each paper.

II.1. LONGITUDINAL DATA AND POPULATION SAMPLING (all 3 populations)

The three populations of roe deer have been subjected to a long-term monitoring with some annual Capture-Mark-Recapture sessions for more than 15 years (since 1977 at Chizé, 1975 at Trois Fontaines, and 1988 at Bogesund). Each year, during winter, roe deer were captured (with box traps at Bogesund and with nets at Chizé and Trois Fontaines), sexed, aged, measured (e.g., body mass, antler size) and individually marked with plastic ear-tags and eventually collars. Age was either known definitively (animals first caught as new-born fawns or fawns <1 year old) or estimated from tooth eruption and wear (Cederlund *et al.* 1992). In the three sites, a high proportion of the population was marked during each year of the study (over 70% in Chizé and Trois Fontaines) so that reliable estimates of population size were available for each year and longitudinal life-history of individuals can be recovered, to investigate many issues in population dynamics and evolutionary ecology. At Chizé and Trois Fontaines, the estimation of population density was based on the generalisation of the

Cormack-Jolly-Seber model (see Gaillard *et al.* 2003a). At Bogesund, it was based on the Lincoln-Petersen model (see Kjellander 2000).



Photos of the traps (A) and nets (B) used to catch roe deer (C) at Bogesund and Chizé & Trois Fontaines respectively. The photo B was not taken at Chizé or Trois Fontaines but on another French roe deer study site (Aurignac).

Experimental manipulation of density through hunting and/or removals took place in all three study areas, so that marked between-year differences occurred in population density (see Figure 13).

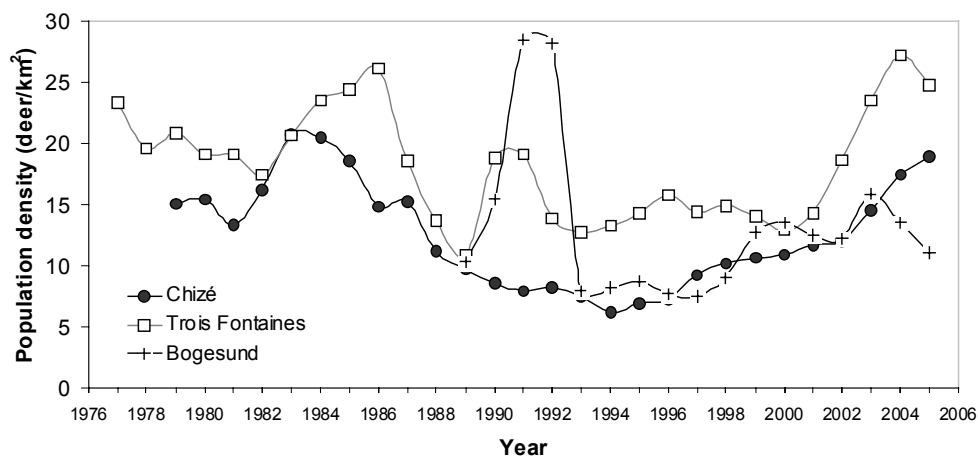


Figure 13. Variation of roe deer density in the three studied populations since the beginning of the long-term study.

II.2. MOLECULAR ANALYSES (Bogesund and Trois Fontaines)

During the study period, the managed population of Chizé has experienced substantial fluctuations, going through abundance from 150 to 550 individuals older than 1 year old (density variation: 5.8-21.0 deers / 100 ha). Through management, the numbers were indeed controlled by a combination of natural, density-dependent and artificial factors (Gaillard *et al.*

1993a). At Trois Fontaines, the population was roughly kept constant in size throughout the study period (at about 200-250 individuals older than 1 year old in March, i.e. a density of 18.4 deers/100ha) by removals for translocations (Gaillard *et al.* 1993a), with however a significant increase of the population density for 4 years because of a stop of the prelevments between 2001 and 2004 (Gaillard pers. com.). At Bogesund, due to experimental manipulation, the roe deer population density varied during the study period (Kjellander 2000). After an increase from 1989 to 1992, the population was reduced to less than 10 deer per km² in 1993. Since 1998, the population has increased again except for the last three years.

II.2. MOLECULAR ANALYSES (Bogesund and Trois Fontaines)

II.2.1. Considerations on the lifetime breeding success as proxy of fitness

Fitness is a pivotal concept to any empirical study testing evolutionary theories (Endler 1986). Yet, if there is a general agreement on the definition of fitness – most authors agree that fitness equates to some measure of genetic contribution to future generations; Endler 1986; Charlesworth 1994 – its measure remains largely controverted and many methods have been proposed to estimate it.

First, fitness can be measured on two different hierarchical levels: the individual and the population (in this later case, fitness quantifies population growth rate). Here, I was interested in individual-based estimate of fitness. Indeed, studying the ultimate benefits and the evolutive function of male territoriality in roe deer implies to gain good estimates of male individual fitness in order to be able to analyse the variance in the success between males and to find important correlates with this variance.

Second, while it is possible to estimate a long-term fitness by evaluating the long-term genetic contribution an individual makes to future generation (e.g., the total number of gene copies a focal individual transmits to all descendants after a given number of generations; see Brommer *et al.* 2004), long term fitness estimates are difficult to develop and single-generation estimates of fitness well capture the long-term genetic contribution to the population (see Brommer *et al.* 2004 for a test). Hence, most empirical studies use generation-based proxies for individual fitness.

Two broad classes of per generation fitness estimates are conventionally used in the literature (Brommer *et al.* 2004). First, rate-sensitive fitness estimates (e.g., λ_{ind}) take into account both the number of offspring produced and the age of the parent when these offspring

were produced. They discount offspring production at later ages and thereby put a premium on starting to reproduce early in life. Second, rate-insensitive estimates (e.g., lifetime reproductive success, noted LRS) only represent the number of offspring produced and ignore the timing of reproduction. They are highly influenced by the age of the first reproduction, but also by the life span. In contradiction with LRS, λ_{ind} considers the repartition and the success of the lifetime events all along the life of the individual (Brommer *et al.* 2002). Although λ_{ind} better fits with the general theoretical definition of the individual genetic fitness, empirical studies usually use the rate-insensitive LRS to estimate individual fitness (e.g., Clutton-Brock 1988). LRS has thus been used in most of the few previous studies that have quantified the causes of variation in individual male fitness of large herbivores (e.g., in red deer: Clutton-Brock *et al.* 1988; but see the use of λ_{ind} in roe deer: Kjellander *et al.* 2004). This single-generation LRS estimate was shown to be a valid demographic proxy of long-term genetic contribution to the population (see Brommer *et al.* 2004) and seems especially to be a good proxy of fitness in large mammals (Clutton-Brock 1988). For natural scenarios, rate sensitivity does not seem to improve estimates of individual-level fitness (Brommer *et al.* 2004). The first reason is that fitness payoff from offspring produced late in life is too strongly de-emphasised by rate sensitivity (Brommer *et al.* 2004). Second, rate insensitivity will buffer variation in offspring value against erroneously inflating the fitness contributions of offspring of different value produced during the life of the parent (Brommer *et al.* 2004). Finally, reproductive timing is certainly an important selective force at times, but its magnitude and sign may change on a shorter timescale than the life span of an individual parent, depending whether population is growing or is shirking (Brommer *et al.* 2004). In this study, I therefore used the single generation rate-insensitive fitness estimate LRS (defined as the total number of independent offspring produced by the individual during its life span) to estimate individual fitness. I also used the yearly reproductive success (YRS), defined as the total number of offspring produced in a year by each member of a set of known individuals (Grafen 1988).

Notice that per generation measures of individual fitness were developed for cases when generation time does not vary between individuals (Fisher 1930) and where the population was at equilibrium. In this case, the mean of LRS from one generation to the next is a valid short-term estimate of mean fitness (Coulson *et al.* 2006). However, in cases where generations overlap and there is substantial inter-individual variation in generation length (most iteroparous species) or when populations fluctuates over time, the mean per generation estimates of fitness do not give mean fitness. This can lead to selection and heritability being

confounded (Coulson *et al.* 2006). One way to solve this problem is to estimate fitness as the relative performance of individuals over a period of time shorter than the generation (e.g., time intervals between breeding seasons). Coulson *et al.* (2006) have thus recently proposed a new approach allowing the estimation of an individual's contribution to population growth over a time step from life history and population data. The number of surviving offspring produced over a time step, that are still alive at the end of the time step, plus one if the parent survived is measured and referred as individual performance. For each individual within a population at each time, the individual performance is removed and population growth is recalculated. This approach takes the realized population growth over a time period and asks how each individual contributed to it directly (Coulson *et al.* 2006).

Although it is relatively easy to decide how the variation in breeding success should be estimated, collecting the relevant data poses a variety of problems, especially in long-lived and highly mobile animals like cervids (Clutton-Brock 1987).

Though reproductive success can be used as a valid proxy of fitness provided that it quantifies the propagation success of an individual's genes through the subsequent generations, variation in reproductive success is often calculated in practice in vertebrates over a single breeding season or few a part of individual's lifespan (Howard 1979; Clutton-Brock 1988). However, since it is on individual differences in LRS that selection will usually operate (Falconer 1960; Maynard Smith 1969), measures calculated over shorter periods are only valid in so far as they reflect variation in LRS (Clutton-Brock 1987), that is probably very seldom. They often either under- or over-estimate variation in LRS. First, male reproductive success often varies between breeding seasons and this variation in yearly success may cause over-estimation of the variation in LRS (Clutton-Brock 1982). Second, if individuals that are particularly successful during their peak period are likely to die earlier (because of trade-off between survival and reproduction) than those that expend less effort, variation in yearly success will over-estimate variation in LRS (Clutton-Brock 1987). This has been shown in mountain sheep rams (Geist 1971), but it is not always the case because of differences in individual quality (Clutton-Brock & Harvey 1979). Third, where age exerts an important effect on success, variation within seasons calculated across animals of different ages is likely to over-estimate variation in LRS (Clutton-Brock *et al.* 1979; Clutton-Brock 1987). Fourth, estimates of variation in success will be affected by the sample of males included, since in particular unsuccessful individuals are often less visible (Clutton-Brock 1987). This can be the case even if LRS is used. For example, mean and variance in LRS can

be estimated among all males conceived, among all males born, among those surviving the neonatal period, among those breeding at least once. These four biases are likely to affect male breeding success stronger than female breeding success, and polygynous species stronger than monogamous ones (Clutton-Brock 1987). It is therefore important to use longitudinal studies to estimate reproductive success on the long-term to investigate patterns in individual fitness (Clutton-Brock 1988).

In addition, measures of LRS have commonly been calculated by counting offspring that are either still dependent of their parents (e.g., Clutton-Brock 1988), either independent offspring (e.g., Gaillard *et al.* 2000b), or breeding offspring (e.g., Clutton-Brock 1988). Brommer *et al.* (2004) have shown that estimates of LRS based on offspring that are recorded breeding correlate better with estimated genetic contribution to the population than estimates based on dependent offspring. However, recruitment is notoriously more difficult to measure (e.g., because of young dispersion). Besides, it seems that male ungulates generally exert little influence on the survival of their offspring, so that differential genetic success arises primarily from differences in their mating contributions (Owen-Smith 1977). In polygynous breeding systems, differences in mate number are usually the most important source of variation in male success (Bateman 1948; Wade 1979; Wade & Arnold 1980). In this study, because a proportion of the fawns were caught as neonates for which the fate was unknown, I used male lifetime breeding success (LBS), defined as the number of born offspring sired by a male, as a proxy of individual male fitness. Although this measure does not integrate a juvenile survival component, fawn survival should be almost exclusively affected by maternal rather than by paternal influences in roe deer (Gaillard *et al.* 2000a) and so male LBS should be a valid proxy to estimate male LRS.

II.2.2. Tissue sampling

From 1988 onwards at Bogesund and 1975 at Trois Fontaines, roe deer (including 8 month-old fawns) were caught each winter (see above). From 1997 onwards at Bogesund and 1985 at Trois Fontaines, neonates were also caught by hand every spring, just after birth (May-June). Mother-offspring relationships were elucidated by direct observation of fawns with their mothers immediately after birth or during autumn (after the summer rut ends roe deer fawns continue to associate with their mother; Linnell *et al.* 1998b). Finally, during the study period, some roe deer have occasionally been shot or removed in order to manipulate experimentally the roe deer population density within the two populations (see Gaillard *et al.*

1993a, 2003a; Kjellander 2000 for more details). In both populations (from 1988 at Bogesund and 1994 at Trois Fontaines), tissue samples for DNA genotyping were collected from individuals caught for the first time and from unmarked shot roe deer. A small (approximately 2 x 2 mm) piece of ear skin tissue was usually removed using sheep ear-notching pliers. However, samples taken on newborn fawns from 1997 to 2003 were hair samples (N = 146). Notice that sampled fawns from a given cohort can become candidate parents for later fawn cohorts provided that they survive to sexual maturity, and that candidate fathers and mothers can be potential parents for several successive fawn cohorts. This allowed us to sample a total of 1757 different individuals at Bogesund (of which 338 fawns with unknown mothers or unsampled known mother and 267 fawns with sampled known mother) and 1298 different individuals at Trois Fontaines (of which 660 fawns with unknown mothers or unsampled known mother and 120 fawns with sampled known mother).

II.2.3. Microsatellite genotyping

Molecular analyses (see Figure 14) were performed at the French laboratory “Centre de Biologie et de Gestion des Populations” (INRA Montpellier).

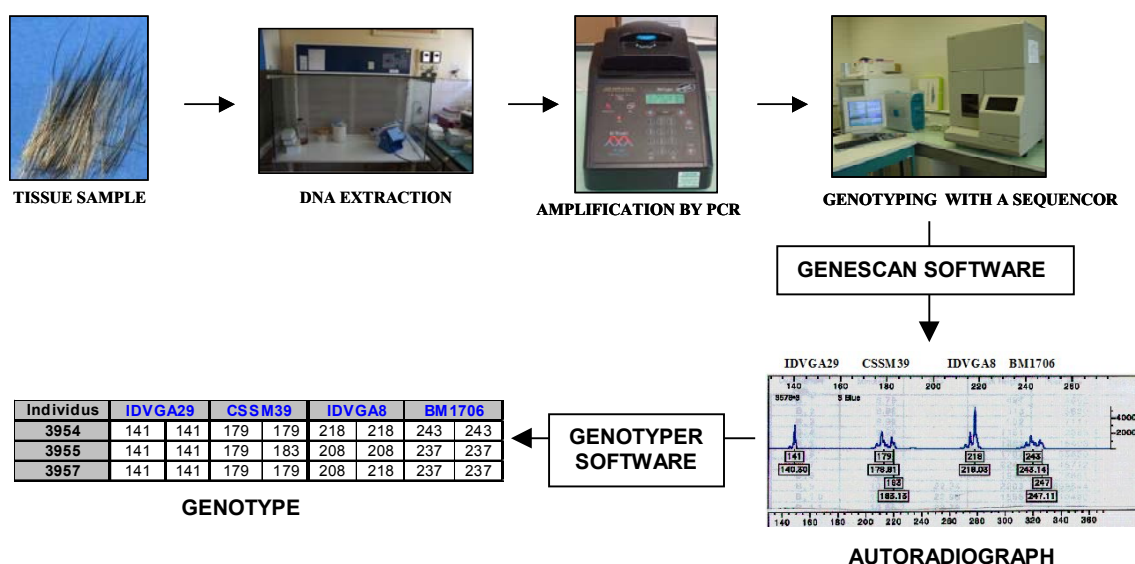


Figure 14. Steps of the molecular analyses.

We used 22 microsatellite markers (microsatellites, or Simple Sequence Repeats (SSRs), are polymorphic loci where short sequences of DNA are repeated in tandem arrays and which are typically neutral and co-dominant; see Table 3 for the list) initially isolated from other

ungulate species (Galan *et al.* 2003; Vial *et al.* 2003), except for Roe5, Roe6, Roe8 and Roe9 isolated specifically from roe deer (Fickel & Reinsch 2000). These 22 microsatellites were divided into two multiplex kits of 11 microsatellites each (Galan *et al.* 2003 unpubl.). Genotyping was carried out using 22 microsatellite markers at Bogesund (see Table 3A), but only 12 of those 22 microsatellite markers at Trois Fontaines (see Table 3B) because of the higher polymorphism of this population.

Table 3. Descriptive statistics for the microsatellite loci used to genotype Bogesund (A) and Trois Fontaines (B) DNA samples.

(A)	Locus	k	N	H _O	H _E	Excl _{1st}	Excl _{2nd}	Null allele freq	F _{IS} (W&C)	HW (excess)	HW (deficit)
	IDVGA29	2	1642	0.328	0.333	0.055	0.139	0.0071	0.006	0.622	0.555
	CSSM39	5	1640	0.613	0.610	0.200	0.348	-0.0032	0.033	0.530	0.472
	IDVGA8	2	1631	0.372	0.374	0.070	0.152	0.0032	-0.056	0.343	0.813
	BM1706	3	1640	0.098	0.097	0.005	0.046	-0.0078	-0.029	0.801	1.000
	OARFCB304	8	1615	0.693	0.695	0.288	0.464	-0.0001	0.012	0.494	0.513
	HUJ1177	5	1629	0.480	0.588	0.197	0.372	0.1238	0.208	0.997	0.002
	BMC1009	5	1642	0.574	0.584	0.185	0.348	0.0098	-0.025	0.199	0.809
	BM848	3	1593	0.631	0.645	0.208	0.352	0.0097	0.030	0.682	0.323
	CSSM41	3	1580	0.551	0.555	0.154	0.275	0.0042	-0.000	0.350	0.664
	BM757	8	1638	0.777	0.790	0.413	0.592	0.0070	-0.022	0.153	0.839
	CSSM43	2	1631	0.110	0.113	0.006	0.053	0.0116	-0.060	0.618	1.000
	Roe8	7	1622	0.575	0.582	0.193	0.362	0.0080	-0.026	0.364	0.640
	SR-CSRP1	4	1550	0.247	0.263	0.035	0.135	0.0239	-0.068	0.261	0.833
	Roe9	3	1631	0.441	0.447	0.100	0.223	0.0063	-0.047	0.632	0.365
	KCNA44	5	1630	0.771	0.787	0.396	0.575	0.0101	-0.023	0.443	0.538
	Roe6	4	1630	0.489	0.491	0.120	0.202	0.0021	-0.052	0.284	0.743
	Roe5	4	1621	0.752	0.637	0.218	0.374	-0.0981	-0.124	0.028	0.971
	ILST030Q	5	1625	0.675	0.687	0.263	0.429	0.0098	-0.009	0.695	0.301
	MAF70	5	1632	0.580	0.559	0.159	0.265	-0.0203	-0.098	0.786	0.213
	MB26	2	1631	0.422	0.425	0.090	0.167	0.0034	0.041	0.756	0.394
	BL42	4	1629	0.643	0.655	0.226	0.381	0.0100	0.063	0.817	0.184
	ILST011	4	1631	0.692	0.678	0.257	0.429	-0.0121	-0.067	0.238	0.777

(B)	Locus	k	N	H _O	H _E	Excl _{1st}	Excl _{2nd}	Null allele freq	F _{IS} (W&C)	HW (excess)	HW (deficit)
	IDVGA29	2	1259	0.292	0.302	0.046	0.128	0.0179	-0.008	0.6216	0.6484
	CSSM39	6	1255	0.781	0.782	0.394	0.574	-0.0004	0.028	0.6272	0.3670
	IDVGA8	6	1261	0.731	0.743	0.339	0.516	0.0076	0.007	0.2382	0.7644
	BM1706	9	1248	0.664	0.682	0.296	0.484	0.0113	0.042	0.7659	0.2449
	OARFCB304	20	1247	0.780	0.809	0.485	0.660	0.0188	0.128	0.9800	0.0214
	HUJ1177	10	1262	0.777	0.784	0.407	0.585	0.0046	0.097	0.9428	0.0590
	BMC1009	6	1262	0.655	0.703	0.284	0.454	0.0365	0.069	0.9299	0.0725
	BM848	7	1235	0.731	0.758	0.361	0.541	0.0170	0.087	0.9322	0.0728
	NVHRT48	3	1268	0.423	0.425	0.090	0.223	0.0060	0.011	0.4848	0.5239
	CSSM43	3	1263	0.554	0.539	0.145	0.285	-0.0141	0.043	0.8355	0.1714
	BM757	12	1259	0.770	0.795	0.434	0.612	0.0161	0.093	0.9651	0.0336
	CSSM43	6	1241	0.724	0.704	0.290	0.462	-0.0172	-0.087	0.2731	0.7545

Note: Parameters estimated using CERVUS on all genotyped individuals: *k* = number of alleles, *N* = number of individuals genotyped, *H_O* = observed heterozygosity, *H_E* = expected heterozygosity, *Excl_{1st}* = exclusion probability of first parent, *Excl_{2nd}* = exclusion probability of second parent (when one parent is known), *Null allele freq* = estimated frequency of null alleles. Parameters estimated using GENEPOP on the 1992 and 2003 fawn cohorts with siblings removed at Bogesund and Trois Fontaines, respectively (*N* = 133 and 97 respectively): *F_{IS}* (W and C) = estimate of Weir and Cockerham's *F_{IS}*, *HW (excess)* = probability test for an excess of heterozygotes, *HW (deficit)* = probability test for a deficit of heterozygotes.

DNA extraction from skin biopsy samples was carried out either using DNeasy[®] 96 Tissue Kit (Qiagen) or PUREGENE[®] DNA Purification Kit (Gentra systems). DNA extraction from hair samples was performed using the Chelex 100 resin method (Biorad) as described by Walsh *et al.* (1991) in a room dedicated to processing rare DNA. For each individual, we extracted a minimum of 10 hair follicles with visible roots, as recommended by Goossens *et al.* (1998) for a single-tube approach. We amplified microsatellites using the polymerase chain reaction (PCR). For skin samples, the procedure is described in Galan *et al.* (2003). For hair samples, we used the multiple-tube approach, as recommended by Navidi *et al.* (1992) and Taberlet *et al.* (1996) for low-DNA samples, with 3 replications of DNA amplification and genotyping per extraction (preliminary tests comparing genotypes from skin versus hair samples of the same individual indicated that 3 repetitions were required to determine a consensus genotype that matched the correct genotype). Amplification was performed separately for each of the 22 or 12 microsatellites at Bogesund and Trois Fontaines respectively, with the same PCR conditions. The samples were run on a monicapillary genotyper ABI PRISM 310 DNA (Applied Biosystems). GENESCAN 3.1 and GENOTYPER 2.5 softwares (Applied Biosystems, Foster city, California, USA) were used to size alleles based on a size standard and to score microsatellites on autoradiographs.

II.2.4. Test of the suitability of microsatellite markers

Prior to paternity analyses, we looked for a deficit or an excess of heterozygotes using a Hardy-Weinberg exact test implemented in the program GENEPOP 3.4 (Raymond & Rousset 1995), for each locus separately and globally, by a Markov chain method (1000 dememorizations, 100 batches and 5000 iterations per batch). The linkage disequilibrium between pairs of loci was also tested with GENEPOP, which computes Fisher's exact test for each table of contingency of the frequency of alleles for all pairs of loci using a Markov chain (1000 dememorizations, 100 batches and 5000 iterations per batch). As multiple test tended to increase type I errors, we performed an adjustment by controlling the false discovery rate (FDR) (Benjamini & Hochberg 1995; Storey 2002), using GeneTS package on R 2.2.1. software. This approach offers an easily interpretable mechanism to control the proportion of significant results that are in fact type I errors while simultaneously allowing type II errors to be reduced. The above tests were performed on a subset of the whole sample, i.e. individuals born in 1992 at Bogesund (N = 133) and 2003 at Trois Fontaines (N = 97; years with the highest sample size) after removing siblings, in order to reduce multigenerational effects.

Allelic frequency and paternity exclusion probabilities were estimated with CERVUS 2.0 (Marshall *et al.* 1998) on the whole sample set. CERVUS was also used to determine the observed and expected heterozygosity, and the null allele frequency for each locus and across all loci. I finally evaluated available power for distinguishing between individuals using the program GIMLET (Valière 2002), which determines the probability of identity (i.e. the probability that two randomly selected genotypes match by chance; Paetkau and Stroberg 1994), for each locus and across all loci. I also calculated the probability that two siblings drawn at random from the population would have identical multilocus genotypes (Waits *et al.* 2001) for each locus and across all loci.

At Bogesund, between 2 and 8 alleles per locus were identified (mean = 4.23) and expected heterozygosity ranged from 0.097 to 0.790 (mean = 0.527) among the 22 microsatellite loci (see Table 3A). There was no significant heterozygote excess or deficit at any single locus, ($p > 0.05$), except for the HUI1177 locus (test of heterozygote deficit: $p = 0.022$). Following correction for multiple, there was no evidence for significant linkage disequilibrium between any pair of loci, except for HUI1177 and Roe5. Finally, the estimated frequency of null alleles was negative or low (freq < 0.02), except for HUI1177 (freq = 0.12). Hence, we decided to remove the HUI1177 locus for parentage analysis. The total exclusionary power of the 21 retained microsatellites was 0.9997 when one parent was known and 0.9850 when both parents were unknown. The probability of identity over all loci was low: 5.14×10^{-12} among all individuals and 1.10×10^{-5} among siblings.

At Trois Fontaines, between 2 and 20 alleles per locus were identified (mean = 7.50) and expected heterozygosity ranged from 0.302 to 0.909 (mean = 0.669) among the 12 microsatellite loci (see Table 3B). The estimated frequency of null alleles was negative or low (freq < 0.04). There was no significant heterozygote excess at any single locus, nor over all loci combined ($p > 0.05$). Two loci however (OARFCB304 and BM757) presented a deficit in heterozygotes ($p = 0.021$ and 0.034 respectively). Following correction for multiple comparisons, there was no evidence for significant linkage disequilibrium between any pair of loci, except for BM1706 and OARFCB304. Hence, we decided to remove the OARFCB304 locus but to keep BM757 locus for parentage analysis. The total exclusionary power of the 11 retained microsatellites was 0.998882 when one parent was known and 0.977188 when both parents were unknown.

II.2.5. Limitation, identification and quantification of genotyping errors

Laboratory genotyping accuracy rarely exceeds 99% (Marshall *et al.* 1998). Genotyping error rates are expected to increase with both the number and the polymorphism of genotyped loci; and genotyping errors are supposed to be more abundant when employing non-invasive tissue-sampling like hairs (Hoffman & Amos 2005). Source of genotyping error can be various and include poor amplification, misprinting, incorrect interpretation of stutter patterns and artefact peaks, contamination, mislabelling or data entry errors (Bonin *et al.* 2004). We were particularly careful to drive error rates as low as possible through a combination of specific quality control protocols. We included a previously typed sample in each amplification as a reference. As mentioned above, we used the multiple-tubes approach (Taberlet *et al.* 1996) to genotype hair samples. We favoured automated scoring of autoradiographs by GENOTYPER software. However, we checked the results manually and confirmed the assigned genotypes by independent blinding scoring repetitions by two experienced scoring people. We used reference samples to control scoring. All reactions yielding uncertain genotypes (e.g. with faint or unclear bands) were repeated. However, we discarded samples with systematic genotyping problems. We checked the reliability of all rare alleles ($N < 10$), by rescored the autoradiographs corresponding to these alleles. We finally used three methods for estimating genotyping error rate (see below). This allowed us to identify many typing errors in our dataset. When an error was found, we checked the autoradiograph in order to identify the cause. All obvious scoring errors were corrected before performing paternity analyses. Concerning the other types of errors which were not possible to correct, we removed the erroneous allele and let a gap for the concerned allele.

The three methods which allowed us to estimate genotyping error rate were the following.

First, in order to fulfil some gaps in the genotypes of 294 individuals from Bogenesund at 21 microsatellite loci, we independently repeat-genotyped at all loci for these individuals. We used this opportunity to compare the two sets of genotypes and identify the discrepancies between all set of loci but the ones with gaps, and estimate an error rate among all compared genotypes. We showed that the typing error rate for our dataset was 3.81% per locus or 2.51% per allele. Given this observed allele-mistyping rate, we may expect one in every 1.25 complete genotypes to contain a mistyped locus. This is particularly high. However, because these repeats were not a random sample of the genotype data (they concerned samples for

which the full genotype could not be established from the first run), this error rate is certainly an over-estimate. They were therefore probably more problematic than the average samples. Besides, most errors came from the same single locus PCR and involved the same type of repeated errors. Hence, errors were not independent.

Second, we used the program CERVUS 2.0 (Marshall *et al.* 1998) to check known mother-fawn pairs in order to identify genotyping errors from mismatches between mothers and their offspring (i.e. genotypes that do not share a common allele) in both populations. The error rate estimated by CERVUS based on these mismatches was defined as the replacement of the true genotype with a genotype selected at random under Hardy-Weinberg assumptions and was calculated using the formula given in Marshall *et al.* (1998). To avoid overestimation of the error rate, all mother-offspring pairs must be independent, and so no single individual were included both as an offspring and mother. Because our data set included a number of mother with multiple offspring, we randomly chose a single fawn from each of these individuals so that no mother was included more than once. We checked 101 and 37 independent known mother-fawn pairs from Bogesund and Trois Fontaines respectively. A total of 26 pairs (34.6% of total pairs checked) and 13 pairs (35.1%) mismatched at Bogesund and Trois Fontaines respectively, with a number of mismatches per pair ranging from 1 to 6 at Bogesund (mean = 2.11, SD = 1.42), and from 1 to 4 at Trois Fontaines (mean = 2.08, SD = 1.19). A mismatch could be due either to genuine non-relationship, or to a typing error in the offspring or the known mother genotypes. Several mother-offspring pairs mismatching up to 3 loci were clearly ascribed to scoring or typographical error and so we had a priori expectation that these pairs mismatching up to 3 loci (N = 21) may represent cases of typing errors in the genotypes of the fawn or the mother. Mother-offspring pairs mismatching at more than 3 loci (N = 5) may probably represent cases where the fawn did not belong to the supposed mother, and they were removed from the database of known mother-fawn pairs. When we counted only mother-offspring pairs that mismatched at up to 3 loci in the analysis, the genotyping error rate was 3.7% and 8.7% per locus at Bogesund and Trois Fontaines respectively. These error rates included only genotyping errors that can be detect by Mendelehian transmission.

Finally, we examined concordance among the genotypes of individuals that were erroneously resampled at Bogesund (N = 27). We identified discrepancies between the two sets of genotypes and estimated an error rate among all compared genotypes. The typing error rate was thus equal to 1.41%. This error rate accumulates the effects of all potential uncertainty error sources (from the sampling to the scoring). It should therefore be the highest

of our three genotyping error rate estimations. Yet, it was lower than other estimated error rates. It is probably because the sample size was low (N=27) compared to the recommendations of Bonin *et al.* (2004) to obtain an accurate estimation of the error rate (the number of blind replicates should represent 5-10% of the samples, that is in our study 83 individuals).

In our dataset, identified genotyping errors seem to be largely due to misinterpreting allele banding patterns such as misprinting (i.e. amplification products are generated than can be misinterpreted as true alleles) and incorrect interpretation of stutter bands (i.e. bands generated by slippage of Taq polymerase during PCR) and artefact peaks, or null alleles (i.e. allele non-amplification resulting from primer binding site mutation) and allelic dropout (i.e. stochastic failure of one allele to amplify).

II.2.6. Paternity analyses

Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall *et al.* 1998). For each parent-offspring pair, the program calculates a LOD score (logarithm of the likelihood ratio). This score is the likelihood of maternity and paternity of a particular candidate parent relative to an arbitrary individual. Using allele frequency data from the population, the program runs a simulation to estimate the critical difference in LOD score between the most likely and next most likely candidate parent (δ) necessary for assignment at greater than 95% or 80% confidence levels. The simulation incorporates user-defined input parameters such as the total number of candidate parents, the proportion of these parents that have been sampled, the frequency of gaps and the genotyping error rate (i.e. proportion of loci typed incorrectly, averaged across loci and individuals) in the genetic data. SanCristobal & Chevalet (1997) have shown that with CERVUS, as long as the error rate is fixed to a value greater than zero, the choice of error rate does not have a major impact on confidence or success rate. We therefore decided to fix the error rate to 1%.

For Bogenlund, the observed rate of missing data, estimated across all typed samples by the allele frequency module of CERVUS, was set at 98.7% of loci typed. Based on long-term CMR and hunting databases, and yearly field observations of animals, we listed the candidate fathers and mothers for each cohort of fawns. Both males and females were considered to be candidate parents for a given fawn cohort if they were defined as alive and potentially reproductive in the previous rut. The last potential participation in the rut for an individual was defined in relation to the moment it was either found dead or last recorded

alive. The first potential participation in the rut was set at 1 year-old for females and 2 years old for males in relation to the age of sexual maturity in roe deer. When the age of a candidate parent was estimated from tooth wear ($N = 269$ females and 162 males), the first year of potential participation in the rut was back-dated by one year in order to take into account potential error in the estimation of age (Hewison *et al.* 1999). The inclusion of candidate parents for which age was estimated should not have a great impact on our results, since we did not analyse the age-dependence of male breeding success. However, note that if some immature males are erroneously considered as candidate fathers in a given year due to inaccurate age estimation, the number of unsuccessful breeding males may be somewhat over-estimated. For this reason, we did not include estimated age males in our analyses of yearly breeding success and, in our analyses of lifetime breeding success, we compared the results with and without estimated age males. The proportion of known candidate parents sampled varied among cohorts but was always higher than 80% for fathers and 76% for mothers. In order to take into account potential unknown candidate parents in the population, we decided to fix the proportion of candidate parents sampled to a conservative value of 75% for all years and for both sexes. The total number of candidate parents present in the population was then calculated for each cohort as the total number of sampled candidate parents present in the population divided by 0.75. Notice that previous work has demonstrated that the simulation outcome is relatively insensitive to the number of candidates (Pemberton *et al.* 1999). Sample sizes of data used for paternity analyses are given in Table 4A.

For Trois Fontaines, the observed rate of missing data, estimated across all typed samples by the allele frequency module of CERVUS, was set at 96.7%. We listed the candidate fathers and mothers sampled for each cohort of fawns based on long-term CMR and hunting databases. Both males and females were considered to be candidate parents for a given fawn cohort if they were defined as alive and potentially reproductive in the previous rut. The last potential participation in the rut for an individual was defined in relation to the moment it was either found dead or 3 years after it was last recorded alive (since about 85% of the individuals survived each year). The first potential participation in the rut was set at 1 year-old for females and 2 years old for males in relation to the age of sexual maturity in roe deer. When the age class of a candidate parent was estimated from tooth wear (Class II: 2-3 years old, Class III: 3-7 years old, Class IV: >7 years old), the first year of potential participation in the rut was estimated using a conservative criteria (Hewison *et al.* 1999). The total number of potential parents for each cohort of fawns was estimated based on CMR methods (references). Sample sizes of data used for paternity analyses are given in Table 4B.

Table 4. Sample size for paternity analyses at Bogesund (A) and Trois Fontaines (B).

(A)

Fawn cohort	Rut year	Number of sampled fawns	Number of sampled fawns with sampled known mother	Number of sampled candidate father	Number of sampled candidate mother	Estimated number of candidate father in the population	Estimated number of candidate mother in the population
1988	1987	4	0	40	79	53	105
1989	1988	6	0	54	102	72	136
1990	1989	12	0	66	129	88	172
1991	1990	6	0	83	152	111	203
1992	1991	131	18	123	184	164	245
1993	1992	48	6	116	220	155	293
1994	1993	14	1	51	112	68	149
1995	1994	14	1	34	81	45	108
1996	1995	10	6	34	84	45	112
1997	1996	22	6	34	84	45	112
1998	1997	24	19	31	72	41	96
1999	1998	45	25	34	77	45	103
2000	1999	41	29	42	89	56	119
2001	2000	46	41	44	89	59	119
2002	2001	30	24	62	81	83	108
2003	2002	54	30	64	81	85	108
2004	2003	69	41	70	86	93	115
2005	2004	29	20	51	63	68	84
2006	2005	29	13	44	70	59	93
MEAN		33.4	14.7	56.7	101.8	75.6	135.8
SD		30.0	14.0	26.4	41.6	35.2	55.5
MAX		131	41	123	220	164	293
MIN		4	0	31	63	41	84

(B)

Fawn cohort	Rut year	Number of sampled fawns	Number of sampled fawns with sampled known mother	Number of sampled candidate father	Number of sampled candidate mother	Estimated number of candidate father in the population	Estimated number of candidate mother in the population
1994	1993	7	0			124	161
1995	1994	25	0	23	22	112	157
1996	1995	50	2	23	26	120	131
1997	1996	52	1	23	46	102	152
1998	1997	44	1	49	66	113	109
1999	1998	50	3	73	88	96	143
2000	1999	40	7	133	116	84	134
2001	2000	73	6	205	162	122	127
2002	2001	77	12	255	192	123	186
2003	2002	114	21	283	232	209	208
2004	2003	104	14	320	272	223	288
2005	2004	101	24	343	318	254	290
2006	2005	42	30	307	282	223	294
MEAN		59.9	9.3	169.8	151.8	146.5	183.1
SD		32.0	10.1	128.9	106.1	57.9	66.4
MAX		114	30	343	318	254	294
MIN		7	0	23	22	84	109

Because one of the input parameters for the simulation varied between years and sexes (i.e. the total number of candidate parents present in the population), to generate the critical δ values for 95% and 80% confidence levels, we carried out a separate simulation for each fawn cohort and for each sex of parent. Then, using these sex- and cohort-specific critical δ values, we performed a separate parentage analysis for each fawn cohort and each sex of parent. Initially, we ran a maternity analysis for each cohort to assign females to fawns with unknown mothers (i.e. those never observed in the field). From this, we retained only those mother-offspring associations which were assigned with 95% confidence by CERVUS. We then

combined these assigned maternities with known maternities from field observations and, for each cohort, subsequently conducted the paternity analysis. 442 fawns at Bogesund and 161 fawns at Trois Fontaines were thus successfully assigned by CERVUS to a male at the 80% level of confidence.

II.2.7. Estimation of male breeding success and the opportunity for sexual selection

After determining the distribution of paternities among males, we estimated yearly breeding success (YBS; the total number of paternities assigned at the 80% confidence level) for each known-aged male and for each reproductive season during which the male was considered as a candidate father. We also estimated lifetime breeding success (LBS; the total number of independent offspring produced by a male during its lifespan) of each male for which data were available for the whole lifespan and which died of natural causes. Importantly, notice that my estimations of YBS and LRS were minimal estimations of YBS and LRS (with an unknown under-estimation) because all fawns could not have been caught each year in the study population. This was further discussed in the discussion part of the thesis.

Two kinds of measures of variation in male reproductive success are commonly used to estimate the opportunity for sexual selection. First, variance in reproductive success among males relative to variance in female success (e.g., Ralls 1977; Payne 1979). Second, variance in male reproductive success relative to the success of the average male, commonly used under the following form: variance in male reproductive success divided by the square of mean reproductive success (also called standardised variance in male breeding success, and noted I ; Crow 1958; Wade 1979; Wade & Arnold 1980; Arnold & Wade 1984). The former measure has the disadvantage that it can be affected either by the extent to which male success varies or by the extent to which female success varies. Since the aim of calculating such measures is usually to make comparisons between sexes or populations, it is preferable to adopt the latter measure (Clutton-Brock 1987). In this study, I used both approaches, estimating the standardised variance in male reproductive success I_{male} and the ratio of the total opportunity for selection in the two sexes $I_{\text{male}} / I_{\text{female}}$. These two measures are thought to be positively correlated with the opportunity for sexual selection (Clutton-Brock 1983, 1988) and to represent an upper limit to the strength of directional sexual selection (Wade and Arnold 1980).

II.3. FIELD ECOLOGY STUDIES (Bogesund)

I performed intensive field-work at Bogesund from late March to late August (during the territorial period) in both 2004 and 2005. The field-work was of two types:

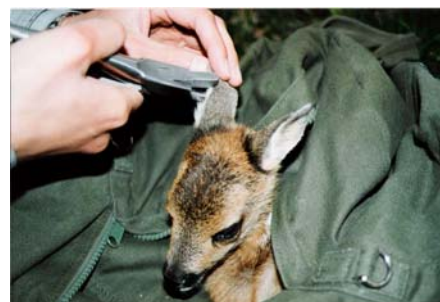
- long-term monitoring: fawn capture, pellet-group counts, roe deer resighting for Petersen density estimation;
- specific field-work for my thesis: mainly intensive radio-tracking and vegetation sampling;

II.3.1. Fawn capture

Neonates were caught by hand just after birth in May-June 2004, 2005 and 2006. Marked females were visited regularly before birth period to monitor udder and belly size evolution and predict when females will give birth. Once females were suspected to have given birth, we observed does until they visited their hidden fawns. We usually captured fawns after the mother had moved away. We also found fawns in the vicinity of bed sites of previously marked siblings. At capture, neonates were weighed, sexed, and marked with little metallic eartags with an individual number. Some neonates were also equipped with a radio-transmitter (65-70 g, Televilt TVP Positioning AB, Lindesberg, Sweden). We monitored marked fawn survival and position daily for up to 4-6 weeks of age and 1-2 times per week thereafter.



A



B



C

Photos of a field-worker capturing a fawn (A), of DNA sampling (B) and of a fawn with a radio-collar (C).

II.3.2. Pellet-group counts and estimation of a local population abundance

We carried out a faecal pellet-group count census (Neff 1968; Cederlund & Liberg 1995) over the entire 2,600 ha roe deer research area, both in 2004 and 2005, in the very first days of April, immediately after snow melt. The 604 sample plots were circular, their size were 10 m² and they were distributed regularly along North-South transects in order that they cross varying slope aspects and altitudinal zones. Transects were spaced 400 m apart, and plots 100 m apart on the transects. Each plot location was georeferenced and the plots were searched with a GPS. Because new pellets that have deposited since defoliation could be distinguished from old pellets in relation to dead leaves and needles that covered the latter but not the former (Kjellander 2000) when the survey is conducted in the spring (Robinette *et al.* 1958), we used a standing crop design with temporary plots. We considered that no pellet degradation occurred during winter due to snow cover and low temperatures. Each plot have been systematically read twice, clockwise and counterclockwise. The total number of pellet groups was recorded on each plot. A minimum of 10 pellets are needed to constitute a group. Moose was the only other deer species in the area, so the risk of counting faeces of other species than roe was excluded.



A



B

Photos of a roe deer pellet-group (A) and of a field-worker reading a plot (B).

We interpolated the number of pellet groups on each plot using a statistical prediction. As this variable was discrete, we used Model-based Geostatistics (Diggle *et al.* 1998), that is, a Generalized Linear Model (McCullagh & Nelder 1989) with a random spatial component. We used the Poisson model and so we assumed that the defecation count at the site x follows, given a non-observed gaussian random field S , a Poisson variable of intensity $\lambda(x)$ such that $\text{Log}(\lambda(x)) = \alpha + S(x)$ where S is centred ($E(S(x)) = 0$) and has a stationary covariance function

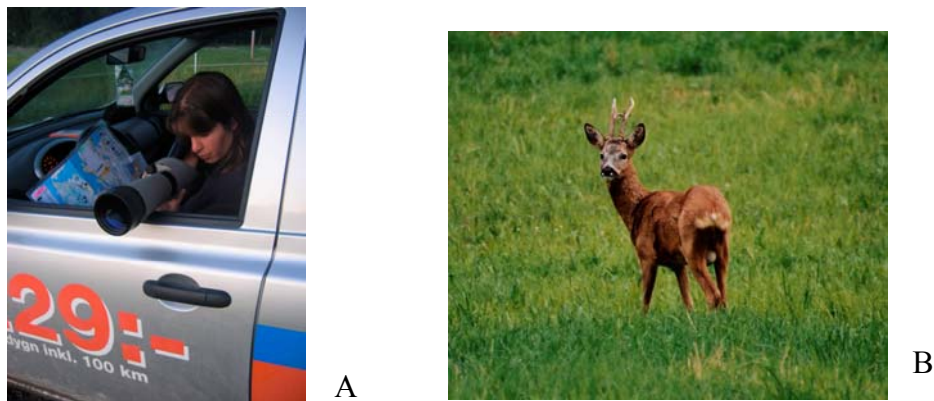
($E(S(x)S(y)) = C(x-y)$). From observed counts, a parametric model was estimated for the covariance by a MCMC maximum likelihood approach (Christensen 2004). The statistical prediction was then performed using a simple kriging procedure on simulated potential values of S at observed sites, given the data, to obtain by an empirical mean of simulations the best prediction of S at a non-observed site (Zhang 2002). Finally, a back transformation was performed that took into account a correction for bias to obtain the prediction of the Poisson intensity which is also the prediction for the count. We performed the preliminary variogram inspection, model fitting and model-based kriging with the *geoRglm* package (Christensen & Ribeiro 2005). We interpolated the number of pellet groups in order to obtain a value every 100 m over the whole study area.

We estimated the total number of pellet groups within each male's territory for 2004 and 2005 as the sum of the point estimates falling within each territory using Arcview 3.2 software. We used this value as a relative index of local roe deer abundance. Although pellet group counts have been criticised as a method to estimate absolute population density (e.g., Robinette *et al.* 1958; Putman 1984), we considered that they provide an informative index of relative animal abundance which was adequate for our purposes (see Forsyth *et al.* 2007 and Discussion of the thesis).

II.3.3. Capture-Mark-Resighting (Petersen method)

The population density was determined using a Petersen estimate which is based on the ratio of marked and unmarked individuals at recapture (Caughley 1977), with about 20-70% of the population being marked with radio-collars. The recapture part of this method consisted of visual observations (with binoculars) where the ratio of marked/unmarked deer was recorded (Strandgaard 1967). Critical assumptions for the general mark-resighting model are: 1) the probability of sighting of marked and unmarked animals is the same, 2) marked and unmarked animals are correctly classified, 3) marked animals are randomly distributed throughout the population, or at least resighting effort is randomly distributed throughout the population, 4) each animal has an identical, but independent probability of being resighted, 5) the number of marked animals in the population is known that in turn assumes markers are not lost or accounted for, and 6) the population is geographically and demographically close (i.e. no immigration, emigration, recruitment, or deaths occur during the population surveys in a geographically defined area).

The census was performed on the 1200 ha of the study area in April and September 2004 and 2005. Same effort was allocated throughout the study area. In each occasion, we continue the resighting until reaching 250 individuals observed, in order to achieve a specified level of precision. I did not use directly results of this method of estimation of population density in my thesis and so I will not further detail this method.



Photos of a field-worker counting deer from the car with a monocular (A) and of a roe buck (B).

II.3.4. Radio-tracking and estimation of the size of males' territory

A variable number of caught individuals were equipped every year with radio-collars (TXT-2Sm, 151 or 152 MHz radio-transmitters delivered by Televilt International AB, Lindesberg, Sweden), weighing 250-300 g, and with a mortality function, with a maximum battery life-span of 5 years, and bearing number plates for individual recognition. I intensively radio-tracked all males and all females equipped with radio-collars and older than 1 year of age during the ruts (from mid-July to mid-August) 2004 (N = 26 for males and 16 for females) and 2005 (N = 22 for males and 22 for females). I also intensively radio-tracked males during the period of territory establishment (April-May) in 2004 and 2005. The animals' status as alive or dead was determined based on activity indication in the radio signal and movement since the previous position was taken. Suspected deaths were checked by a flushing effort.

Radio-tracking was conducted from the ground with Televilt RX-810 and RX-98 receivers and a 4-element Yagi antenna. Animals were located by triangulation from at least three points along roads or hills. They were tracked from 0 to 3 times per 24 hour period, both at daytime, and during night, dusk, and dawn. According to White & Garrot (1990), two locations can be considered as independent if the time between them is superior to the time

necessary to the animal to cross through its home range. About 30 mn are necessary for the roe deer, when its average speed is 1 km/h, and the home range surface is 500 x 500 m (25 ha). A minimum of 3 hours always passed between two successive locations to avoid temporal autocorrelation of the data.



A



B



C

Photos of a field-worker radio-tracking a roe deer (A), of a doe with a radio-collar (B) and of a field-worker reporting an animal position on the map of the study area .

A study of radio-tracking accuracy was performed in August 2005. We randomly chose 20 positions (with known coordinates) among all fixes taken during the 2005 rut for all the radio-tracked individuals, placed test transmitters at these 20 positions using a GPS 12 XL (12 channel, GARMIN, accuracy < 20 meters) and then took fixes on them. We measured the distance between our fixes and the real positions of the collars. The mean error was 41.0 ± 41.6 m. Radio-tracking positions were digitalised in a geographic information system (Arcview 3.2) and analysed using the Spatial Analyst and Animal Movement extensions to Arcview (Hooge & Eichenlaub 1997).

Male territory size and female home range size were estimated using the Kernel method (i.e. a parametric estimator that describes the range as a probability density function; Worton 1989) with the 90% isocline and the least square cross validation calculation for the smoothing parameter, as recently recommended by Börger *et al.* (2006). To calculate the appropriate proportion of fixes by which a home range or a territory is defined, I collected a large number of fixes from a range of males in 2004 during the territory establishment period,

plotted a graph of range size (estimated by Kernel 90%) versus the number of locations using a bootstrap procedure and identified the point at which the gradient of the slope changes. The asymptote was achieved after about 25-35 locations depending of the male, which was of the same range of the recommended standard of 30 fixes proposed by Kenward (1987). Hence, we chose to collect 30 fixes per male and per rut.

II.3.5. Vegetation sampling and map of habitat quality

During the ruts 2004 and 2005, we performed a systematic vegetation sampling over the 2,500 ha study area comprising 357 point locations. Points were located 200 meters apart on a North-South transect, and all transects were separated by 200 meters. In 2005, however, point locations were shifted 100 meters to the North and 100 meters to the East compared with 2004. For each point, the habitat was classified as young forest (tree height < 5 m), intermediate forest (5-15 m), old forest (>15 m), clear-cut, crop fields, fallow/meadow, human area (e.g., garden, road), or pasture. Vegetation cover was estimated within a circle of 2 metre radius (12.56 m²) for three different strata (0-20 cm, 20-50 cm and 50-150 cm) with a three category scale (0-10%, 10-50%, >50%). Bilberry cover was estimated within a circle of 10 meter radius (314 m²) and coded as absent, 0.1-10%, 10-50% or >50%. Bilberry has been shown to be one of the primary winter food resources for roe deer in Scandinavia (e.g., Cederlund *et al.* 1980; Mysterud *et al.* 1998). Vegetation sampling was carried out using a wooden frame of 25 x 25 cm. All vegetation inside the frame was identified to the species level and cut at the following heights: 0-20 cm, 20-50 cm and 50-150 cm (maximum browsing height for a roe deer).



Photos of a field-worker sampling the vegetation within the wooden frame.

Each sample was labelled and stored frozen in a paper bag. All samples were later thawed, dried at 60° C for three days and then weighed on a scale to the nearest 0.01 g. For each sampling point, we then estimated the biomass of crop plants (i.e. oat, wheat, barley), berry plants (i.e. *Vaccinium* spp., *Ribes* spp.), pasture plants (i.e. *Trifolium* spp. and *Vicia* spp.), various grasses, and the total biomass of consumed plants. Plants consumed by roe deer were determined based on the analysis of 11 rumen contents from 2 females and 9 males shot during the 2005 rut at Bogesund (C. Vanpé, unpubl. data).

Each of the 10 habitat variables (i.e. 5 factors: habitat, cover 0-20 cm, cover 20-50 cm, cover 0-150 cm, cover of bilberry; and 5 continuous variables: biomass of crop plants, biomass of berries, biomass of pasture plants, biomass of grasses, total biomass of consumed plants) was entered in a Geographic Information System (ArcView 3.2), mapped, and interpolated over the whole study area. To build the raster interpolated map for each habitat variable, cell size was fixed to 25 x 25 m and the number of neighbouring cells used in the interpolation was fixed to one so that all the cells with missing values took the value of the nearest sampling point. To identify the specific resource attributes that best reflect habitat quality (in terms of attractivity for females), we first analysed habitat selection by females during the rut by performing an Ecological-Niche Factor Analysis (ENFA; Hirzel *et al.* 2002), using the *enfa* function of the *adehabitat* package (Calenge 2006) for the R 2.4.1 statistical software (R Development Core Team; Ihaka & Gentleman 1996). The study area was modelled as a raster map (each pixel representing a resource unit) in relation to the 10 habitat variables. We used the 30 positions of the 29 females radio-tracked in 2004 or 2005 during the rut (when a female was radio-tracked in both years, we only used positions from 2004 to avoid pseudo-replication) to determine resource units used by females. All pixels on the raster map of the whole study area were considered to be available resource units for females. To determine the specific resource attributes that best reflect the suitability of an area for females, we interpreted the marginality axis of the ENFA (see Hirzel *et al.* 2002 for further details). The marginality axis was mainly explained by the following habitat variables (see Figure 15): biomass of crop plants (coefficient = 0.57), biomass of various grasses (coefficient = 0.37), vegetation cover of the strata 20-50 cm and 50-150 cm (coefficients = 0.28 and 0.32 respectively), crop field habitat (coefficient = 0.28), biomass of consumed plants (coefficient = 0.21), intermediate forest habitat (coefficient = -0.21) and cover of bilberry (coefficient = -0.30). That is, for these variables, female roe deer used habitat non-randomly in relation to the mean available habitat with regard to the corresponding variable (see Hirzel *et al.* 2002). This

analysis showed that females tended to avoid the intermediate age forest habitat with high cover of bilberry (negative values of marginality), while they selected crop field habitats with high biomass of crop plants, and high vegetation cover (positive values of marginality). We derived a habitat suitability map, from the results of the ENFA, by assigning a numerical value to each raster map unit of the study area based on its position in this ecological space relative to the average niche of the species in the marginality analysis.

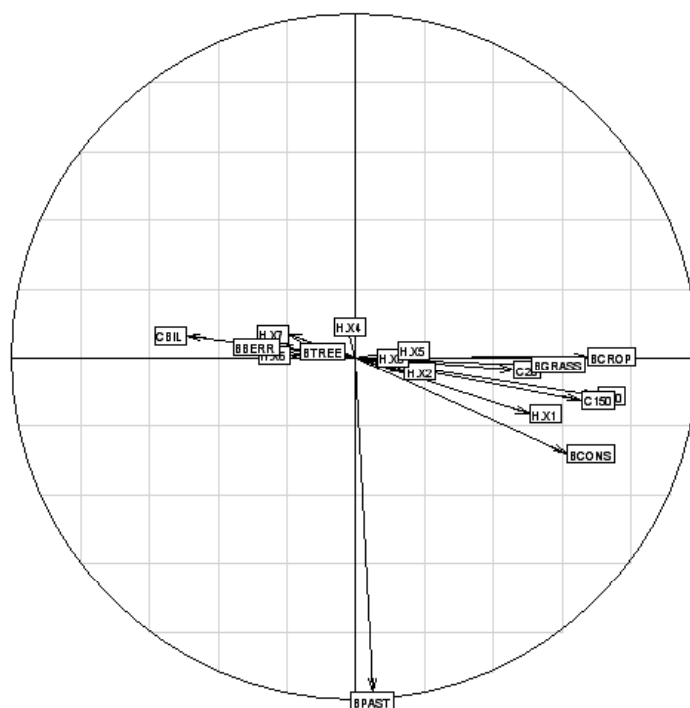


Figure 15. Position of each variable on the graph plotting the singularity (Y axis) against the marginality (X axis) of the ENFA.

Note: CBIL = cover bilberry, BBERR = biomass of berries, BTREE = biomass of trees, H.X1 = crop field, H.X2 = fallow and meadow, H.X3 = young forest, H.X4 = human area, H.X5 = pasture, H.X6 = old forest, H.X7 = intermediate aged forest, BGRASS = biomass of various grasses, BCROP = biomass of crop plants, BPAST = biomass of pasture plants, BCONS = total biomass of consumed plants, C20 = cover 0-20 cm, C50 = cover 20-50 cm, C150 = cover 50-150 cm.

PART 1

VARIATION IN MALE BREEDING SUCCESS AND OPPORTUNITY FOR SEXUAL SELECTION



**Roe deer fawn
(photograph by Cécile Vanpé)**

PAPER 1

Mating system, sexual dimorphism and the opportunity for sexual selection in a territorial ungulate

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Abstract

In mammals, species with high sexual size dimorphism tend to have highly polygynous mating systems associated with high variance in male lifetime reproductive success (LRS), leading to a high opportunity for sexual selection. However, little information is available for species with weak sexual size dimorphism. In a long-term study population, we used parentage analysis based on 21 microsatellite markers to describe, for the first time, variance in male lifetime breeding success (LBS) of roe deer, a territorial ungulate where males weigh less than 10% more than females. LBS ranged from 0 to 14 (mean = 4.54, variance = 15.5) and its distribution was highly skewed, with only a few males obtaining high LBS and many males failing to breed or siring only one fawn. As predicted for polygynous species with low sexual size dimorphism, the standardised variance in male LBS was low ($I_m = 0.75$) and was only slightly higher than the standardised variance in female LRS ($I_f = 0.53$), suggesting a low opportunity for sexual selection. The I_m value reported here for roe deer is much lower than values reported for highly dimorphic ungulates such as red deer ($I_m > 3$). We suggest that, along a continuum of opportunity for sexual selection, roe deer occupy a position closer to monogamous and monomorphic territorial ungulates than to highly polygynous, sexually dimorphic ungulates with dominance-rank based mating systems such as harems or roving mating systems.

Keywords: *Capreolus capreolus*, microsatellite, paternity analysis, lifetime reproductive success, roe deer, ungulates.

Introduction

Measuring the opportunity for sexual selection is crucial for addressing many questions in behavioural ecology (such as the evolution of sexual size dimorphism, conspicuous male traits, alternative mating tactics, and sex-biased parental investment; Andersson, 1994) and population dynamics (such as effective population size; Begon, 1984). Sexual selection theory predicts that the opportunity for sexual selection is strong when reproductive success varies widely among males, with a few males highly successful at mating and many others males failing to mate or siring only one (or a few) offspring (Darwin, 1871). This has led to the general expectation of an association between strong sexual selection, high mating polygyny, and high variance in male reproductive success (Andersson, 1994; Huxley, 1938; Wade, 1979). Several authors have thus proposed the use of variance in male reproductive success as a measure of the opportunity for sexual selection (e.g., Arnold and Wade, 1984; Payne, 1984; Wade and Arnold, 1980).

The evolution of male-biased sexual size dimorphism is thought to have evolved principally as the result of intra-sexual competition over mates, given the scenario of high variance in male reproductive success (Andersson, 1994; Darwin, 1871). In mammals, the level of sexual size dimorphism is linked to the level of polygyny (e.g., for a review: Alexander et al., 1979; in ungulates: Loison et al., 1999). As a rule, highly dimorphic species are highly polygynous, resulting in high variance in male mating success in a wide range of taxa, including primates (e.g., Clutton-Brock et al., 1977), pinnipeds (e.g., in elephant seal *Mirounga angustirostris* (Gill, 1866): LeBoeuf and Reiter, 1988) and ungulates (e.g., in red deer *Cervus elaphus* (Linnaeus, 1758): Clutton-Brock et al., 1988).

However, the general pattern relating variation in male reproductive success, sexual size dimorphism, and level of polygyny in mammals remains unclear for several reasons. First, attempts to estimate variance in male reproductive success have traditionally relied on short term data and behavioural observations of the number of copulations or the number of social associations during which a male may have exclusive access to a female (see Clutton-Brock, 1988). But, since intense competition between males typically restricts effective reproductive activity to a few years of their total adult life span, short-term data may grossly over-estimate variation in lifetime reproductive success (Clutton-Brock, 1988). Second, the recent development of molecular biology tools has revealed some discrepancies between behavioural and genetic estimates of male reproductive success (e.g., Amos et al., 1993; Coltman et al., 1999), mainly due to extra-pair copulations in socially monogamous species

(e.g., Goossens et al., 1998) and to ‘sneaky’ mating tactics of subordinate males in polygynous species (e.g., Coltman et al., 1999). One important consequence of this is that while variance in male reproductive success may be higher than expected in monogamous monomorphic species, it may be lower than expected in polygynous dimorphic species (Andersson, 1994). Finally, the available information on variance in male lifetime reproductive success in mammals is limited to a few studies and concerns almost exclusively highly polygynous and dimorphic species (e.g., in red deer: Marshall, 1998; Pemberton et al., 1992; bighorn sheep *Ovis canadensis* (Shaw, 1804): Coltman et al., 2002; Soay sheep *Ovis aries* (Linnaeus, 1758): Coltman et al., 1999; Pemberton et al., 1999; but see data for the weakly dimorphic harbour seal *Phoca vitulina* (Linnaeus, 1758): Coltman et al., 1998). This precludes any meta-analysis to detect general patterns in the opportunity for sexual selection among mammals, which would be very useful to better understand the evolution of mating systems (Andersson, 1994).

The aim of this study was therefore to provide the first genetic estimate of variance in male lifetime breeding success and the opportunity for sexual selection in an ungulate with low sexual size dimorphism, the European roe deer *Capreolus capreolus* (Linnaeus, 1758). For this, we used microsatellite and paternity analysis in a long-term monitored population in Sweden. Roe deer males weigh less than 10% more than females (Andersen et al., 1998), defend spatially stable territories, usually from 3 years of age (Hewison et al., 1998), and party size is supposed to be low (generally < 5; Liberg et al., 1998). Hence, we predicted that the standardised variance in male breeding success would be much lower in roe deer compared to ungulate species with more pronounced sexual size dimorphism.

Materials and methods

Study species

The European roe deer is a small-sized cervid (adults weigh about 20-30 kg). Females are non-territorial. During the rutting period, they live solitarily, or with fawns, in overlapping home ranges (Bramley, 1970). Although female roe deer are monestrous, 98% of adult females in a population are generally fertilised (Hewison, 1996; Hewison and Gaillard, 2001). Females normally give birth for the first time at 2 years of age (3-4 years in poor habitats and/or at high density; Gaillard et al., 1992), and thereafter every year, to 1-3 neonates (most commonly twins) in May-June (Gaillard et al., 1998b). Males become sexually mature as

yearlings, but usually do not defend territories before 3 years of age (4 years at high density; Strandgaard, 1972; Vincent et al., 1995). The territorial period runs from early spring (in March-April) until late August-early September, encompassing the rut which takes place from mid-July to mid-August (Bramley, 1970). The spatial system of the two sexes is independent and male territories can include all, or part of, the home ranges of several females (generally 1-5, but up to 10; Bramley, 1970; Strandgaard, 1972).

Study site and data collection

The study area was situated at Bogesund (59°23' N, 18°15' E), a mainland peninsula surrounded by water on all sides except to the north, situated on the coast of the Baltic Sea on the inner portion of the Stockholm Archipelago, within the hemi-boreal zone in east-central Sweden. The habitat is fragmented, with approximately 65% forest, 25% fields, and 10% bed rock and bogs. The climate is mild, characterised by moderate winters, with snow cover usual from late December to early March, and relatively warm and dry summers (Kjellander et al., 2006). The only natural predator of roe deer fawns is the red fox *Vulpes vulpes* (Linnaeus, 1758). The 2,600 ha roe deer research area constituted the major part of the Bogesund peninsula, divided into a 1,250 ha western experimental area where hunting was controlled and a 1,350 ha eastern control area where hunting continued normally (see Kjellander, 2000 for more details).

The present work was carried out in the western part where the roe deer population has been monitored intensively since 1988 by an annual Capture-Mark-Recapture (CMR) procedure (Kjellander et al., 2006). From 1988 onwards, roe deer (including 8 month-old fawns) were caught each winter in box traps, sexed and individually marked with plastic ear-tags. In addition, from 1997 onwards, neonates were caught by hand every spring (May-June), sexed, and marked with small metallic numbered ear-tags. Fawns were thus marked either during their first winter (all caught fawns before 1997 and almost half of the caught fawns from 1997 onwards; N = 379) or right after birth (half of the caught fawns from 1997 onwards; N = 228). Mother-offspring relationships were elucidated by direct observation of fawns with their mothers immediately after birth or during autumn (after the summer rut ends roe deer fawns continue to associate with their mother; Linnell et al., 1998) for the fawns caught immediately after birth. The year of birth of individual animals was either known definitively (animals first caught as new-born fawns or juveniles <1 year old), or estimated from tooth eruption and wear (Cederlund et al., 1992) examined during capture or after death

(see below for how potential error in age estimation from tooth wear was handled in the analysis).

Tissue sampling, DNA extraction and microsatellite genotyping

We collected tissue samples for DNA genotyping from individuals caught for the first time and from unmarked shot roe deer. We usually removed a small (approximately 2 x 2 mm) piece of ear skin tissue using sheep ear-notching pliers. However, samples taken on newborn fawns from 1997 to 2003 were hair samples (N = 146). We sampled in total 605 fawns born from 1988 to 2005 (of which 267 had a known mother), 231 candidate fathers and 352 candidate mothers (see Electronic appendix 1). Notice that sampled fawns from a given cohort can become candidate parents for later fawn cohorts provided that they survive to sexual maturity, and that candidate fathers and mothers can be potential parents for several successive fawn cohorts.

Genotyping was carried out using 22 microsatellite markers (see Electronic appendix 2) initially isolated from other ungulate species (Galan et al., 2003; Vial et al., 2003), except for Roe5, Roe6, Roe8 and Roe9 isolated specifically from roe deer (Fickel and Reinsch, 2000). These 22 microsatellites were divided into two multiplex kits of 11 microsatellites each (Galan et al., 2003, unpubl.). DNA extraction from skin biopsy samples was carried out either using DNeasy[®] 96 Tissue Kit (Qiagen) or PUREGENE[®] DNA Purification Kit (Gentra systems). DNA extraction from hair samples was performed using the Chelex 100 resin method (Biorad) as described by Walsh et al. (1991) in a room dedicated to processing rare DNA. For each individual, we extracted a minimum of 10 hair follicles with visible roots, as recommended by Goossens et al. (1998) for a single-tube approach. We amplified microsatellites using the polymerase chain reaction (PCR). For skin samples, the procedure is described in Galan et al. (2003). For hair samples, we used the multiple-tube approach, as recommended by Navidi et al. (1992) and Taberlet et al. (1996) for low-DNA samples, with 3 replications of DNA amplification and genotyping per extraction (preliminary tests comparing genotypes from skin versus hair samples of the same individual indicated that 3 repetitions were required to determine a consensus genotype that matched the correct genotype). Amplification was performed separately for each of the 22 microsatellites with the same PCR conditions. The samples were run on a monicapillary genotyper ABI PRISM 310 DNA (Applied Biosystems). GENESCAN 3.1 and GENOTYPER 2.5 softwares (Applied Biosystems, Foster city, California, USA) were used to size alleles based on a size standard and to score microsatellites on autoradiographs.

Tests of microsatellite markers

Prior to paternity analyses, we checked for Hardy-Weinberg equilibrium, for each locus separately and globally, with exact tests using GENEPOP 3.4 (Raymond and Rousset, 1995) and the Markov chain method (1000 dememorizations, 100 batches and 5000 iterations per batch). The linkage disequilibrium between pairs of loci was tested with GENEPOP by computing Fisher's exact test for each contingency table of allele frequencies for all pairs of loci using a Markov chain (1000 dememorizations, 100 batches and 5000 iterations per batch). As performing multiple tests tends to increase type I errors, we implemented the false discovery rate (FDR) (Benjamini and Hochberg, 1995; Storey, 2002), using the GeneTS package in the R 2.2.1. software. This approach offers an easily interpretable way to control for the proportion of significant results that are in fact type I errors, while simultaneously ensuring that type II errors remain low (no loss of power). The above tests were performed on a subset of the whole sample, i.e. individuals born in 1992, in order to reduce multigenerational effects. Allelic frequencies and paternity exclusion probabilities were estimated with CERVUS 2.0 (Marshall et al., 1998) over the whole sample set. CERVUS was also used to determine the observed and expected heterozygosity and the null allele frequency for each locus and across all loci. We evaluated available power for distinguishing between individuals using the program GIMLET (Valière, 2002), which determines the probability of identity (i.e. the probability that two randomly selected genotypes match by chance; Paetkau and Stroberg, 1994), for each locus and across all loci. We also calculated the probability that two siblings drawn at random from the population would have identical multilocus genotypes (Waits et al., 2001) for each locus and across all loci.

Paternity assignment

Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall et al., 1998). For each parent-offspring pair, the program calculates a LOD score (logarithm of the likelihood ratio). This score is the likelihood of maternity and paternity of a particular candidate parent relative to an arbitrary individual. Using allele frequency data from the population, the program runs a simulation to estimate the critical difference in LOD score between the most likely and next most likely candidate parent (δ) necessary for assignment at greater than 95% or 80% confidence levels. The simulation incorporates user-defined input parameters such as the total number of candidate parents, the proportion of these parents that have been sampled, the frequency of gaps and the genotyping

error rate (i.e. proportion of loci typed incorrectly, averaged across loci and individuals) in the genetic data. The observed rate of missing data was estimated across all typed samples by the allele frequency module of CERVUS and set at 98.7% of loci typed. From independent repeat-genotyping of 294 samples at 21 microsatellite loci, we observed that the typing error rate for our data set was 3.81% per locus (Vanpé et al., unpubl. data). However, because these repeats were not a random sample of the genotype data (they concerned samples for which the full genotype could not be established from the first run), this error rate is certainly an over-estimate. In addition, San Cristobal and Chevalet (1997) have shown that with CERVUS, as long as the error rate is fixed to a value greater than zero, the choice of error rate does not have a major impact on confidence or success rate. We therefore decided to fix the error rate to 1%.

Based on long-term CMR and hunting databases, and yearly field observations of animals, we listed the candidate fathers and mothers for each cohort of fawns. Both males and females were considered to be candidate parents for a given fawn cohort if they were defined as alive and potentially reproductive in the previous rut. The last potential participation in the rut for an individual was defined in relation to the moment it was either found dead or last recorded alive. The first potential participation in the rut was set at 1 year-old for females and 2 years old for males as a function of the age of sexual maturity in roe deer. When the age of a candidate parent was estimated from tooth wear ($N = 269$ females and 162 males), the first year of potential participation in the rut was back-dated by one year in order to take into account potential error in the estimation of age (Hewison et al., 1999). The inclusion of candidate parents for which age was estimated should not have a great impact on our results, since we did not analyse the age-dependence of male breeding success. However, note that if some immature males are erroneously considered as candidate fathers in a given year due to inaccurate age estimation, the number of unsuccessful breeding males may be somewhat over-estimated. For this reason, we did not include estimated age males in our analyses of yearly breeding success and, in our analyses of lifetime breeding success, we compared the results with and without estimated age males. The proportion of known candidate parents sampled varied among cohorts but was always higher than 80% for fathers and 76% for mothers. In order to take into account potential unknown candidate parents in the population, we decided to fix the proportion of candidate parents sampled to a conservative value of 75% for all years and for both sexes. The total number of candidate parents present in the population was then calculated for each cohort as the total number of sampled candidate parents present in the

population divided by 0.75. Notice that previous work has demonstrated that the simulation outcome is relatively insensitive to the number of candidates (Pemberton et al., 1999).

Because one of the input parameters for the simulation varied between years and sexes (i.e. the total number of candidate parents present in the population), to generate the critical δ values for 95% and 80% confidence levels, we carried out a separate simulation for each fawn cohort and for each sex of parent. Then, using these sex- and cohort-specific critical δ values, we performed a separate parentage analysis for each fawn cohort and each sex of parent. Initially, we ran a maternity analysis for each cohort to assign females to fawns with unknown mothers (i.e. those never observed in the field). From this, we retained only those mother-offspring associations which were assigned with 95% confidence by CERVUS. We then combined these assigned maternities with known maternities from field observations and, for each cohort, subsequently conducted the paternity analysis.

Statistical analyses

Although individual fitness (*sensu* Darwin) is not necessarily easily defined and its definition is highly context dependent, most authors agree that fitness equates to some measure of genetic contribution to future generations (Brommer et al., 2004) and empirical studies conventionally use lifetime reproductive success (LRS, usually defined as the number of offspring surviving to breeding age sired by a parent) as a valid single-generation proxy of long-term genetic contribution (see Brommer et al., 2004; Clutton-Brock, 1988). In this study, because a proportion of the sampled fawns were caught as neonates for which the fate was unknown, we used male lifetime breeding success, defined as the number of born offspring sired by a male, as a proxy of individual male fitness. Although this measure does not integrate a juvenile survival component, fawn survival should be almost exclusively affected by maternal rather than by paternal influences in roe deer (Gaillard et al., 2000). Hence, the inclusion in the analysis of fawns caught during their first winter is unlikely to introduce any systematic bias in terms of the distribution of paternities among individual males.

After determining the distribution of paternities among males, we estimated yearly breeding success (YBS; the total number of paternities assigned at the 80% confidence level) for each known-aged male and for each reproductive season during which the male was considered as a candidate father. We also estimated lifetime breeding success (LBS; the total number of independent offspring produced by a male during its life span) of each male for which data were available for the whole life span and which died of natural causes. We restricted LBS analyses to male cohorts born prior to 1999 for which all, or almost all, males

had died at the end of the year 2005 (number of known candidate fathers for a given cohort still alive in 2005 < 4).

Variance in male LBS is the product of several components: the variance in LBS due to non breeders (individuals with LBS = 0) and, within breeders, the variation in reproductive life span (number of potential breeding seasons), annual fecundity (breeding success per season), and their covariance. To examine the contribution of these different components to the variance in male LBS, we used Brown's methodology for the analysis of the variance and covariance of products of random variables (Brown, 1988; Brown and Alexander, 1991; see also Coltman et al. 1999 for an application in Soay sheep). We also tested the hypothesis that male reproductive success was distributed randomly by comparing the observed number of assigned paternities with the number expected under a Poisson distribution with the same mean. Finally, we estimated the opportunity for sexual selection in roe deer by calculating the standardised variance in male reproductive success (I_m), i.e. the ratio of variance in male reproductive success to the square of the mean male reproductive success, which represents an upper limit to the strength of directional sexual selection (Wade and Arnold, 1980). However, this measure of opportunity for sexual selection does not take into account variation in female reproductive success and so we also calculated the ratio of the total opportunity for sexual selection in the two sexes (I_m/I_f ; Wade and Arnold, 1980), which should be positively correlated with the intensity of sexual selection (Clutton-Brock 1983, 1988). For that, we estimated female LRS on 28 known-aged females, based on direct observation of fawns with their mothers in late September (Kjellander, 2000; Kjellander et al., 2004; C. Vanpé, unpubl. data). We considered the number of fawns observed at the end of September to represent the number of weaned offspring for a given female observed at least three times with the same number of fawns at heel. Females were born from 1988 to 1998. We used only does for which data were available for the whole life span and which died of natural causes.

Results

Test of microsatellite markers

Between 2 and 8 alleles per locus were identified (mean = 4.23) and expected heterozygosity ranged from 0.097 to 0.790 (mean = 0.527) among the 22 microsatellite loci (see Electronic appendix 2). There was no significant heterozygote excess or deficit at any single locus, nor over all loci combined ($p > 0.05$), except for the HUI1177 locus (test of

heterozygote deficit: $p = 0.022$). Following correction for multiple comparisons (231 tests, critical $p = 0.000216$, minimum observed $p = 0.00043$), there was no evidence for significant linkage disequilibrium between any pair of loci, except for HUI1177 x Roe5 ($p = 0.00022$). Finally, the estimated frequency of null alleles was negative or low ($\text{freq} < 0.02$), except for HUI1177 ($\text{freq} = 0.12$). Hence, we decided to remove the HUI1177 locus for parentage analysis. The total exclusionary power of the 21 retained microsatellites was 0.999675 when one parent was known and 0.985035 when both parents were unknown. The probability of identity over all loci was 5.14×10^{-12} among all individuals and 1.10×10^{-5} among siblings.

Distribution of paternities between males and variance in male YBS

Of the 605 fawns sampled between 1988 and 2005 (see Electronic appendix 1), the mother's identity was known from behavioural observations for 267. From the maternity analyses performed using CERVUS, we identified the mother of a further 15 fawns at the 95% confidence level. We were then able to assign paternity to 442 fawns at the 80% confidence level (73% of the total 605), of which 235 were also assigned at the 95% confidence level (see Electronic appendix 1). Because very few fawns were sampled and assigned fathers from 1988 to 1991 ($N < 13$ at the 80% confidence level) compared to the potential number of fawns born in the population during these years of high density (see Electronic appendix 1), we removed these 4 years from the subsequent analyses of male YBS and LBS so as not to bias the results towards non breeding males. Sample size was thus 428 paternities assigned at the 80% confidence level (100 from known-aged males), of which 232 were also assigned at the 95% confidence level (60 from known-aged males).

Within a single reproductive season, the number of paternities assigned per known-aged male and per year ranged from 0 to 5 fawns ($N = 231$, $\text{mean} \pm \text{SE} = 0.69 \pm 0.07$; see Fig. 1). After removing all fawns with unknown mothers ($N = 37$), the fawns of a single known-aged male involved up to 3 different females, but note that this is a conservative value.

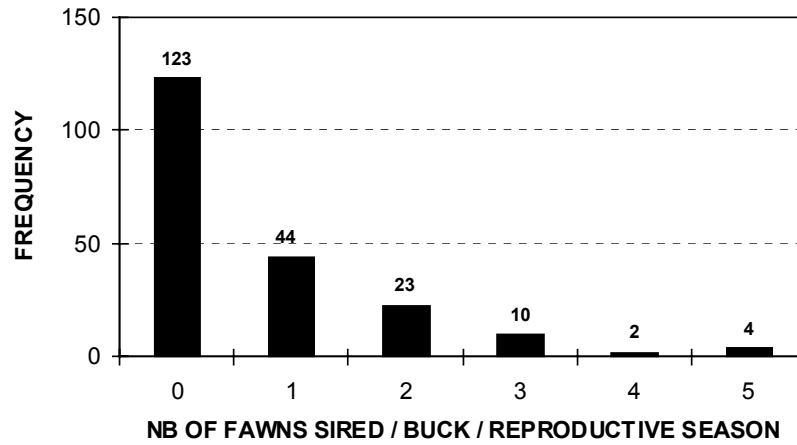


Figure 1. Frequency distribution of paternities assigned per buck (> 1 year of age) and per year (assignments at the 80% confidence level) pooled over all years for all known-aged males ($N = 206$).

Note: Numbers above bars give exact frequencies.

Variance in male LBS

Of the 231 sampled candidate fathers, we could estimate the number of paternities assigned per male over the whole life span (LBS) for 24 candidate fathers (of which 9 were known-aged males). Of the 109 paternities assigned at the 80% confidence level to these 24 males, 66 were also assigned at 95% confidence level, 24 had an unknown mother, 77 had a known mother based on behavioural observations and 8 had a known mother based on maternity analyses. LBS among all males ranged from 0 to 14 (mean \pm SE = 4.54 ± 0.80 , variance = 15.5; see Fig. 2). The distribution of paternities over the lifetime deviated significantly from a Poisson distribution of the same mean ($\chi^2 = 8.05$, df = 1, $p = 0.0045$), indicating that LBS was not randomly distributed among bucks (see Fig. 2). The 3 most successful males (i.e. about 13% of the 24 candidate fathers considered in LBS analyses) sired at least 10 fawns each, totaling 36 fawns together, which represents 33% of the assigned fawns. When we removed non-breeders ($N = 2$), the mean LBS (\pm SE) was 4.95 ± 0.82 . The two components of male LBS varied widely between individuals: reproductive life span ranged from 2 to 11 years (mean \pm SE = 6.38 ± 0.59), while fecundity ranged from 0 to 1.6 fawns sired per year of reproductive life (mean \pm SE = 0.67 ± 0.09). We calculated that about 88% of the variance in male LBS was due to breeders (that sired at least one fawn during their lifetime) and 12% to non breeders (that failed to breed at all). In addition, among breeders, variation in average fecundity contributed most to the variance in male LBS (56%), while variation in reproductive life span contributed somewhat less (33%), and the covariance

between these two components contributed only 11%. The number of successful breeding years of a male was highly positively correlated to its reproductive life span (Spearman correlation test: $r_s = 0.67$, $p < 0.001$).

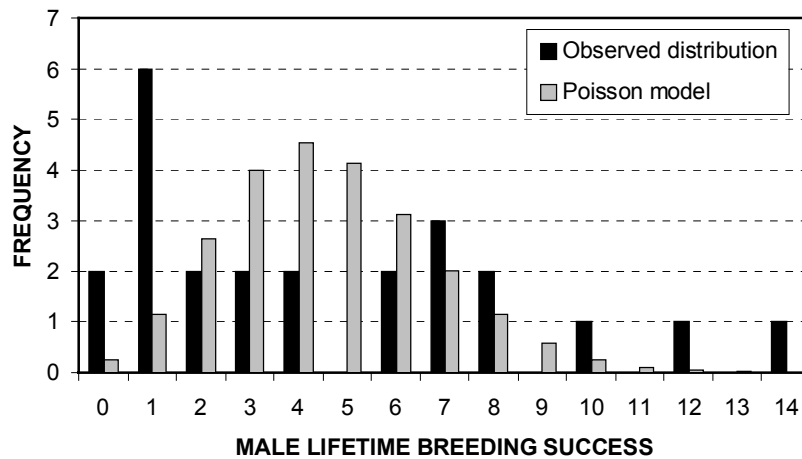


Figure 2. Comparison of the observed frequency distribution of lifetime breeding success among bucks (both with known age and estimated age, $N = 24$) with a Poisson distribution with the same mean.

Note: We used only bucks for which data were available for the whole lifespan, which died of natural causes, and whose cohort was entirely, or almost entirely, extinct at the end of 2005. In black: observed distribution. In grey: Poisson distribution with the same mean.

When considering only known-aged males ($N = 9$), the results followed an almost identical pattern, as LBS still ranged from 0 to 14 fawns (mean = 4.78, variance = 20.69), reproductive life span also ranged from 2 to 11 years (mean = 5.33, variance = 8.75), and annual fecundity ranged from 0 to 1.6 fawns (mean = 0.83, variance = 0.33). Furthermore, in this sample subset, about 80% of the variance in male LBS was due to breeders, of which variation in reproductive life span and variation in average fecundity contributed respectively to 34% and 54%. Consequently, we chose to consider LBS data for both known-aged and estimated age males in the following analyses of opportunity for sexual selection.

Opportunity for sexual selection

The opportunity for sexual selection was calculated both as the standardised variance in male LBS (I_m) and as the ratio of the standardised variance in male LBS to the standardised variance in female LBS (I_m/I_f). Based on LBS, I_m was 0.75 when considering all males and 0.60 when considering successful breeders only. This indicated that only a little of the standardised variance in LBS among all males was due to the inclusion of individuals that

obtained no matings (I_m among successful breeders = 80% of I_m among all males). Early mortality also affected the opportunity for sexual selection. When only individuals with a reproductive life span superior or equal to 4 years were included ($N = 18$), I_m was 0.52, which is equal to 69% of the standardised variance in LBS among all males. LRS of known-aged female roe deer (see Fig. 3) was found to range from 0 to 12 fawns ($N = 28$, mean = 4.19, variance = 9.27). Consequently, we estimated that the standardised variance in female LRS (I_f) was 0.53 and hence, the variance ratio I_m/I_f was 1.42.

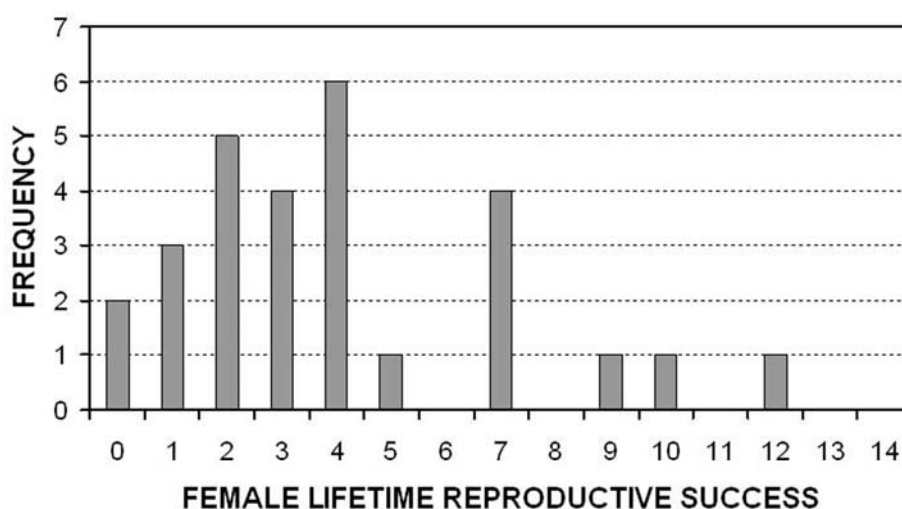


Figure 3. Distribution of lifetime reproductive success among known-aged does ($N = 28$).

Note: Data were based on direct observations of weaned fawns at heel at the end of September. Females were born between 1988 and 1998. We used only does for which data were available for the whole life span and which died of natural causes.

Discussion

In this paper, we used molecular paternity analysis to provide the first information on variance in male reproductive success and the opportunity for sexual selection in an ungulate species with low sexual size dimorphism. As expected, in line with the low level of sexual size dimorphism of roe deer (Andersen et al., 1998), we obtained a low standardised variance in male LBS, characteristic of a weakly polygynous mating system with a low opportunity for sexual selection.

Our results revealed that there was significant reproductive skew in roe deer, with several males siring no fawns or only one fawn and the most successful males siring up to 14 offspring over their lifetime (mean = 4.54, variance = 15.5). The maximum number of offspring sired per male was, however, lower in roe deer than in more sexually dimorphic

ungulate species. In red deer, based on behavioural observations, Clutton-Brock et al. (1988) have reported that LRS varied from 0 to 32 calves surviving to the age of two years (mean = 5.41, variance = 41.9) among mature stags. In Soay sheep, male LRS ranged from 0 to 19 offspring (mean = 0.73, variance = 3.53; Pemberton et al., 1999 based on molecular tools).

One striking result from this study is that the variance in male LBS among breeders was a result of both variation in average fecundity (56%) and variation in reproductive life span (33%). This is in contrast to highly polygynous mammals, where variation in annual fecundity is usually the single largest component of fitness variation among breeding males (Clutton-Brock, 1988), possibly because the age of successful reproduction is usually limited to a few years in these species. In red deer, for example, based on behavioural estimates of male LRS, Clutton-Brock et al. (1988) reported a contribution of 32% for variance in annual fecundity, but of only 7% for variance in reproductive life span. Variance in longevity accounted for about 25% of the variance in male LRS in American pronghorn *Antilocapra americana* (Ord, 1815), an ungulate with a level of sexual size dimorphism intermediate between red deer and roe deer (Byers, 1997).

We also estimated the standardised variance in LBS (I_m), which represents an upper limit to the strength of directional sexual selection, to infer the opportunity for sexual selection in this territorial ungulate. A truly monogamous mating system should have a I_m value of zero, whereas mating systems with moderate to strong levels of polygyny should have positive I_m values (e.g., ranging from five to 50 in pinnipeds: Boness et al., 1993). As expected, in line with the low level of sexual size dimorphism of roe deer (Andersen et al., 1998), we obtained a low value of I_m (0.75 when considering all males, and 0.60 when considering successful breeders only), characteristic of a weakly polygynous mating system. To take into account variation in female reproductive success, we also calculated the ratio of the total opportunity for sexual selection in the two sexes (I_m/I_f). We estimated that the standardised variance in female LRS (I_f) was 0.53 and the variance ratio I_m/I_f was 1.42. In polygynous species, I_f is expected to be lower than I_m (Clutton-Brock, 1988). Our results supported this prediction, but interestingly, the difference between sexes was very low compared to highly dimorphic species (e.g., in red deer, $I_m/I_f = 9.85$ and 3.53 based on behavioural observations of LBS and LRS respectively: Clutton-Brock et al., 1988). Hence, again, these results support our prediction of a low level of polygyny and a low opportunity for sexual selection in roe deer.

Note, however, that since we succeeded in assigning paternity to only 73% of the sampled fawns, and since not all fawns born in each cohort were sampled, we have certainly

under-estimated the YBS and the LBS of most males. In particular, we have likely over-estimated the number of non-breeding males. Indeed, we actually found that a surprisingly high proportion of the variance in male LBS (i.e. 12%) was due to non breeders that failed to sire any fawns during their lifetime. We have probably also under-estimated the maximum number of fawns that a male can sire per year and during his lifetime. For example, one male, which was not included in YBS analyses because his age was estimated, sired up to 6 fawns per year, and one male, which was not included in LBS analyses because he died during hunting aged 9 years, sired 15 fawns during his lifetime. However, while the mean LBS was clearly under-estimated, it is unclear whether the variance was under- or over-estimated. Also, the results are in agreement with predictions based on the current knowledge of roe deer life-history (see Hewison et al., 2005) and on the low level of sexual size dimorphism in this species. Finally, the under-estimation of mean male LBS should lead to an over-estimation of the ratio I_m/I_f . Hence, our result is conservative, further supporting the prediction of a weakly polygynous mating system in roe deer.

In addition, while female LRS estimate was based on the number of weaned fawns at heel at the end of September, our measure of male LRS did not include an offspring survival component. As previously mentioned, this is not expected to affect variance in male LRS much (Gaillard et al., 2000), since male ungulates generally exert little influence on the survival of their offspring, so that differential genetic success arises primarily from differences in their mating contributions (Owen-Smith 1977). In contrast, offspring survival may be the most important component of variation in female reproductive success in large mammals (e.g., in red deer: Clutton-Brock et al., 1988; roe deer: Gaillard et al., 2000). In roe deer, the most critical stage for fawn survival is concentrated in the neonatal period during the first months of life (Gaillard et al., 1998a; Linnell et al., 1998). Hence, by measuring female LBS as the number of fawns at heel at the end of September, we captured most of the variance in female LRS due to fawn survival.

Jarman (1983) suggested that there is a continuum of sexual selection intensity in African antelopes, from monogamous and monomorphic species to highly polygynous and dimorphic species. We investigated whether this hypothesis was supported in ungulates in general by comparing published values of I_m , preferentially based on genetic paternity analysis, for species with varying levels of sexual size dimorphism (see Fig. 4). In agreement with the predicted pattern, studies of ungulates with moderate to high male-biased sexual size dimorphism (males >30% heavier than females) reported much larger values of I_m than the value we obtained for roe deer (see Fig. 4).

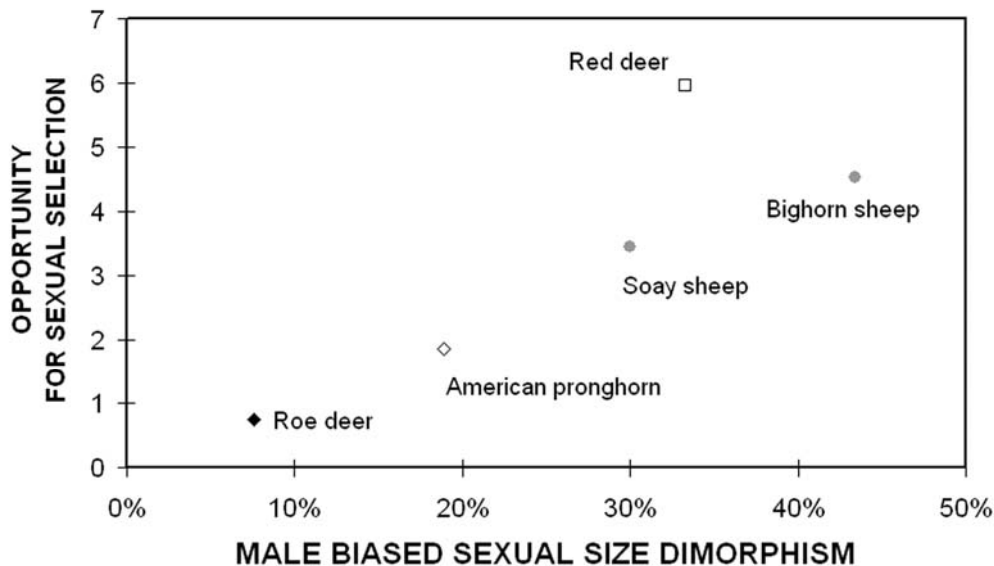


Figure 4. Opportunity for sexual selection in relation to the degree of male-biased sexual size dimorphism across different ungulate species.

Note: Sexual size dimorphism data are estimated from mean male and female body mass data from Weckerly (1998). Estimations of the opportunity for sexual selection are based on published data of standardised variance in male lifetime reproductive success or lifetime breeding success among all males (I_m): for roe deer (this study), for red deer (Marshall, 1998), for Soay sheep (Coltman et al., 1999), for bighorn sheep (Coltman et al., 2002), and for American pronghorn (Byers, 1997). Black diamonds: territorial species. Grey filled circles: tending/roving species. Black open squares: harem-holding species. Black open diamonds: species with a mixed territorial / harem-holding mating system.

Notice that these values are, however, lower ($3 < I_m < 6$ among all males) than those of pinniped species with moderate to strong levels of polygyny ($I_m > 5$; Boness et al., 1993). Interestingly, the values obtained by Byers (1997) for the American pronghorn based on behavioural observations of mating success ($I_m = 1.08$ when considering the number of matings, but 1.87 based on the number of offspring surviving to weaning; $I_m/I_f = 1.44$) were quite similar to the values we obtained for roe deer. Unfortunately, there is a lack of genetic data on standardised variance in male LBS of monomorphic and monogamous ungulate species in the literature for comparison with roe deer. However, we can expect that the value of I_m for such species may be even lower than the value we found in roe deer, converging towards zero. We therefore suggest that, along a continuum of opportunity for sexual selection in ungulates from monogamous and monomorphic species to highly polygynous and sexually dimorphic species, roe deer occupy an intermediate position, which is likely to be closer to monomorphic species than to highly dimorphic species. Our results also seem to support the view that territorial species such as roe deer or the American pronghorn (the American pronghorn has a mixed territorial / harem-holding mating system; see Byers, 1997 for more details) tend to have a lower opportunity for sexual selection than species with

dominance-rank based mating systems (e.g., harem-holding, roving) such as red deer, bighorn sheep or Soay sheep. It is, however, less clear whether, for a given level of polygyny, sexual size dimorphism, variance in male reproductive success and the opportunity for sexual selection should be consistently higher for species with dominance rank-based mating systems compared to territorial species (Clutton-Brock, 1988). Much more data for ungulate species exhibiting various levels of sexual size dimorphism and different mating systems is needed to investigate this issue.

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Electronic appendix 1. Sample size and assignment results for each cohort of fawns.

Fawn cohort	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	Total
Total nb of sampled fawns (nb with known mother)	4 (0)	6 (0)	12 (0)	6 (0)	131 (18)	48 (6)	14 (1)	14 (1)	10 (6)	22 (6)	24 (19)	45 (25)	41 (29)	46 (41)	30 (24)	54 (30)	69 (41)	29 (20)	605 (267)
Nb of candidate fathers sampled	40	54	66	84	104	116	51	34	34	34	31	34	41	41	56	58	63	39	231
Nb of candidate mothers sampled	78	102	129	152	184	220	112	80	83	83	66	70	84	83	73	74	72	36	352
Estimated nb of candidate fathers in the population	53	72	88	111	164	155	68	45	45	45	41	45	56	59	83	85	93	68	
Estimated nb of candidate mothers in the population	105	136	172	203	245	293	149	108	112	112	96	103	119	119	108	108	115	84	
Nb of fathers assigned at 95% confidence level			3		40	11	2	2	3	6	17	16	23	25	15	24	33	15	235
Nb of fathers assigned at 80% confidence level	1	4	7	2	80	29	9	12	6	12	23	37	34	37	25	45	55	24	442

Note: nb = number.

Electronic appendix 2. Descriptive statistics for the 22 microsatellite loci.

Locus	k	N	H _O	H _E	Excl _{1st}	Excl _{2nd}	Null allele freq	F _{IS} (W&C)	HW (excess)	HW (deficit)
IDVGA29	2	1642	0.328	0.333	0.055	0.139	0.0071	0.006	0.622	0.555
CSSM39	5	1640	0.613	0.610	0.200	0.348	-0.0032	0.033	0.530	0.472
IDVGA8	2	1631	0.372	0.374	0.070	0.152	0.0032	-0.056	0.343	0.813
BM1706	3	1640	0.098	0.097	0.005	0.046	-0.0078	-0.029	0.801	1.000
OARFCB304	8	1615	0.693	0.695	0.288	0.464	-0.0001	0.012	0.494	0.513
HUJ1177	5	1629	0.480	0.588	0.197	0.372	0.1238	0.208	0.997	0.002
BMC1009	5	1642	0.574	0.584	0.185	0.348	0.0098	-0.025	0.199	0.809
BM848	3	1593	0.631	0.645	0.208	0.352	0.0097	0.030	0.682	0.323
CSSM41	3	1580	0.551	0.555	0.154	0.275	0.0042	-0.000	0.350	0.664
BM757	8	1638	0.777	0.790	0.413	0.592	0.0070	-0.022	0.153	0.839
CSSM43	2	1631	0.110	0.113	0.006	0.053	0.0116	-0.060	0.618	1.000
Roe8	7	1622	0.575	0.582	0.193	0.362	0.0080	-0.026	0.364	0.640
SR-CSR1	4	1550	0.247	0.263	0.035	0.135	0.0239	-0.068	0.261	0.833
Roe9	3	1631	0.441	0.447	0.100	0.223	0.0063	-0.047	0.632	0.365
KCNA44	5	1630	0.771	0.787	0.396	0.575	0.0101	-0.023	0.443	0.538
Roe6	4	1630	0.489	0.491	0.120	0.202	0.0021	-0.052	0.284	0.743
Roe5	4	1621	0.752	0.637	0.218	0.374	-0.0981	-0.124	0.028	0.971
ILST030Q	5	1625	0.675	0.687	0.263	0.429	0.0098	-0.009	0.695	0.301
MAF70	5	1632	0.580	0.559	0.159	0.265	-0.0203	-0.098	0.786	0.213
MB26	2	1631	0.422	0.425	0.090	0.167	0.0034	0.041	0.756	0.394
BL42	4	1629	0.643	0.655	0.226	0.381	0.0100	0.063	0.817	0.184
ILST011	4	1631	0.692	0.678	0.257	0.429	-0.0121	-0.067	0.238	0.777

Note: Parameters estimated using CERVUS on all genotyped individuals: k = number of alleles, N = number of individuals genotyped, H_O = observed heterozygosity, H_E = expected heterozygosity, Excl_{1st} = exclusion probability of first parent, Excl_{2nd} = exclusion probability of second parent (when one parent is known), Null allele freq = estimated frequency of null alleles. Parameters estimated using GENEPOP on the 1992 fawn cohort with siblings removed (N = 133): F_{IS} (W&C) = estimate of Weir and Cockerham's F_{IS}, HW (excess) = probability test for an excess of heterozygotes, HW (deficit) = probability test for a deficit of heterozygotes.

PART 2

AGE-RELATED VARIATION IN MALE BREEDING SUCCESS



**Roe buck engages in a “chase court” with a doe
(photograph by Bruno Lourtet)**

PAPER 2

Age-specific variation in male breeding success and mating tactics of roe deer

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Abstract

We investigated age-specific variation in male yearly breeding success in two contrasted populations of the territorial European roe deer (*Capreolus capreolus*), using microsatellite genotyping and paternity analyses. Yearly breeding success was markedly age-structured. In both populations, male breeding success was low at 2 years of age, peaked at 3-8 years of age (the prime-age stage), and then declined from 8 years of age onwards. We thus found that 2-year-old roe bucks are able to successfully breed, but only a few individuals of particularly high phenotypic quality are able to hold a territory during the rut at that age. The marked senescence we reported for males older than 8 years of age in male breeding success could be due to a loss of territorial-based dominance.

Keywords: age of first breeding, *Capreolus capreolus*, microsatellites, paternity analyses, senescence, territoriality.

Introduction

Age is known to structure markedly most life history traits of vertebrate populations (Charlesworth 1994; Gaillard et al. 2000). In particular, age is an important determinant of survival (e.g., Caughley 1966; Loison et al. 1999) and individual mating success (e.g., LeBœuf 1974; Kodric-Brown 1983; Berger 1986; Clutton-Brock 1988; Owen-Smith 1993; Byers 1997). Therefore, studying age-specific rates of reproduction and survival is a crucial issue in population ecology (Caughley and Sinclair 1994; Tuljapurkar and Caswell 1996; Coulson et al. 2001) and life-history theory (Stearns 1992).

According to the principle of energy allocation (Cody 1966; Williams 1966), the amount of energy available is limited, so that trade-offs in the amount of energy allocated to growth, survival and reproduction are expected to occur (Stearns 1992). In iteroparous species, current reproduction should thus be balanced against future survival (basis for senescence theory; Hamilton 1966; Kirkwood and Rose 1991) and future reproduction (basis for reproductive costs; Williams 1966). This may explain why in large mammals, at both population and individual levels, reproductive performance and survival peak for prime-age adults (Gaillard et al. 2000 for a review on large herbivores; Caughley 1966; Loison et al. 1999; Gaillard et al. 2003b for survival; Clutton-Brock et al. 1982; Byers 1997; McElligott and Hayden 2000; Ericsson et al. 2001; McElligott et al. 2003 for reproduction). However, some authors have reported an increased mating success with increasing age (e.g., Coltman et al. 1999; Coltman et al. 2001). Such increased performance with increasing age could be linked to a potential increase in average individual quality with increasing age through a “selective (dis)appearance” effect (Vaupel et al. 1979; van de Pol and Verhulst 2006). Indeed, high-quality individuals live longer than poor quality ones (Gaillard et al. 2000) and thereby increase in proportion within a cohort with increasing age (Bérubé et al. 1999; Weladji et al. 2006). As a result, an increase in mean breeding performance amongst the older age classes is likely to occur at the population level, potentially masking within-individual patterns of senescence (Cam et al. 2002; Nussey et al. 2006). Hence, assessing age-dependence of mating success ideally requires longitudinal data on marked known-aged individuals over their whole life span, which is rarely the case for wild large mammals.

In ungulates, the available studies on age-dependent variation in male breeding success are limited to highly dimorphic and polygynous species, with dominance-rank based mating systems, such as red deer *Cervus elaphus* (Clutton-Brock et al. 1982), fallow deer *Dama dama* (McElligott and Hayden 2000), bighorn sheep *Ovis canadensis* (Coltman et al.

2001), or Soay sheep *Ovis aries* (Coltman et al. 1999). No study has as yet focussed on a species where territoriality is the main male mating tactic. Life history theory predicts that given an age- (or stage-) structured life history tactic, there exists an optimal way to partition lifetime reproductive effort at each age (or stage) so that individual fitness is maximized (Fisher 1930; Cole 1954; Williams 1966; Charlesworth 1994). In territorial species, we should expect that age-specific variation in male reproductive success is strongly linked to age-specific variation in territorial status, so that the mating tactic itself is expected to shape age-specific variation in mating success (see Yoccoz et al. 2002 for similar arguments on the harem-based mating tactic of red deer) because territoriality is generally viewed as a prerequisite to mate for male roe deer (e.g., Johansson 1996).

The aim of this study was therefore to investigate age-specific variation in male yearly breeding success of a territorial species, the European roe deer *Capreolus capreolus* (e.g., Bramley 1970), using genetic paternity analyses. We analysed two unique data sets collected from two contrasted populations of roe deer monitored for more than 15 years in Sweden and France, including known-aged males up to 12 and 13 years of age respectively (for an observed maximal male longevity in roe deer of 14 years of age; Loison et al. 1999). In addition to age-dependent variation in male yearly breeding success (YBS), we investigated individual trajectories over the entire lifetime for few males for which data were available. Age is known to be an important source of variation in roe deer female fecundity (Danilkin and Hewison 1996; Gaillard et al. 1992, 1998; Hewison 1996; Hewison et al. 2002). In contrast, no reliable information is available on age-specific variation in male breeding success in this species. Previously studies (i.e. Johansson 1996) was based on direct observations and did not include known-aged individuals. We tested whether variation in male yearly breeding success in relation to age conformed to the dome-shaped relationship in accordance with the general pattern observed among large mammals for most life history traits related to performance. As senescence has been reported in roe deer after 7 years of age for survival of both sexes and for male antler size (Gaillard et al. 1993, 2004; Vanpé et al. 2007), after 10 years of age for body mass (Pettorelli et al. 2002), and after 12 years of age for female reproductive output (Gaillard et al. 1998), we expected to find sometimes a decrease in male mating success among old males after 7 years of age. Finally, we addressed the question of the age of first mating for young males in relation to first territory establishment. Indeed, although roe deer males become sexually mature at about 15 months of age, most studies reported that roe deer males do not usually defend territories prior to 3 or 4 years of age (Bramley 1970; Strandgaard 1972; Kurt 1991; Vincent et al. 1995), and whether 2 year-old

males can be fully territorial and successfully mate is, to date, controversial (see Liberg et al. 1998).

Materials and methods

Study sites and data collection

We used data from two long-term monitored populations of roe deer: Bogesund, a 2,600 ha area of fragmented habitat located in central eastern Sweden (59°23'N, 18°15'E); and Trois Fontaines, a 1,360-ha enclosed forest in eastern France (48°43'N, 2°61'E) (see Vanpé et al. 2007 for more details). The populations of Bogesund and Trois Fontaines have been intensively monitored since 1988 and 1975, respectively, using Capture-Mark-Recapture (see e.g., Gaillard et al. 2003a and Kjellander 2000 for further details). Each year during winter, roe deer were captured in box traps (at Bogesund) or nets (at Trois Fontaines), and individually marked. In addition, since 1997 at Bogesund and 1985 at Trois Fontaines, neonates have been caught by hand every spring, just after birth (May-June), and individually marked. Mother-offspring relationships were, as far as possible, elucidated by direct observation of fawns with their mothers just after birth or during autumn. During the study period, some roe deer were occasionally shot or removed in order to manipulate experimentally population density (see Gaillard et al. 1993, 2003a; Kjellander 2000 for further details). The age of individuals in the two populations was either known definitively (captured as fawns in spring or winter), or estimated from tooth wear (Cederlund et al. 1991) examined during winter captures or after shooting. As ages estimated from tooth wear are likely to be inaccurate (see Hewison et al. 1999 for a test using known-aged roe deer), in this paper we only used known-aged individuals for analyzing age-dependence of male breeding success.

Microsatellite and paternity analysis

Since 1988 at Bogesund and 1994 at Trois Fontaines, ear skin tissue samples have been collected from all individuals caught for the first time or shot as unmarked roe deer. We thus sampled a total of 1757 and 1298 individuals at Bogesund and Trois Fontaines, respectively. Genotyping was carried out using 21 microsatellite markers at Bogesund (see Vanpé et al. unpubl. data), but only 11 of these 21 microsatellite markers at Trois Fontaines because of the higher polymorphism of this population (see Vanpé et al. unpubl. data.). Genotyping methods have been detailed in Vanpé et al. (unpubl. data). The total exclusionary

power of the set of microsatellite markers used at Bogesund and Trois Fontaines was 0.9997 and 0.9989, respectively, when one parent was known, and 0.9850 and 0.9772, respectively, when both parents were unknown. Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall et al. 1998) and using the user-input parameters defined in Vanpé et al. (unpubl. data). We successfully assigned 442 and 161 fawns at Bogesund and Trois Fontaines, respectively, to a given father at the 80% level of confidence.

Estimation of male breeding success

After determining the distribution of paternities among males, we estimated yearly breeding success (YBS) for each known-aged male and for each breeding season during which the male was considered as a candidate father. Because a proportion of the sampled fawns was caught as neonates for which the fate was unknown, we defined YBS as the number of fawns born in a given cohort and sired by a given male. We thus estimated YBS as the total number of paternities assigned to a given male in a given year at the 80% confidence level. Because very few fawns were assigned prior to 1991 (Bogesund) and 1997 (Trois Fontaines), we restricted our analyses to fawns born after these years. Note that our estimates of YBS were minimum estimates (with an unknown rate of under-estimation), because it was not possible to catch all fawns born within each year.

Statistical analyses

To analyse the influence of age on YBS (discrete response variable) at the population level (Fig. 1), we used a Generalized Linear Mixed Model (GLMM) implemented in the glmmADMB module (H. Skaug, D. Fournier and A. Nielsen) of the software R 2.3.1 (R Development Core Team 2004). Parameters are estimated by maximum likelihood using the Laplace approximation to evaluate the marginal likelihood (Skaug and Fournier 2005). YBS was modelled as a poisson distribution (see MacLoughlin et al. 2006 for a similar approach on red deer females). As we suspected that many males were identified as unsuccessful simply because we did not catch the fawns they sired, we used a zero-inflated model. Hence, with probability '1-pz' YBS comes from a Poisson distribution, and with probability 'pz' YBS is zero (Bohning et al. 1999). Note, however, that while sampling only a variable proportion of fawns born in a given cohort will lead us to underestimate YBS, this should not influence the relationship between YBS and age because there is no a priori reason to suspect that fawns sired by males of a given age were systematically more or less likely to be sampled than those

sired by males of other ages. Age was fitted as a fixed effect and individual identity as a random effect, thus controlling for the likely heterogeneity among individuals (Vaupel et al. 1979) and for problems of pseudo-replication when using repeated measures from the same animals at different ages (Hurlbert 1984).

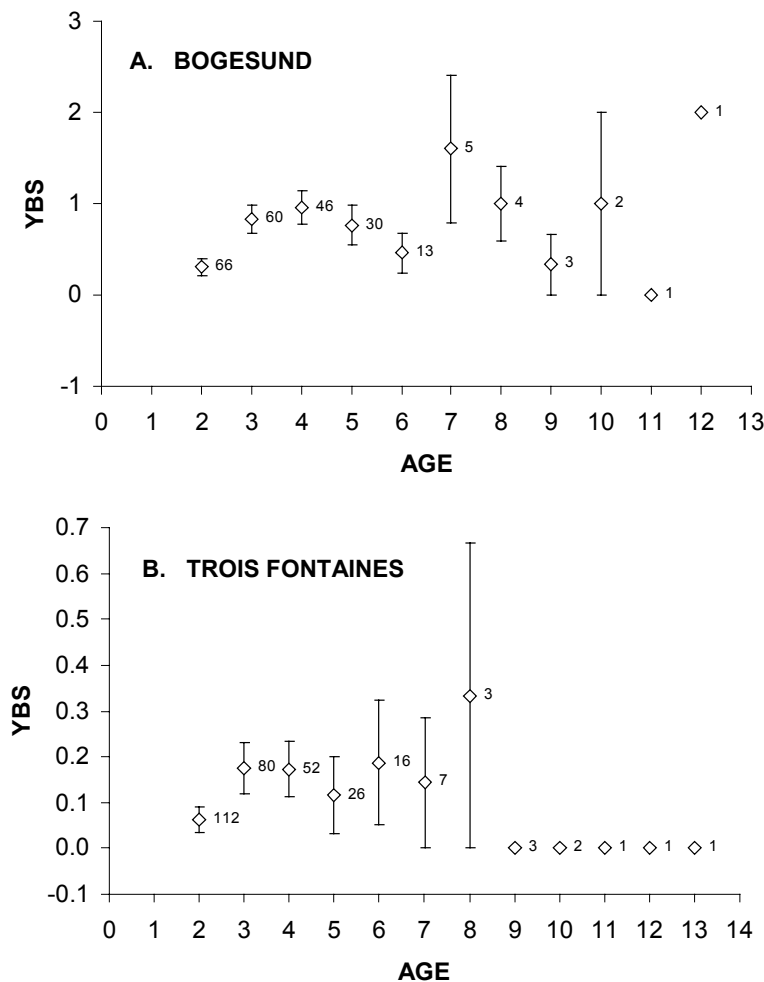


Figure 1. Age-specific estimates of male yearly breeding success (YBS) observed at Bogesund (A) and Trois Fontaines (B). Error bars show standard errors. The sample sizes for each age class are also given.

We first looked for the best model to account for age-specific variations in YBS in each population independently, by comparing the model without any age-dependence (i.e., constant YBS over ages) with models including age fitted as a continuous covariate (by fitting polynomial functions of various orders) or as a discrete factor (2 age-class model: 2 year-olds, and older ages; 3 age-class model (2, 3-7, >7): 2 year-olds, 3-7 year-olds, and older ages; 3 age-class model (2, 3-8, >8): 2 year-olds, 3-8 year-olds, and older ages; Table 1A). Each fitted model corresponds to different biological hypotheses (e.g., continuous increase with age,

dome-shaped variation). The three-age-class model is considered typical for ungulates (Gaillard et al. 2000). Then, we pooled data for both populations and tested the effects of age and population, as well as their interaction, on male YBS (Table 1A). Model selection was performed using the small-sample-size corrected Akaike Information Criterion (AICc), as recommended by Burnham and Anderson (2002). We selected the model with the smallest AICc (i.e., the best compromise between accuracy and precision). When two models differ in their AICc values by less than 2 units, both can be considered competitive for interpretation (Burnham and Anderson 2002). The confidence intervals of the predictions of zero-inflated GLMM models were built using the classical asymptotic theory of log-likelihood ratio test adapted to this special case (Cox and Hinkley 1992, pp. 218-222). Finally, the individual-based data allowed us to compare breeding success for the same individual at different ages for 5 known-aged males from Bogesund. By doing this, we were able to control for possible differences in individual quality among males on YBS estimates.

Results

Age of fathers at fawn conception and age of first breeding attempt

At Bogesund, the age (at fawn conception) of the fathers of the 90 fawns that were sired by known-aged males ranged from 2 to 12 years (Fig. 2). The age of first conception (i.e. first successful breeding) of the 44 known-aged fathers ranged from 2 to 5 years (mean \pm SE = 2.98 ± 0.85), with a median at 3 years old. At Trois Fontaines, the age (at fawn conception) of the fathers of the 39 fawns that were sired by known-aged males ranged from 2 to 8 years (Fig. 2). The age of first conception of the 20 known-aged fathers ranged from 2 to 7 years (mean \pm SE = 3.30 ± 0.25), with a median at 3 years old.

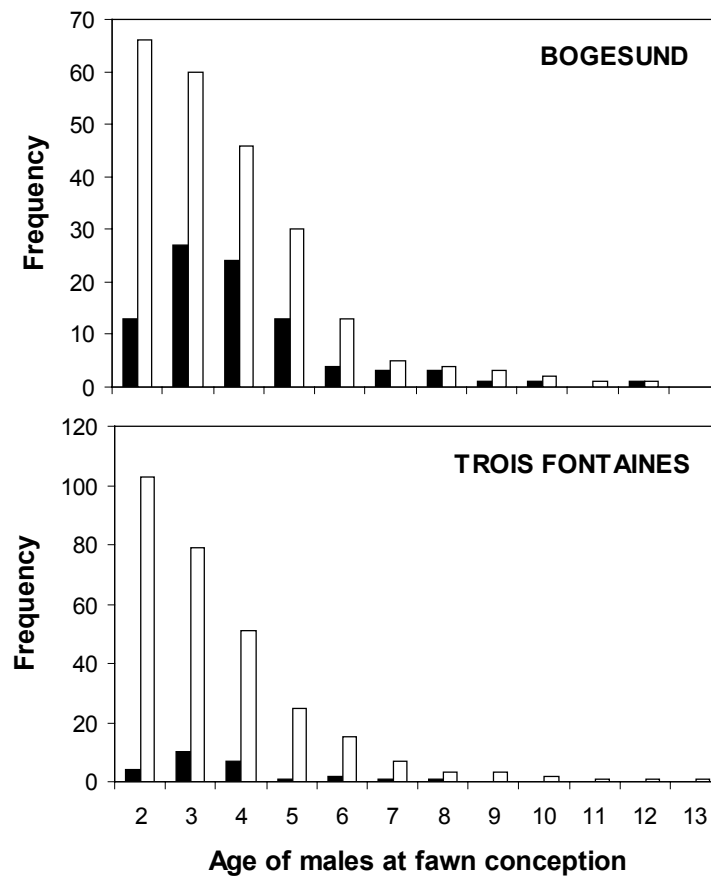


Figure 2. Frequency of the different ages among successful breeders (in black) and candidate fathers (in white) at Bogesund and Trois Fontaines.

Variation in YBS with age (transversal data)

At Bogesund, the best age-dependent model of variation in male YBS included 2 age-classes (i.e. 2 year-olds, and older ages; Table 1A). Two-year-old males had a lower YBS (mean = 0.31, IC = [0.13, 0.37]) than older males (mean = 0.85, IC = [0.47, 0.84]). However, the best two-age-class model and 2 models including 3 age-classes (i.e. 2, 3-7, >7 and 2, 3-8, >8) had very similar AICc (Table 1A), indicating substantial support for the three-age-class models. Thus, 3-8 year-old males had higher YBS (mean = 0.69, IC = [0.46, 0.86]) than younger (mean = 0.25, IC = [0.13, 0.37]) and older (mean = 0.46, IC = [0.13, 1.05]) males (see Fig. 3A). Note that the variance in observed YBS among males older than 8 was particularly high.

At Trois Fontaines, the best age-dependent model included 3 age-classes (i.e. 2, 3-8, >8; Table 1A). Males of 3-8 years old had a higher YBS (mean = 0.10, IC = [0.04, 0.16]) than both younger (mean = 0.03, IC = [0.01, 0.08]) and older (mean = 0.00, IC = [0.00, 0.05])

males (see Fig. 3B). Note that all males older than 8 years old in our sample (N = 8) failed to successfully breed. However, both three-age-class models, the quadratic model and the two-age-class model (i.e. 2, >2) had very similar AICc (Table 1A), indicating substantial support for these models too.

Table 1. Model selection for age-specific variation in male breeding success for each of the studied populations (A) and for both populations pooled (B).

(A)

		null	age	age ²	age ³	2 ac (2, >2)	3 ac (2,3-7,>7)	3 ac (2,3-8,>8)
Bogesund	k	3	4	5	6	4	5	5
	AIC _c	480.5	481.4	480.1	475.1	468.3	469.3	469.8
	ΔAIC _c	12.2	13.1	11.7	6.8	0.0	0.9	1.5
Trois Fontaines	k	3	4	5	6	4	5	5
	AIC _c	236.0	238.0	233.4	235.3	233.8	232.5	232.4
	ΔAIC _c	3.6	5.6	1.0	3.0	1.4	0.1	0.0

(B)

	null	age	age ²	2 ac (2, >2)	3 ac (2,3-7,>7)	3 ac (2,3-8,>8)	pop	pop + age	pop + age ²	pop + 2 ac (2, >2)	pop + 3 ac (2,3-7,>7)	pop + 3 ac (2,3-8,>8)	pop x age	pop x age ²	pop x 2 ac (2, >2)	pop x 3 ac (2,3-7,>7)	pop x 3 ac (2,3-8,>8)
k	3	4	5	4	5	5	4	5	6	5	6	6	6	8	6	8	8
AIC _c	760.7	762.3	753.8	741.6	740.5	740.1	716.2	717.7	712.0	700.3	699.9	699.7	721.5	713.4	704.3	703.1	700.9
ΔAIC _c	61.1	62.7	54.1	41.9	40.8	40.4	16.6	18.1	12.4	0.7	0.2	0.0	21.9	13.7	4.7	3.5	1.2

Note: Model selection was performed using the small sample correction Akaike Information Criterion (AIC_c), as recommended by Burnham and Anderson (2002). ΔAIC_c are the AIC_c differences between the given model and the best model (the model with the lowest AIC_c). The selected model appears in bold and outlined in grey. k = number of parameters. + : additive effect. x : interaction effect. null = constant model. age = age fitted as a covariable. age² = age fitted as a quadratic function. age³ = age fitted as a cubic function. 2 ac (2, >2) = age fitted as a factor with two age classes (i.e., 2, >2 years old). 3 ac (2, 3-7, >7) = age fitted as a factor with three age classes (i.e., 2, 3-7, >7 years old). 3 ac (2, 3-8, >8) = age fitted as a factor with three age classes (i.e., 2, 3-8, >8 years old). pop = population fitted as a 2 level factor (Bogesund, Trois Fontaines).

When we pooled data of both populations in a single analysis, the best model included additive effects of the population and of a 3 age class term (i.e. 2, 3-8, >8; Table 1B). YBS

followed a similar pattern in both populations, in that it was lower for 2 year-olds, higher for males of 3-8 years, and then lower again for older males. In addition, YBS was lower for a given age class at Trois Fontaines than at Bogesund. However, the other model including 3 age-classes (i.e. 2, 3-7, >7) with the additive effect of the population, and the model including 2 age-classes (i.e. 2, >2) with the additive effect of the population had very similar AICc values to this model (Table 1B). From the second of these two models, YBS was lower for 2 year-old males compared to older males to a similar degree in both populations, and was lower for a given age class at Trois Fontaines compared to Bogesund.

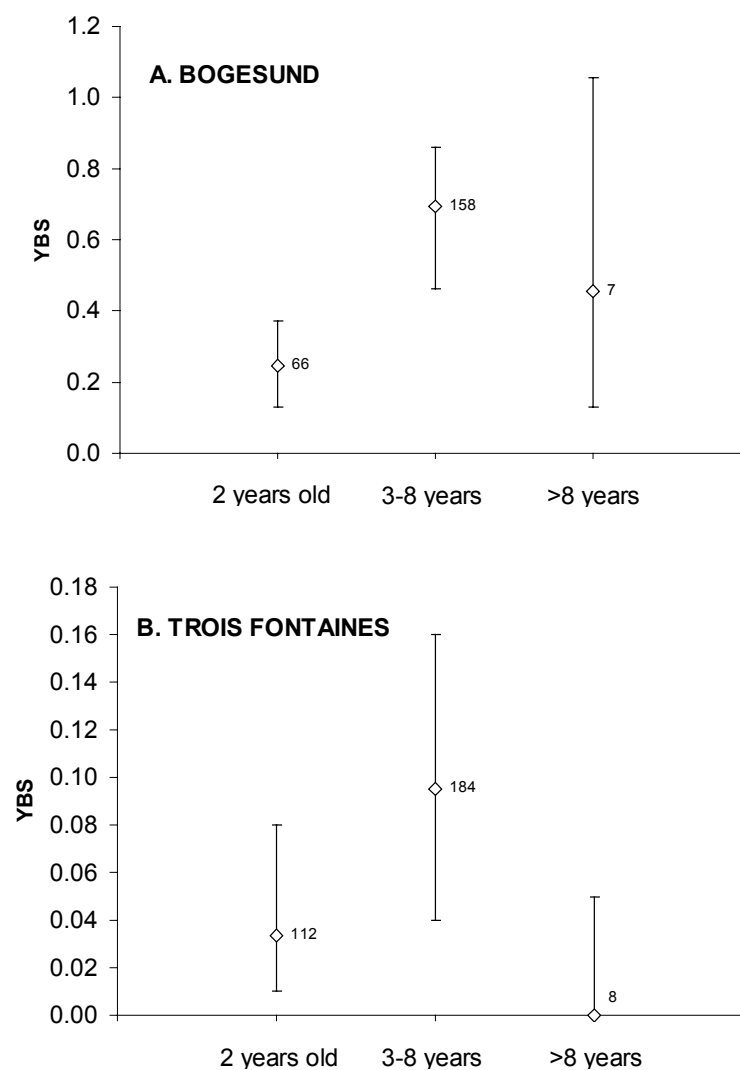


Figure 3. Age-specific estimates of male yearly breeding success (YBS) predicted by the model with age fitted as a factor with 3 age classes (2, 3-8, >8) at Bogesund (A) and Trois Fontaines (B). Error bars show 95% confidence intervals built using the classical asymptotic theory of log-likelihood ratio test adapted to this special case (Cox and Hinkley 1992). The sample sizes of each age class are also given.

Proportion of successful breeders in each age class

When combining all the reproductive seasons for which we had data, 2 year-old males were strongly under-represented in the total number of known-aged successful breeders (only about 15% of fathers in both populations as compared to 29% and 35% of candidate males at Bogesund and Trois Fontaines, respectively; Fig. 2). Males of 3-8 years of age accounted for the largest proportion of paternities ($> 80\%$ in both populations), while they represented only 68% and 61% of candidate fathers at Bogesund and Trois Fontaines, respectively. Lastly, males older than 8 were neither over- nor under-represented as fathers at Bogesund (they represented 3% of fathers and 3% of candidate males) and were not represented among fathers at Trois Fontaines while they represented 3.4% of candidate males. Hence, at Bogesund, the proportion of successful breeders was similar in 3-8 year-olds and older males (about 45%), but higher in these age classes than in younger males (about 20%). At Trois Fontaines, the proportion of successful breeders was larger in 3-8 year-olds (12%) than in either older or younger males (0% and 4%, respectively).

Variation in YBS with age (individual trajectories)

By looking at the age-specific variation in YBS for 5 known-aged males from Bogesund for which we had longitudinal data over their lifetime (Fig. 4), we found that the most successful male (male 130) sired 14 fawns during its lifetime.

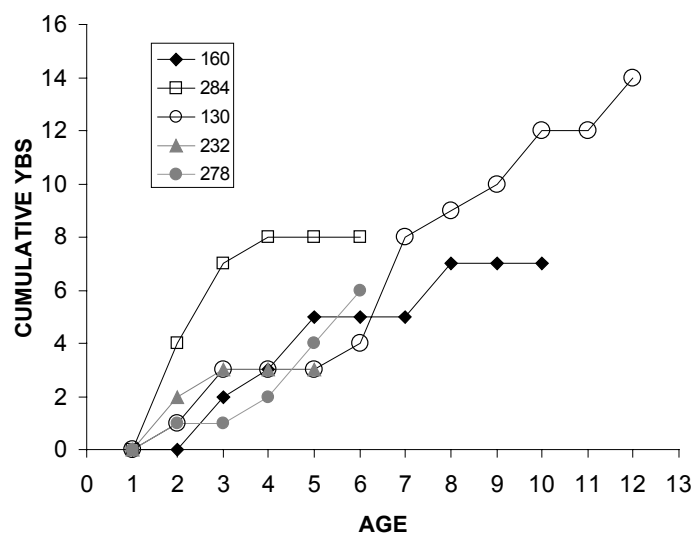


Figure 4. Cumulative yearly breeding success (YBS) with age of 5 known-aged males (each type of symbol corresponds to a different individual) at Bogesund for which we had information over the lifetime.

This male started to breed successfully at 2 years of age (1 fawn sired) and was the most iteroparous individual (11 years of breeding). In contrast, the two most successful males at 2 and 3 years of age (male 232 and 284) rapidly ceased to breed (at 4 and 5 years of age, respectively) and died one year later. The male (male 160) that did not breed as a 2 year-old had a relatively high lifetime breeding success (7 fawns sired), with a high level of iteroparity (9 years of breeding). Finally, the last male (male 278) regularly breed each year (except at 3 years of age) from 2 years of age up to this death at 6 years of age.

Discussion

In this paper, we reported the first analysis of age-specific variation in male YBS of roe deer. Results were highly similar in the two contrasting studied populations. Male reproductive performance was highly variable in relation to age, and from the best-fitting model we identified three distinct stages (2, 3-8, >8), supporting the dome-shaped pattern of variation commonly reported for age-dependent variation in life-history traits of ungulates (Gaillard et al. 2000). Indeed, male YBS was low at 2 years of age, peaked at 3-8 years of age (the prime-age stage), and then declined from 8 years of age onwards. We thus provided evidence that 2-year-old males can successfully breed, although at a much lower rate than older males, and that reproductive senescence among males occurs at approximately 8 years of age.

Age of first successful breeding and first territory establishment in young adults

Although roe deer males become sexually mature at about 15 months of age, yearlings have never been reported to be fully territorial before 2 years-of age, nor to mate in any previous study as far as we know (Hewison et al. 1998; Liberg et al. 1998). While several authors (Strandgaard 1972; Ellenberg 1978; Andersen et al. 1995; Johansson 1996) have reported that 2-year-old males could occupy territories, and Johansson (1996) and Börger (2006) have observed that non-territorial young adult males could play an active role during the rut (either as satellites or peripherals; see Liberg et al. 1998 for further details), repeatedly challenging territorial males, none of the previous studies provided evidence that these young males could actually sire fawns. Our study, in two contrasted populations, provides the first evidence that this is the case. Two-year-old males represented about 15% of fathers in both populations. They had lower average YBS than older males at both Bogesund and Trois

Fontaines. This difference was due to the low proportion of 2-year-old males that were successful, rather than to a low number of fawns sired (when successful) in a given year.

An interesting question is whether the few 2-year-old successful breeders were all territorial or whether non-territorial 2-year-old males were also able to successfully breed. Although we did not have information on the territorial status for all the successful breeding males, those 2 year-old males which were successful at Bogesund tended to be heavier and to have longer antlers than unsuccessful ones (C. Vanpé, unpubl. data). In addition, the only 2-year-old male (out of 4 monitored and radio-tracked) that successfully fathered a fawn at Bogesund in spring 2005 exhibited all the characteristics of a territorial animal (i.e., home range size similar to that of older territory-holders, no overlap of core areas with any territory of neighbouring older males), whereas two of the three others that failed to breed were non-territorial (one satellite and one peripheral, observations by C.V.). This territorial male that successfully bred as a 2-year-old was the heaviest and had the longest antlers for his age-class (24.5 kg vs. 19.7 kg (SD = 0.7) and 100.7 mm vs. 35.7 mm (SD = 31.0) for the successful and the unsuccessful 2 year-old males, respectively; C. Vanpé, unpubl. data). This suggests that the rare successful breeding events among 2-year-old males may concern only the few individuals of particularly high phenotypic quality which are able to hold a territory during the rut. While non-territorial 2-year-old males may adopt sneaky tactics (satellital or peripheral; see Liberg et al. 1998) to attempt to mate with unattended females, their mating success is likely very low. Females seem to avoid non-territorial young males and even vocally protest when courted by them, provoking territorial males to attend (Liberg et al. 1998; Börger 2006). In addition, territorial males invariably chase away young non-territorial males, especially when they attempt to court a female (Börger 2006). In support of this, we found that most males did not sire fawns before 3 years of age, when they had almost attained their adult body mass (Pettorelli et al. 2002) and antler size (Vanpé et al. 2007). Hence, roe bucks commonly obtained their first reproductive success several years after physiological maturity, suggesting the existence of a kind of social age threshold for mating (Jarman 1983).

Senescence and alternative mating tactics in old males

In both populations, males older than 7-8 years of age tended to have a lower breeding success than prime-age males, providing evidence for senescence in male YBS. However, while at Trois Fontaines all 8 males older than 8 failed to breed (probably due to the low sample size of males older than 8 years of age and the high proportion of males for which we could not catch the fawns in this population), at Bogesund the variance in YBS among the 7

senescent males was high, with some old males being able to sire as many fawns as prime-age males, and other old males being unsuccessful.

Results we reported at Bogesund are in line with several studies of Scandinavian roe deer populations in which a loss of territorial specific dominance has been reported for some males during their last rutting seasons before death (Bramley 1970; Andersen et al. 1995). Old males may sometimes be evicted by a younger male, and should restrict their movements to a small area (Johansson 1996), with limited participation in the rut (Kurt 1991). It is likely that such males have a lower breeding success than fully territorial males. The high variance in breeding success we found for old males at Bogesund also nicely matches the hypothesis that some males older than 7 years of age with high body mass and large antlers may still be able to defend their territory and remain highly competitive, whereas others with low body mass and small antlers may not (see Vanpé et al. 2007 for further details).

We also analysed the individual YBS trajectory of 5 known-aged males from Bogesund, thus taking into account between-individual differences in quality (Clutton-Brock 1988). Because better individuals often live longer (Gaillard et al. 2000), average quality, and thereby average breeding success, should increase with increasing age at the population level, potentially masking senescence. Although further studies are needed, these few data seem to indicate that longevity is an important component of lifetime breeding success of roe deer males. The consequences of such individual heterogeneities need to be investigated more closely in the future.

Comparison with other ungulate species

We showed that roe deer males breed, on average, for the first time at 3 years of age, when they generally acquire the ability to hold a territory. Moreover, while there was a decline in breeding success from 8 years of age onwards in both populations studied, some old males go on to breed successfully in one population. Male roe deer seem thus to have a higher level of iteroparity than males of highly dimorphic and polygynous species such as red deer. Males we monitored over their lifetime at Bogesund successfully bred in up to 5 consecutive years and had up to 8 successful breeding attempts during their lifetime. In contrast, red deer males successfully bred some years between 5 and 11 years of age (Clutton-Brock et al. 1982). As longevity rather than very successful years seems to account for among-male variance in lifetime breeding success of roe deer, reproductive costs (e.g. shorter life spans) for highly successful males (Geist 1971) seem unlikely to occur. However, the

marked age-structure of male YBS in roe deer needs to be taken into account in order to avoid over-estimation of the opportunity for sexual selection and the intensity of selection on age-related male traits (Clutton-Brock 1988).

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PART 3

PHENOTYPIC TRAITS AS SEXUALLY SELECTED TRAITS



**Young roe buck with asymmetric antlers
(photograph by Olivier Villa)**

PAPER 3

Antler size provides an honest signal of male phenotypic quality in roe deer

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Antler Size Provides an Honest Signal of Male Phenotypic Quality in Roe Deer

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ABSTRACT: Identifying factors shaping secondary sexual traits is essential in understanding how their variation may influence male fitness. Little information is available on the allocation of resources to antler growth in territorial ungulates with low sexual size dimorphism. We investigated phenotypic and environmental factors affecting both absolute and relative antler size of male roe deer in three contrasting populations in France and Sweden. In the three popu-

lations, we found marked age-specific variation in antler size, with an increase in both absolute and relative antler size between yearling and prime-age stages, followed by a decrease (senescence) for males older than 7 years. Antler size increased allometrically with body mass. This increase was particularly strong for senescent males, suggesting the evolution of two reproductive tactics: heavy old males invested particularly heavily in antler growth (potentially remaining competitive for territories), whereas light old males grew small antlers (potentially abandoning territory defense). Finally, environmental conditions had little effect on antler size: only population density negatively affected absolute antler size in one of the three populations. Antler size may therefore provide an honest signal of male phenotypic quality in roe deer. We discuss the implications of these results in terms of territory tenure and mating competition.

Keywords: allometry, *Capreolus capreolus*, climate, population density, secondary sexual trait, senescence.

Antlers and horns of ungulates have been subject to great interest since Darwin (1859, 1871) developed his theory of sexual selection, as they represent one of the most spectacular examples of male secondary sexual traits in vertebrates. Several hypotheses have been put forward to explain the evolution of horns and antlers (see reviews by Geist [1966]; Clutton-Brock [1982]; Andersson [1994]; Lincoln [1994]), most of which relate to the framework of male-male competition over mates. Horns in bovids and antlers in cervids are used as weapons for attack and defense against rival males during the mating season. Closely related to this, they may also function as indicators of male strength and fighting ability in display toward other males. In addition, females may use the traits as reliable signals reflecting sexual vigor and genetic quality when choosing mates. In all cases, a large trait is advantageous and, if heritable, will evolve, as there may thus be positive feedback between the effects of intrasexual combat among males and female choice (Wong and Candolin 2005). These behavioral advantages of large horns and antlers should translate into reproductive success, with larger-horned/antlered males siring more offspring, irrespective of age and body size (in reindeer *Rangifer tarandus* [Espmark 1964], bighorn sheep *Ovis canadensis* [Coltman

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et al. 2001], red deer *Cervus elaphus* [Kruuk et al. 2002], and Soay sheep *Ovis aries* [Preston et al. 2003]).

According to the conditional handicap theory (Zahavi 1977; Pomiankowski 1987; Iwasa et al. 1991), secondary sexual traits such as antlers, to serve as honest signals of male quality for choosy females, are expected to be strongly condition dependent and costly to produce and maintain, particularly for males in poor condition (e.g., Kotiaho 2000). While several studies have shown a correlation between antler size or shape and body size or mass (e.g., in roe deer *Capreolus capreolus* [Pélabon and Van Breukelen 1998] and red deer [Mysterud et al. 2005]), condition dependence has rarely been fully demonstrated (for a general review on sexual ornaments, see Cotton et al. 2004). There is also some evidence that antlers are costly sexual traits. Møhen et al. (1999) estimated that energy requirements for antler growth by moose (*Alces alces*) were half as much as energy requirements for summer fat and protein deposition. Hence, if we assume that antlers are honest quality traits, choosing a male with large weapons might lead to short-term direct benefits for females, such as access to good-quality territories, paternal care, or male sexual vigor (Price et al. 1993), or long-term indirect benefits, such as high genetic quality of offspring, to the extent that these benefits are heritable (Fisher-Zahavi's handicapped sexy son model, combining both Fisherian runaway and good-genes processes; Fisher 1915; Møller and Alatalo 1999; Eshel et al. 2000; Kokko et al. 2003). Recently, antler size in red deer stags has been shown to be heritable (Kruuk et al. 2002), positively related to the probability of becoming a harem holder in stags (Bartos and Bahbouh 2006), and positively related to relative testes size and sperm velocity (Malo et al. 2005). This suggests that antler size in red stags is an honest signal of male quality, which may be used by females to choose mates.

Identifying the factors shaping antler and horn size is therefore essential for a better understanding of how weapon size variation may influence male fitness in ungulates (Prichard et al. 1999), but studies of variation in secondary sexual traits are comparatively scarce. Previous studies have mainly focused on nonterritorial species with a high level of sexual size dimorphism (e.g., in moose [Solberg and Saether 1994], red deer [Schmidt et al. 2001; Mysterud et al. 2005], bighorn sheep [Festa-Bianchet et al. 2004], and reindeer [Weladji et al. 2005]). Few studies have investigated age-dependent variation in antler size in territorial species and/or in species with low sexual size dimorphism. Yet, these species are particularly interesting because they are expected to be only weakly polygynous, with reduced potential for sexual selection by male-male competition, compared to species with high sexual size dimorphism and harem-holding or lekking mating systems (e.g., Wade 1979; Andersson 1994), and the opportunity

for female mate choice may also be higher because females have greater, unimpeded access to assess either the male or his territory (Min 1997).

In this study, we therefore analyzed variation of antler size in roe deer, a medium-sized territorial deer with a low level of sexual size dimorphism (Andersen et al. 1998), using individual-based long-term data of known-age males from three contrasting populations. We analyzed how male age, population density, climate, habitat quality, and resource abundance influenced absolute and relative antler size (i.e., before and after controlling for the allometric relationship between antler size and body mass, respectively) to test the following predictions.

1. *Age-specific changes of absolute and relative antler size.* Age is known to structure markedly most life-history traits of vertebrate populations (Charlesworth 1994). In large mammals, three main life cycle stages are generally recognized: a juvenile stage, a prime-age stage, and a senescent stage (Gaillard et al. 2000). Individual performance typically peaks during the prime-age stage (for reviews on birds and large herbivores, respectively, see Bennett and Owens 2002; Gaillard et al. 2000), as reported for survival (e.g., Caughley 1966; Loison et al. 1999) but also for antler size (e.g., in red deer; Mysterud et al. 2005). We therefore expected to find larger antlers in prime-age males than in younger and older males (prediction 1a). While senescence (i.e., a decline in performance with increasing age) has been documented in several large herbivores for body mass (e.g., on red deer; Mysterud et al. 2001), reproduction (e.g., on moose; Ericsson et al. 2001), and survival (for a review, see Gaillard et al. 2003b), clear evidence of senescence in sexually selected traits such as antler size or horn growth are comparatively scarce (but see in ibex *Capra ibex* [Von Hardenberg et al. 2004], moose [Saether and Haagenrud 1985], and red deer [Mysterud et al. 2005]). We therefore tested for senescence in antler size in roe deer (prediction 1b). Because large, costly traits can be physiologically afforded only by individuals of superior condition, we expected antler size to be strongly condition dependent (e.g., Andersson 1994; Mysterud et al. 2005), predicting a positive allometric relationship between antler size and body mass (prediction 1c; e.g., Huxley 1931).

2. *Responses of absolute and relative antler size to environmental factors.* Because antlers are cast and regrown each year and are costly to produce, we should expect a strong relationship between energy allocation to antler growth and current environmental conditions (Andersson 1994). Several studies of ungulates have reported a negative effect of increasing population density and harsh climatic conditions on antler size or horn growth (e.g., in white-tailed deer *Odocoileus virginianus* [Ashley et al. 1998], bighorn sheep [Jorgenson et al. 1998], red deer [Schmidt et al. 2001; Mysterud et al. 2005], and roe deer [Pélabon and

Van Breukelen 1998]). These effects may reflect the impact of environmental factors on overall body size or, alternatively, their impact on energy allocation to antler growth. Few studies have distinguished between these two possibilities (but see in red deer; Mysterud et al. 2005). We investigated the effects of environmental conditions on antler size, predicting that both absolute and relative antler size should decrease under harsh conditions, that is, with increasing population density (prediction 2a) and summer dryness (prediction 2b). The negative effects of harsh environmental conditions on antler size or horn growth are commonly interpreted as resulting from decreased forage availability and quality (e.g., Skogland 1983; Fowler 1987; Weladji et al. 2005). Several studies have demonstrated a direct relationship between antler size or horn growth and food quantity or quality (e.g., Schmid 1955), but these studies have been commonly based on experimental manipulation of food (but see Festa-Bianchet et al. 2004), which may not replicate food stress typical of natural conditions (see Cotton et al. 2004; Putman and Staines 2004). Here, we investigated the influence of spatiotemporal variation in habitat quality on antler size by looking at the effects of natural variations in acorn mast abundance and habitat quality. We expected to find larger antlers, in both absolute and relative terms, in favorable years when acorn mast production was high (prediction 2c) and in the richest habitats (prediction 2d).

Material and Methods

Study Species

The European roe deer is a small-sized cervid (adults weigh about 20–30 kg) with low sexual size dimorphism (males are less than 10% heavier than females; Andersen et al. 1998). In this species, only males carry antlers, and in contrast to most other deer species, male roe deer grow antlers during the winter (i.e., during the period of food restriction), mainly from December to early March. The antler cycle is controlled mainly by testosterone secretions (Sempéré 1982), and males are territorial from early spring to the end of the rut (late August–early September). While buck kids first develop a small button on top of their pedicle before growing small antlers at 1 year old, classically with two spikes, subadult and adult bucks usually develop a four-point and five-point/six-point head, respectively. However, there are large individual differences in antler size and shape, even within an age class, and antler size is generally considered as an unreliable indicator of age (e.g., Prior 2000).

Study Sites and Roe Deer Populations

We used data from three contrasting populations of European roe deer: Chizé, a 2,614-ha enclosed forest located in western France (46°06'N, 0°26'W); Trois Fontaines, a 1,360-ha enclosed forest located in eastern France (48°43'N, 2°61'E); and Bogesund, a 2,600-ha area of fragmented habitat (with 65% forest) located in the central eastern part of Sweden (59°23'N, 18°15'E). While Chizé has a temperate oceanic climate, with mild winters and hot and dry summers, and Trois Fontaines has a continental climate characterized by moderately severe winters, with low temperatures and rainy summers (Gaillard et al. 1997), Bogesund has a continental climate under the influence of the Baltic Sea, with relatively harsh snowy winters and mild and dry summers (Kjellander 2000). More details can be found in articles by Gaillard et al. (1997) and Kjellander et al. (2006). The three populations have been monitored for more than 16 years on the basis of annual capture-mark-recapture sessions involving known-age animals. Because a high proportion of roe deer were marked each year in all three sites, reliable estimates of annual population size were available (for Chizé and Trois Fontaines, see Gaillard et al. 2003c; for Bogesund, see Kjellander 2000). Experimental manipulation of density through hunting and/or removals took place in all three study areas, so marked between-year differences occurred in population density (see fig. B1 in the online edition of the *American Naturalist*; for further details, see Gaillard et al. 1993, 2003c; Kjellander 2000; Kjellander et al. 2006).

Morphometric Measurements

We used data from annual winter captures (January–March) in each site. Antler length was measured to the nearest 0.5 cm along the external side of the main beam, from the base of the antler to the top of the main beam. When both antlers were measured, the average length was retained. Measurements from cleaned antlers were removed from the analyses ($N = 124$ at Chizé and $N = 96$ at Trois Fontaines) so that we considered only antlers still in velvet (i.e., still growing). Antler length was considered as a proxy for antler size. Note that strong allometric relationships generally occur among morphometric traits; hence, antler length is expected to reliably index antler size. We used body mass (measured to the nearest 0.1 kg) to assess relative antler size. Note that roe deer are income breeders with few fat reserves (see Andersen et al. 2000); hence, body mass has been reported to be a better measure of phenotypic quality than body condition (Toigo et al. 2006).

When an individual was caught more than once in a given year, only the latest measures of antler length and

body mass were used. All roe deer included in our analyses were first caught within their first year of life, when tooth eruption patterns enable young-of-the-year and older animals to be discriminated without error (Flerov 1952). The analyses included 451 measurements of 216 roe deer at Chizé, 271 measurements of 158 roe deer at Trois Fontaines, and 130 measurements of 56 roe deer at Bogesund.

Climatic Data

We obtained meteorological data from Météo France and from the Swedish Meteorological and Hydrological Institute. We calculated a monthly Gaussen (1954) summer hydric index (June–August) as the amount of precipitation minus twice the mean temperature (for previous applications to ungulates, see Gaillard et al. 1997; Garel et al. 2004; Toigo et al. 2006). This index has been widely used in plant biogeography and climatology (e.g., Walter and Lieth 1960) because of the strong correspondence with plant distributions. The hydric index measures the water available for vegetation (Dajoz 1973), and the summer hydric index is known to influence the duration of green forage, as well as its quality (Becker et al. 1994). We calculated a yearly summer hydric index as the average of the monthly indexes for June, July, and August. The summer hydric index of the year i was expected to affect antler growth from January to March of the year $i + 1$. We did not use measures of winter climate in the present analyses because we did not find any effect of winter conditions on various roe deer life-history traits in previous work (for Chizé and Trois Fontaines, see Gaillard et al. 1996; for Chizé and Bogesund, see Kjellander et al. 2006) or on roe deer antler size in preliminary analyses of the present data at Bogesund.

Resource Availability and Habitat Quality

Acorn mast production was recorded by a commercial seedling producer (Svenska Skogsplantor AB) at several different locations in southern Sweden but not at Bogesund itself. However, mast years occur concomitantly across the entire Swedish range of oak (G. Hamilton, Swedish National Board of Forestry, unpublished data). From the recorded data, we distinguished two types of mast years: in poor years, mast harvest varied between 0 and 500 kg, while in true mast years, it varied between 1.5 and 4 t (Kjellander et al. 2006). The effect of acorn mast years on antler size at Bogesund was investigated by fitting this parameter as a two-modality factor (poor vs. true mast year) in the models. A positive effect of mast on fawn body mass has been previously reported at Bogesund (Kjellander et al. 2006).

At Chizé, we distinguished two main habitats of con-

trasting quality within the reserve (see, e.g., Pettoirelli et al. 2005). The northern area is covered by a 1,397-ha oak forest in which the preferred food plants of roe deer in spring and summer occur more frequently and have a higher nitrogen content than in the southern part of the reserve, which is covered by a 1,143-ha limestone beech forest (Pettoirelli et al. 2001). We therefore included habitat quality at Chizé as a two-modality factor (poor vs. rich) in the models. To attribute a habitat type to each roe deer captured, we used its capture site (for further details, see Pettoirelli et al. 2003). Adult roe deer living in forests in continental Europe are highly sedentary (Strandgaard 1972; Pettoirelli et al. 2003), so we can reliably assume that individuals were captured in the habitat type where they lived at this scale. Habitat quality has been previously shown to affect several life-history traits at Chizé (Pettoirelli et al. 2001, 2002, 2003).

Statistical Analyses

Because the antler size measurements were taken during the period of antler growth and because we considered only antlers still growing, we first controlled for capture date (as the Julian date, with January 1 as day 1) by adjusting antler size to February 14 (i.e., the median date of the whole capture period) in the three sites. Although antler growth is a nonlinear process (Goss 1983; for roe deer, see Rösig 1908), in this study, data collection was restricted to a quite short period of time for which the relationship between antler length and date was well described by a linear model (correlation between residuals from linear models and residuals obtained including a quadratic function; Bogesund $R^2 = 0.996$; Chizé $R^2 = 0.966$; Trois Fontaines $R^2 = 0.937$). We did not adjust body mass to a standard date at Bogesund and Trois Fontaines because we did not find any significant change of body mass with Julian date (common slope of the linear regression between body mass and Julian date \pm SE = -0.0014 ± 0.0134 , $t = -0.107$, $P = .92$ and 0.0030 ± 0.0087 , $t = 0.348$, $P = .73$, for Bogesund and Trois Fontaines, respectively). Such an adjustment was necessary, however, at Chizé (slope = -0.0248 ± 0.0073 , $t = -3.413$, $P < 10^{-3}$). The standardized measures of antler size and body mass were ln transformed to fit homoscedasticity requirements.

We used linear models to assess the factors influencing antler size. The mean number of measures per individual (\pm SD) was 2.08 ± 1.60 (range = 1–9) at Chizé, 1.72 ± 1.06 (range = 1–6) at Trois Fontaines, and 2.32 ± 1.25 (range = 1–6) at Bogesund. To control for repeated measures of the same individuals over the study period, male identity was entered as a random factor in mixed models. While fitting random effects may be prob-

lematic when only one measure is available for some individuals (see Crawley 2002), it was not a problem in our case because we fitted random effects only on the intercept, not on the slope. To check this empirically, we redid the analysis, excluding individuals for which we had only one measure. Because we obtained nearly identical results, we chose to present the analysis of the full data set here. Model selection was performed using the Akaike Information Criterion (AIC), as recommended by Burnham and Anderson (2002). A smaller AIC value corresponds to a better fit of the model to the data (i.e., the best compromise between accuracy and precision). However, when the difference between AIC values of two competing models was less than 2, we used the criterion of parsimony, selecting the simpler of the two models (Burnham and Anderson 2002). We used a backward procedure by fitting first the more complicated model, then removing interactions, and, last, removing the main effects of factors. All the analyses were performed using the R 2.2.1 statistical package (R Development Core Team 2004). We used the “lme” function (included in the “nlme” R package) for fitting mixed-effects models (Pinheiro and Bates 2000), using the maximum likelihood estimation procedure.

We first fitted several age-dependent models (for details, see table A1) to determine the pattern of age-specific changes of antler size. We then determined the allometric relationship between antler size and body mass by testing the effect of body mass, population, and age on antler size, as well as all their two-way and three-way interactions. For comparisons among populations, we restricted the analysis to a common range of body mass (i.e., ln-transformed values from 2.94 to 3.47; $N = 436$ at Chizé, $N = 271$ at Trois Fontaines, and $N = 117$ at Bogesund). For each age class within each population, we then estimated (i) the annual mean absolute antler size and (ii) the annual mean of the residuals from the selected allometric model as a measure of relative antler size. We investigated the effects of environmental variables on age-specific variation across years in both absolute and relative antler size in each site. At Chizé and Trois Fontaines, we tested the main effects of age (three age classes), population density (estimated in March–April of the year of antler growth), and the summer hydric index (of the previous year), as well as their two-way and three-way interactions. At Bogesund, for both yearlings and prime-age males (senescent males were eliminated because of low sample size; for details, see table C1 in the online edition of the *American Naturalist*), we tested the main effects of population density, the summer hydric index, and acorn mast abundance (of the previous autumn), as well as their two-way and three-way interactions. To be able to compare the effects of these three factors among and between populations, we standardized all the environmental variables

within each population so that they had a mean of 1 and a standard deviation of 1. The summer hydric index and population density were not correlated at Chizé ($r = 0.186$, $P = .18$) or Bogesund ($r = -0.031$, $P = .45$). However, a negative correlation between the summer hydric index and population density occurred at Trois Fontaines ($r = -0.45$, $P = .01$), which may complicate interpretation if both variables appear in the selected model. Finally, we tested the influence of habitat quality on antler size at Chizé by comparing the selected age-specific model with and without the additional effect of habitat quality. The details concerning model selection for environmental effects are provided in table C2 in the online edition of the *American Naturalist*.

Results

Antler Growth Models

Antler growth was investigated in each of the three sites from the beginning of January to the end of March. The linear model selected to standardize antler size data explained 4.2%, 34.1%, and 43.5% of the variation in antler size at Chizé, Trois Fontaines, and Bogesund, respectively. The low value for Chizé was expected because the data collection period occurred toward the end of antler growth in this population, when antler size no longer increased over time. Indeed, antler size increased over the winter capture period with different speed among sites. Growth rate was five times lower at Chizé (mean \pm SE = 0.4 ± 0.1 mm/day; fig. 1) than at Bogesund and Trois Fontaines, which had similar growth rates (2.1 ± 0.2 and 2.0 ± 0.2 mm/day, respectively). However, standardized antler size on February 14 was much higher at Chizé (mean \pm SE = 195.6 ± 1.4 mm) and Trois Fontaines (199.6 ± 2.7 mm) than at Bogesund (98.6 ± 4.1 mm).

Age-Specific Variations in Absolute Antler Size

A three-age-class model best accounted for age-specific changes of standardized antler size in all three study populations (see table A1). Antler size increased from yearlings to prime-age males, peaked for prime-age males, and then decreased in senescent males (fig. 2), as predicted in prediction 1a. We therefore detected a general senescence process in roe deer antler size in all populations, from 8 years onward, as predicted in prediction 1b. However, the magnitude of senescence markedly differed among populations. Between prime-age and senescent stages, absolute antler size decreased by only 6.1% at Chizé but by 23.2% and 46.0% at Trois Fontaines and Bogesund, respectively. Indeed, while senescent males had larger antlers than year-

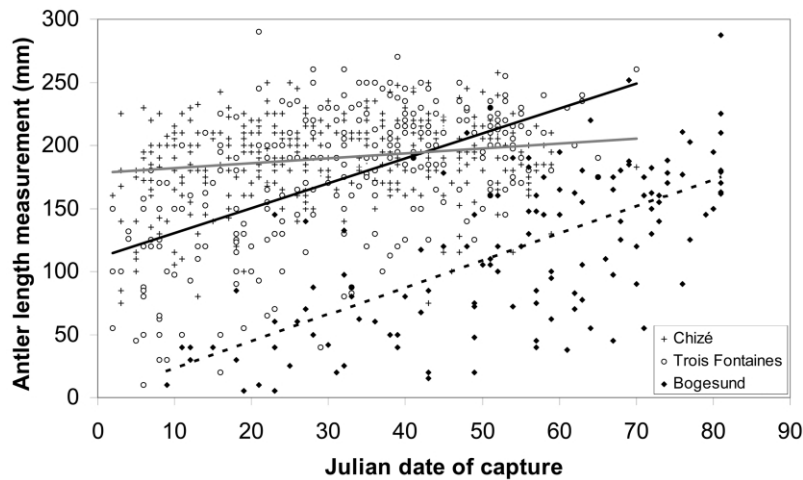


Figure 1: Antler growth models at Chizé (crosses, gray line), Trois Fontaines (circles, black line), and Bogesund (diamonds, dashed line).

lings at Chizé, they had shorter ones at Trois Fontaines and Bogesund (fig. 2).

Allometric Variation in Antler Size

The best model describing allometric variation in antler size was the full model (AIC = 44.80 vs. 65.86 when removing the population \times age class \times body mass three-way interaction), which included the effects of body mass, age (three age classes), and population, as well as all their two-way and three-way interactions. As predicted (prediction 1a), within a given population, prime-age males had larger antlers for a given body mass than did yearlings and senescent males (fig. 3). In addition, as predicted (prediction 1c), a positive allometric relationship occurred between antler size and body mass in the three sites and for all age classes (fig. 3).

Within a given population, the slope of the allometric relationship did not differ between prime-age males and yearlings in all three populations ($t = 0.218$, $P = .83$ at Chizé; $t = 0.275$, $P = .78$ at Trois Fontaines; and $t = -0.614$, $P = .54$ at Bogesund; fig. 3). However, interestingly, antler size at Bogesund increased significantly more strongly with increasing body mass in senescent males than in younger males (mean slope difference \pm SE between senescent males and yearlings: 5.052 ± 1.025 , $t = 4.930$, $P < 10^{-4}$; between senescent males and prime-age males: 5.351 ± 0.975 , $t = 5.487$, $P < 10^{-4}$; fig. 3). Although not significant, the same trend occurred at both Chizé (mean slope difference \pm SE between senescent males and yearlings: 0.253 ± 0.372 , $t = 0.680$, $P = .50$; fig. 3) and Trois Fontaines (1.077 ± 0.611 , $t = 1.763$, $P = .08$; fig. 3). That is, light senescent males had smaller antlers than both

yearlings and prime-age males, but the antlers of the heaviest senescent males were of similar size to those of prime-age males.

Effects of Environmental Conditions on Antler Size

At Chizé, the best model accounted for 40% of the variation in absolute antler size across years and included the additive effects of age (three age classes), the summer hydric index, and population density, as well as the two-way interaction between age and the hydric index (AIC = -147.3 vs. -144.9 for the same model without the two-way interaction; see table C2). Age accounted for 27.5% and environmental drivers for 12.4% of the variance (including 6.7% by population density). Antler size significantly decreased with increasing population density (as expected in prediction 2a) to the same degree for all age classes (slope \pm SE = -0.02 ± 0.01 , $t = -2.36$, $P = .02$; table 1). The effect of the summer hydric index on absolute antler size was slight and age specific, that is, a nonsignificant negative trend in yearlings (slope \pm SE = -0.03 ± 0.02 , $t = 1.76$, $P = .08$; table 1) and no effect in prime-age and senescent males (slope \pm SE = 0.0009 ± 0.016 , $t = 0.58$, $P > .1$ and 0.03 ± 0.02 , $t = 1.64$, $P > .1$, respectively; table 1), contrary to prediction 2b. Finally, the additive effect of the habitat factor (AIC = -423.6) did not improve the selected model at Chizé (three age classes; AIC = -431.9). Hence, contrary to our prediction 2d, individual habitat quality did not affect absolute antler size at Chizé. By comparing the retained model (AIC = -147.3) with the retained model plus an additive effect of year (fitted as a factor; AIC = -144.5), we estimated that the proportion of annual var-

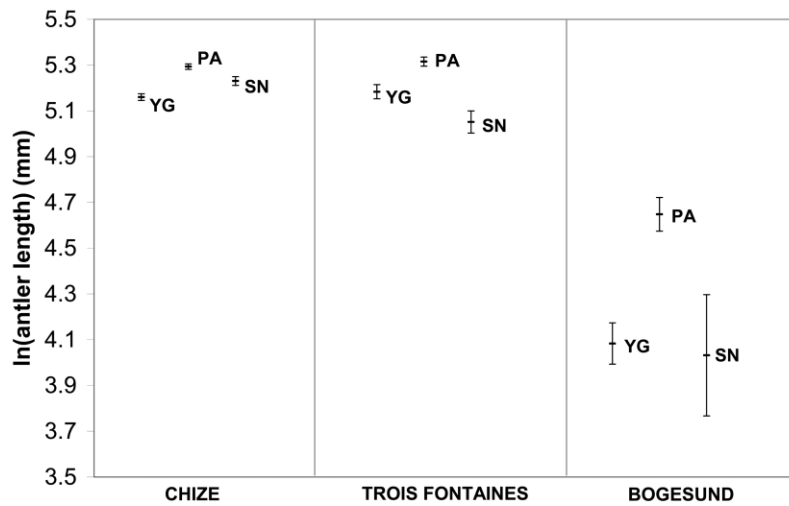


Figure 2: Differences of mean ln-transformed antler size (in mm) between yearlings (YG), prime-age males (PA), and senescent males (SN) in the three studied populations at Chizé, Trois Fontaines, and Bogesund. Estimates are based on the model with three age classes that was selected in each population. Error bars represent standard errors of the estimates.

iation in absolute antler size accounted for by the environmental drivers (12.4%) was lower than the proportion that remained unexplained (28.1%).

At Trois Fontaines, the best model explaining annual variation in absolute antler size was the constant model without any effect of environmental factors (see table C2). Hence, contrary to predictions 2a and 2b, neither population density nor the summer hydric index influenced absolute antler size. Similarly, at Bogesund, for both yearlings and prime-age males, the best model accounting for annual variation in absolute antler size was the constant model without any effect of environmental factors (see table C2). Hence, contrary to predictions 2a, 2b, and 2c, the summer hydric index, population density, and acorn mast abundance did not influence absolute antler size at Bogesund.

The best models explaining variation in relative antler size across years at Chizé, Trois Fontaines, and Bogesund were the constant models without any effect of environmental factors, except for prime-age males at Bogesund, where the best model accounted for 43% of the annual variation in relative antler size and included the effect of population density only (AIC = -12.5 vs. -8.4 for the constant model; see table C2). Thus, contrary to predictions 2b, 2c, and 2d, the hydric index, acorn mast abundance, and the habitat quality had no effect on relative antler size in all three populations. There was also little support for prediction 2a because at Chizé, Trois Fontaines, and Bogesund, for yearlings, relative antler size was not affected by population density, although relative antler size did decrease with increasing density at Bogesund

for prime-age males (slope \pm SE = -0.11 ± 0.04 , $t = -2.58$, $P = .03$).

Discussion

Our results indicate that changes in age and body mass were more influential than changes in environmental factors in shaping the variation observed in roe deer antler size in all the three populations we studied, as expected in general for deer (e.g., Clutton-Brock 1982; Andersson 1994). In accordance with our prediction 1a, prime-age males had larger antlers and allocated more energy to antler growth than yearling and senescent males. These results provide support for the mating strategy-effort hypothesis (Yoccoz et al. 2002), which predicts that reproductive effort peaks in prime-age males, because they are most often harem holders or territory owners, compared to young and senescent males. Our results are also in agreement with prediction 1b because males from 8 years of age onward grew smaller antlers than prime-age males, demonstrating, for the first time, clear evidence of senescence in antler size of roe deer. Previous studies have been unable to document this phenomenon because of the lack of data from known-age animals (e.g., Pélabon and Van Breukelen 1998), given the large errors obtained when aging roe deer from tooth wear (see Hewison et al. 1999). A similar decrease of absolute antler size in old males has previously been reported in dimorphic species of large herbivores such as moose (Saether and Haagenrud 1985), white-tailed deer (Scribner et al. 1989), and red deer (Mysterud et al. 2005), although not consistently (in red deer, see, e.g.,

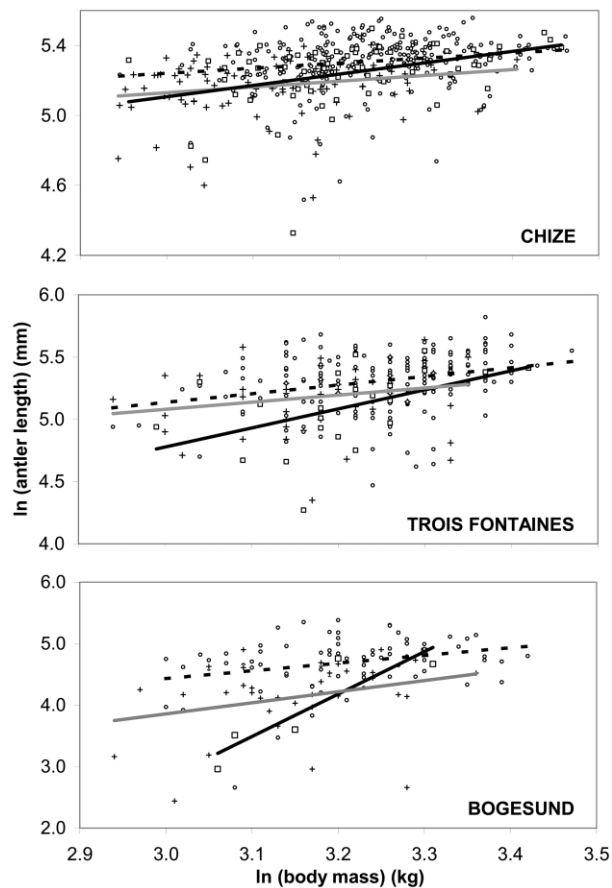


Figure 3: Allometric relationships between ln-transformed antler size (in mm) and ln-transformed body mass (in kg) in yearlings (*crosses*, *gray line*), prime-age males (*circles*, *dashed line*), and senescent males (*squares*, *solid line*) in the three studied populations at Chizé, Trois Fontaines, and Bogesund.

Kruuk et al. 2002). Interestingly, the onset of senescence in antler size of roe deer occurs at the same time as the onset of senescence in survival rate (Gaillard et al. 1993, 2004), suggesting that antler size may be an honest signal of male health and quality. In line with prediction 1c, we also found that antler size increased with increasing body mass in all the three populations and for all age classes. This suggests that antler size in roe deer is condition dependent because only the heavy males can afford long, costly antlers. Finally, contrary to predictions 2a, 2b, 2c, and 2d, our results suggest that environmental variables have little influence on antler size. Of the tested environmental variables, only population density had any significant influence on antler size. The absence of an effect of climate on antler size might be due to the low variation in conditions, notably at Bogesund, and/or the lack of food

stress related to harsh climatic conditions over the study period.

While these results underline the general importance of age and body mass over environmental factors for determining roe buck antler size, comparison of the three contrasting populations highlights some further interesting patterns. First, standardized antler size (on February 14) was much higher at Chizé and Trois Fontaines than at Bogesund, while antler growth rate was much lower at Chizé than at Trois Fontaines and Bogesund. This is because data collection occurred toward the end of the antler growth period at Chizé, while it occurred in the middle and at the beginning of antler growth at Trois Fontaines and Bogesund, respectively. These results highlight the contrasting phenology in antler growth between the three populations. In the more southerly French populations, antler growth occurs earlier than at Bogesund, presumably linked to the earlier onset of spring and the territorial and sexual cycle of roe deer males. Similarly, but to a lesser extent, spring is somewhat later in the harsh continental climate of Trois Fontaines compared to Chizé, which is under oceanic influences; hence, antler growth is later.

Second, we found that the magnitude of senescence on antler size was much higher at Trois Fontaines than at Chizé and much higher at Bogesund than in the two French populations. From the ranking of senescence rate in our three populations, it seems that the magnitude of senescence increases with winter severity. Similarly, Gaillard et al. (1993) have previously reported a stronger senescence for roe deer survival at Trois Fontaines compared to Chizé. Furthermore, in the three populations, antler size tended to increase more strongly with increasing body mass for senescent males than for yearling and prime-age males. This general pattern was especially marked at Bogesund, where the difference in slope between senescent males and younger males was statistically significant, possibly because the marked senescence rate at Bogesund provided the necessary conditions to trigger a contrasting pattern of allocation in antler growth between light and heavy senescent deer, whereas the lower senescence rate at Trois Fontaines and Chizé did not. Indeed, in the two French populations, when we restricted the analysis to very old deer (10 years of age and older), the slope of the antler size–body mass relationship was steeper (mean slope difference \pm SE between males 10 or more years old and yearlings: 0.319 ± 0.243 at Chizé and 1.434 ± 0.870 at Trois Fontaines) than when considering the whole senescent age class (mean slope difference \pm SE between males 8 or more years old and yearlings: 0.253 ± 0.372 at Chizé and 1.077 ± 0.611 at Trois Fontaines). These results show that while the heaviest senescent males allocated as much energy to antler size as did prime-age males of similar body mass, light senescent males allocated much less than

Table 1: Best models describing the response of antler size to environmental variables

	LS estimate	SE	<i>t</i>	<i>P</i>
Absolute antler size at Chizé:				
Intercept	5.1827	.0161	322.289	.000
Age PA – YG	.1232	.0227	5.421	.000
Age SN – YG	.0698	.0250	2.797	.007
Density	–.0249	.0105	–2.357	.021
HI	–.0287	.0163	–1.755	.084
Age (PA – YG) × HI	.0380	.0228	1.666	.100
Age (SN – YG) × HI	.0616	.0260	2.374	.021
Relative antler size at Bogesund in PA:				
Intercept	–.0097	.0349	–.279	.786
Density	–.1087	.0421	–2.582	.030

Note: Parameter estimates are shown as least square (LS) estimate and standard error (SE) and test statistics as *t* and *P*. The best model describes the response of absolute ln-transformed antler size to environmental variables at Chizé and relative ln-transformed antler size to environmental variables at Bogesund in prime-age males. YG = yearlings, PA = prime-age males, SN = senescent males, HI = summer hydric index. Parameters for the terms including age PA – YG and age SN – YG are given as the differences between the given age level (PA and SN, respectively) and the reference age level YG.

did light younger males. This suggests that for senescent males, antler growth is more costly for poor-condition males than for good-condition males, as assumed by the handicap theory (e.g., Kotiaho 2000). We suggest that two alternative reproductive tactics may have evolved among senescent males, who are particularly sensitive to harsh environmental conditions (e.g., Clutton-Brock et al. 1982; Clutton-Brock and Albon 1983; Albon et al. 1983). First, heavy (i.e., high-quality) senescent males may exhibit a risk-prone tactic by investing heavily in antler growth in order to develop antlers of sufficient size to remain competitive against younger males, thereby allowing them to continue to defend their territory so as to maximize mating opportunities and hence lifetime reproductive success. Second, light (i.e., low-quality) senescent males may exhibit a conservative tactic, being unable to divert a large amount of energy to antler growth and so having inferior competitive ability than heavier and/or younger males. We speculate that these light old males might find it difficult to successfully defend a territory that may preclude them from mating. In support of this idea, Johansson (1996) observed that three of the five senescent males that she monitored in Sweden during their last rutting season before death were still actively territorial, were involved in male-male conflicts, and also courted and mated females, whereas the two others were evicted from their territory by younger males, subsequently remaining in restricted areas, and did not participate in any rutting activities at all (see also Liberg et al. 1998).

Third, the only effects of population density were on absolute antler size at Chizé and relative antler size at Bogesund in prime-age males (i.e., antler size decreased with increasing density). This was, in part, expected because the Chizé population has experienced substantial

density variation over the study period (range = 6.2–20.7 deer/km²), and density-dependent responses have been previously reported for several life-history traits (Boutin et al. 1987; Gaillard et al. 1992, 1996, 1997; Pet-torelli et al. 2002; Kjellander et al. 2006), while no evidence of density dependence has so far been reported in the highly productive population of Trois Fontaines (see Gaillard et al. 1993, 1996, 1997, 2003a). The absence of an effect on relative antler size at Chizé suggests that the observed effect of population density on absolute antler size simply translated an effect on body mass. At Bogesund, while density-dependent responses have also been reported (Kjellander 2000; Kjellander et al. 2006), the absence of any density effect on absolute antler size here may be due to the weak density variation and low number of years for this study (see fig. B1; table C1). The significant effect of density on relative antler size in prime-age males was due to one exceptional high-density year (1992) when relative antler size was particularly low. Because sample size for this year was particularly low (see table C1), no firm conclusions can yet be drawn.

While most studies dealing with sexual selection have focused on highly sexually dimorphic ungulate species with a dominance-based mating system, such as red deer or Soay sheep, little is known about male mating tactics in territorial species with low sexual dimorphism, such as roe deer. We suspect that antler size in roe deer, as a major sexually selected trait, may play a crucial role in determining male mating success. A common view is that antlers, as weapons that can potentially inflict serious injury, may allow males to successfully defend their territory and so to control an area within which they may mate females without being harassed by rival males (e.g., Andersen et al. 1998). However, although they are monoestrous, female

roe deer may be courted and mated by several males because their ranges may overlap several male territories (Strandgaard 1972; Andersen et al. 1998), and a significant proportion (up to one-third) may make short (less than 48 h) rut excursions outside their normal home range, potentially mating with a nonneighboring male (see anecdotal observations in Norway [Linnell 1994; Andersen et al. 1995], Sweden [Liberg et al. 1998], Italy [San José and Lovari 1998], and France [M. Pellerin, S. Said, and J.-M. Gaillard, unpublished data]). Hence, territorial males may not be able to fully monopolize females during rut, and female mate choice probably also greatly influences male mating success in this species. Furthermore, in territorial species, dominance between males is generally location dependent, with males dominant inside their territory but subordinate outside (Owen-Smith 1977; for roe deer, see Hewison et al. 1998). In support of this idea, a very recent article on roe deer convincingly showed that territory holders consistently won male-male fights within their territories but not outside (Hoem et al., forthcoming). The authors concluded that roe deer territoriality was a low cost–low benefit process, which could be a tactic to reduce the frequency of potentially dangerous fights. Contrary to fights in harem-holding or lekking species, direct male-male fights are rather infrequent in territorial species. Even in the case of an intrusion of a rival male inside a territory, display behaviors (e.g., parallel walk, head shaking, scraping) often allow males to resolve conflicts without resorting to fighting (Liberg et al. 1998; Hoem et al., forthcoming). Hence, we suggest that in territorial species such as the roe deer, antler size may be a major cue in male display and female mate choice, acting as a reliable and honest signal of individual male phenotypic quality (our results). In support of this, Hoem et al. (forthcoming) showed that male-male fights escalated more and were more complex when the difference in antler size between combatants was smaller. Wahlström (1994) also found a positive correlation between yearling antler size and testicle

size in roe deer, indicating that antler size may reflect male fertility and sexual vigor, because testes size determines sperm production rate (Møller 1989). Furthermore, it seems that territorial males may evaluate the potential threat of yearlings, in terms of mating competition, by using yearling antler size as an honest indicator of phenotypic quality (Strandgaard 1972): yearlings with large antlers and large testes are more frequently victims of aggressive acts from territorial males and hence tend to disperse more (Strandgaard 1972; Wahlström 1994). Linking studies of antler size variation, territorial behavior, female choice, and genetic paternity in roe deer should provide a better understanding of how and why reproductive success varies in this weakly dimorphic territorial ungulate.

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APPENDIX A

Model Selection for the Effects of Age on Antler Size

Table A1: Model selection for age-specific changes in absolute ln-transformed antler size in the three studied populations

	Null	Age	Age ²	Age ³	Full classes	Three classes	Four classes
Chizé:							
df	3	4	5	6	15	5	6
AIC	−376.7	−367.4	−396.4	−396.0	−366.9	−431.9	−423.9
ΔAIC	55.1	64.4	35.5	35.8	64.9	.0	8.0

Table A1 (Continued)

	Null	Age	Age ²	Age ³	Full classes	Three classes	Four classes
Trois Fontaines:							
df	3	4	5	6	15	5	6
AIC	15.9	22.6	11.8	21.1	31.2	−5.5	.4
ΔAIC	21.4	28.1	17.3	26.6	36.7	.0	5.9
Bogesund:							
df	3	4	5	6	12	5	6
AIC	251.2	255.2	240.8	251.2	239.4	227.0	231.2
ΔAIC	24.2	28.3	13.9	24.2	12.4	.0	4.2

Note: Model selection was performed using the Akaike Information Criterion (AIC) as recommended by Burnham and Anderson (2002). ΔAIC is the AIC difference between the given model and the best model. The selected model appears in bold. Null = constant model. Age = model with age fitted as a covariable. Age² = model with age fitted as a quadratic function. Age³ = model with age fitted as a cubic function. Full classes = model with age fitted as a factor with as many age classes as observed different ages. Three classes = model with age fitted as a factor with three age classes (i.e., 1, 2–7, 8+ years). Four classes = model with age fitted as a factor with four age classes (i.e., 1, 2, 3–7, 8+ years).

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Appendix B from C. Vanpé et al., “Antler Size Provides an Honest Signal of Male Phenotypic Quality in Roe Deer”
(Am. Nat., vol. 169, no. 4, p. 481)

Temporal Variation in Population Density in the Three Studied Populations

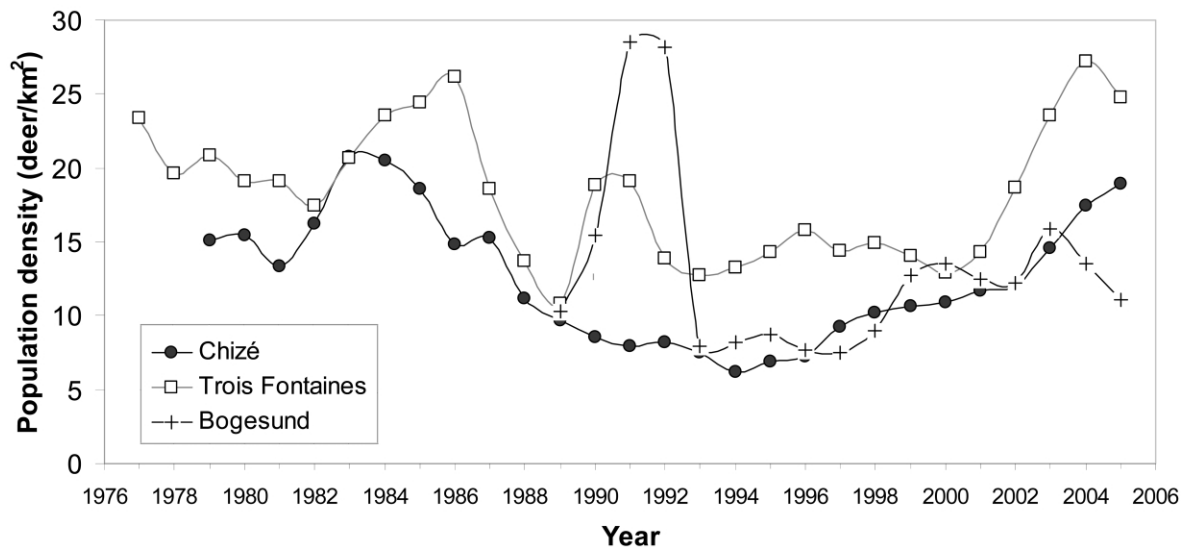


Figure B1: Yearly estimates of roe deer population density (in deer/km²) at Chizé from 1979 to 2005, Trois Fontaines from 1977 to 2005, and Bogesund from 1989 to 2005.

Appendix C from C. Vanpé et al., “Antler Size Provides an Honest Signal of Male Phenotypic Quality in Roe Deer”
(Am. Nat., vol. 169, no. 4, p. 481)

Sample Size and Model Selection Procedure for the Effects of Environmental Conditions on ln-Transformed Antler Size

Table C1

Sample size per year and per age class in the three studied populations

	Chizé			Trois Fontaines			Bogesund		
	YG	PA	SN	YG	PA	SN	YG	PA	SN
1979	2	0	0
1980	6	3	0
1981	2	7	0
1982	4	9	0	1	11	0
1983	5	5	0	2	11	0
1984	2	14	0	4	6	0
1985	0	5	0	5	6	0
1986	1	9	1	0	3	0
1987	3	12	3	0	0	0
1988	5	9	4	0	0	0
1989	4	12	3	3	12	1
1990	5	9	7	1	0	0	2	0	0
1991	1	9	6	2	7	0	2	0	0
1992	4	12	1	2	0	0	2	2	0
1993	1	9	1	2	11	0	0	1	0
1994	4	11	4	0	3	0	2	0	0
1995	1	8	2	3	19	1	0	3	0
1996	4	9	4	4	16	2	0	3	0
1997	6	13	4	4	9	5	0	0	0
1998	9	15	6	3	12	1	0	0	0
1999	4	16	4	3	10	2	2	2	0
2000	3	8	2	1	3	0	2	2	1
2001	2	18	4	1	12	2	14	5	1
2002	2	15	1	2	15	3	3	16	1
2003	4	11	4	4	14	1	3	13	3
2004	13	10	5	5	6	2	5	17	0
2005	14	13	3	4	7	2	4	19	0

Note: YG = yearlings, PA = prime-age males, SN = senescent males.

Table C2

Model selection procedure for the effects of environmental conditions on ln-transformed antler size across years in the three studied populations

	Age	Acorn mast abundance	Density	HI	Age × HI	Age × density	Density × HI	Acorn × HI	Acorn × density	Age × density × HI	Acorn × density × HI	df	AIC	ΔAIC
Chizé:														
Absolute antler size:														
	X		X	X	X							8	-147.3	.0
	X		X	X	X	X						10	-146.8	.5
	X		X	X	X		X					9	-145.9	1.4
	X		X	X	X	X	X					11	-145.0	2.3
	X		X	X								6	-144.9	2.4
	X		X		X							7	-143.4	3.9
	X		X	X	X	X	X			X		13	-143.3	4.0
	X		X	X			X					7	-143.0	4.3
	X		X	X		X	X					9	-142.7	4.6
Relative antler size:														
												2	-210.8	.0
			X									3	-210.4	.4
				X								3	-208.9	1.9
			X	X								4	-208.4	2.4
	X		X	X			X					5	-206.5	4.3
	X		X	X								6	-205.4	5.4
	X		X	X	X							8	-205.3	5.5
	X		X	X	X	X						10	-204.6	6.2
	X		X	X	X			X				9	-203.6	7.2
	X		X	X				X				7	-203.5	7.3
	X		X	X		X	X					9	-202.7	8.1
	X		X	X	X	X	X					11	-202.6	8.2
	X		X	X	X	X	X			X		13	-199.6	11.2
Trois Fontaines:														
Absolute antler size:														
	X			X								5	-19.6	-2.0
	X											4	-19.5	-1.9
				X								3	-17.9	-.3
	X		X	X								6	-17.7	-.1
	X		X									5	-17.7	-.1
												2	-17.6	.0
	X		X	X	X	X						10	-16.5	1.1
	X		X	X				X				7	-16.3	1.3
	X		X					X				7	-16.3	1.3
	X		X	X		X						8	-16.2	1.4
			X	X								4	-16.2	1.4
	X		X	X	X	X	X					11	-14.7	2.9
	X		X	X		X	X					9	-14.6	3.0
	X		X	X	X		X					9	-13.4	4.2
	X		X	X	X	X	X			X		13	-11.9	5.7
Relative antler size:														
												2	-57.1	.0
			X									3	-56.6	.5
			X									3	-55.4	1.7
			X	X								4	-54.6	2.5

Table C2 (Continued)

	Age	Acorn mast abundance	Density	HI	Age × HI	Age × density	Density × HI	Acorn × HI	Acorn × density	Age × density × HI	Acorn × density × HI	df	AIC	ΔAIC
	X			X								5	-53.7	3.4
	X		X									5	-52.3	4.8
	X		X	X								6	-51.7	5.4
	X		X	X	X	X						10	-51.6	5.5
	X		X			X						7	-51.0	6.1
	X		X	X		X						8	-50.7	6.4
	X		X	X	X	X	X					11	-50.3	6.8
	X		X	X		X	X					9	-49.3	7.8
	X		X	X	X							8	-49.1	8.0
	X		X	X	X		X					9	-47.8	9.3
	X		X	X	X	X			X			13	-47.7	9.4
Bogesund:														
Yearlings:														
Absolute antler size:														
												2	17.0	.0
				X								3	17.2	.2
	X											3	17.5	.5
	X			X								4	18.2	1.2
			X	X								4	18.6	1.6
	X		X									4	19.2	2.2
	X		X	X								5	20.1	3.1
			X	X			X					5	20.6	3.6
	X		X	X			X	X	X			8	20.7	3.7
	X		X	X			X					6	22.1	5.1
	X		X	X				X				6	22.1	5.1
	X		X	X			X	X				7	22.3	5.3
	X		X	X			X	X	X		X	9	22.6	5.6
	X		X	X				X	X			7	23.9	6.9
	X		X	X			X		X			7	24.0	7.0
Relative antler size:														
			X	X								4	13.4	-1.0
												2	14.4	.0
			X									3	14.5	.1
			X	X								5	15.3	.9
	X		X	X				X	X			7	15.7	1.3
	X			X								3	15.7	1.3
	X		X	X			X		X			7	15.9	1.5
	X		X									4	16.4	2.0
	X		X	X				X				6	16.6	2.2
	X		X	X					X			6	16.7	2.3
	X			X								4	16.8	2.4
	X		X	X			X	X	X		X	9	17.4	3.0
	X		X	X			X	X				7	17.5	3.1
	X		X	X			X	X	X			8	17.7	3.3
	X			X				X				5	18.4	4.0
Prime-age males:														
Absolute antler size:														
			X									2	-10.1	.0
												3	-10.0	.1

Table C2 (Continued)

	Age	Acorn mast abundance	Density	HI	Age × HI	Age × density	Density × HI	Acorn × HI	Acorn × density	Age × density × HI	Acorn × density × HI	df	AIC	ΔAIC
		X	X						X			5	-8.0	2.1
		X										3	-7.2	2.9
		X	X									4	-6.9	3.2
		X	X	X				X	X			6	-6.3	3.8
		X	X	X					X			6	-6.3	3.8
		X	X	X				X				6	-6.3	3.8
		X		X				X				5	-5.7	4.4
		X	X	X								5	-5.4	4.7
		X	X	X			X	X	X		X	7	-4.3	5.8
		X	X	X			X	X	X			7	-4.3	5.8
		X	X	X			X	X				7	-4.3	5.8
		X	X	X			X		X			7	-4.3	5.8
Relative antler size:														
			X									3	-12.5	.0
		X	X									4	-10.4	2.1
		X	X	X								5	-8.5	4.0
		X	X						X			5	-8.5	4.0
												2	8.4	4.1
		X	X	X			X	X	X		X	7	-6.8	5.7
		X	X	X			X	X	X			7	-6.8	5.7
		X	X	X			X		X			7	-6.8	5.7
		X	X	X			X	X				7	-6.8	5.7
		X	X	X				X	X			6	-6.6	5.9
		X	X	X					X			6	-6.6	5.9
		X	X	X				X				6	-6.6	5.9
		X										3	-6.4	6.1
		X		X				X				5	-2.4	10.1

Note: Model selection was performed using the Akaike Information Criterion (AIC) as recommended by Burnham and Anderson (2002). However, when the difference between AIC values of two competing models was less than 2, we used the criterion of parsimony, selecting the simpler of the two models (Burnham and Anderson 2002). X indicates that the term is included in the model. ΔAIC is the AIC difference between the given model and the selected model. The selected models appear in bold. Age = age fitted as a factor with three age classes (i.e., yearlings, prime-age males, and senescent males). Density = population density. HI = summer hydric index.

PAPER 4

Is bigger better in a low sexual size dimorphic ungulate? Continued sexual selection on male body mass and antler size in roe deer

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(Data from Trois Fontaines should be added to this manuscript before publication)

Abstract

Most studies of sexual selection in mammals have focussed on highly dimorphic species with dominance-based mating systems, in which size-dependent male-male competition and variance in male reproductive success are tightly linked. By comparison, little is known about sexual selection in mammals with low sexual size dimorphism and territorial mating system, where the traits under selection might be less obvious. We examined continued sexual selection on male body mass and antler size in European roe deer *Capreolus capreolus*, a territorial ungulate in which males are less than 10% heavier than females. Yearly breeding success increased with both body mass and antler size. High body mass and large antlers may be advantageous to roe bucks for two reasons: (i) they enhance fighting ability and dominance, so allowing males to better defend their territory and access mates, and/or (ii) they attract females, because they are honest signals of male phenotypic quality. This study provides the evidence that strong effects of male body mass or size on male yearly breeding success can occur in ungulate species with low sexual size dimorphism if body mass and/or size are also strongly selected in females.

Keywords: *Capreolus capreolus*, microsatellites, paternity analysis, male breeding success, sexually selected traits, sexual selection.

Introduction

Sexual selection was defined by Darwin (1871) as the selection acting on individual traits of one sex (usually males) that affect mating success or fertilization. Sexual selection theory predicts that the opportunity for sexual selection is strong when males compete intensely for mates, creating the potential for reproductive success to vary widely among males (Darwin 1871). However, sexual selection can only occur if variation in reproductive success is correlated with phenotypic variation (Andersson 1994). Hence, to measure selection in progress, a trait-related measure is required. Systematic relationships between mating success and trait variation are evidence of continued sexual selection.

There is wide acceptance of the idea that male-biased sexual dimorphism in body size and weaponry has evolved principally as the result of intra-sexual competition over mates (Darwin 1871; Andersson 1994). Hence, quantitative demonstrations of sexual selection on male phenotypic traits in empirical studies have usually focussed on male body mass or size and weapon size (see Andersson 1994). In ungulates, a positive correlation between male body mass or size and male yearly breeding success has been reported in Soay sheep *Ovis aries* (Preston et al. 2001) and bighorn sheep *Ovis canadensis* (Coltman et al. 2001). The assumption here is that large body size or mass confers an advantage in dominance contests, frontal combats involving pushing, or endurance rivalry, and so in male access to females. Similarly, large horn or antler size or mass has been found to be associated with increased male yearly breeding success in red deer *Cervus elaphus* (Kruuk et al. 2002), bighorn sheep (Coltman et al. 2001), and Soay sheep (Preston et al. 2003), notably due to the advantage that antlers and horns confer in intrasexual combat and so in access to receptive females. But while those size-dimorphic ungulate species with harem-holding or roving mating systems have received much attention, very little information is available about continued sexual selection on male phenotypic traits in ungulate species with low sexual size dimorphism and in territorial species. This information would be particularly interesting because the intensity of sexual selection on phenotypic traits is expected to vary widely in relation to the level of sexual size dimorphism and the mating system (Andersson 1994).

In species with low sexual dimorphism, the traits under selection are likely to be less obvious than in highly dimorphic species. First, in monomorphic or low dimorphic species, males are commonly more active than females in display or territory defense, suggesting that males may be subject to stronger sexual selection than females, but with mainly behavioural rather than morphological consequences (Andersson 1994). Hence, it has been proposed that

male behavioural characteristics might be stronger determinants of reproductive success than physical ones such as body mass or antler size in these species (hypothesis 1, in roe deer *Capreolus capreolus*: Strandgaard 1972). Second, agility, implying small body size, may be important in determining male mating success, through scramble competition or courtship in territorial species (agility-hypothesis; Andersson 1994), and so sexual selection may rather favor low body size or mass (hypothesis 2). However, as suggested by Clutton-Brock (1987), it is not the extent to which male success varies that will determine the development of sexual dimorphism, but the comparative effects of particular traits on breeding success in males and females. Hence, it is also possible that a strong sexual selection occurs on male body mass, with large body mass resulting in a higher breeding success, if body mass has also a key role in female fecundity and hence is selected for in both sexes (hypothesis 3).

In territorial species, predictions in terms of sexual selection are also commonly difficult to express due to location-dependent dominance (Owen-Smith 1977) and the potential role of both phenotypic traits and territory characteristics in determining male breeding success. In a resource defense polygyny mating system, males gain access to females indirectly, by defending an area with vital resources for females (Emlen and Oring 1977). Hence, we can expect that male contests have favored male phenotypic traits, such as body mass and weapon size, which enhance strength and ability to fight and defend a mating territory. However, whereas frontal combats between rival males are common in dominance-rank based mating systems, physical male-male interactions are usually rather infrequent in territorial species, since male dominance is mainly location-specific and display behaviors often allow males to resolve conflicts without resorting to fighting (Owen-Smith 1977; Hoem et al. 2007). In addition, in a resource defense polygyny mating system such as territoriality, female choice should be mainly directed not towards the males themselves, but towards the quantity or quality of the resources that the males are defending. But, as pointed out by Balmford et al. (1992), male quality and territory quality are often inter-correlated. Indeed, intra-sexual competition among males is likely to produce a situation where the most competitive males occupy the territories preferred by females. Hence, females may choose the best males, and male-male competition should ensure that the best males occupy the best territories. It is, however, also possible that females gain by choosing males with respect to characteristics other than those important in intra-sexual competition that may be reliable indicators of male phenotypic quality.

The role of body mass and weapon size in determining male breeding success is still largely unexplored in territorial ungulate species with low sexual size dimorphism. The aim of

this study was therefore to investigate this issue in a wild population of European roe deer, a territorial species in which males are less than 10% heavier than females (Andersen et al. 1998). We explored continued sexual selection on male body mass and antler size using genetic estimates of male yearly breeding success. Because of the low sexual size dimorphism of roe deer and in support with Strandgaard's (1972) hypothesis (similar to hypothesis 1), we expected that male body mass and antler size were little correlated with male yearly breeding success in this species.

Materials and methods

Study population

The study site is situated at Bogesund, a 2,600 ha area of fragmented habitat in central eastern Sweden (59°23'N, 18°15'E; see Vanpé et al. 2007 for more details). The roe deer population of Bogesund has been intensively monitored since 1988 with annual Capture-Mark-Recapture procedures (see Kjellander 2000 for more details). Each year, during winter, roe deer were captured in box traps, sexed and individually marked. Neonates were also caught by hand every spring, just after birth (May-June), from 1997 onwards. Mother-offspring relationships were elucidated by direct observation of fawns with their mothers just after birth or during autumn. Since 1992, some roe deer were occasionally shot in order to experimentally manipulate roe deer population density within the research area (see Kjellander 2000 for more details).

Phenotypic measurements

We used measures of antler size and body mass collected both during winter captures and summer/autumn hunting. Antler length of males was measured to the nearest 0.5 cm along the external side of the main beam, from the base of the antler to the top of the main beam. For antlers still in velvet measured during winter captures, we calculated the residuals of the measurements by fitting a linear regression of antler size on capture date (for more details, see Vanpé et al. 2007). For hard antlers measured on shot individuals during summer or autumn, we used untransformed raw measures. Body mass of males was measured to the nearest 0.1 kg. While body mass measures collected during winter captures were live weights, body mass measures from shot individuals were dressed weights. Hence, we used four measures to describe phenotypic quality (see Table 1): residual soft antler size (RSAS), hard antler size (HAS), live weight (LW) and dressed weight (DW). As age estimates based on

tooth wear are likely to be inaccurate (Hewison et al. 1999) and because most individuals in this study were of estimated age, we could not control for age-related variation in these measures. We therefore considered only males of 2 years of age or older at fawn conception during the rut for this study.

Paternity analysis and estimation of male breeding success

From 1988 onwards, tissue samples were collected for DNA genotyping from all individuals caught for the first time and unmarked shot roe deer. This allowed us to sample a total of 1757 different individuals. Genotyping of the DNA samples of all individuals was carried out using 21 microsatellite markers (see Vanpé et al. unpubl. data). Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall et al. 1998) and the user-defined input parameters detailed in Vanpé et al. (unpubl. data). 442 fawns at Bogesund were thus successfully assigned by CERVUS to a male at the 80% level of confidence. After determining the distribution of paternities among males, we estimated yearly reproductive success for each male and for each breeding season during which the male was considered as a candidate father. Because a proportion of the sampled fawns were caught as neonates for which the fate was unknown, we used male yearly breeding success (YBS) as a proxy of male yearly reproductive success. This was defined as the number of born offspring sired by a male in a given year and calculated as the total number of paternities assigned at the 80% confidence level to a given male in a given year. Because very few fawns were sampled and assigned fathers for the cohorts from 1988 to 1991 compared to the potential number of fawns born in the population during these years of high density, we restricted our analyses to fawns born after 1991 (see Vanpé et al. unpubl. data).

Statistical analyses

Systematic relationships between reproductive success and trait variation are evidence of continued sexual selection on secondary trait variation (Andersson 1994). We used a Generalized Linear Mixed Model implemented in the glmmADMB module (H. Skaug, D. Fournier and A. Nielsen) of the software R 2.3.1 (R Development Core Team 2004) to analyse the effect of our 4 phenotypic trait variables on male YBS. Parameters are estimated by maximum likelihood using the Laplace approximation to evaluate the marginal likelihood (Skaug and Fournier 2005). YBS was modelled as a poisson distribution. As we suspected that many males were identified as unsuccessful simply because we did not catch the fawns they sired, we used a zero-inflated model. Hence, with probability '1-pz' YBS comes from a

Poisson distribution, and with probability 'pz' YBS is zero (Bohning et al. 1999). Individual identity was fitted in the mixed models as a random effect, thus controlling for the innate variation among individuals. Model selection was performed using the small sample size corrected Akaike Information Criterion (AICc), as recommended by Burnham and Anderson (2002). A smaller AICc value corresponds to a better fit of the model to the data (i.e., the best compromise between accuracy and precision). The effects of the different phenotypic measures on YBS were tested separately because they were recorded for different males (i.e. shot animals, live captures, etc). For each variable, we tested the constant model against the model including the effect of the phenotypic measure as a covariable. Finally, we tested simultaneously for the effect of live weight and residual antler size corrected for the allometric relationship with body mass (residual of SRAS on LW = RRSAS) on YBS using individuals for which both winter capture measures were available. In this case, we tested the additive effect of the two measures and their two-way interaction effect by simplifying the full model using a backward stepwise selection procedure.

Results

For all the 4 tested phenotypic trait measures (i.e. DW, LW, RSAS, HAS), the model including the measure performed better than the constant model (Table 1). All 4 phenotypic trait variables had a positive effect on male YBS (Table 1 and Figure 1). However, for RSAS, the constant model had a very similar AICc value to the model including the covariable (Table 1), indicating that the effect of RSAS on YBS, if it did occur, was slight. There also seemed to be a threshold below which male YBS was almost always zero (about 16 kg for DW, 20 kg for LW and 15 cm for HAS; Figure 1).

Table 1. Results of the model selection testing for the effects of the 4 phenotypic trait measures on male yearly breeding success.

phenotypic trait	measured variable	period	AICc model with covariable	AICc constant model	equation of the best model
BODY MASS	dressed weight	summer/autumn hunting	150.71	157.54	$E(YBS) = (1 - 0.46398) \exp(0.3277 \times DW - 6.6650)$
	live weight	winter captures	541.67	562.72	$E(YBS) = (1 - 0.26741) \exp(0.1827 \times LW - 4.7818)$
ANTLER SIZE	hard antler size	summer/autumn hunting	81.81	86.95	$E(YBS) = (1 - 0.50200) \exp(0.0239 \times HAS - 5.3672)$
	residual soft antler size	winter captures	225.78	226.29	$E(YBS) = (1 - 0.39685) \exp(0.0059 \times RSAS - 0.1258)$

Note: AICc = Akaike Information Criterion corrected for small sample size. YBS = yearly breeding success, DW = dressed weight, LW = live weight, HAS = hard antler size, RSAS = residual soft antler size.

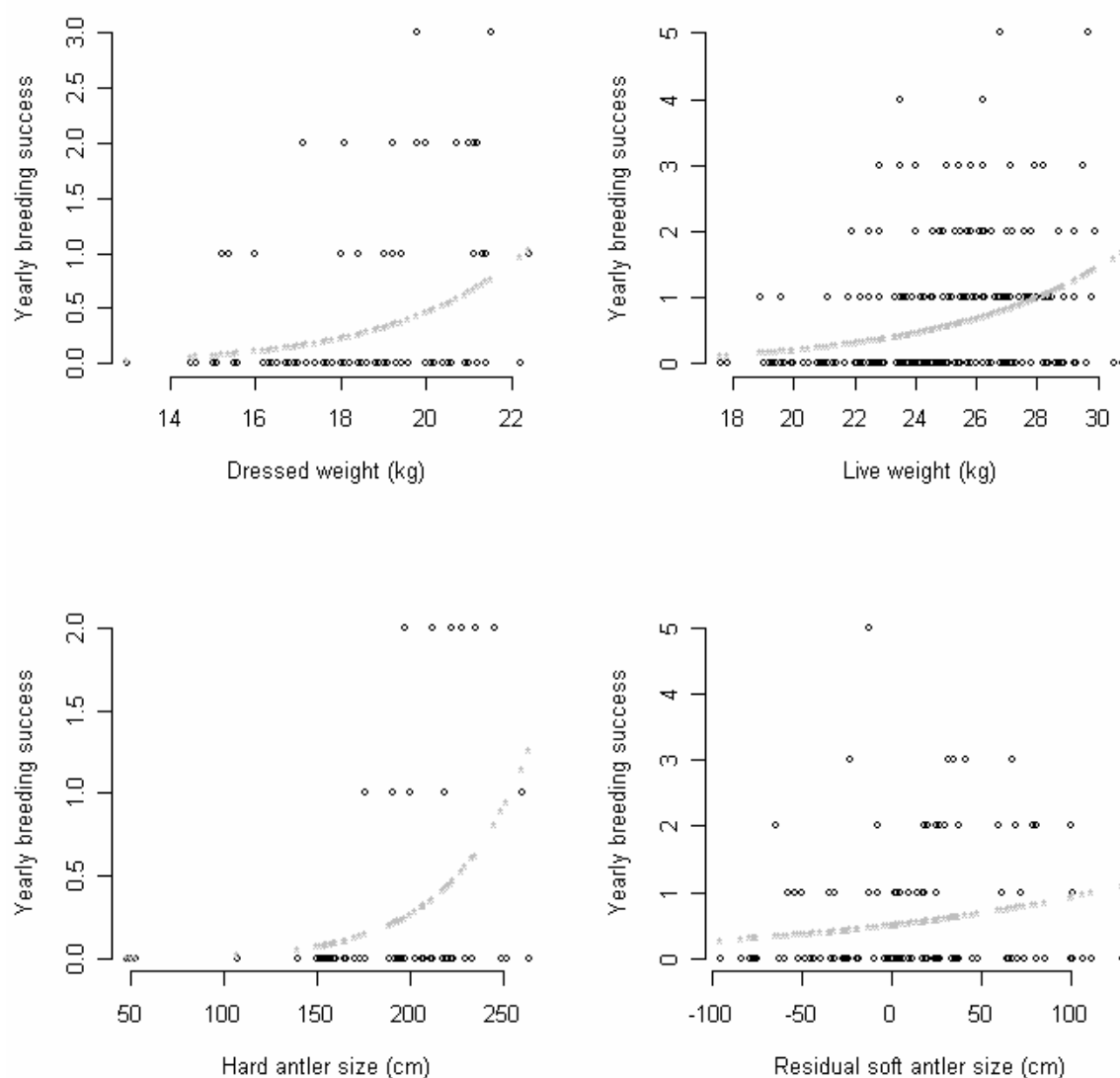


Figure 1. Variation in male yearly breeding success in relation to (A) dressed weight (kg) of animals shot during summer/autumn, (B) live weight (kg) of animals caught during winter, (C) hard antler size (cm) of animals shot during summer/autumn, and (D) residuals (in relation to date measured; cm) of soft antler size of animals caught during winter.

Note: Black open circles = observed data. Grey stars = values predicted by the zero inflated generalized linear mixed model, with breeding success modelled as a poisson distribution with a logit link function.

The results of the analysis testing for the combined effect of LW and RRSAS (residual of SRAS on LW) showed that the best fitting model included the simple effect of live weight only ($E(YBS) = (1-0.32075) \exp(-5.4035 + 0.2074 LW)$; Table 2). Hence, this suggests that antler size for a given body mass may have no direct effect on male YBS and that the observed effect of antler size documented above may simply reflect the correlated effect of body mass on male YBS. However, the model including the additive effect of LW and

RRSAS had a very similar AICc value to the selected model, indicating substantial support for this model too (Table 2).

Table 2. Results of the model selection testing for the effect of live weight (LW) and residual antler size corrected for the allometric relationship with body mass (residual of SRAS on live weight = RRSAS) on yearly breeding success using individuals for which both winter capture measures were available (N=101).

models	AICc	Δ AICc
RRSAS + LW + RRSAS : LW	223.53	3.86
RRSAS + LW	221.43	1.77
RRSAS	227.25	7.59
LW	219.66	0.00
constant	225.40	5.73

Note: Model selection was performed using the small sample correction Akaike Information Criterion (AICc) as recommended by Burnham and Anderson (2002). Δ AICc are the AICc differences between the given model and the best model (the model with the lowest AICc). The selected model appears in bold.

Discussion

For the first time, we provide evidence of continued sexual selection on secondary sexual trait variation in a territorial ungulate with low sexual size dimorphism. Specifically, we have shown that YBS was positively correlated with both body mass and antler size in male roe deer. However, when antler size is corrected for the allometric relationship with body mass, it seems that there is no real direct effect of antler size per se on male YBS.

At least three non exclusive hypotheses may explain the increase of YBS with body mass and antler size that we observed. First, heavy males with large antlers may have better competitive, fighting abilities and endurance than other males, which may allow them to defend a territory which provides greater access to mates during the entire rut period. In support of this interpretation, we previously showed that territory size, which has a positive effect on male access to females and male YBS, tended to increase with body mass in all male roe deer and also with antler size in sub-adults (Vanpé et al. unpubl.). In addition, Hoem et al. (2007) have shown that being resident and having longer antlers were the most important factors determining who wins fights, and that both antler size and age determined territorial status of roe bucks. However, direct male-male fights are rather infrequent in roe deer because of the site-dependent dominance (Owen-Smith 1977; Hewison et al. 1998) and display behaviours often allow males to resolve conflicts without resorting to costly fighting (Liberg

et al. 1998; Hoem et al. 2007). Several studies have shown that antler size may be one of the main cues used by males to assess their rival's individual fighting ability (Strandgaard 1972; Hoem et al. 2007). Males may therefore assess each other in part by the size of antlers, avoiding fights with superior competitors (Hoem et al. 2007).

Second, heavier males with larger antlers may be chosen by females for mating, as body mass and antler size have been shown to be reliable indicators of male phenotypic quality (see Vanpé et al. 2007). In addition, Wahlström (1994) found a positive correlation between yearling antler size and testicle size in roe deer, indicating that antler size may reflect male fertility and sexual vigor, because testes size determines sperm production rate (Møller 1989). Hence, by choosing sexual partners on the basis of large antler size or high body mass, does may ensure that they mate with a high quality male. From this, they may gain either direct benefits, such as high male sexual vigor and protection against harassment by other males (see reviews by Price et al. 1993 and Andersson 1994), or indirect benefits, such as bearing offspring of high quality (reviewed in Kokko et al. 2003).

Third, as we did not control for the effects of age, we cannot discard the hypothesis that the observed increase of YBS with body mass and antler size at least partly reflects an increase of YBS with age. However, among known-aged males that failed to breed ($N = 156$), 37% were 2-year-old males (at fawn conception), 60% were 3-7-year-old males and 3% were older males. In addition, YBS did not continuously increase with age. YBS was shown to be smaller in two-year-old males than in prime-age males (3-8 years of age), to peak in prime-age males and then to decline for the oldest ages (Vanpé et al. unpubl.). Hence, it is unlikely that the increase of YBS with body mass and antler size simply reflects an increase of YBS with age.

The effect of antler size on male breeding success no longer held when we corrected antler size for the allometric relationship with body mass. That is, for a given body mass, antler size had no influence on male YBS. Hence, it seems that the observed effect of antler size on male YBS simply reflects the correlated effect of body mass on male breeding success. However, we could only investigate the effect of antler size after correction for body mass using RSAS, which had only a slight effect on male YBS (Figure 1), and the model including both RSAS and LW obtained substantial support too (Table 2). Hence, before totally discarding a possible direct antler size effect on male YBS, further analyses should be performed.

There are few empirical evidence of continued sexual selection on male body mass and antler or horn size in large mammals in the literature, based on genetic estimates of male

YBS, for comparison with my results on roe deer; and comparisons between studies are difficult because of differences in methods. In Soay sheep, Preston et al. (2003) found a strong positive relationship between horn length (irrespective of age, body size, condition and testes size; effect \pm SE = 0.00730 ± 0.00222), but not body size, and paternity success, whereas Preston et al. (2001) reported that body size was a significant predictor of siring success (effect = 0.119 ± 0.0331). In bighorn sheep, Coltman et al. (2001) showed that mating success increased with weight and horn size (range of within-year correlation coefficients = 0.171-0.657 and 0.151-0.576, respectively), with horn length increasingly positive in correlation with mating success in older rams (effect horn length = 0.022 ± 0.016 , effect age x horn length = -0.014 ± 0.006 , effect age² x horn length = 0.0016 ± 0.0005). In red deer, the mass of a male's antlers in a given year had a significant effect on his annual breeding success, with a stronger effect for younger males, even when including leg length in the model to remove any correlated selection on body size (effect antler mass = 0.00365 ± 0.000613 , effect age x antler mass = -0.000598 ± 0.000245 ; Kruuk et al. 2002). However, there was no evidence of a relationship between leg length and YBS (Kruuk et al. 2002). But all these studies focussed on highly dimorphic ungulate species with dominance-rank based mating systems, for which a strong effect of body mass and antler or horn size on male YBS was expected. In territorial species with low a level of sexual size dimorphism such as roe deer, predictions were less obvious.

We provided evidence for a significant continued sexual selection on male body mass, with high body mass favoring high breeding success in roe deer. Hence, the hypotheses of the weak role of male body mass and of selection for agility and small size to explain the evolution of the low sexual size dimorphism in roe deer were not supported. Rather, our results seem to be consistent with the hypothesis of Clutton-Brock (1987), suggesting that the development of low sexual size dimorphism in polygynous species may be a result of a parallel selection for high body mass or size in females. Indeed, in roe deer, body mass and size are known to strongly influence female fecundity (Gaillard et al. 1992, 2000; Hewison 1996; Hewison and Gaillard 2001). This study thus provides the evidence that strong effects of male body mass or size on male breeding success can occur in ungulate species with low sexual size dimorphism if body mass and/or size are also strongly selected in females.

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PART 4

ROLE OF THE TERRITORY IN MALE BREEDING SUCCESS AND EVOLUTION OF TERRITORIALITY



**Jumping roe deer
(photograph by Olivier Villa)**

PAPER 5

Access to mates in roe deer is determined by the size of a male's territory, but not its habitat quality

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Summary

Territoriality is commonly associated with a resource defence polygyny mating strategy, where males are expected to gain access to females by anticipating how resources will influence female distribution and competing for resource-rich sites to establish their zone of dominance. We tested this hypothesis in a population of European roe deer (*Capreolus capreolus*) by simultaneously assessing the influence of resources on female distribution and the influence of female distribution on male distribution and breeding success using paternity analyses. Females did not fully distribute themselves among male territories in relation to resources. As a result, relative female abundance in a male's territory depended on its size, but not its habitat quality. In turn, relative female abundance in a male's territory determined, at least partially, his breeding success. Interestingly, male territory size and, hence, male access to females, was partly determined by male body mass (all males) and by residual antler size (sub-adults only). The latter result suggests that large antlers may be important to young males for establishing their first territory, which is then usually retained for all subsequent reproductive seasons. To conclude, although territoriality of male roe deer has certainly evolved as a tactic for ensuring access to mates, our results suggest that it does not really conform to a conventional resource defence polygyny strategy, as males seem to gain no obvious benefit in terms of enhanced access to mates by defending a territory in an area of high habitat quality. This may explain the stability of male territories between years, suggesting that male territoriality conforms to an “always stay” and “low risk - low gain” mating strategy in roe deer.

Keywords: antler size, body mass, breeding success, *Capreolus capreolus*, mating strategies, resource defence polygyny.

Introduction

In mammals, where males usually provide no parental care and have the higher reproductive potential, female reproductive success is directly constrained by access to the resources necessary to breed and to meet the energy requirements of gestation and lactation, whereas male reproductive success is limited more by access to potential partners (Trivers 1972). This has consequences for theoretical predictions of animal distribution. First, female distribution should depend primarily on resource dispersion (modified by predation pressure and the costs and benefits of associating with other individuals). Second, males should distribute themselves in relation to female distribution (modified by male density), at least during the breeding period, in order to gain access to as many mates as possible (Emlen and Oring 1977).

Males can either directly compete for mates, or indirectly compete for resources that influence female distribution (Emlen and Oring 1977). The economics of these two mating strategies depends mainly on the defensibility of females, which is directly related to their density and distribution, female range size and female group size and stability, and indirectly to the distribution of resources (Clutton-Brock 1989). When females are spatially and temporally predictable (e.g., when they occupy stable small ranges containing clumped and high-quality food resources), the most economic mating strategy should be to adopt a “resource defence polygyny” tactic (e.g., territoriality; Emlen and Oring 1977), where males gain access to females by anticipating how resources will influence female distribution and competing for resource-rich sites to establish their zone of dominance.

Male territoriality is commonly associated with a resource defence polygyny strategy. In ungulates, in which male territoriality is widespread (see Owen-Smith 1977), the evolution of male territoriality as a mating strategy analogous to resource defence polygyny has been suggested for various species (e.g., in Grevy’s zebra *Equus grevyi*: Klingel 1974; roe deer *Capreolus capreolus*: Putman 1988, Wahlström 1994, Johansson 1996, Liberg et al. 1998; hippopotamus *Hippopotamus amphibius*: Nowak 1991; wildebeest *Connochaetes gnou*: Estes 1969; Reeves’s muntjac *Muntiacus reevesi*: Dubost 1970; sika deer *Cervus nippon*: Miura 1984). However, no study has as yet tested this hypothesis by simultaneously assessing the influence of resources on female distribution and the influence of female distribution and resource dispersion on male distribution and mating success.

The roe deer is a small ungulate in which adult males are strongly territorial (Bramley 1970; Strandgaard 1972; Liberg et al. 1998). The only information available on the influence

of habitat quality and female distribution on male mating success in this species is based on observations of mating and territorial behaviours (Strandgaard 1972; Johansson 1996). Behavioural data almost certainly provide poor estimates of male breeding success, given that multiple mating commonly occurs (Danilkin and Hewison 1996; Liberg et al. 1998) and that roe deer are cryptic and often occupy dense forest habitat. These studies suggest that male mating success may be limited by the number of female home ranges which overlap a male's territory (Johansson 1996). In addition, Johansson's observations suggest that the quality of male territories, but not their size, positively influences mating success, as males with clover fields within their territory were more successful, supporting the resource defence polygyny hypothesis. But territories in roe deer are stable, with little change of boundaries and size between years (Bramley 1970; Johansson 1996; Hewison et al. 1998; Linnell and Andersen 1998). Territory boundaries may possibly even outlast the tenancy of any single individual (Strandgaard 1972). This is unexpected in a resource defence polygyny strategy, in which males should maximise their access to potential mates by maximising their zone of dominance and/or the habitat quality within that zone. Hence, in order to elucidate the adaptive value of territoriality as a resource defence polygyny mating strategy, we need data on the number of genetic paternities obtained by males in relation to their ranging behaviour (Hewison et al. 1998).

The aim of this study was to investigate this issue in a roe deer population situated in Sweden, testing the following predictions. First, we expected female abundance within a male's territory to increase with territory size (prediction 1). Second, if male territoriality evolved as a resource defence polygyny mating strategy, females should be distributed in relation to resources. The "Ideal Free Distribution" hypothesis (IDF; Fretwell and Lucas 1970) states that, in the absence of constraints on movement, individuals are expected to be distributed so that differences in local densities reflect differences in habitat quality. As a result, resources are equally shared among individuals and fitness is equal in all habitats (Fretwell and Lucas 1970). Although most wild populations do not conform to the assumptions of the IFD, this model is useful for predicting patterns of foraging behaviour and testing hypotheses in behavioural ecology (Calsbeek and Sinervo 2002). Assuming that females are free to distribute themselves in relation to resources, we expected female abundance within a male's territory to increase with habitat quality for a given territory size (prediction 2). Third, territoriality should secure mating access to resident females for the territorial male. Hence, we expected a male's breeding success to depend on female abundance within his territory (prediction 3). Males should attempt to enhance their mating

success by either enlarging their zone of dominance, or by occupying areas particularly favoured by females, or both. Hence, we also expected male breeding success to increase with territory size and/or territory habitat quality (prediction 4). Finally, we should expect substantial male-male competition to occupy the “best” territories (providing access to the highest numbers of females). Hence, the best territories should be occupied by the best competitors in male-male contests. We, therefore, expected a positive correlation between the suitability of the territory in terms of access to females, and male attributes which reflect ability to fight and dominate, such as age, body mass and antler size (prediction 5).

Materials and methods

Study species

The roe deer is a selective feeder, preferentially feeding on forbs, seeds and deciduous browse rich in soluble nutrients (Tixier and Duncan 1996). This makes them adapted to exploit the early stages of forest succession where preferred foods are most abundant (Wahlström 1995). It is an income breeder (Andersen et al. 2000), relying on food intake rather than body reserves to cope with the marked increase in energy requirements during late gestation - early lactation. Females are considered as non-territorial, living solitarily, or with their fawns, during summer in overlapping home ranges (Bramley 1970; Strandgaard 1972; Wahlström and Kjellander 1995). The spatial system of the two sexes is independent so that a female's home range may overlap several male territories (Hewison et al. 1998; Liberg et al. 1998). Male territoriality is seasonal. Adult males are considered as fully territorial, but only during spring-summer (Liberg et al. 1998). Territories are established in early spring (March-April) and maintained until late August - early September, just after the July-August rut (e.g., Bramley 1970; Strandgaard 1972). Although males become sexually mature as yearlings, they usually do not defend territories until two, three or four years of age, depending on population density (see Liberg et al. 1998 for more details).

Study site

The study was carried out in the 1,250 ha western part of Bogesund (59°23' N, 18°15' E), a 2,600 ha mainland peninsula situated on the coast of the Baltic Sea on the inner portion of the Stockholm Archipelago, within the hemiboreal zone in east-central Sweden. The habitat is fragmented, with approximately 65% woodland, 25% fields and 10% bed rocks and bogs (Kjellander 2000). The dominant coniferous tree species are Norway spruce *Picea abies*

and Scots pine *Pinus sylvestris*, while deciduous species including birch *Betula* spp., aspen *Populus tremulus* and oak *Quercus robur* are also common. Dwarf shrubs, primarily bilberry *Vaccinium myrtillus* and cranberry *Vaccinium vitis idae*, are patchily distributed as ground cover in mature forest stands, while numerous herbs are abundant in most habitats (Kjellander 2000). Some agricultural fields are re-sown in early autumn, but most are ploughed after harvest, remain fallow during winter and are sown in spring (Kjellander 2000). Common crops are oat *Avena sativa*, wheat *Triticum* spp., barley *Hordeum* spp. and pasture plants such as *Trifolium* spp. and *Vicia* spp. Fenced pastures with livestock (horses, cows or sheep) occupy less than half of the agricultural land. In addition, numerous small meadows and abandoned fields lie fallow. The only natural predator of roe deer fawns is the red fox *Vulpes vulpes* (Kjellander and Nordström 2003).

Data collection and analyses

The Bogesund population of roe deer has been monitored intensively since 1988 by an annual Capture-Mark-Recapture programme. Each winter, roe deer were caught in box traps, sexed and individually marked with plastic ear-tags (see Kjellander 2000 for more details). A variable number of caught individuals were also equipped with radio collars (TXT-2Sm, 151 or 152 MHz transmitters, Televilt International AB, Lindesberg, Sweden). Age was either known definitively (animals first caught as new-born fawns or juveniles <1 year old) or estimated from tooth eruption and wear (Cederlund et al. 1992) during capture or after death. Hewison et al. (1999) have shown that age estimations based on tooth wear are inaccurate in roe deer, especially for the oldest ages. Hence, we considered two age classes only, sub-adults (2 years old; all known-aged) and adults (>2 years old; both estimated and known-aged males). Body mass was measured to the nearest 0.1 kg, while antler size was measured to the nearest 0.5 cm and standardised to the 14th of February (see details in Vanpé et al. 2007).

Radio-tracking and estimation of territory size

We intensively radio-tracked all males and females equipped with radio-collars and older than 1 year of age during the ruts (i.e. from mid-July to mid-August) of 2004 (N = 25 males and 16 females) and 2005 (N = 23 males and 22 females, of which 15 and 9 were the same individuals as in 2004, respectively). Radio-tracking was conducted from the ground with Televilt RX-810 and RX-98 receivers and a 4-element Yagi antenna. Animals were located from 0 to 3 times per 24 hour period (including day, night, dusk and dawn) by

triangulation from at least three points along roads or hills, with a minimum of 3 hours between successive locations. A study of radio-tracking accuracy performed in August 2005 showed that the mean error of localisations was 41.0 ± 41.6 meters (C. Vanpé, unpubl. data). We collected 30 fixes per individual and per rut, which is the recommended standard proposed by Kenward (1987). Radio-tracking positions were digitised in a geographic information system (Arcview 3.2) and analysed using the Spatial Analyst and Animal Movement extensions to ArcView (Hooge and Eichenlaub 1997). Male territory size and female home range size were estimated using the Kernel method (Worton 1989) with the 90% isocline and the least square cross validation calculation for the smoothing parameter, as recently recommended by Börger et al. (2006). We discarded from the following analyses one 2-year-old male that failed to breed and had a home range pattern characteristic of a non-territorial satellite sub-adult (a small home range (15.9 ha) with a core area (defined as the 50% kernel isocline) almost entirely overlapping the territory of an adult male).

Pellet-group counts for estimating an index of relative local female abundance in each territory

We carried out a faecal pellet-group count census (Neff 1968; Cederlund and Liberg 1995) over the entire 2,600 ha roe deer research area, both in 2004 and 2005, in early April, immediately after snow melt. The 604 sample plots (10 m²) were circular and distributed regularly every 100 m along north-south transects, with 400 m between neighbouring transects. We considered that no pellet degradation occurred during winter due to snow cover and low temperatures. Because new pellets that have deposited since defoliation could be distinguished from old pellets in relation to dead leaves and needles that covered the latter but not the former (Kjellander 2000), we used a standing crop design. The total number of pellet groups (with a minimum of 10 pellets per group) was recorded on each plot.

We interpolated the number of pellet groups on each plot using a statistical prediction. As this variable was discrete, we used Model-based Geostatistics (Diggle et al. 1998), that is, a Generalized Linear Model (McCullagh and Nelder 1989) with a random spatial component. We used the Poisson model and so we assumed that the defecation count at the site x follows, given a non-observed gaussian random field S , a Poisson variable of intensity $\lambda(x)$ such that $\text{Log}(\lambda(x)) = \alpha + S(x)$ where S is centred ($E(S(x)) = 0$) and has a stationary covariance function ($E(S(x)S(y)) = C(x-y)$). From observed counts, a parametric model was estimated for the covariance by a MCMC maximum likelihood approach (Christensen 2004). The statistical

prediction was then performed using a simple kriging procedure on simulated potential values of S at observed sites, given the data, to obtain by an empirical mean of simulations the best prediction of S at a non-observed site (Zhang 2002). Finally, a back transformation was performed that took into account a correction for bias to obtain the prediction of the Poisson intensity which is also the prediction for the count. We performed the preliminary variogram inspection, model fitting and model-based kriging with the geoRglm package (Christensen and Ribeiro 2005). We interpolated the number of pellet groups in order to obtain a value every 100 m over the whole study area.

We estimated the total number of pellet groups within each male's territory for 2004 and 2005 as the sum of the point estimates falling within each territory using Arcview 3.2 software. We used this value as an index of relative local roe deer abundance. We corrected this value using an estimation of the local sex ratio, defined as the proportion of mature females caught in each trap zone (N = 7) during winter captures, in order to obtain an index of relative abundance of mature females in each territory. We assumed that relative female abundance in winter was an informative reflection of relative female abundance in summer, since roe deer home ranges are globally stable between seasons (Hewison et al. 1998) and adult mortality is generally low (Gaillard et al. 1993). Although pellet group counts have been criticised as a method to estimate absolute population density (e.g., Robinette et al. 1958; Putman 1984), we considered that they provide an informative index of relative animal abundance which was adequate for our purposes (see Forsyth et al. 2007).

Vegetation sampling and identification of the specific resource attributes that reflect habitat quality for females

During both ruts we performed a systematic vegetation sampling over the 2,500 ha study area comprising 357 point locations. Points were located 200 meters apart on a North-South transect, and all transects were separated by 200 meters. In 2005, however, point locations were shifted 100 meters to the North and 100 meters to the East compared with 2004. For each point, the habitat was classified as young forest (tree height < 5 m), intermediate forest (5-15 m), old forest (> 15 m), clear-cut, crop fields, fallow/meadow, human area (e.g., garden, road), or pasture. Vegetation cover was estimated within a circle of 2 metre radius (12.56 m²) for three different strata (0-20 cm, 20-50 cm and 50-150 cm) with a three category scale (0-10%, 10-50%, >50%). Bilberry cover was estimated within a circle of 10 meter radius (314 m²) and coded as absent, 0.1-10%, 10-50% or >50%. Bilberry has been

shown to be one of the primary winter food resources for roe deer in Scandinavia (e.g., Cederlund et al. 1980; Mysterud et al. 1998). Vegetation sampling was carried out using a wooden frame of 25 x 25 cm. All vegetation inside the frame was identified to the species level and cut at the following heights: 0-20 cm, 20-50 cm and 50-150 cm (maximum browsing height for a roe deer). Each sample was labelled and stored frozen in a paper bag. All samples were later thawed, dried at 60° C for three days and then weighed on a scale to the nearest 0.01 g. For each sampling point, we then estimated the biomass of crop plants (i.e. oat, wheat, barley), berry plants (i.e. *Vaccinium* spp., *Ribes* spp.), pasture plants (i.e. *Trifolium* spp. and *Vicia* spp.), various grasses, and the total biomass of consumed plants. Plants consumed by roe deer were determined based on the analysis of 11 rumen contents from 2 females and 9 males shot during the 2005 rut at Bogesund (C. Vanpé, unpubl. data).

Each of the 10 habitat variables (i.e. 5 factors: habitat, cover 0-20 cm, cover 20-50 cm, cover 0-150 cm, cover of bilberry; and 5 continuous variables: biomass of crop plants, biomass of berries, biomass of pasture plants, biomass of grasses, total biomass of consumed plants) was entered in a Geographic Information System (ArcView 3.2), mapped, and interpolated over the whole study area. To build the raster interpolated map for each habitat variable, cell size was fixed to 25 x 25 m and the number of neighbouring cells used in the interpolation was fixed to one so that all the cells with missing values took the value of the nearest sampling point. To identify the specific resource attributes that best reflect habitat quality (in terms of attractivity for females), we first analysed habitat selection by females during the rut by performing an Ecological-Niche Factor Analysis (ENFA; Hirzel et al. 2002), using the *enfa* function of the *adehabitat* package (Calenge 2006) for the R 2.4.1 statistical software (R Development Core Team; Ihaka and Gentleman 1996). The study area was modelled as a raster map (each pixel representing a resource unit) in relation to the 10 habitat variables. We used the 30 positions of the 29 females radio-tracked in 2004 or 2005 during the rut (when a female was radio-tracked in both years, we only used positions from 2004 to avoid pseudo-replication) to determine resource units used by females. All pixels on the raster map of the whole study area were considered to be available resource units for females. To determine the specific resource attributes that best reflect the suitability of an area for females, we interpreted the marginality axis of the ENFA (see Hirzel et al. 2002 for further details). The marginality axis was mainly explained by the following habitat variables: biomass of crop plants (coefficient = 0.57), biomass of various grasses (coefficient = 0.37), vegetation cover of the strata 20-50 cm and 50-150 cm (coefficients = 0.28 and 0.32 respectively), crop field habitat (coefficient = 0.28), biomass of consumed plants (coefficient

= 0.21), intermediate forest habitat (coefficient = -0.21) and cover of bilberry (coefficient = -0.30). That is, for these variables, female roe deer used habitat non-randomly in relation to the mean available habitat with regard to the corresponding variable (see Hirzel et al. 2002). This analysis showed that females tended to avoid the intermediate age forest habitat with high cover of bilberry (negative values of marginality), while they selected crop field habitats with high biomass of crop plants, and high vegetation cover (positive values of marginality). We derived a habitat suitability map, from the results of the ENFA, by assigning a numerical value to each raster map unit of the study area based on its position in this ecological space relative to the average niche of the species in the marginality analysis. We then used this map to derive mean habitat quality within each male's territory.

Paternity analysis and estimation of male breeding success

From 1988 onwards, tissue samples were collected for DNA genotyping from all individuals caught for the first time and unmarked shot roe deer. From 1997 onwards, tissue samples were also collected from neonates caught by hand in springtime, just after birth (May-June). This allowed us to sample a total of 1757 different individuals. We usually removed a small (approximately 4 x 4 mm) piece of ear skin tissue using sheep ear-notching pliers. Mother-offspring relationships were elucidated by direct observations of marked fawns with their mothers just after birth or during autumn. Genotyping of the DNA samples of all individuals was carried out using 21 microsatellite markers (see Vanpé et al. unpubl.). In this study, we focused on caught fawns from the cohorts 2005 (N = 29) and 2006 (N = 29). We aimed to identify the father of these fawns in order to estimate yearly breeding success of the males radio-tracked during the 2004 and 2005 ruts. Parentage was assessed using a likelihood-based approach with the program CERVUS 2.0 (Marshall et al. 1998) and the user-defined input parameters detailed in Vanpé et al. (unpubl.). We listed 57 sampled candidate mothers and 51 sampled candidate fathers for the 2005 fawn cohort, and 73 sampled candidate mothers and 63 sampled candidate fathers for the 2006 fawn cohort. In total (both years pooled), we were able to assign 26 fawns to the 31 different radio-tracked males. Yearly breeding success (YBS) was defined as the number of fawns assigned to a male (at the 80% confidence level) in a given year.

Statistical analyses

To test our predictions, we used mixed linear models (either simple or generalized) implemented in R 2.4.1 statistical package (R Development Core Team 2004), where male identity was entered as a random factor to control for repeated measures of the same individual. Model selection was performed using the small sample size corrected Akaike Information Criterion (AICc) as recommended by Burnham and Anderson (2002). The best model was taken as the one with the smallest AICc value (i.e., the best compromise between accuracy and precision). The index of relative female abundance in a male's territory was log-transformed to normalize data in models where it was the dependant variable.

To test predictions 1 and 2, we used the "lme" function (included in the "nlme" R package) for fitting linear mixed-effects models (Pinheiro and Bates 2000), using the maximum likelihood estimation procedure. To identify territory characteristics (territory size, habitat quality, or both) that could reflect territory suitability in terms of access to females for males, we compared the model relating the index of relative female abundance in a male's territory to territory size with the constant model. We also compared the model describing the relationship between the index of relative female abundance in a male's territory (corrected for territory size) to the mean habitat quality index within the territory with the constant model.

To relate YBS (discrete response variable) to individual-based measures describing the males' territory (i.e. relative index of local female abundance in the territory, territory size, mean habitat quality index within the territory) to test predictions 3 and 4, we used two different complementary methods. First, we used a Generalized Linear Mixed Model (GLMM) implemented in the glmmADMB module (H. Skaug, D. Fournier and A. Nielsen). Parameters are estimated by maximum likelihood using the Laplace approximation to evaluate the marginal likelihood (Skaug and Fournier 2005). YBS was modelled as a poisson distribution (see MacLoughlin et al. 2006 for a similar approach on red deer females). As we suspected that many males were identified as unsuccessful simply because we did not catch the fawns they sired, we used a zero-inflated model. Hence, with probability '1-pz' YBS comes from a Poisson distribution, and with probability 'pz' YBS is zero (Bohning et al. 1999). We compared each model including the simple effect of the index of relative female abundance in the territory, territory size, and the mean habitat quality index within the territory, with the constant model. Second, we tested the effect of male YBS (fitted as a factor with 3 levels: 1 fawn, 2 fawns, 3 fawns) on each of the three individual-based measures describing a males' territory. Because of the incomplete sampling of fawns born in 2005 and 2006, we restricted our analyses of male YBS to those males for which we could assign at

least one fawn (the territory of males for which we could not assign any fawn was most often in parts of the study area where fawn capture was more difficult).

Finally, to examine prediction 5, we tested the additive effects of male age class (sub-adults vs. adults), residual antler size (antler size corrected for the allometric relationship between antler size and body mass; see Vanpé et al. 2007) and body mass, as well as their two-way interactions, on territory characteristics (territory size and/or habitat quality index in a male's territory) which reflect the suitability of territories in terms of access to mates for males. We used two separate models (one for antler size and one for body mass) as both data were not always available for all males.

Results

Characteristics determining relative local female abundance in a male's territory

The model including an effect of territory size on the log-transformed index of relative female abundance in the territory ($AICc = 284.33$) described the data better than the constant model ($AICc = 312.44$). Hence, as expected (prediction 1), as territory size increased, relative female abundance in the territory also increased (mean slope \pm SE = 0.041 ± 0.006). The model including an effect of the habitat quality index in a male's territory, corrected for territory size, on the log-transformed index of relative female abundance in the territory ($AICc = -177.83$) performed less well than the constant model ($AICc = -179.91$). Hence, relative female abundance (range: 1.02 to 34.7) seems not to be affected by the habitat quality of the territory, contrary to prediction 2. These results indicate that the suitability of a male's territory in terms of access to females seems to be best reflected by territory size, but not by its habitat quality.

Effect of relative female abundance in a male's territory on male yearly breeding success

Comparing the GLMM models, the constant model performed slightly better ($AICc = 99.47$) than the model including the effect of relative female abundance in a male's territory ($AICc = 100.47$), indicating the lack of a marked effect of female abundance on male YBS. However, there was a trend for an increase of male YBS with the index of relative female abundance in their territory described by the equation: $E(YBS) = (1 - 0.42) \exp(-0.5023 + 0.0532 \text{ relative female abundance})$ (see Figure 1A).

Interestingly, the linear mixed model including an effect of male YBS on the log-transformed index of relative female abundance in a male's territory ($AICc = 37.81$) described

the data better than the constant model ($AICc = 41.11$), indicating that the relative female abundance in a male's territory varied among the 3 levels of male breeding success. Males that sired 3 fawns had a higher index of relative female abundance in their territory (mean \pm SE = 2.88 ± 0.30) than males that sired 2 (1.50 ± 0.30) or 1 fawns (1.82 ± 0.16 ; see Figure 1B). This result therefore supports, at least partially, our prediction 3. Notice, however, that there were only 3 males that sired 3 fawns in our data set and that there was no difference in relative female abundance in a male's territory between males that sired 1 fawn and 2 fawns.

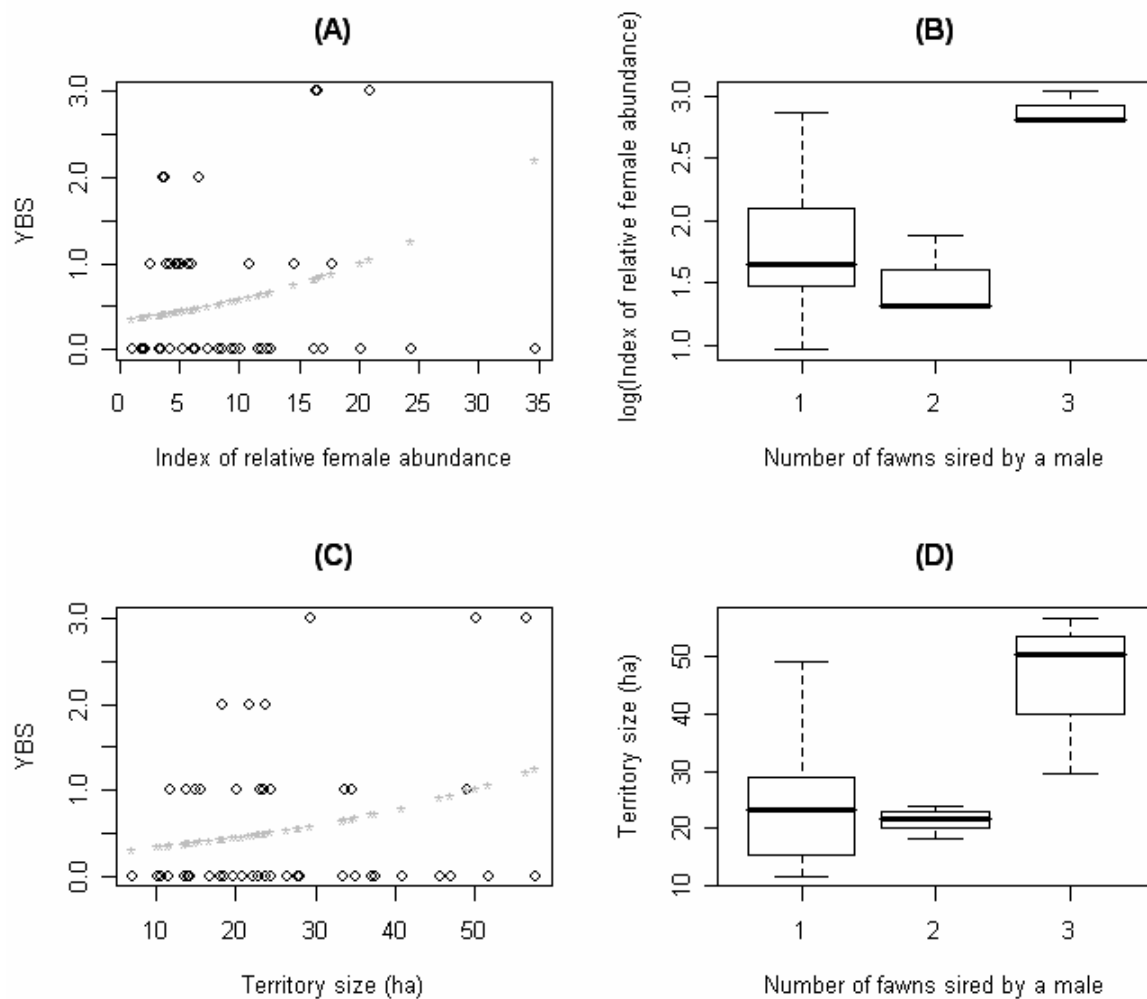


Figure 1. Variation in male yearly breeding success (YBS) with the index of relative local female abundance in his territory (A) and with male territory size (C), and variation in the log-transformed index of relative female abundance in a male's territory (B) and variation in male territory size (D) with the number of fawns sired by a male (successful breeders only).

Note: Black open circles = observed data. Grey stars = values predicted by the zero inflation generalized linear mixed model.

Effect of territory size and habitat quality on male yearly breeding success

Comparing the GLMM models, the constant model performed slightly better ($AICc = 99.47$) than the model including the effect of territory size ($AICc = 101.68$), indicating the lack of a marked effect of territory size on male YBS. However, there was a trend for an increase in male YBS with male territory size described by the equation: $E(YBS) = (1 - 0.3693) \exp(-0.8422 + 0.0267 \text{ territory size})$ (see Figure 1C). In contrast, the constant model performed much better ($AICc = 99.47$) than the model including an effect of territory habitat quality ($AICc = 104.03$). Therefore, our index of territory habitat quality had no effect on male YBS.

The linear mixed model including an effect of male YBS on territory size ($AICc = 141.68$) described the data better than the constant model ($AICc = 142.82$), indicating that territory size varied among the 3 levels of male breeding success. Notice, however, that the two models had very similar $AICc$ values. Males siring 3 fawns had a larger territory (mean \pm SE = 45.42 ± 6.31) than males siring 2 fawns (21.32 ± 6.31) or 1 fawn (24.08 ± 3.29 ; see Figure 1D). However, there was no significant difference in territory size between males that sired 1 fawn and 2 fawns. Hence, this result supports, at least partially, our prediction 4. In contrast, the linear mixed model including an effect of male YBS on the index of habitat quality ($AICc = 28.94$) performed less well than the constant model ($AICc = 33.45$), indicating that territory habitat quality did not vary among the 3 levels of male breeding success.

Effect of male phenotypic attributes on territory size

The best linear mixed model testing the effect of male body mass and age class (sub-adults vs. adults) on territory size was the model including the simple effect of body mass ($AICc = 354.95$ vs. 356.15 for the constant model). Hence, body mass had a positive effect on male territory size (mean slope \pm SE = 1.32 ± 0.84 ; see Figure 2). In contrast, the best model testing the effect of male residual antler size and age class on territory size was the constant model ($AICc = 356.15$ vs. 356.82 for the model with the simple effect of residual antler size and 356.94 for the model including the additive effects of antler size, age class and their two-way interaction term). Notice, however, that the $AICc$ values of these models were very similar, providing substantial support for these models too (see Burnham and Anderson 2002). It seems that territory size increased with male residual antler size in sub-adults (mean slope \pm SE = 0.58 ± 0.24), but was not affected in adults (0.04 ± 0.05 ; see Figure 3). These

results therefore partially support prediction 5. Notice, however, that the data set included only 4 sub-adult individuals.

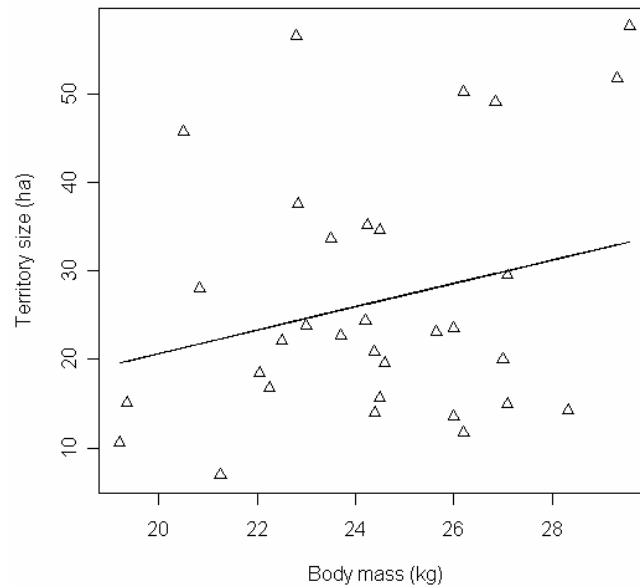


Figure 2. Effect of male body mass (kg) on territory size (ha).

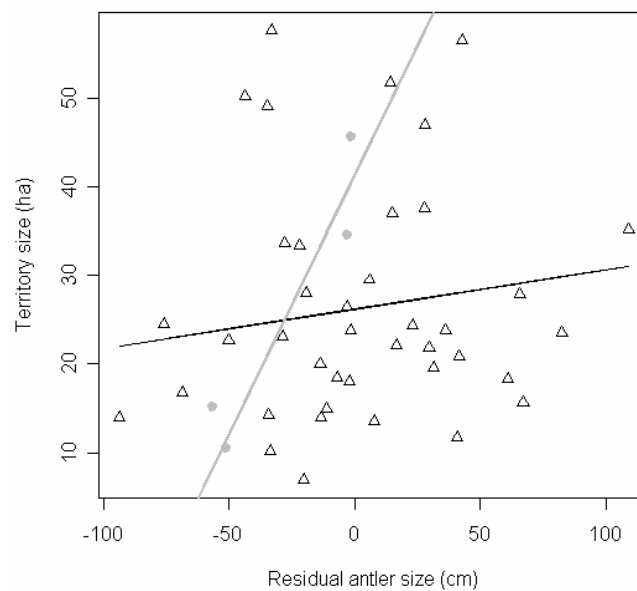


Figure 3. Effect of male residual antler size (cm; standardized to the 14th of February and then corrected for the allometric relationship between antler size and body mass; see Vanpé et al. 2007) on territory size (ha) in sub-adults (grey filled circles, grey line) and adults (black open triangles, black line).

Discussion

Our results show that female abundance within a male's territory depends on the size of his territory, as expected from prediction 1, but not on his habitat quality, contrary to prediction 2. This is contrary to expectations if we assume that females distribute themselves freely, in relation to resource distribution, as predicted by the IFD model (Fretwell and Lucas 1970). In support of predictions 3 and 4, territory size and female abundance within the territory, in turn, seem to determine male breeding success, at least partially. Finally, in support of prediction 5, male body mass in all males and antler size in sub-adults only had a positive effect on male territory size. Hence, our results do not really conform to expectations if male territoriality in roe deer was a conventional resource defence polygyny strategy (sensu Emlen and Oring 1977), because males seem to aim to defend a territory as large as possible, irrespective of its attractivity to females in terms of habitat resources.

We showed that relative female abundance in a male's territory was not related to its habitat quality, which seems to contrast with predictions under the resource defence polygyny hypothesis. These results also differ from the observations of Johansson (1996) who reported that male mating success in roe deer was related to territory quality, but not territory size: males who occupied a territory which included clover fields were more successful than other males. Strandgaard (1972) also noticed that the quality of crops influenced the number of females staying on a given territory. However, Johansson (1996) used behavioural estimates of mating success, which are certainly poor indicators of true male breeding success, particularly as multiple mating commonly occurs (Liberg et al. 1998). In addition, both studies used a subjective categorical variable to describe habitat quality based on the assumption that clover fields were the preferred resource selected by females. To our knowledge, our study is the first to use a niche analysis to determine the specific resource attributes that reflect habitat quality of a male's territory in terms of access to females. Several other studies of territorial ungulates have demonstrated a direct relationship between the quality of male territories and access to potential mates (e.g., in American pronghorn *Antilocapra americana*: Kitchen 1974; puku *Kobus vardoni* and topi *Damaliscus lunatus* antelopes: Balmford et al. 1992; impala *Aepyceros melampus* and waterbuck *Kobus defassa*: Jarman 1974; in a territorial population of red deer *Cervus elaphus*: Carranza 1995). However, none of these studies had access to the data of a reliable estimate of male breeding success which are essential to fully test the resource defence polygyny mating hypothesis.

The absence of a relationship between the index of habitat quality and relative female abundance in a male's territory observed in our study may be due to several factors. First, our estimation of relative female abundance within a male's territory was based on the assumption that local female density in winter was a relevant estimate of local female density in summer, since female home ranges are globally stable between seasons (Hewison et al. 1998). However, some seasonal migrations can occur in yearling and 2- and 3-year-old females between mother-fawn separation and home range establishment (see Wahlström and Liberg 1995). This may potentially result in a redistribution of young females between the winter and rut periods, but concerns only a certain proportion of the total number of females. Second, the use of pellet group counts to reflect spatial variation in relative deer abundance has not been fully tested at the present time. However, it has been suggested that pellet-group counts should provide an informative index of relative animal abundance (e.g., Forsyth et al. 2007), especially in northern areas (such as Scandinavia), where pellet decay rate is negligible during winter. Third, although our index of habitat quality integrated a number of habitat variables such as habitat type, vegetation cover, and the biomass of various kinds of plants, it may still not adequately reflect the suitability of an area for females. Fox predation, for example, is known to be a strong determinant of summer fawn survival and variation in female reproductive success at Bogesund (Kjellander et al. 2004a). Hence, predation avoidance may swamp the role of food resources and vegetation cover in determining female distribution. However, a preliminary analysis suggests that the number of fox dens present within a male's territory has no effect on the index of relative female abundance in a male's territory or on male breeding success (C. Vanpé, unpubl. data). A fourth possibility is that females may not be free to distribute themselves in relation to resources because, for example, of social constraints. Indeed, the IFD model is not appropriate when some individuals can monopolize resources by securing the highest quality areas while forcing inferior competitors into suboptimal habitats (e.g., in the case of territoriality or dominance hierarchies, "Ideal Despotism Distribution" model, Fretwell 1969). Female roe deer are considered as non-territorial, except maybe during fawning site defence (Liberg et al. 1998), because they commonly live in overlapping home-ranges. However, this overlap often concerns close relatives (see Liberg et al. 1998), with matrilineal associations common due to extensive female philopatry (see Hewison et al. 1998). Hence, we cannot rule out the possibility that dominance relationships between unrelated females impose a constraint on female ranging behaviour. Indeed, female home range size seems to decrease with increasing population

density (Kjellander et al. 2004b) and aggressive behaviours between females seem to be common (e.g., Johansson 1996; Börger 2006).

If females do not fully distribute themselves as a function of resources, males will be unable to “predict” the distribution of potential mates by anticipating how resource distribution influences female dispersion. Hence, in contrast to the expectations under resource defence polygyny (Elmen and Oring 1977), males should show no interest in competing for resource-rich sites to establish their zone of dominance. We showed that, to some degree, local female abundance in a male’s territory increased with territory size and, as a result, had a positive influence on male YBS. This suggests that, to maximize fitness, males should attempt to enlarge their territory in order to maximize their chance of encountering receptive females. Interestingly, previous studies have reported that although roe bucks have to re-establish their territory each year in spring, most of them show high fidelity to the area where they established their first territory (Liberg et al. 1998). In addition, territories are remarkably stable from year to year, with little change of borders and size (e.g., Bramley 1970; Johansson 1996; Linnell and Andersen 1998), even when the distribution of resources or females changes markedly between years (Strandgaard 1972). Territory borders may even persist after the death of an owner and the take-over of a new occupant (Strandgaard 1972; Cederlund et al. 1994), usually an immigrating buck or a non-territorial sub-adult (Cederlund et al. 1994; Johansson 1996). These observations suggest that males do not constantly attempt to enhance their mating success by either enlarging their zone of dominance or by occupying areas particularly favoured by females (Hewison et al. 1998), contrary to expectations for a conventional resource defence polygyny strategy.

Our results also showed that body mass tended to have a positive effect on territory size in all males, and interestingly, that residual antler size had a strong positive effect on territory size in sub-adults only. Hence, among territorial sub-adults, heavy individuals with large antlers are the best competitors, able to defend the largest territories, with the highest access to mates. This also suggests that male phenotypic traits, and especially antler size, which reflect the ability of males to fight are particularly important during the key period where males establish their first territory. These traits, therefore, partially determine access to mates for a male in his first year of territoriality, but also probably for his entire lifetime, because of the pronounced spatial stability of both sexes. In addition, since we found that territory size and relative female abundance in a male’s territory partially affected his breeding success, it is likely that body mass and antler size of sub-adult males will influence both current and lifetime breeding success. Hence, the establishment of a male’s first territory

may play a more important role in determining fitness than previously thought. The identification of the proximate and ultimate determinants of the characteristics of a male's first territory is thus essential to better understand variation in male fitness in roe deer.

It should be noted, however, that we did not find very strong relationships between male YBS and territory size and between male YBS and relative female abundance in a male's territory. In addition, while the most successful males (siring at least 3 fawns) had the largest territories and, as a result, access to the highest number of females, we did not observe any differences between males siring 1 fawn and males siring 2 fawns in either territory size or relative female abundance. This could be due to low sample size, but may also be explained by the fact that males probably do not have full mating monopoly inside their territory. Indeed, in roe deer, 30 to 50% of females make short excursions outside their normal home range during the rut, traversing several territories, and potentially consorting and mating with other males, before returning (see Liberg et al. 1998 for more details). In addition, females whose range overlaps several male territories move frequently between them during oestrus, being courted and mated repeatedly, by one or more territory holders (Liberg et al. 1998). The above suggests that female roe deer may take an active role in mate searching and mate choice, and this may explain why male breeding success is not more closely linked to the number of females present within his territory.

To sum up, although territoriality of male roe deer has certainly evolved as a tactic for ensuring access to mates (Hewison et al. 1998), our results suggest that it does not entirely conform to a resource defence polygyny strategy (*sensu* Emlen and Oring 1977). We speculate that social constraints may govern, at least partly, the distribution of female roe deer at the local scale, and that variation in the number of females within a male's territory probably depends mainly on the resultant annual variation in female distribution (Bramley 1970; Strangaard 1972), since territory boundaries and size are highly stable between years. Our results are therefore in agreement with the view that male territoriality conforms to an "always stay" and "low risk - low gain" strategy in roe deer (see Linnell and Andersen 1998), where males do not compete intensely for territories and mating (at least once they have established their first territory). Rather, males gain the benefits of site familiarity and reduced frequency of dangerous fights with rival males by remaining in the same area where they are dominant (Owen-Smith 1977). The result of successful territory establishment is thus more likely to be the delimitation of an area in which bucks can court and mate without interference because they are dominant, rather than direct and automatic access to females (Cederlund and Liberg 1995; Hoem et al. 2007). In this way, roe deer territoriality may differ somewhat from

territoriality of most other ungulates, for which previous studies have demonstrated a direct relationship between territory quality and mate access (e.g., in impala and waterbuck: Jarman 1974; American pronghorn: Kitchen 1974; puku and topi antelopes: Balmford et al. 1992), suggesting a better fit with the conventional resource defence polygyny model than for roe deer. We therefore suggest that resource defence polygyny should not be considered as a homogeneous mating strategy. There are actually no discrete distinctions between the different types of polygynous mating systems described by Emlen and Oring (1977) and, as Jarman (1974) pointed out, “any attempt to subdivide a continuum creates problems”. The variability of polygynous mating systems would be probably more realistically described as a continuum extending from resource defence polygyny to female defense polygyny, with roe deer occupying an intermediate position.

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PART 5

A FIRST STEP TOWARDS THE FEMALE POINT OF VIEW: FEMALE MULTIPLE MATING



**Roe does
(photograph by Olivier Villa)**

PAPER 6

Multiple paternity is likely but infrequent in the polytocous European roe deer

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Abstract

Although multiple paternity (defined as the presence of at least two fathers for a single litter) has been documented in various polytocous taxa, including birds and mammals, there is so far little evidence for it in large herbivores. Because roe deer females are polytocous and mate repeatedly during oestrus, they are likely candidates for multiple paternity. To test for this, we analysed a panel of microsatellite markers and performed paternity analyses in two wild contrasted populations of European roe deer in Europe (Bogesund in Sweden and Trois Fontaines in France). We found that 24.2% of litters (2 of 15 and 13 of 49 at Trois Fontaines and Bogesund, respectively) were potentially sired by more than one male. However, in 13 of the 15 litters with potential multiple paternity, at least one fawn was assigned a father with only 80% confidence. Of the other two cases (one in each population), only one (from Trois Fontaines) provided strong support in favour of multiple paternity, since both fawns were assigned a different father with 95% confidence and neither had any mismatched locus with their putative father. We conclude that multiple paternity likely occurs in roe deer, but is infrequent. That female roe deer participate in multiple mating could be a mechanism to ensure fertilisation during their short and single annual oestrus, rather than a way to increase genetic diversity.

Keywords: *Capreolus capreolus*; fertilisation insurance; microsatellites; multiple mating; paternity analysis; territoriality

Introduction

Historically, male mating systems and reproductive success in mammals have been investigated by intensive behavioural studies, monitoring the number of copulations or social associations during which a male may have exclusive access to a female (e.g., Clutton-Brock 1988). However, the use of behavioural observations to quantify reproductive success may lead to incorrect assignment of offspring to particular individuals, especially when multiple mating occurs. With the recent development of molecular tools (particularly microsatellite markers) and sophisticated analytical methods in population genetics, an alternative approach is now available for assessing male mating tactics and reproductive success using paternity analysis (e.g., Marshall *et al.* 1998). This approach allows assessment of male reproductive success in species where direct observation of mating behaviour is virtually impossible (e.g., in dense habitat or at night), and has dramatically altered our understanding of breeding tactics of many species, for example, by revealing extra-pair copulations, “sneaky” tactics and multiple paternities (e.g., Birkhead *et al.* 1990; Gibbs *et al.* 1990; Amos *et al.* 1993; Goossens *et al.* 1998; Coltman *et al.* 1999; DeYoung *et al.* 2002).

Multiple paternity is a result of insemination of a female by at least two males to produce a single litter or brood. The discovery of multiple paternity in the wild has important implications in terms of population genetics. By enhancing genetic diversity among offspring of a given litter, multiple paternity can play an important role in the maintenance of genetic variation, influencing effective population size (Sugg & Chesser 1994). Although multiple paternity (defined as the presence of at least two fathers for a single litter) has been documented in various polytocus taxa, including birds (e.g., Petrie & Kempenaers 1998) and mammals (e.g., Birdsall & Nash 1973; Schenk & Kovacs 1995; Say *et al.* 1999; Waser & DeWoody 2006), there is so far little evidence for it in large herbivores. Multiple paternity has been documented in a free-ranging population of pronghorn *Antilocapra americana* (Carling *et al.* 2003) and in two enclosed populations of white-tailed deer *Odocoileus virginianus* (De Young *et al.* 2002; Sorin 2004). However, multiple paternity in large herbivores has not yet been investigated in a territorial species such as the European roe deer *Capreolus capreolus* (Andersen *et al.* 1998).

Male territoriality is commonly viewed as a mating tactic to ensure paternity by monopolising oestrous females present within a defined area of dominance (Owen-Smith 1977). However, a female’s home range may overlap several territories (Owen-Smith 1977) and females can move between neighbouring territories during the rut, encountering several

potential mates (e.g., in roe deer: Liberg *et al.* 1998). The discovery of multiple paternity in a territorial ungulate species would require us to revise our view of territorial mating systems in large herbivores, particularly with regard to party size, the operational sex ratio (see Emlen & Oring 1977) and, hence, the opportunity for sexual selection. Numerous hypotheses have been proposed to understand multiple mating by females in terms of direct benefits (e.g., fertilisation insurance, access to food or nuptial gifts, avoidance of male harassment; Reynolds 1996) or genetic benefits (e.g., sperm competition, increasing genetic diversity among offspring via multiple paternity; Reynolds 1996; Newcomer *et al.* 1999). A high level of multiple paternity would lend support for the genetic diversity hypothesis, while a low level of multiple paternity in populations where most females successfully breed would suggest that multiple mating is a mechanism to ensure fertilisation.

Roe deer females are polytocous (up to four fawns, most often two; Andersen *et al.* 1998). During oestrus, females are courted and mated repeatedly and frequently (Danilkin & Hewison 1996), hence, roe deer females are likely candidates for multiple paternity. However, there is only one very short annual oestrus (24-36 hours; Hoffmann *et al.* 1978) and, although multiple mating occurs, it is not clear whether a female mates repeatedly with the same partner or with different males. Using a panel of microsatellite markers and paternity analyses, we investigated multiple paternity in roe deer from two contrasted and intensively monitored populations.

Materials and methods

Study populations

Bogesund is a 2,600 ha area of fragmented habitat in central eastern Sweden (59°23'N, 18°15'E), while Trois Fontaines is a 1,360-ha enclosed forest in eastern France (48°43'N, 2°61'E) (see Vanpé *et al.* 2007 for further details). These populations have been intensively monitored by Capture-Mark-Recapture (see Gaillard *et al.* 2003 and Kjellander *et al.* 2006 for further details) since 1988 and 1975, respectively. Each winter, roe deer are captured and individually marked. Occasionally, some are also shot or removed for release elsewhere. Since 1997 at Bogesund and 1985 at Trois Fontaines, new-borns are marked in May-June. Mother-offspring relationships are assessed by direct observation of fawns with their mothers just after birth or during autumn.

Tissue sampling and molecular analysis

Tissue samples were collected for DNA genotyping from all individuals caught for the first time (from 1988 and 1994 at Bogesund and Trois Fontaines, respectively). We sampled a total of 1757 individuals at Bogesund and 1298 individuals at Trois Fontaines. Genotyping was performed using 21 microsatellite markers at Bogesund (see Vanpé *et al.* in press for details) and 11 of these same markers at Trois Fontaines (because of higher polymorphism at this site). The total exclusionary power of the set of microsatellite markers used at Bogesund and Trois Fontaines was 0.9997 and 0.9989, respectively, when one parent was known, and 0.9850 and 0.9772, respectively, when both parents were unknown.

Prior to paternity analyses, we checked for Hardy-Weinberg equilibrium for each locus separately and globally with exact tests using GENEPOP 3.4 (Raymond & Rousset 1995) and the Markov chain method (1000 dememorizations, 100 batches and 5000 iterations per batch). Linkage disequilibrium between pairs of loci was tested with GENEPOP by computing Fisher's exact test for each contingency table of allele frequencies for all pairs of loci using a Markov chain (1000 dememorizations, 100 batches and 5000 iterations per batch). As performing multiple tests tends to increase type I errors, we implemented the false discovery rate (Benjamini & Hochberg 1995) using the GeneTS package in the R 2.2.1. software. The above tests were performed on a subset of the whole sample (i.e. individuals born in 1992 at Bogesund and 2003 at Trois Fontaines, the years with the highest sample size) in order to reduce multigenerational effects. In both populations, there was no significant heterozygote excess nor deficit at any single locus, with the exception of a deficit for the BM757 locus at Trois Fontaines ($p = 0.021$). A deviation from Hardy-Weinberg equilibrium at a single locus is not likely to seriously bias likelihood values estimated across many loci and so we retained this locus for paternity analyses. Following correction for multiple comparisons, there was no evidence for significant linkage disequilibrium between any pair of loci in either population.

Paternity analysis

Parentage was assessed using a likelihood-based approach implemented in CERVUS 2.0 (Marshall *et al.* 1998). For each parent-offspring pair, the program calculates a LOD score (logarithm of the likelihood ratio). This score is the likelihood of maternity and paternity of a particular candidate parent relative to an arbitrary individual. Using allele frequency data from the population, the program runs a simulation to estimate the critical difference in LOD score between the most likely and next most likely candidate parent (δ) necessary for assignment at the 95% or 80% confidence levels. The simulation incorporates the definition

of user-defined input parameters such as the total number of candidate parents, the proportion of these parents that have been sampled, the frequency of gaps and the genotyping error rate in the genetic data. The observed rate of missing data was estimated across all typed samples by the allele frequency module of CERVUS and set at 98.7% of loci typed at Bogesund and 96.7% at Trois Fontaines. Since as long as the error rate is fixed to a value greater than zero, the choice of error rate does not have a major impact on confidence or success rate (San Cristobal & Chevalet 1997), we fixed the error rate to 1% for both populations.

In each population, and for the fawns of each cohort, we listed the candidate fathers and mothers sampled based on long-term CMR, hunting databases and yearly field observations of animals. Both males and females were considered to be candidate parents for a given fawn in a given cohort if they were defined as alive and potentially active in the previous rut. The first potential participation in the rut was set at 1 year of age for females and 2 years of age for males (based on the age of sexual maturity in roe deer). The last potential participation in the rut for an individual was defined at Bogesund in relation to the moment it was either found dead or last recorded alive, and at Trois Fontaines in relation to the moment it was either found dead or 3 years after it was last recorded alive (about 85% of males and 92% of females survive from one year to the next at Trois Fontaines; Gaillard *et al.* 1993). When the age of a candidate parent was estimated from tooth wear, the first year of potential participation in the rut was evaluated by using a conservative criterion in order to limit the effects of age estimation errors in the list of candidate parents for the fawns of each cohort (Hewison *et al.* 1999). As a result, some individuals may have been included in the list of candidate parents for the fawns of a given cohort although they were not actually candidates, but not the reverse. At Trois Fontaines, the total number of potential parents for the fawns of each cohort was estimated based on CMR methods (e.g., Gaillard *et al.* 2003). At Bogesund, the proportion of known candidate parents sampled varied among cohorts, but was always higher than 80% for fathers and 76% for mothers (see Vanpé *et al.* in press). In order to take into account potential unknown candidate parents in this population, we decided to fix the proportion of candidate parents sampled to a conservative value of 75% for all years and for both sexes. The total number of candidate parents present in Bogesund population was then calculated for the fawns of each cohort as the total number of sampled candidate parents present in the population divided by 0.75.

442 fawns at Bogesund and 161 fawns at Trois Fontaines were successfully assigned a father at the 80% confidence level. Our null hypothesis was that paternity for each litter could be assigned to a single male. Based on identification of loci mismatches between known

mothers and their fawns, we estimated a genotyping error rate of 3.7% at Bogesund and 8.7% at Trois Fontaines. Because, on average, 0.77 and 0.95 locus per individual was thus expected to be erroneous at Bogesund and Trois Fontaines respectively, we restricted our analyses to polytocus litters for which all fawns had no more than 1 mismatched locus with their purported father to avoid erroneous conclusions due to genotyping errors. We firmly rejected the null hypothesis when at least two offspring within a given litter were assigned different males with 95% confidence and each had no mismatched locus with their purported father.

Results

At Bogesund, 47 twin litters and 2 triplet litters were assigned fathers. Of these, 13 (27%) revealed possible multiple paternity (Table 1a) involving 27 fathers, of which 17 were assigned with 80% confidence and 10 with 95% confidence. Fawns within a single litter were assigned different fathers with 95% confidence in only one case, however both of these fawns had one mismatched locus with their putative father (Table 1a).

Table 1. Details on paternity assignments of litters sired by more than one male at Bogesund (A) and Trois Fontaines (B).

(A)

	all fathers assigned at 95% confidence level	all fathers assigned at 80% confidence level	at least 1 father assigned at 80% confidence level	total number of litters
all fathers had 0 mismatch with their fawn	0 (22)	0 (0)	4 (9)	4 (31)
all fathers had 1 mismatch with their fawn	1 (1)	2 (2)	0 (2)	3 (5)
at least 1 father had 1 mismatch with its fawn	0 (2)	2 (3)	4 (8)	6 (13)
total number of litters	1 (25)	4 (5)	8 (19)	13 (49)

(B)

	all fathers assigned at 95% confidence level	all fathers assigned at 80% confidence level	at least 1 father assigned at 80% confidence level	total number of litters
all fathers had 0 mismatch with their fawn	1 (5)	0 (1)	0 (6)	1 (12)
all fathers had 1 mismatch with their fawn	0 (0)	0 (0)	0 (0)	0 (0)
at least 1 father had 1 mismatch with its fawn	0 (1)	0 (0)	1 (2)	1 (3)
total number of litters	1 (6)	0 (1)	1 (8)	2 (15)

Note: Numbers represent the number of litters for which paternity was shared between at least two males. Numbers in brackets represent the total number of polytocus litters in each category.

At Trois Fontaines, we assigned paternity for 15 litters, of which only 2 (13%) revealed possible multiple paternity (Table 1b). These litters involved 4 fathers, of which 1 was assigned with 80% confidence and 3 with 95% confidence. Fawns within a single litter were assigned different fathers with 95% confidence in only one case, and, in this case, neither fawn showed any mismatched locus with their putative father (Table 1b).

Discussion

In total, we identified 15 litters (13.3% at Trois Fontaines and 26.5% at Bogenlund of all polytocous litters) for which paternity within a given litter was shared between two males, indicating, for the first time, potential multiple paternity in roe deer. We cannot exclude the possibility, however, that errors in paternity assignment accounted for some of these observations. Indeed, in 13 of these litters, at least one fawn was assigned a father with only 80% confidence. In the other 2 cases (one in each population), only one (Trois Fontaines) provided strong support in favour of multiple paternity, since both fawns were assigned a different father with 95% confidence and neither had any mismatched locus with their putative father. Hence, multiple paternity in roe deer is, at best, a rare event.

In fact, considering only cases where at least two offspring were assigned different fathers with 95% confidence and each had no mismatched locus with their purported father, we rejected our strict null hypothesis of no multiple paternity for none of 22 polytocous litters (0%) at Bogenlund and 1 of 5 polytocous litters (20%) at Trois Fontaines. In comparison Carling *et al.* (2003) reported multiple paternity in 44% of polytocous litters assigned with 80% confidence in American pronghorn, but only one case for which both offspring were assigned different fathers with 95% confidence. In white-tailed deer, De Young *et al.* (2002) and Sorin (2004) reported multiple paternity in 26% and 22% of polytocous litters assigned with 95% confidence respectively, although the former study concerned a captive population at unusually high density.

In our study, although the most likely father differed between litter-mates in 15 cases, there was an alternative candidate with a positive LOD score (see Marshall *et al.* 1998) and few mismatched loci who was common to all litter members in 11 of them. In addition, there were often less (or the same number of) mismatches between offspring and this alternative father than with the purported father. In these cases, the alternative male could have fathered both fawns, but erroneously not be identified as the most likely father by CERVUS. This could be either because of genotyping error leading to mismatches between the true father and

the fawn and/or because the two candidate fathers were related (e.g., full or half sibs) and therefore had genotypes which were compatible with the fawn. Even in the only case for which paternity was assigned at the 95% confidence level for both fawns and no mismatches occurred, the second most likely father was common to both fawns and also had no mismatches with either. Only 4 litters (all Bogesund) included siblings that did not share any likely father.

As our results indicate that the frequent multiple mating of females seems to lead to, at most, very few multiple paternities in roe deer, the genetic diversity hypothesis is not a likely candidate to explain this behaviour. We suggest, instead, that females mate repeatedly with one or more males to ensure fertilisation, and that this is particularly important for roe deer, given that females have a single short annual oestrus. This fertilisation insurance mechanism ensures that adult females have a very high probability of conceiving each year (typically > 0.95, Gaillard *et al.* 1992; Hewison 1996). In contrast, the genetic diversity hypothesis, via postcopulatory or cryptic choice, has been suggested to explain multiple mating by females in American pronghorn (Carling *et al.* 2003) where active female mate choice and multiple ovulation occur. Further research is needed to clarify the adaptive function of multiple mating and multiple paternity in ungulates.

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DISCUSSION



**A roe buck engaging in a courtship, sniffing a doe's genital area
(photograph by Olivier Villa)**

I. SYNTHESIS OF MAIN RESULTS

The main results of this study concern the variance in breeding success among males, the determinants of this variance, and the evolution of territoriality in roe deer. The originality of this work lies with the combined use of molecular techniques, longitudinal capture-recapture data and ecological field work to investigate in details the mating system of roe deer in two free-ranging populations, using an evolutionary approach. I present the first ever data, based on genetic paternity analyses, on the opportunity for sexual selection and the sexually selected traits in a territorial ungulate with low sexual size dimorphism.

- **PAPER 1:** As expected for a species with low sexual size dimorphism, the variance in male (minimal) lifetime breeding success is low in roe deer, suggesting a low opportunity for sexual selection. In particular, it is much lower than that of highly polygynous and sexually dimorphic species such as red deer, bighorn sheep and Soay sheep.
- **PAPER 2:** Yearly breeding success is lower among 2 year-old males than 3-8 year olds, peaks in prime-age males (3-8 years of age), and then declines for males older than 8 years of age. Successful 2-year-old breeders may include the few individuals of high phenotypic quality which are able to establish a territory at this early age. The occurrence of senescence might be linked to the loss of dominance of some low quality males older than 8 years of age.
- **PAPER 3:** Antler size mainly reflects male age and body mass, and is more resilient to variation in environmental conditions such as climate, food resources and density. Hence, antler size in roe deer appears to be a honest signal of male phenotypic quality. By choosing their sexual partners on the basis of their large antlers, females might thus ensure that they mate with a high quality male. Males may also use antler size of rival males as a cue to assess the possibility of winning a fight in order to control and monopolize more females for reproduction.
- **PAPER 4:** Both male body mass and antler size (not corrected for body mass) have a positive effect on male yearly breeding success, through their role in fighting ability and dominance, but also probably in female mate choice, as honest signals of male quality. The low sexual size dimorphism in roe deer may have evolved because of the key role of body mass in the fitness of both males and females.

- **PAPER 5:** Territory size, but not the quality of the habitat within the territory, positively affects male access to females and male yearly breeding success. Territoriality conforms to an “always stay” and “low risk - low benefit” tactic, where males, once they have established their first territory, do not compete intensely for territories and mating by attempting to enlarge their area of dominance and/or to occupy an area attracting for females in terms of resources. Male territoriality in roe deer thus differs from a conventional resource defence polygyny mating system.
- **PAPER 6:** Multiple paternity occurs, but rarely, in roe deer. Although females have a single short oestrus, the proportion of reproducing adult females is generally very high. Hence, females may mate repeatedly with one or more males to ensure fertilisation, rather than to increase genetic diversity within a given litter.

II. DISCUSSION AND PERSPECTIVES

II.1. VARIANCE IN MALE BREEDING SUCCESS AND THE OPPORTUNITY FOR SEXUAL SELECTION IN ROE DEER

II.1.1. First data on male lifetime breeding success in roe deer based on molecular analyses

This study provides the first data on the distribution of paternities among males and the variance in male breeding success in a wild population of European roe deer, based on genetic analyses (Paper 1). Results show that roe bucks sired between 0 and 6 fawns per year, and between 0 and 14 fawns over their entire life span, with a mean of 4.54, a variance of 15.5, and a standardized variance in lifetime breeding success (LBS) of 0.75. In addition, after removing all fawns with unknown mothers ($N = 37$), the fawns of a single known-aged male come from up to 3 different females, but note that this is a conservative value. Hence, as expected, in line with the low level of sexual size dimorphism of roe deer (Andersen *et al.* 1998), I obtained a low standardized variance in male LBS ($I_m = 0.75$), characteristic of a weakly polygynous mating system with low opportunity for sexual selection.

I could not include the results of the Trois Fontaines paternity analyses in Paper 1, because the genetic data for this population were obtained right at the end of my Ph.D. I thus attempt here to compare patterns of variance in male breeding success observed in the two studied populations, Bogesund and Trois Fontaines. Due to practical problems (in particular, a large part of the DNA samples from Trois Fontaines, including adults from the first study years, was damaged during storage and, as a result, could not be genotyped), I could only estimate the variation in yearly breeding success (YBS), but not minimum LBS, among successful breeders using the Trois Fontaines genetic data. I observed basically a similar distribution of YBS in both populations (see Figure 16). In both populations, whereas more than 50% of successful breeders sired a single fawn, very few males had a YBS > 3 fawns (< 8%). This provides confirmation of the results found at Bogesund, although I could not compare, in the same way, data on male LBS between the two populations.

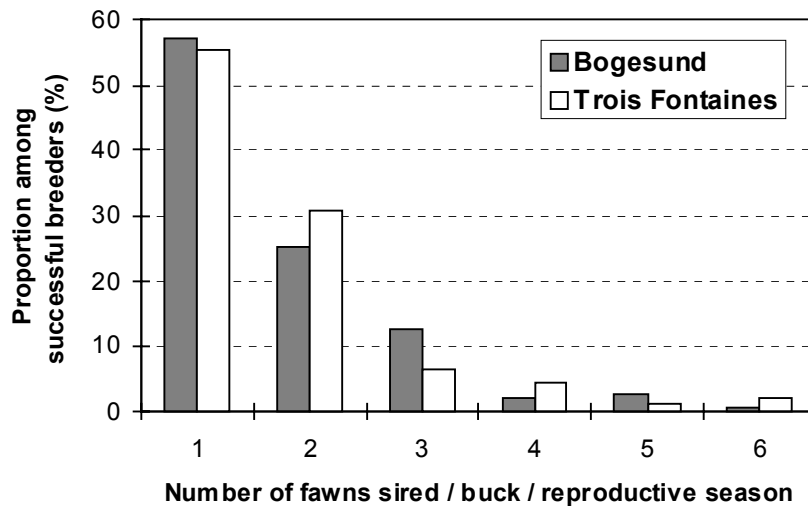


Figure 16. Distribution of paternities of successful breeders at Bogesund and Trois Fontaines.

I should, however, be cautious before drawing conclusions on the absolute level of polygyny in roe deer. Several limits may have affected the estimates of variance in male LBS at Bogesund.

First, in a wild free-ranging population of roe deer, it is impossible to catch all fawns born in a given year, especially because of the dense habitat, the cryptic nature and the hiding behavioural tactic of fawns after birth (Espmark 1969), and the high number of fawns produced each year (almost all females > 2 years of age give birth most often to two fawns). It is, however, difficult to estimate the proportion of fawns caught each year at Bogesund. We know that about 95% of females are fertilized each year and that does typically give birth to 2 fawns each year (Gaillard *et al.* 1992; Hewison & Gaillard 2001). Based on this information and the estimate of the number of potential mothers present each year on the study area, I can roughly estimate that between 2 and 32% of fawns were caught each year at Bogesund (mean \pm SD = 13.4 ± 9.5). Notice, however, that these estimates are highly conservative (these are minimum estimates). The capture success was very low during the first years of the study (from 1988 to 1991; mean \pm SD = 2.4 ± 0.9 %) due to a low effort and inexperienced field-worker. Hence, I restricted the analysis of breeding success to the cohorts after 1991 (mean estimated proportion of fawns caught \pm SD = 16.4 ± 8.5). Still, as a consequence of the low proportion of fawns caught in the population each year, the number of non-breeders among males was likely to have been over-estimated, and the success of most males should have been under-estimated. Unfortunately, it is very difficult to assess the magnitude of this biases

on the resultant variance in male breeding success. However, while the mean LBS was clearly under-estimated, it is unclear whether the variance was.

Second, in this study, because the fate was unknown for a proportion of the sampled fawns which were caught as neonates, we used the number of born offspring sired by an individual, as a proxy of individual fitness. Although this measure does not integrate a juvenile survival component, there is no evidence that fawn mortality varied systematically between the offspring of different bucks and I would expect fawn survival to be almost exclusively affected by maternal rather than by paternal influences in roe deer (Gaillard *et al.* 2000a). As a consequence, this potential problem should not have biased much my estimation of male breeding success, except maybe if the most successful males are systematically in the best habitats where fawn survival is higher, in particular during years with harsh climatic conditions (Pettorelli *et al.* 2005).

Finally, I could estimate male LBS for only a low sample size of males, for which breeding success was available for the whole lifespan and which died of natural causes. To reduce the bias toward individuals dying young, I also restricted my analyses to male cohorts born prior to 1999 for which all, or almost all, males had died at the end of the year 2005. As a result, the estimation of mean and variance of male LBS was based on a sample size of only 24 males, despite having genotyped a total of 231 potential candidate fathers. It is thus important to confirm the results found by estimating LBS with a larger sample size, including entire cohorts and to compare estimates of variance in LBS between different cohorts. In roe deer, strong cohort effects have been shown on fawn survival (see Gaillard *et al.* 1993b, 1997).

To sum up, although several biases may have affected the estimate of variance in male LBS, I have no reason to believe that these biases may have strongly under-estimated it to the extent that the variance in roe deer could actually reach values similar to highly polygynous and dimorphic ungulate species. I am thus confident that there is a low level of polygyny in roe deer. In addition, my results are in agreement with what was predicted based on the actual knowledge of roe deer life-history (see Hewison *et al.* 2005). However, although I found a low variance in male LBS in roe deer, the estimated value was somewhat larger than expectations based on observations of territorial behaviour. In roe deer, almost all males of three years of age or older are commonly thought to be capable of defending a territory, direct fights over territories are quite rare and loss of territory tenureship is almost exclusively due to the death of the territorial male (see Hewison *et al.* 1998; Liberg *et al.* 1998). Hence, male-male competition for access to mates is commonly thought to be low (Hewison *et al.* 1998),

although solid data are scarce. My results showed, however, that of the 24 males for which we could estimate LBS at Bogesund, the 3 most successful males (13% of candidate fathers) sired at least 10 fawns each, representing together 33% of the assigned fawns (Paper 1). This suggests a quite high reproductive skew among males, raising the question of the factors that are responsible for this variance in breeding success among males in this territorial species with low sexual size dimorphism.

II.1.2. An attempt to compare estimates of the variance in male lifetime reproductive success between different ungulate species

There are few empirical estimates of male LRS or LBS in large mammals in the literature for comparison with my results on roe deer (see Appendix 1), and comparisons between studies are difficult because of differences in methods and criteria that may cause bias (Coltman *et al.* 1999a). First, some studies are based on behavioural observations of mating and courting behaviours (e.g., Clutton-Brock *et al.* 1982, 1988; Börger 2006), whereas others used genetic paternity assignment (e.g., Marshall 1998; Coltman *et al.* 1999a; this study). Behavioral observations may tend to underestimate the true success of dominant males and overestimate the contribution of low-ranking males (e.g., in red deer: Pemberton *et al.* 1992). Second, some studies include the survival of offspring as a component of male lifetime reproductive success (LRS estimate; e.g., Clutton-Brock *et al.* 1988; Marshall 1998), whereas others do not (LBS estimate; e.g., Coltman *et al.* 1999a; this study). However, offspring survival should be almost exclusively affected by maternal rather than by paternal influences (e.g., Gaillard *et al.* 2000a). Hence, although LRS and LBS are not strictly comparable, comparisons between studies using LRS and LBS to estimate the variance in male reproductive success should be globally valid, except if strong correlation occurs between male reproductive success and habitat quality through fawn survival (see above). Third, some studies include all males (e.g., Clutton-Brock *et al.* 1988; Coltman *et al.* 1999a, 2002), whereas others include only males that reached the age of sexual maturity (e.g., Clutton-Brock *et al.* 1982; this study) and/or successful breeders (e.g., Clutton-Brock 1987; Coltman *et al.* 1999a; this study). The variance in male LRS is expected to be substantially lower when considering only those males that successfully bred than among all males or even all mature males (see Clutton-Brock *et al.* 1988; Marshall 1998; Coltman *et al.* 1999a; this study). Fourth, some studies (e.g., Coltman *et al.* 1999a) consider only entire cohorts (i.e. only cohorts for which all individuals are dead in order to avoid bias linked to low quality males

which die first), whereas others (e.g., Clutton-Brock *et al.* 1982; Pemberton *et al.* 1999) do not. It is important to consider entire cohorts, because nonbreeders make a significant contribution to the estimate for the total opportunity for selection. In addition, LBS can be influenced by environmental conditions in the year of birth (e.g., population density, climate; Rose *et al.* 1998; Coltman *et al.* 1999b).

In Paper 1, I attempted to compare my results on the standardized variance in male LBS in roe deer with published data on other ungulate species for which methods of estimation of male LRS or LBS were as similar as possible with the methods I used (see studies in grey in Appendix 1). All but one of these studies were based on molecular analyses. I was indeed obliged to include the behavioural study on American pronghorn in order to include data on a low sexual size dimorphic species for comparison with roe deer. All but one (“LRS” was estimated for only 6 seasons in bighorn sheep; Coltman *et al.* 2002) of these studies estimated LRS over the entire lifetime. These studies also usually included all males or all mature males. Hence, although all the methods of these 5 studies were not strictly identical, my comparative analysis should be globally valid because I did not analyse absolute values of variance in male LRS but rather their relative position on the continuum of opportunity for sexual selection based on their I_m values (see Paper 1). As expected, I found that roe deer had a much lower I_m value ($I_m = 0.75$) than highly dimorphic species, such as red deer (5.97), bighorn sheep (4.52) or Soay sheep (3.46), but only a slightly lower I_m value than the American pronghorn (1.08), which has a level of sexual size dimorphism intermediate between roe deer and the above-cited highly dimorphic species (see Appendix 1 and Paper 1).

II.1.3. New insights on the pattern of variation in the opportunity for sexual selection among ungulate species

As sexual selection theory predicts (Darwin 1871), when the opportunity for sexual selection is strong, a few males are highly successful at mating while many other males go unmated. A close relationship was thus expected between party size, level of sexual size dimorphism, variance in male reproductive success and the opportunity for sexual selection in ungulates (Clutton-Brock *et al.* 1977; Alexander *et al.* 1979; Harvey & Mace 1982). Jarman (1983) thus suggested that in African antelopes, a continuum of opportunity for sexual selection may occur between monomorphic and monogamous species at the lower end with similar life-history traits in both sexes to highly dimorphic and polygynous species at the upper end with contrasted life-history traits between males and females. In ungulates, in

agreement with this prediction, species with high sexual size dimorphism and high polygyny level, such as red deer, bighorn sheep or Soay sheep, have a high variance in male reproductive success and so a strong opportunity for sexual selection (see Figure 17).

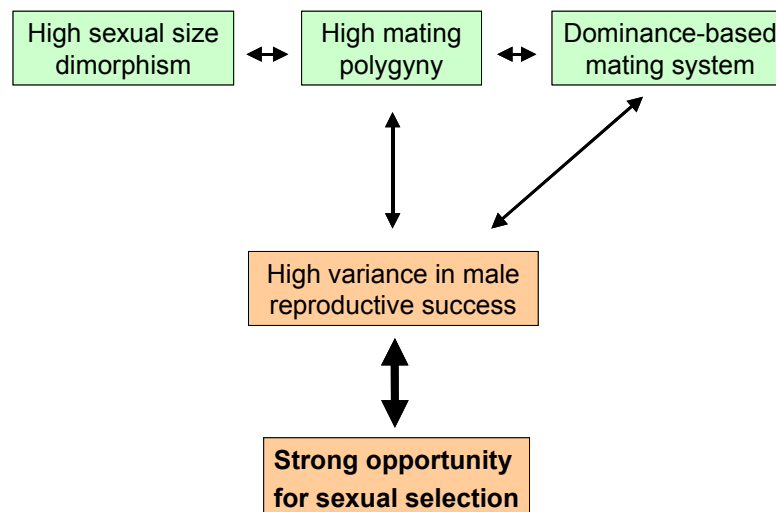


Figure 17. Illustration of the relationships occurring in red deer, Soay sheep and bighorn sheep, between sexual size dimorphism, mating polygyny, mating system, variance in male reproductive success and opportunity for sexual selection.

Unfortunately, there was a lack of genetic data in the literature on monomorphic or weakly dimorphic ungulate species to confirm whether such species do have, conversely, a weak variance in male LRS (but see in the monogamous rodent *Peromyscus californicus*: Ribble 1992; in the weakly dimorphic harbor seal: Coltman *et al.* 1998; and in the monogamous ungulate Kirk's dik dik based on yearly reproductive success: Brotherton *et al.* 1997). My thesis provided the first genetic data to investigate this issue in ungulates, using the case of roe deer. I found that the I_m value of roe deer was much smaller than published I_m values of highly dimorphic ungulate species, such as red deer, Soay sheep or bighorn sheep (see above). Hence, my results tend to support the hypothesis that low dimorphic ungulate species tend to have a low variance in male reproductive success.

Clutton-Brock (1987) pointed out that monomorphic and low sexual size dimorphic species may sometimes reach similar levels of variance in male LRS as highly dimorphic species, since the level of sexual size dimorphism is likely to be more strongly linked to the differential effect of body mass or size on the variance in LRS between males and females than to variance in male LRS itself. In ungulates, I speculate that this is unlikely. Indeed, I noticed that highly polygynous and dimorphic ungulate species which had a high variance in

male LRS commonly had dominance-rank based mating systems (i.e. harems, roving systems or leks), in which body mass or size play a key role in male access to females through dominance rank and fighting ability. Conversely, monomorphism and low sexual size dimorphism are commonly linked to territorial mating systems, in which male body mass or size may not be as crucial to male-male competition over mates because of the site-dependent dominance which allows to solve most of male-male conflicts without involving fighting (i.e. territorial males are dominant inside their territory but subordinate outside), and the mating system is commonly monogamous or oligogynous (i.e. slightly polygynous). Gaillard (1988) thus proposed a continuum among cervid species from primitive species, with low adult body mass, no or a low level of sexual dimorphism, a monogamous territorial mating system, living in closed forest habitats (e.g., *Muntiacus* or *Hydropotes*) to more “developed” species, with high adult body mass, high level of sexual dimorphism, a polygynous and social mating system, living in opened habitats (e.g., *Cervus* or *Dama*). Hence, it is likely that monomorphic and low dimorphic ungulate species should commonly have lower variance in male LRS than highly dimorphic ungulate species. Note however that it does not mean that the variance ratio in male and female LRS is always lower in monomorphic and low dimorphic species than in highly dimorphic species. Carranza (1996) reported a negative relationship between sexual size dimorphism and litter size in mammals. Hence, monomorphic and low dimorphic mammal species may have a larger variance in female LRS than highly dimorphic mammal species.

Hence, my comparative analysis based on genetic estimates of the variance in male LRS in several ungulate species seems to support the view of a continuum of opportunity for sexual selection, from monomorphic and monogamous species with territorial mating systems to highly dimorphic and polygynous species with dominance-rank based mating systems (see Figure 18). Along this continuum, roe deer probably occupies a position closer to monogamous and monomorphic territorial ungulates than to highly polygynous, sexually dimorphic ungulates with dominance-rank based mating systems (see also Gaillard 1988). However, much more data for ungulate species exhibiting low sexual size dimorphism or monomorphism and territorial mating systems is needed to test the generality of this pattern. By comparing values of I_m for lekking, harem-holding and roving/tending species, after correcting for variation in sexual size dimorphism, it would be possible to evaluate the impact of mating system variation on sexual selection.

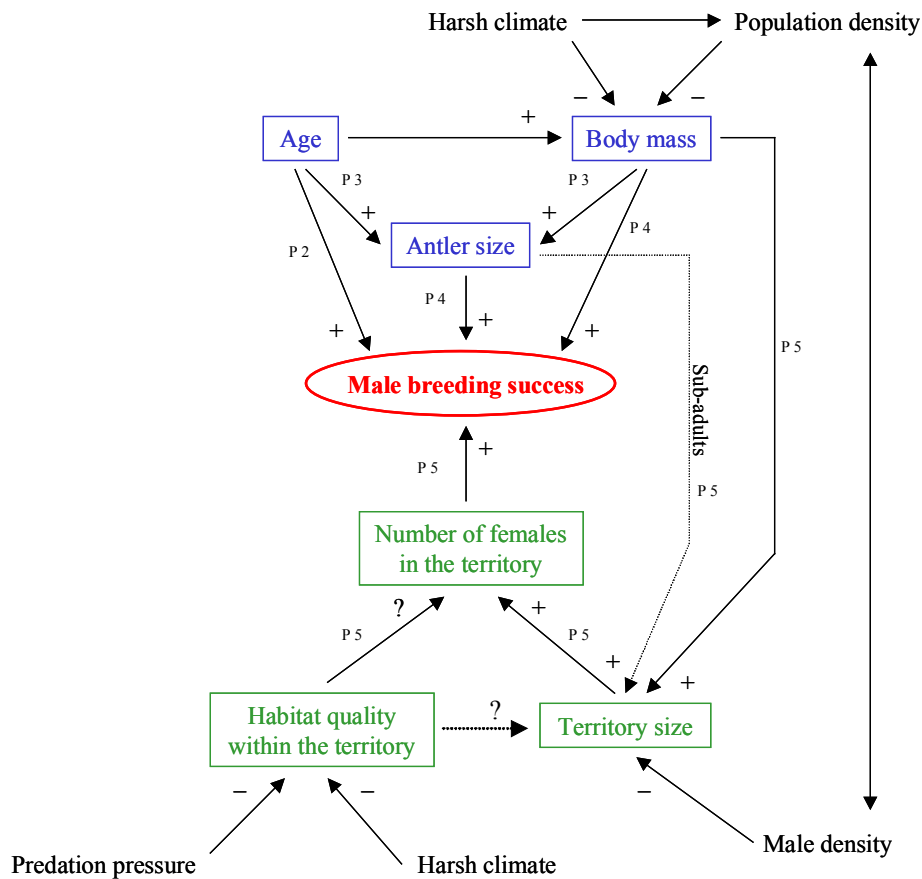


Figure 19. Summary of the relationships (+ : positive effects, - : negative effects) found in my different papers (papers P2, P3, P4, P5) between phenotypic traits (in blue), territory characteristics (in green) and male breeding success in roe deer up to 7-8 years of age (before senescence).

II.2.1. Age

Male YBS was found to be age-related (Paper 2) and age-specific variation was basically similar to trends reported for most other long-lived mammals (e.g., Clutton-Brock *et al.* 1988). In the both studied populations (Bogesund and Trois Fontaines), YBS was smaller at 2 years of age than at 3-8 years of age (prime-age males), peaked in prime-age males and finally tended to decline for the oldest ages. The first increase of male YBS with age may be explained by the increasing breeding experience of males and also body growth that is only complete at 3-4 years of age, which may allow them to better defend their territory and compete for access to females and/or to be preferentially chosen by females. Males older than 8 years of age tended to have globally a lower YBS than prime-age males, providing evidence for a senescent effect (see Paper 2). The decline of YBS for the oldest ages was strongly marked only at Trois Fontaines (all the 8 males older than 8 years of age failed to successfully

breed). At Bogesund, while most old males seemed to have a low YBS, few of them obtained as many paternities as prime-age males. Interestingly, the onset of senescence in male YBS of roe deer may occur globally at the same time as the onset of senescence in survival (Gaillard *et al.* 1993a, 2004) and in antler size (see Paper 3), at about 7-8 years old. This suggests that these phenomena may be mechanistically linked. But although annual male YBS was found to be age-related, marked variation still occurred among males of the same age class (especially among males older than 8 years of age at Bogesund), suggesting that there are other unidentified determinants of male YBS.

II.2.2. Body mass and antler size

In Paper 4, I found that body mass and antler size positively affected male YBS. A common view is that antlers in roe deer are used by males as weapons to successfully defend their territory and so to control an area within which they may mate females without being harassed by rival males. But body mass of roe bucks is also likely to play a role in fighting between males for the defence of territories, by enhancing male strength, and/or in endurance rivalry, by allowing males to be active during the whole rut period which lasts about 1 month. In support of this, I found, in Paper 5, that body mass in all males and antler size in 2-year-old males had a positive effect on male territory size, which was a key determinant of the abundance of potential mates in a male's territory.

However, contrary to harem-holding, roving or lekking ungulate species, direct male-male fights are rather infrequent in territorial species such as roe deer. Dominance is location-dependent, with males being dominant within their territory, but subordinate outside (Owen-Smith 1977; Hewison *et al.* 1998). A recent paper on roe deer has showed that territory holders consistently won male-male conflicts, including fights, within their territories but not outside (Hoem *et al.* 2007). Even in the case of an intrusion of a rival male inside a territory, display behaviours (e.g., parallel walk, head shaking, scraping) often allow males to resolve conflicts without resorting to costly fighting (Liberg *et al.* 1998) and antler size seems to be one of the cues used by males to assess their rival's individual fighting ability (Hoem *et al.* 2007). Hoem *et al.* (2007) have thus showed that male-male fights escalated more and were more complex when the difference in antler size between rival males was smaller. When the difference in antler size was large, male-male interactions often ended without involving dangerous fighting. Furthermore, it seems that territorial males may evaluate the potential threat of yearlings, in terms of mating competition, by using yearling antler size as an honest

indicator of phenotypic quality (Strandgaard 1972): yearlings with large antlers and large testes are more frequently victims of aggressive acts from territorial males and hence tend to disperse more (Strandgaard 1972; Wahlström 1994). Territoriality associated with male display and the use of antler size as a honest signal of male fighting ability are likely to be a tactic in roe deer to reduce the frequency of potentially dangerous fights. This is expected in an ungulate species with sharp antlers or horns, such as roe deer, in which direct fights are not only costly in terms of energy expenditure, but also can potentially inflict serious injury and even sometimes lead to death (Danilkin & Hewison 1996). The results of this study support this view. Paper 3 provides evidence that antler size of male roe deer mainly reflects their age and body mass, and is more resilient to variation in environmental conditions such as climate, food resources and population density. Since body mass and age are both reliable descriptors of individual quality and have been shown to affect the ability to fight and the dominance of males in most vertebrates (see Clutton-Brock 1988a), antler size can be considered as a honest signal of male individual quality in roe deer. Males may thus use antler size and body mass of rival males as a cue to assess the possibility of winning a fight in order to control and monopolize territory providing access to more females for reproduction.

In addition, females may use male antler size and body mass as cues to assess male quality. I showed in Paper 3 that antler size in roe deer was a reliable indicator of male phenotypic quality, as assessed by age and body mass. In addition, Wahlström (1994) found a positive correlation between yearling antler size and testicle size in roe deer, indicating that antler size may reflect male fertility and sexual vigor, because testes size determines sperm production rate (Møller 1989). By choosing their sexual partners on the basis of their large antlers, does may thus ensure that they mate with a high quality mate. Females may then gain either direct benefits, such as high male sexual vigor and protection against harassment by other males, or indirect benefits, such as bearing offspring of high quality.

II.2.3. The abundance of females in territories

Male territories in roe deer are commonly large enough to include the home ranges of several females. From 0 to 3 females (Bramley 1970; but up to 10 females, Strandgaard 1972) commonly live within a male's territory, probably depending on population density and operational sex ratio. It seems likely that males mostly mate with those females with which their range wholly or partly overlaps (Hewison *et al.* 1998). But does the number of females present within a male's territory determine his reproductive success? Based on behavioural

estimates of male mating success, Johansson (1996) previously found that the number of females' home range overlapping a male's territory limited his mating success. In Paper 5, I also found that male YBS tended to increase with the index of relative female abundance in a male's territory, but the relationship was not strong. The males siring 3 fawns had a higher index of relative female abundance in their territory than males siring 1 or 2 fawns, but there was no difference in the index of relative female abundance between males siring 1 and 2 fawns.

An explanation to the absence of a strong relationship between male YBS and the index of relative female abundance in a male's territory may be that territoriality in roe deer has long been viewed as a means for males to monopolize females and assure their mating success. However, females have the possibility to leave a male's territory, since their home range is not constrained within a single male's territory (independence of the spatial system of the two sexes, Bramley 1974), and to mate with different males within, or outside of, their home range (Liberg *et al.* 1998). Indeed, some females do make short excursions during the rut, probably to visit a male outside their normal home range (see Liberg *et al.* 1998). Hence, males may not have the entire mating monopoly with the females present on their territory. I discuss further this point later in my discussion. This may explain why, although my results showed that the index of relative female abundance in a male's territory party affected male breeding success, I did not find a strong relationship between male breeding success and the index of relative female abundance in a male's territory.

However, I could not discount the possibility that the absence of a strong relationship between male YBS and the index of relative female abundance in a male's territory resulted from my method of estimation of this index. Pellet-group counts have been criticised as a method to reliably estimate absolute population density (e.g., Robinette *et al.* 1958; Putman 1984; Fuller 1991; White 1992). However, a recent paper showed that pellet group counts provide an informative index of relative variation in local density (Forsyth *et al.* 2007). The authors found three indices (total pellets, pellet groups and pellet frequency) which changed positively and approximately linearly with increasing deer density. However, their estimates of deer density showed a high uncertainty, since they were based on known numbers of deer released and harvested, direct counts from vantage points and annual musters (see Forsyth *et al.* 2007). Hence, this study cannot provide a strong evidence of the reliability of pellet group counts as a method to estimate an index of relative deer abundance. Here, I restricted the use of the pellet-group count method to estimate an index of relative spatial abundance of deer at Bogesund. In Sweden, due to the presence of snow and low temperatures during most of the

period of pellet accumulation, the pellet degradation rate should be very low and spatially homogeneous on the whole study area. One can therefore assume that the relative number of pellet groups accumulated in different areas reflects the relative density of animals in these areas, although this approach has yet to be validated. As Forsyth *et al.* (2007) advised, before using pellet counts as an index of relative abundance, it is better to first evaluate the relationship between the index and population density and this has not been done yet at Bogesund. Hence, as long as the relationship between pellet group counts and deer density has not been evaluated at Bogesund, my results based on the index of relative female abundance should be considered with caution.

II.2.4. Territory size and habitat quality within the male's territory

In territorial species, males have two main options to maximize their access to mates: they can attempt either to enlarge their zone of dominance by maximizing the size of their territory, or to occupy areas particularly favored by females by maximizing, for example, the quality or quantity of food resources, or both. In roe deer, Johansson (1996), using behavioural observations, has previously found that the quality of the territory, but not territory size, may influence male mating success, with males with clover fields in their range having the highest success. In contrast, in Paper 5, I showed that territory size, but not the habitat quality of the territory, affected the index of relative female abundance in a male's territory and, at least partially, male YBS. Males siring 3 fawns had a larger territory than males siring 1 or 2 fawns. Below (Part II.2.6) I discuss the consequences of this result further in terms of adaptive function and the evolution of territoriality.

The quality of a territory in terms of habitat is difficult to define and even more difficult to measure (see Garshelis 2000). Previous studies have used very simple variables to define the habitat quality of a territory (e.g., presence or absence of clover fields; see Johansson 1996). But it is unlikely that such variables reliably reflect the quality of a habitat for females. Roe does have been categorized as income breeders (Andersen *et al.* 2000). As such, they rely on food resource intake rather than on body reserves to cope with the marked increase in energy requirements during the late gestation-early lactation period. Hence, roe does are expected to be particularly sensitive to local spatial variations in food resources. But during spring-summer they also require appropriate habitat for birth and fawn rearing, with enough cover to hide fawns against potential predators. In addition, the roe deer is a selective feeder, preferentially feeding on forbs, seeds and deciduous browse rich in soluble nutrients

(Tixier & Duncan 1996). Hence, both the quality and the quantity, and possibly also the diversity, of food resources are likely to be important for roe deer nutrition. Even all these habitat requirements for females can covary, it may not always be the case and hence, it may be important to take into account all these requirements when attempting to define a measure of habitat quality for females. In paper 5, I tried to identify a measure of habitat quality that integrated numerous characteristics, including habitat type, the biomass of various plant types, the biomass of the main food resources for roe deer, vegetation cover, etc., that were selected for by females, and so that may reliably reflect the quality of the habitat from the female point of view. Using the ecological niche factorial (ENFA, Hirtzel *et al.* 2002) analysis based on radio-tracking data, I identified the main specific resource attributes that determined the distribution of females over the whole study area. I then created a variable integrating this information based on the marginality axis of the ENFA (see Paper 5 and Materials and Methods part of the thesis). I used this variable as a measure of habitat quality within each male's territory in terms of attractivity for females. However, although my index of habitat quality integrated a number of habitat variables, it may still not perfectly reflect the suitability of an area for females. Fox predation pressure, for example, was not considered in my niche analysis. Yet, it is known to be a strong determinant of summer fawn survival and variation in female reproductive success at Bogesund (Kjellander *et al.* 2004). Hence, predation pressure may swamp the role of food resources and vegetation cover in determining female distribution if females select their summer range on the basis of local fox abundance. A preliminary analysis suggests that the number of fox dens present within a male's territory has no effect on the number of females present or on male YBS (C. Vanpé, unpubl. data). However, this is a rough estimation of fox predation pressure, since I did not know whether fox dens were still occupied or not, and no systematic sampling strategy was used to locate fox dens (we noted the position of fox dens that we observed during pellet group counts). It would thus be interesting to further investigate this issue.

To sum up, it is possible that the absence of a relationship between the quality of the habitat within male's territory and the index of relative female abundance in that same territory may be caused by inaccurate measures of habitat quality or relative female abundance. For these reasons, this result should be considered cautiously and more exploration is required regarding methods to reliably estimate local population density (e.g., multi-site CMR models) and more thought is required on what could be a good measure of habitat quality (see Garshelis 2000).

II.2.5. Other potential sexually selected traits

I focussed my study on a few particular male traits which were, to me, the most likely sexually selected traits in roe deer. But it is obvious that other traits may affect male breeding success.

Reby *et al.* (1999) suggested that barking in roe deer was linked, in part, to the expression of territoriality among bucks and may enable them to identify and locate each other, and perhaps to assess dominance status, particularly during barking / counter barking sessions involving several animals. It seems indeed that individual differences in propensity to bark are related to dominance. Male barking characteristics may thus be used by rival males and females as a cue to assess male status, phenotypic quality or ability to fight, and may be an important male sexually selected trait. More research on this topic is required.

Chemical signals are also likely to play a role in roe deer sexual selection (M. Gosling, pers. com.). Roe bucks abundantly mark their territory with scraping (i.e. pawing the ground with the front hooves) and rubbing (rubbing antlers and forehead against stems of trees and bushes; Johansson 1996). Both types of behaviours leave conspicuous marks, but also probably odors, as roe deer have skin glands both on the head and between the digits of the hooves (Raesfeld *et al.* 1985 cited by Johansson 1996; Danilkin & Hewison 1996). Marks are not confined to territory borders and it is mainly male territorial adults that mark (Johansson 1996). Although Johansson (1996) observed that several males, but no females, seemed to respond to either rubs and scrapes, she suggested that marks were primarily signals towards males in roe deer, but that females also utilised them to gain information on the status of males during the rut. More research on this topic is also required.

Finally, Strandgaard (1972) proposed that morphological traits in roe deer may have a rather weak effect on male breeding success compared to behavioural traits. Thus, the degree of aggressivity, for example, may play an important role in male breeding success. Testosterone is an endocrine signal, which plays an important role in normal spermatogenesis, the function of accessory sex glands and the regulation of antler development, rank and mating success (Blottner *et al.* 2006). It is also likely to be linked to male aggressivity. In dabbling ducks *Anas* sp., for example, Poisbleau *et al.* (2005) have thus shown that dominance rank, which is often correlated with aggressivity, was positively related to male testosterone level, but not to morphological characters. Similarly, in chacma baboons *Papio hamadryas ursinus*, males which gained in dominance rank had higher testosterone than males which lost in rank (Beehner *et al.* 2006). Also, male testosterone was positively related

to aggression rates during unstable periods when high rank was being contested. In this species, testosterone may be more important than the rank relationship in predicting the outcome of male-male interactions (Bergman *et al.* 2006). Hence, it would be interesting to investigate the relationship between the level of testosterone during the rut, territorial behaviour and male YBS in roe deer.

II.2.6. New insights into the adaptive function and evolution of male territoriality

I investigated whether male territoriality in roe deer conformed to the hypothesis of a resource defence polygyny mating system. According to this hypothesis, males gain access to mates indirectly by defending a space with resources that are vital for females, and so which are expected to attract them. Females are expected to distribute themselves in relation to these resources and males are expected to attempt to enhance their access to mates by maximizing the quality and/or quantity of these resources within their territory. But for this to be an optimal mating tactic, males should have the monopoly of mating within their territory, or at least, the quality of his territory, and hence the the number of females he succeeds in attracting, should be positively correlated with his mating success.

Results of my Paper 5 suggest that females may not distribute themselves among territories in relation to the quality of the habitat within them. If it is actually the case, males should thus be unable to “predict” the distribution of potential mates by anticipating how resource distribution influences female dispersion. Hence, in contrast to the expectations of resource defence polygyny, males should show no interest in competing for resource-rich sites to establish their zone of dominance, since males with the highest habitat quality within their territory (for a given size of territory) may not have the highest access to females. In support of this result, it is known that territories are highly stable in size and boundaries from year to year, even when changes in habitat composition, the availability of females or the identity of the territory holder occur (Liberg *et al.* 1998). Males may commonly retain the same territory during their entire lifetime or at least during most of their lifetime, and rarely change territory (Liberg *et al.* 1998). This means that males do not constantly attempt to enlarge their territory or challenge the males with the highest quality territories to enhance their access to females, contrary to what is expected for a conventional resource defence polygyny tactic. Consistent with this, Bramley (1970) showed by an experimental manipulation that after the removal of all the females from the territory of a male, the male

continued to defend his territory. In an other large scale experiment where 22 bucks were removed during mid-rut in a 450 ha area, none of the remaining 8 territorial radio-marked males shifted or enlarged their territories, in either the same season or the next (Cederlund *et al.* 1994). The vacancies were instead filled by immigrating bucks. As a result, dominant males may hold “ecologically inferior” territories for many years.

This suggests that, although territoriality of male roe deer has certainly evolved as a tactic for ensuring access to mates (Hewison *et al.* 1998), it does not really conform to a resource defence polygyny tactic (*sensu* Emlen & Oring 1977). Male territoriality in roe deer actually conforms to an “always stay” and “low risk - low gain” tactic (see Linnell & Andersen 1998), where males, once they have established their first territory, do not compete intensely for territories. Rather, males gain the benefits of site familiarity and reduced frequency of dangerous fights with rival males by remaining in the same area where they are dominant (Owen-Smith 1977). The result of successful territory establishment is thus more likely to be the delimitation of an area in which bucks can court and mate without interference because they are dominant, rather than direct and automatic access to females (Cederlund & Liberg 1995; Börger 2006; Hoem *et al.* 2007). In agreement with this hypothesis, Börger (2006) reported that a territorial owner was never observed being disturbed while courting a female inside his own territory.

However, I found a positive relationship between the size of a male’s territory and the index of relative female abundance in the territory, and at least partly between the size of a male’s territory and male YBS (see Paper 5). Hence, although males do not constantly attempt to enlarge their territory to enhance their access to females and commonly retain the same territory during their entire lifetime (see above), male territory size seems to be an important determinant of male access to mates. First territory establishment in young is therefore likely to be a key stage in the life of males. The first territory that young will be able to gain and defend should determine, at least partly, through the size of the territory, their access to mates in their first year of territoriality, but also probably for their entire lifetime, because of the pronounced spatial stability of both sexes, the stability of territories in terms of size and boundaries and the fidelity of males to their first territory. Interestingly, results of Paper 5 showed that body mass tended to have a positive effect on territory size in all males, and above all, that residual antler size had a strong positive effect on territory size in sub-adults only (note however that sample size in sub-adults was low). Hence, phenotypic traits, and especially antler size, may determine the size of the territory that sub-adults managed to establish. Among territorial sub-adults, heavy individuals with large antlers may be the best

competitors, able to evict adult males with the largest territories or at least to establish the largest territories, with the highest access to mates. This may suggest that body mass and antler size of sub-adult males may influence, at least partly, both their current and lifetime access to females. Hence, the establishment of a male's first territory may play a more important role in determining fitness than previously thought. The identification of the proximate and ultimate determinants of the characteristics of a male's first territory is thus essential to better understand variation in male fitness in roe deer.

In this way, roe deer territoriality seems to differ somewhat from the territoriality of most other ungulates, for which previous studies have demonstrated a direct relationship between territory quality and mate access (e.g., in impala and waterbuck: Jarman 1974; American pronghorn: Kitchen 1974; puku and topi antelopes: Balmford *et al.* 1992), suggesting a better fit with the conventional resource defence polygyny model than for roe deer. I therefore suggest that resource defence polygyny should not be considered as a "homogeneous" mating tactic and that the variability of polygynous mating systems characterized by Emlen and Oring (1977) would be probably more realistically described as a continuum extending from lekking and resource defence polygyny to female defence polygyny. Along this continuum, roe deer territoriality would then probably occupy an intermediate position between lekking defence polygyny and resource defence polygyny (see Figure 20).

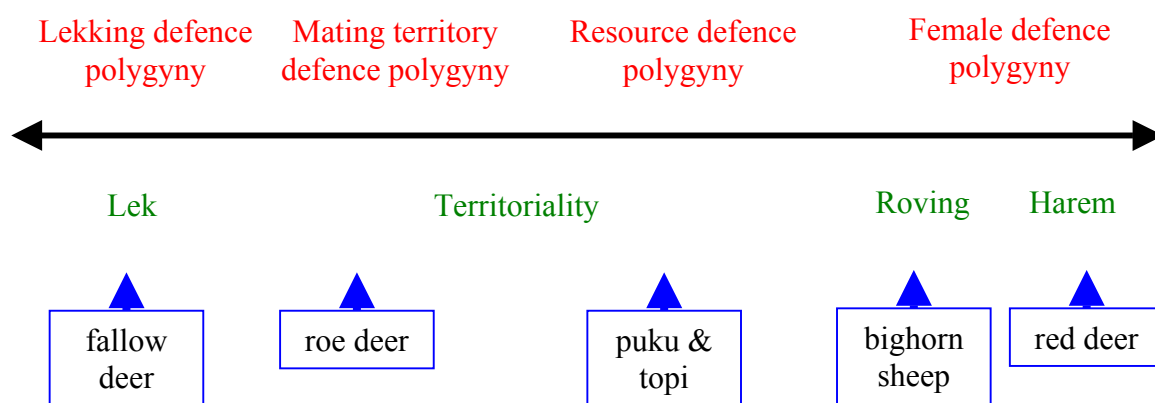


Figure 20. Illustration of the proposed continuum of polygynous mating systems in ungulates.

This would be in agreement with the suggestion of O. Liberg (pers. com.) that male territorial system in roe deer may be a kind of "enlarged lek" (see also Liberg *et al.* 1998), since females

seem to choose males not on the basis of the habitat quality of their territory but on their phenotypic quality. I qualify this intermediate mating system as “mating territory defence polygyny”. However, more empirical work is needed to develop a more comprehensive framework. In particular, an experimental approach could be useful because correlation does not equal causation. For example, to better understand the evolution of the roe deer mating system, it would be interesting to vary artificially the number of females resident and/or the quality of the habitat within territories of different males and monitor the subsequent changes in male ranging behaviour and breeding success.

II.3. COMPARISON OF THE EXTENT AND CAUSES OF VARIATION IN BREEDING SUCCESS IN THE TWO SEXES

As Clutton-Brock (1977) noted, *“if we wish to understand the evolution of sexual differences, we need to investigate the contrasting forms of competition among males and females and the factors determining breeding success in each sex”*. Below, I compare the extent and causes of variation in breeding success in roe deer bucks and does. I compare the distribution of LBS and its components, the effects of age on survival and YBS and the factors that affect YBS in the two sexes.

II.3.1. Comparison of the distribution of lifetime breeding success

Roe does have been reported to give birth to 0-4 fawns per year, with twin litters more common and 4 fawns very rare (3 fawns are also rare in France: < 5%, J.M. Gaillard, pers. com.). They have a very high probability of getting pregnant each year and successfully giving birth to fawns (Gaillard *et al.* 1992; Hewison 1996; Hewison & Gaillard 2001). In most populations of roe deer, nearly all females older than 2 years ovulate and produce fawns (proportion of pregnant adults = 67-100%, with mean = 81%; at Chizé, 98% of females > 20 months breed every year), whereas higher variation occurs in the proportion of yearlings breeding (proportion of pregnant yearlings = 35-100% per population, with mean = 66%; see Hewison 1996, Andersen *et al.* 1998). In comparison, my results showed that about half of prime-age males (3-7 years old) successfully breed each year at Bogesund (Paper 2). Even though this value is surely under-estimated, because a considerable but unknown proportion of fawns in the population were not caught each year (see above), the proportion of successful breeders among males is likely to be much lower than among females.

Surprisingly, although it is quite easy to estimate female breeding success in roe deer by observing fawns with their mother just after birth in roe deer, no study has yet published detailed data on female lifetime reproductive success (LRS) this species (including an estimation of the mean, variance, and standardized variance in LRS) and investigated the respective role of the main components of LRS (i.e. fecundity, life span, age of first breeding, fawn survival) on the variance of female LRS, as has been previously done by Clutton-Brock (1988b) for red deer (but see data on 5-year reproductive success of Gaillard *et al.* 1998a). To be able to compare variance in LRS between the two sexes in roe deer (see Figure 21), I therefore roughly estimated female LRS (not including fawn survival) from a data set of 28 females at Bogesund.

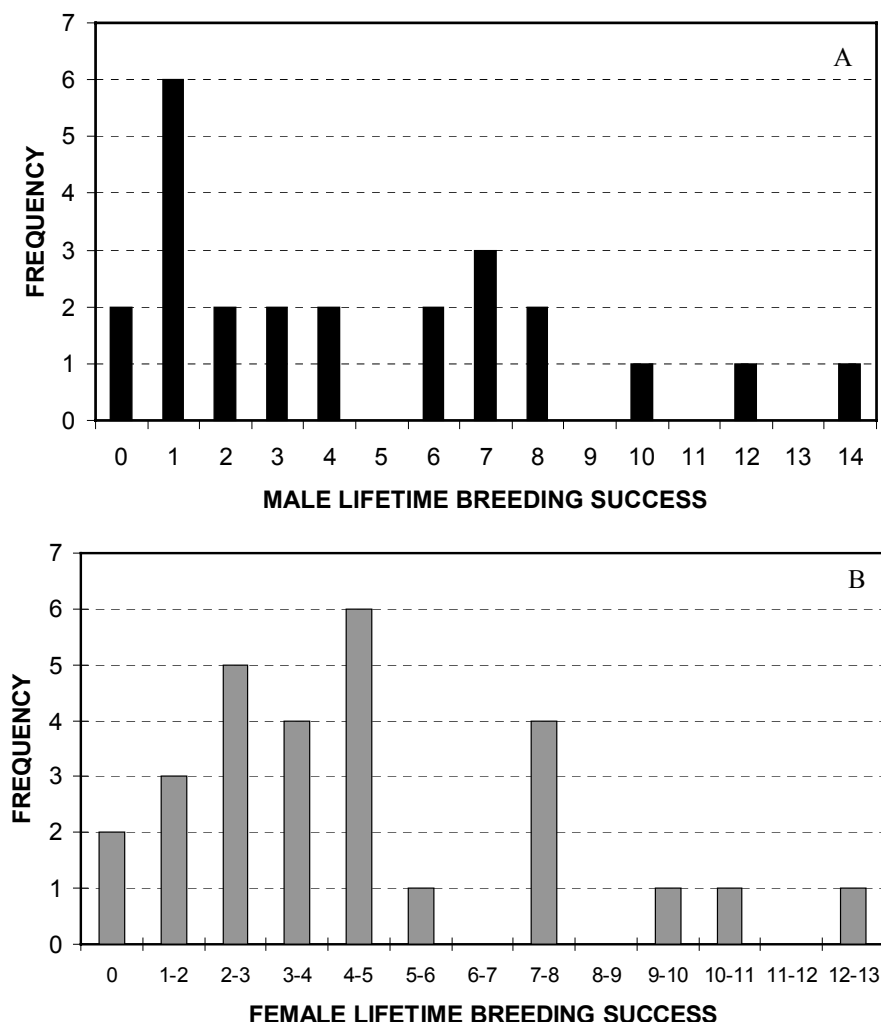


Figure 21. Distribution of lifetime breeding success among bucks ($N = 24$; A) and does ($N = 28$; B). From Paper 1.

I found that LBS varied between 0 and 12 (mean \pm SD = 4.19 ± 3.04). The standardised variance in female LBS (I_f) was thus 0.53 and reproductive lifespan varied between 0 and 10 years (see Table 5). Hence, according to these results, the standardised variance in LBS seemed to be smaller in females than in males, supporting the view of a polygynous mating system. But the variance in female LBS was strikingly large and, as a result, the difference between I_m and I_f was not so marked, and the ratio of the standardized variance in male LBS to the standardized variance in female LBS was low ($I_m/I_f = 1.42$), suggesting an oligogynous mating system (i.e. with a low polygyny level) with low opportunity for sexual selection, supporting the hypothesis of Melis *et al.* (2005).

Table 5. Summary of the main reproductive parameters in male and female roe deer at Bogesund.

	MALES	FEMALES
range of YRS	0 - 6 fawns	0 - 3 fawns
range of LRS	0 - 15 fawns	0 - 12 fawns
mean LRS	4.54	4.19
variance in LRS	15.50	9.27
standardized variance in LRS	0.75	0.53
age of 1st breeding	2 years old	1 year old
reproductive lifespan	0 - 11 years	0 - >10 years

Note: age at 1st breeding = age at 1st breeding at fawn conception.

Note that I found a higher variance and standardized variance of female reproductive success (see Table 5) than Gaillard *et al.* (1998a) who investigated the 5-year reproductive success (including a fawn survival component) of 37 females at Trois Fontaines. The authors reported that females varied greatly in their success, as a consequence of a high family effect: one female did not raise any fawn whereas three females raised 10 fawns over five breeding attempts. The variance in 5-year reproductive success was 7.7 for a mean success of 6.6 fawns and a standardized variance of 0.175.

II.3.2. Comparison of the effects of age on breeding success and survival

Age is an important factor of variation in female fecundity. Females normally attain sexual maturity as yearlings (giving birth at 2 years of age), but under favourable conditions they may already become pregnant as fawns (Hewison 1996; see Andersen *et al.* 1998),

whereas under poor conditions first reproduction is often delayed one year until the age of 3 years old (Hewison 1996; Gaillard *et al.* 1992). Note however that breeding female fawns rarely succeed to successfully raise their offspring. Fecundity at two years old can be lower than in older females (Danilkin & Hewison 1996; Hewison 1996; Andersen *et al.* 1998; but see Gaillard *et al.* 1998a and Figure 22). From 3 years of age, the number of offspring per female and per year remains approximately constant until does are over the age of 12. Thereafter there is a marked decrease in female fecundity (Gaillard *et al.* 1994; see Figure 22), largely due to an increase in the proportion of does that fail to conceive (Gaillard *et al.* 1998b). Hence, for both sexes, YBS is lower among 2-year-olds than among adults and senescence may occur for the oldest ages. However, bucks commonly begin breeding later than does (usually in their second or third year of life at fawn conception).

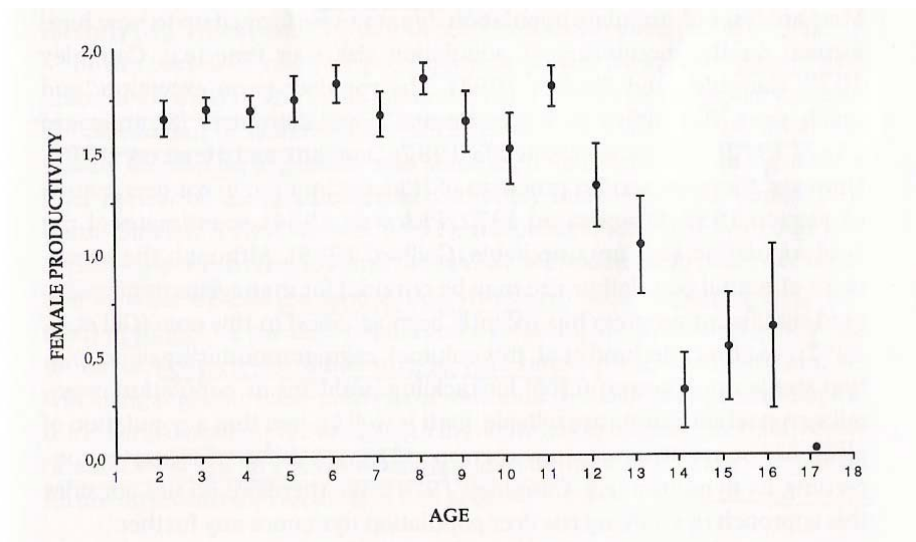


Figure 22. Age-specific female productivity (measured as the product between number of fetuses and probability of pregnancy) from the Chizé population (Sempéré unpubl. data). From Gaillard *et al.* (1998b).

Senescence in breeding success seems also to start earlier in males (at about 7-8 years old) than in females (at about 12 years old; Gaillard *et al.* 1998b; see Figure 22), although a detailed analysis for females is, as yet, lacking. Among animals of both sexes, survival rates are high until the age of eight, when mortality begins to increase (see Figure 23). However, it seems that the survival is always higher in females than in males, possibly due to the costs of territoriality (Gaillard *et al.* 1993a). This marked difference in survival between males and females is surprising for a species with a low polygyny level and a low sexual size dimorphism (Gaillard *et al.* 1998b). It is very close to that observed in highly polygynous and dimorphic species such as red deer. In contrast, life-history traits (e.g., birth weight, postnatal growth rate, summer and winter survival of fawns; for a review, see Gaillard *et al.* 1998b)

during the juvenile stage are very similar. Further research focused on survival differences among males according their breeding success is needed to better understand the causes of the lower survival of males compared to females in roe deer.

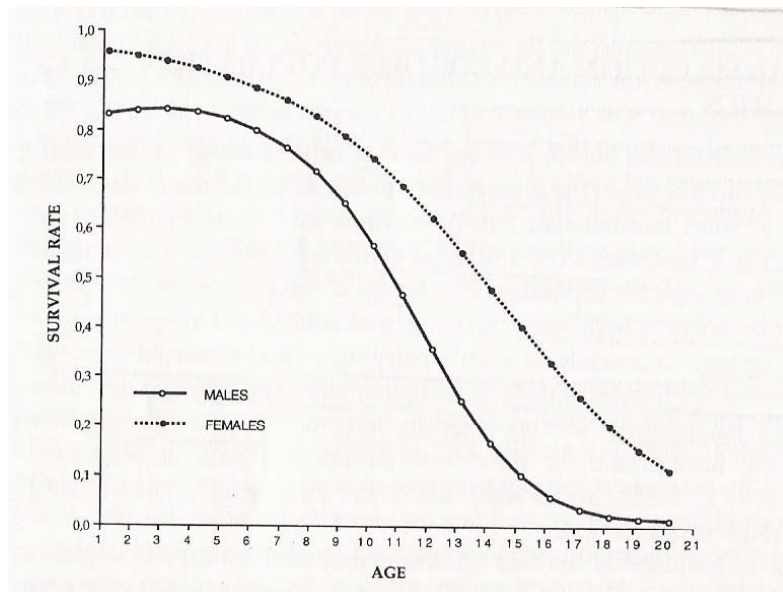


Figure 23. Age-specific survival in bucks and does. From Gaillard *et al.* (1998b).

II.3.3. Comparison of the ultimate factors that affect breeding success

We showed that body mass affected male YBS (Paper 4). Body mass and size also strongly influence female fecundity. Large and heavy females have higher LRS because they live longer (Gaillard *et al.* 2000a), reproduce earlier (Gaillard *et al.* 1992), and have larger litter sizes (Hewison 1996; Hewison & Gaillard 2001) than small and light females. Heavier does in all age classes were more likely to ovulate and produced larger potential litters (Hewison 1996; Andersen *et al.* 1998).

Ecological conditions also have a great effect on female reproductive success. A cohort effect linked to climatic conditions in spring and population density has been demonstrated on fawn survival over the first summer. Birth weight and postnatal growth rate of newborn fawns are higher during springs with less heavy rain in April (Gaillard *et al.* 1993b) and with low density (Gaillard 1994). Some evidence for density-dependent responses have been found in the proportion of 2-year-old females breeding (Gaillard *et al.* 1992), fawn survival rates (Gaillard *et al.* 1997), and the number of fawns recruited into the winter population (Boutin *et al.* 1987). From longitudinal studies of populations, a negative relationship between population density and kid production of females has been established (Boutin *et al.* 1987; Vincent *et al.* 1995). The occurrence of cohort effects has an important

implication concerning the variability among individuals in the number of offspring produced during a lifetime. The numerical cohort effect (i.e. immediate consequences of cohort effect; sensu Gaillard *et al.* 2003b), particularly during harsh conditions, leads to an increase in the variance of LRS between individuals within a population (see Gaillard *et al.* 1998b). Finally, food resources and habitat quality can also influence female reproductive success. Resource restriction may cause an increase in roe deer juvenile mortality, delay the onset of puberty, and decrease female fecundity (see Danilkin & Hewison 1996). Recently, McLoughlin *et al.* (in press) have shown that the habitat quality (defined by habitat components important for food, cover, and edge: meadow, thickets and increased density of road access) in a female's home range was significantly related to their LRS, after correcting for density effects. This is expected because roe deer is an income breeder (Andersen *et al.* 2000), and so females cannot rely on body reserves to meet the high energy demands at the end of gestation and during early lactation. In bucks, the effect of ecological conditions on male reproductive success has been recently investigated based on observations of mating and courting behaviours (Börger 2006). This study showed that local density, together with differences in the local population structure (proportion of adult males, sex ratio), had a pervasive influence on individual variance in mating and courting success. 22% of the variation in the number of mating partners per rut was explained by changes in local population density. The number of females courted per rut also increased with an increase in the proportion of adult males, which suggests it is harder for males to monopolize females at higher densities than at lower densities.

According to Trivers (1972), males are adapted to compete for females while females are adapted to compete for food. My results seem to globally support this view. While fighting ability, through antler size and body mass, territorial status and territory size seem to be important to males for access to mates, body mass seems to be a major determinant of female reproductive success. For females, environmental conditions affecting female body mass, such as the availability of food resources, population density or climatic conditions are also important. These differences in selection pressures may explain the differences in morphology (e.g., presence of antlers and thick neck (during rut) in males but not in females), physiology (e.g., testosterone cycles) or behaviour (e.g., mating territoriality in males, but not in females) between the two sexes. Interestingly, body mass in roe deer seems to have an important role for determining individual fitness in both sexes.

II.3.4. New insights into the evolution of the low sexual size dimorphism in roe deer

There is a wide acceptance of the idea that male-biased sexual dimorphism in body size evolved principally as the result of intra-sexual competition over mates (Darwin 1871; Andersson 1994). In roe deer, sexual size dimorphism is low (Andersen *et al.* 1998). Several hypotheses can be proposed to explain the evolution of this low level of dimorphism. First, male body mass might not play an important role in male-male competition over mates in this territorial species in which combats are rather infrequent due to site-specific dominance (see above). Also, agility, implying a small body size, might be more important in determining male mating success, through scramble competition or courtship, than strength and fighting ability in this territorial species (agility-hypothesis; Andersson 1994). If this is the case, sexual selection might favor low body size and mass. Finally, the low level of sexual size dimorphism might be explained by the key role of body mass in female breeding success (see above), which may favor the evolution of high body mass and size in females also. Indeed, as suggested by Clutton-Brock (1987), it is not the extent to which male success varies that will determine the development of sexual dimorphism, but the comparative effects of particular traits on breeding success in males and females (see Figure 22). “*Monomorphism in size is likely to be found where body size has a similar effect on the breeding success of both sexes whether or not variation in breeding success differs between the sexes*” (Clutton-Brock 1986). Trait variance only establishes the upper limits to the intensity of sexual selection (usually called potential for selection). Its actual intensity is determined by the relationship of breeding success with the trait, in this case, body mass.

Contradicting the first and second proposed hypotheses, my results showed that the body mass of males had a significant positive effect on their YBS (see Paper 4). Hence, my results rather fit the third hypothesis, suggesting that the low level of sexual size dimorphism in roe deer may be due to a parallel selection for body mass in both sexes (see Figure 24). In males, YBS is related in part to weight and fighting skills, while in females, those above a given weight threshold have higher reproductive performance. In addition, weight may not be as crucial to male breeding success in a territorial species as it is in a dimorphic species with dominance-rank based mating systems, due to site-dependent dominance which allows territorial males to solve most male-male conflicts without involving fighting.

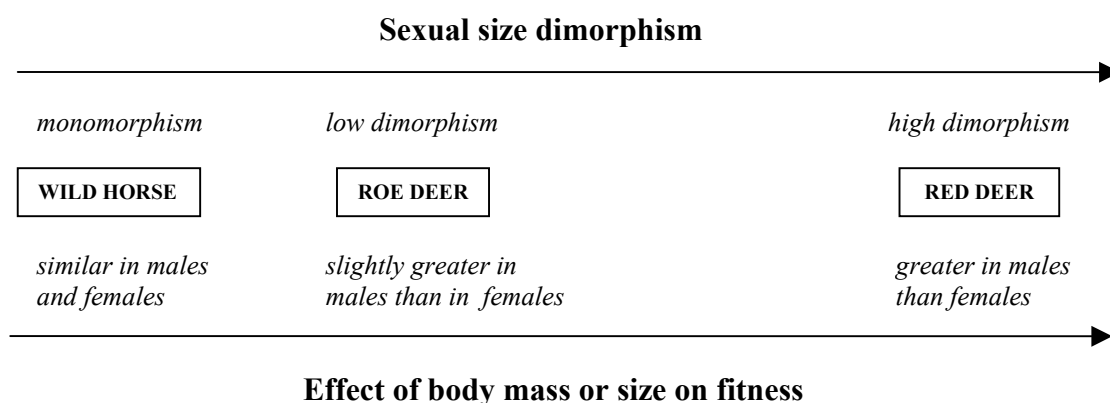


Figure 24. The evolution of sexual size dimorphism in ungulates depends on the relative effect of body mass or size on breeding success in the two sexes.

II.4. ALTERNATIVE MATING TACTICS IN YOUNG AND OLD MALES

In roe deer populations, from wooded areas or woodland-agricultural land mosaic landscapes, territoriality seems to be the main male mating tactic. From earlier studies, no behaviours have been observed in prime-age adult roe bucks during the rut that could clearly be identified as an alternative mating tactic to territoriality (Liberg *et al.* 1998). This lack of alternatives to territoriality in adult roe males is striking when compared to the flexibility of the mating system and mating tactics in fallow deer (Langbein & Thirgood 1989), red deer (Carranza 1995), American pronghorn (Byers & Kitchen 1988; Maher 1994), and bighorn sheep (Coltman *et al.* 2001). However, note that small territorial ungulate species (such as small African bovid species and South-American cervid species: J.M. Gaillard, pers. com.) commonly have a low flexibility of mating systems and mating tactics. The results of my thesis provide new insights into mating tactic plasticity in roe deer, especially in young, but sexually mature, males, and in old males.

In young but sexually mature males (2-year-old males), both territoriality (e.g., Strandgaard 1972; Ellenberg 1978; Johansson 1996) and alternative space use tactics seem to be used during the rut (Johansson 1996). The frequency of territory holding among young males seems to be context-specific: young males may successfully hold territories only when density is low (Kurt 1991; Vincent *et al.* 1995). Some 2-year-old males thus adopt an alternative tactic (called satellites) in which the young male associates with one territorial male, overlapping all or most of his territory. Satellite males may take advantage of the site

dominance of the territorial male to gain access to females, without taking the full costs of this (Johansson 1996). This tactic has already been reported in a few ungulates: in waterbuck (Wirtz 1982), and fallow deer (Moore *et al.* 1995), in which this tactic is restricted to young males, and in white rhinoceros *Cerathotherium simum* (Owen-Smith 1975) and topi (Gosling & Petrie 1990), in which adult males also use this tactic, particularly males that are too small to compete for a dominant position. In roe deer, other 2-year-old males adopt a peripheral tactic, where the animal remains in a restricted buffer area between two territories and makes quick raids into them in search of receptive females (Johansson 1996). However, while non-territorial young adult males are known to play an active role during the rut, and may even sometimes attempt to copulate (Johansson 1996), no previous studies have provided evidence that they could successfully breed.

I showed that 2-year-old males were able to successfully breed but that their YBS was lower than that of prime-age males (see Paper 2). However, this lower YBS was mainly due to the lower proportion of successful breeders among 2-year-old males. Hence, a successful breeding event was uncommon among 2-year-old males, and among successful breeders, 2-year-old males tended to have as much success as prime-age males. I noticed that 2-year-old males that sired fawns tended to be heavier and had larger antlers than 2-year-old males that failed to breed. They also seemed to be territorial. Preliminary results thus suggested that successful breeders among 2-year-old males may concern only the few individuals that have a particularly high phenotypic quality, allowing them to successfully establish and defend a territory. Interestingly, among territorial 2-year-old males, antler size also seemed to determine the suitability of the territory in terms of access to females through territory size (Paper 5). Hence, antler size, which reflects the ability of males to fight, seems to be particularly important during the key period when males attempt to establish their first territory, determining the possibility for 2-year-old males to establish their first territory, but also determining the suitability of their territory in terms of access to mates for their first year of territoriality. This also probably has consequence for their entire reproductive lifetime, since males show a high between year fidelity to the area where they establish their first territory and females are highly sedentary from year to year (Strandgaard 1972).

While low quality non-territorial 2 year-old males may adopt sneaky strategies, as satellites or peripherals, to attempt to mate with unattended females (Johansson 1996; Liberg *et al.* 1998), I speculate that their mating success is very low. Indeed, females seem to flee, and even vocally protest, when courted by non-territorial young males, provoking territorial males to attend (Liberg *et al.* 1998; Börger 2006). In addition, territorial male invariably

chases away any non-territorial young males, especially when they attempt to court a female (Börger 2006). But if non-territorial 2-year-old males have a very low probability to successfully breed, why then do they adopt these likely costly spatial tactics (high costs due to aggressions by territorial males)? It might be that 2-year-old bucks repeatedly challenge the territorial host male and might expect to take over the territory of their host (Johansson 1996). Anecdotal observations by Johansson (1996) have shown that some satellites and peripherals could later evict the territory owner from his territory and that satellites might have a better chance of taking over at least part of a territory the following year than peripherals. Interestingly, there is also some anecdotal evidence that these 2-year-old males (mainly satellites) which take over an already existing territory when they establish themselves as territorial for the first time may have better reproductive prospects than 2-year-old males (all peripherals) that have to carve out a new territory in a peripheral area (Johansson 1996; Liberg *et al.* 1998). Johansson (1996) thus suggested that although satellites may pay a higher cost, they do secure a better future reproductive success, while the peripheral tactic is a low cost alternative with a more uncertain future. This also raises the question of why territorial males accept 2-year-old male satellites within their territory, considering that the presence of these young males may be costly in terms of time and energy spent in conflicts to keep them away from resident females (satellite hosts experienced twice as many conflicts as solitary territory holders and had twice as many conflicts with their own satellite male as with outsiders; Johansson 1996). Furthermore, there is a high risk that they lose the whole, or a part, of their territory to this satellite male the following season. In this context, it would be interesting to investigate the degree of relatedness between satellites and their territorial host males. Indeed, if satellites are closely related to the territorial host males, one may investigate this issue within the framework of kin selection theory (i.e. process by which characteristics are favoured due to their beneficial effects on the survival of close relatives, including offspring and non-descendant kin; Maynard-Smith 1964).

Further research is needed on the relationship between 2-year-old male mating tactics and their current and future reproductive success. In particular, it would be interesting to confirm whether most of successful breeding among 2-year-old males are restricted to the few individuals that succeed to defend a territory as suggested.

Information on the mating behaviours of **old males** is scarce. Johansson (1996) observed that three of the five senescent males that she monitored in Sweden during their last rutting season before death were still actively territorial, were involved in male-male

conflicts, and also courted and mated females, whereas the two others were evicted from their territory by younger males, subsequently remaining in restricted areas inside their former territory, and had a limited participation in the rut (see also Liberg *et al.* 1998). Note however that these results were based on estimated age individuals.

In Paper 2, I found that males older than 8 years of age at Bogesund were usually still able to successfully breed and that the proportion of non-breeders did not differ between prime-age males and older males. Hence, I attributed the decline in YBS that I observed after 7-8 years of age to the fact that successfully breeding old males sired, on average, fewer fawns than successfully breeding prime-age males. However, the variance in YBS was very large among old males at Bogesund. Among the successfully breeding old males, while some managed to remain competitive and to sire as many fawns as prime-age males, others became less competitive and less successful. Interestingly, in Paper 3, I reported a differential allocation of energy to antler growth in males older than 7 years of age which depended on body mass. While the heaviest senescent males allocated as much energy to antler size as prime-age males of similar body mass, light senescent males allocated much less than light younger males. This suggests that two alternative reproductive tactics may have evolved among senescent males. First, high-quality old males with high body mass may express a risk-prone tactic, investing heavily in antler growth in order to develop antlers of sufficient size to remain competitive against younger males, thereby allowing them to continue to defend their territory so as to maximize mating opportunities and, hence, LBS. Second, low-quality old males with low body mass may express a conservative tactic, being unable to divert a large amount of energy to antler growth and so having inferior competitive ability than heavier and/or younger males, potentially precluding them from successfully defending their territory and hence from having a high YBS. Interestingly, these results nicely match Johansson's (1996) behavioural observations. Linking studies of individual phenotypic quality, territorial behaviour and mating tactics and genetic paternity in males older than 8 years of age should provide a definitive test of these speculations.

I found a high number of **prime-age males failing to breed** in both Bogesund and Trois Fontaines populations (see Paper 2). It is likely that most of these non-breeders were “false” non-breeders, due to the unknown proportion of fawns born each year which were not sampled in the two populations. However, in a roe deer population there are certainly some males which fail to breed, at least for a given reproductive season. In support of this, Johansson (1996) observed that some prime-age males were evicted by a younger male and

had little contact with females in a given year, before acquiring a new territory the following year. But even among males for which I was able to estimate LBS, some were unsuccessful for their entire life span. Hence, it seems that there may be some low quality males that consistently fail to breed. Interestingly, Johansson (1996) noticed that some males consistently performed very poorly during the rut (i.e. with very low courting and tending frequencies). They did not loose their territories, but those they occupied seemed of inferior quality, containing no or few females. Hence, although some prime-age males seem to perform more poorly than others, it does not seem that alternative mating tactics have developed among prime-age males.

II.5. THE ROLE OF FEMALES IN ROE DEER SEXUAL SELECTION

Recent findings have shown that in many birds, fishes, anurans, and insects, females play a more active role than previously thought, by engaging in mate choice, mating with more than one male, and/or selecting genetic partners separately from social partners (Reynolds 1996). Sexual selection can continue even after copulation (postcopulatory sexual selection, reviewed in Birkhead & Pizzarri 2002), through (i) cryptic female choice: a female can influence which of several copulatory partners father their offspring (Eberhard 1996; Ben-Ari 2000; Jones 2002), (ii) sperm competition: the sperm of two or more males can compete to fertilize a given set of eggs (Parker & Ball 2005; Simmons 2005). As for pre-copulatory sexual selection, cryptic female choice and sperm competition lead to a host of behavioral, anatomical and physiological adaptations in males and females (see Andersson 1994 for a review).

In territorial species such as roe deer, the potential for mate choice by females is theoretically expected to be high, because females have unimpeded opportunity to assess either the male and/or his territory (see Min 1997). Although they are mono-oestrus, roe does may be courted and mated by several males because their ranges may overlap several male territories (Strandgaard 1972; Liberg *et al.* 1998). In addition, a significant proportion (up to one-third) may make short rut excursions outside their normal home range, crossing the territories of several non-neighbouring males and engaging in courtship activities, and potentially mating with one of these non-neighbouring males (see anecdotal observations in Norway: Linnell 1994, Andersen *et al.* 1995; Sweden: Liberg *et al.* 1998; Italy: San José & Lovari 1998; Börger 2006; and France: M. Pellerin, S. Said, and J.M. Gaillard unpubl. data, M. Hewison, N. Morellet, A. Coulon, B. Cargnelutti, E. Richard unpubl. data). Hence,

territorial males may not be able to fully monopolize females during the rut, and female mate choice probably influences male mating success in roe deer. Females also play an active role during the rut by frequently soliciting courting from specific males (Kurt 1991; Danilkin & Hewison 1996; Börger 2006) or rejecting courting by non-territorial and/or young males through avoidance behaviour and even “vocal protests”, provoking dominant males to interfere, or by continuing to walk when mated by a male so that successful mating is prevented (Liberg *et al.* 1998; Börger 2006). These observations further suggest that females may have some control over whom they mate with. Overt female competition during courting and sexual conflict over mating have even been recently reported (Börger 2006). Börger (2006) observed a few cases of females interrupting a male-female courting sequence by walking between the female and the courting male and blocking the male, or by charging and chasing the courted female, or both. It has also been suggested that female roe deer might be able to control extensively their reproductive output through abortion or selective loss of foetuses, since recent research has shown sex-biased maternal allocation patterns, with heavy females investing more in female offspring (Hewison *et al.* 2005).

In order to better understand the role of females in roe deer sexual selection, I considered the potential benefits of multiple mating and female mate choice in does. Numerous hypotheses have been proposed to explain the benefits of multiple mating for females, which can be categorised as either direct benefits (e.g., fertilisation insurance, access to food or nuptial gifts, male harassment avoidance; Reynolds 1996) or genetic benefits (e.g., sperm competition, increasing genetic diversity among offspring via multiple paternity; Reynolds 1996; Newcomer *et al.* 1999). Due to the long tenure of territories among males, the sedentarity of females and the family unit structure composed of related females, incestuous matings between father and daughter and an elevated level of inbreeding within units may be common in roe deer (Kurt *et al.* 1993). Hence, I expected that female breeding tactics should favour inbreeding avoidance. I investigated whether the benefit of increasing genetic diversity among offspring could explain multiple mating by roe does by studying the possibility that multiple mating of females leads to multiple paternity. Roe deer females are polytocous (up to 4 fawns, most often 2; Andersen *et al.* 1998). During oestrus, females are courted and mated repeatedly and frequently (Danilkin & Hewison 1996), hence, roe deer females are likely candidates for multiple paternity. However, roe does have only one very short annual oestrus (24-36 hours; Hoffmann *et al.* 1978), and while multiple mating occurs, whether a female mates repeatedly with the same male or with different males remains unknown. In Paper 6, I found that multiple paternity most likely occurred in roe deer, but was limited. Frequent

multiple mating results in only very few multiple paternities. The genetic diversity hypothesis is, therefore, not a likely candidate to explain multiple mating in roe deer. I suggest, instead, that females may repeatedly mate to ensure fertilisation. This may explain how roe does manage to have a very high probability of getting pregnant each year (typically > 0.95, Gaillard *et al.* 1992; Hewison 1996), despite their single short oestrus.

It has long been suggested that oestrus females are courted and mated by one of the resident territorial males with which their home range overlaps (see Liberg *et al.* 1998). But as some females make excursions during the rut to “visit” a foreign male, it is clearly possible that this is not always the case. No study has yet been able to demonstrate that these female rutting excursions outside their normal home range coincide with female oestrus, and that females actually mate with the males they visit. However, using paternity analysis, I was able to document that females do mate with, and are fertilised by, a male whose territory does not overlap the female’s home range (C. Vanpé, unpubl. data). Several hypotheses have been proposed to explain the adaptive function of female excursions during the rut: (i) inbreeding avoidance, (ii) incest avoidance, (iii) female interference (“busy” local bucks), (iii) avoidance of male harassment, (iv) active mate choice, (v) avoidance of aggressive interactions with other females. Börger (2006) recently suggested that females may adopt a conditional space use tactic, where the choice of the two alternative tactics ‘stay and compete’ and ‘mate outside the home range’ depends on the availability of males and competition from other females. Investigating the characteristics of the visited foreign males (e.g. phenotypic quality, genetic variation, etc) compared to the local territorial male and/or of the habitat that attracts females constitutes a very interesting future research area (see Liberg *et al.* 1998).

The next step to explore the role of females in roe deer sexual selection will be to further investigate female mate choice. What distinguishes the father of a female’s offspring from the other males with whom the female could have mated? According to the good genes hypothesis, females may be expected to maximize the genetic polymorphism of their offspring, through their mate choice, by mating with a male with a high level of heterozygosity, or to avoid inbreeding by mating with a male with a genotype as different as possible from her own genotype. I plan to investigate this issue using the Bogenlund data on paternity analyses and radio-tracking. I have already calculated four measures of individual heterozygosity or individual inbreeding coefficient (H , d^2 , standardized H , and standardized d^2 ; see Slate & Pemberton 2002) for all genotyped individuals of Bogenlund. H is calculated as

the proportion of typed loci for which an individual is heterozygous. d^2 measures the difference in the number of repeat units between alleles in a genotype as an indication of the time since their coalescence (Goldstein *et al.* 1995; Coulson *et al.* 1998), assuming a step-wise mutation process (Valdes *et al.* 1993). Furthermore, I plan to estimate the degree of relatedness between particular individuals using three measures (Identity index, Queller & Goodnight's index, Lynch & Ritland's index) implemented in the software IDENTIX (Belkhir *et al.* 2002). In the case of females mating with a resident territorial male whose territory overlaps their home range, I plan to compare the individual heterozygosity measures of the father of the female's offspring with the those of the other males whose territory overlaps her home range. I would also like to compare the degree of relatedness between the female and the father of her offspring as well as between the female with other males whose territory overlaps her home range. Also, in the case of females mating with a male from outside her home range, I plan to compare the individual heterozygosity measures between the local males whose territory overlaps a female's home range and the true father of her fawns, as well as the degree of relatedness between the female and the true father of her fawns and between the female and the males whose territory overlaps her home range.

A female might choose the most heterozygous male through physical cues. Brown (1997) suggested that the expression of physical qualities in males such as vigor, condition-sensitive ornaments and symmetry, may directly reflect individual heterozygosity at key loci or many loci. Multilocus heterozygosity is often correlated with fitness-associated traits (David 1998; Hansson & Westerberg 2002) and with fitness (in birds: Hansson *et al.* 2001; in mammals: Coltman *et al.* 1998; Slate *et al.* 2000). My preliminary results seem to suggest that antler size in yearlings and body mass in old males (>7 years of age) tend to increase with individual heterozygosity, but that individual heterozygosity had no effect on male YBS (C. Vanpé, unpubl. data).

II.6. LET'S GO FURTHER: FROM THEORETICAL KNOWLEDGE ON MATING SYSTEMS AND SEXUAL SELECTION TO APPLIED ISSUES IN CONSERVATION AND POPULATION MANAGEMENT

A good understanding of mating systems and sexual selection, in complement to population dynamics and habitat studies, is of particular concern for solving applied issues such as wildlife management and conservation biology (see Caro 1998; Gosling & Sutherland 2000). Yet, although evolutionary and behavioural ecology studies have already proved to be

very useful, for example, for choosing the best individuals for breeding translocation or reintroduction programs (e.g., Sigg *et al.* 2005), for investigating the impact of trophy hunting on population dynamics and genetic variability (e.g., Festa-Bianchet 2002), or for studying the viability of small populations through the estimation of effective population size and inbreeding depression (e.g., Morrow & Fricke 2004), such studies are still poorly used in wildlife conservation programs and management plans. Below, I would like to advocate the usefulness of studies on mating systems and sexual selection in ungulates for their conservation and population management.

Analyses of population dynamics or demography usually consider only the female segment of the population (Caswell 2001). It is, indeed, assumed implicitly that there are a sufficient number of males available for the females to find an appropriate mate (male availability does not limit female reproduction), that males will be born and die at the same rate as females, and that the number of males does not affect the dynamics or the demographic characteristics of the females (Saether *et al.* 2004; Rankin & Kokko 2007). However, recent studies have suggested that these assumptions may not always be valid, due to effects of adult sex ratio on temporal and spatial variation in reproductive traits (e.g., in moose: Saether *et al.* 2003, 2004; red deer: Clutton-Brock *et al.* 2002), effect of males on the population dynamics by being a component of population density (e.g., Mysterud *et al.* 2002), and effect of males on the demographic rates of females through their behaviour (e.g., infanticide, mate searching behaviour, male harassment, male resource use; Swenson *et al.* 1997; Mysterud *et al.* 2002; Rankin & Kokko 2007). Hence, it is important to consider the effects of both sexes on demographic processes in a population (Mysterud *et al.* 2002) and to consider the mating system and sexual selection in any assessment of population extinction risk (e.g., Kokko & Brooks 2003; Rowe & Hutchings 2003; Saether *et al.* 2004). Saether *et al.* (2004) have shown, for example, that demographic stochasticity is weaker and the estimated time to extinction is considerably shorter for a monogamous than for a polygynous mating system. Polygyny level may also affect the influence of skewed sex ratios on female fecundity. In general, even in harvested populations with highly skewed sex ratios, males are usually able to fertilise all females, but this may not be the case in a species with a low polygyny level and with a territorial mating system such as roe deer. Hence, the mating system should be considered when performing population viability analysis based on counts of total population size (Saether *et al.* 2004). In addition, one-sex population models should be abandoned in favour of two-sex models, particularly when thinking about conservation

(Saether *et al.* 2004) or biological control programmes (Ferguson *et al.* 2005; Schliekelman *et al.* 2005). Studies of mating systems and sexual selection in ungulates should help to better predict the influence of males on population dynamics or demography, and better manage populations.

The mating system, polygyny level, social organisation, and differential dispersal patterns between the sexes have important consequences for the distribution of genetic variability between populations and between individuals within populations (Chesser & Ryman 1986; Chesser 1991; Sugg & Chesser 1994; Sugg *et al.* 1996; Chesser 1998). For instance, a mating system with a high polygyny level, where a few males monopolise most of the matings, should tend to limit population genetic diversity, whereas a mating system with a low polygyny level, where almost all males participate in reproduction and transmit their genes to subsequent generations, should favour population genetic diversity. In the former case, temporary removal of dominant males and careful manipulation of a population's social structure could help conservation biologists and wildlife managers to reduce the effects of inbreeding on populations (e.g., in Cuban iguanas *Cyclura nubila*: Alberts *et al.* 2003). This strategy may be most effective for small, genetically-compromised, endangered species that show strong polygyny, with a few dominant males monopolising territories and females. After the dominant males are removed from their home ranges, new males should take over their roles and females should have access to a more diverse set of males (or genes).

A good understanding of the polygyny level and of the determinants of variance in male reproductive success may be very useful for choosing the best individuals for reintroduction, translocation, or captive breeding programs, and to estimate the optimal proportion of males and females that should be introduced (e.g., Sigg *et al.* 2005). If the polygyny level is high, it may not be necessary to introduce as many males as females to maximise future recruitment in the population. While in a strictly monogamous system, the lack of males may reduce the reproductive output of females, in a polygynous mating system, these effects are likely to be greatly reduced because a single male can fertilise multiple females. A good knowledge of age-specific variation in male reproductive success and survival may also be of help to know whether young individuals or prime-age individuals should be favoured. In the same way, if body mass and weapon size are key determinants of dominance status and male access to mates, it may be better to favour heavy males with large weapons if we want to maximise the reproductive success of males.

Humankind exerts an ever growing selection pressure on animal populations through its activities (e.g., roads, dams, introduction of exotic species, pollution, over-fishing), and, in particular, through hunting. It has been recently shown that selective hunting in a bighorn sheep population represented a significant artificial selection pressure (Coltman *et al.* 2003). However, the effects of selective hunting regimes on wild populations have received little consideration up to now among both biologists and wildlife managers (but see reviews by Festa-Bianchet 2003; Harris *et al.* 2002). This is surprising because sport hunting alters population density, sex ratio, and age distribution (Wall 1989; Ginsberg and Milner-Gulland 1994; Solberg *et al.* 2000), all of which potentially influence population genetics. Four potential effects of sport hunting have been reported: (i) it may alter the rate of gene flow among neighbouring demes (e.g., in bighorn sheep: Hogg 2000), (ii) it may alter the rate of genetic drift (random change in gene frequencies between generations) through its effect on genetically effective population size (e.g., in moose and white-tailed deer: Ryman *et al.* 1981; bighorn sheep: Fitzsimmons *et al.* 1997), (iii) it may decrease fitness through the deliberate culling of individuals with traits deemed undesirable by hunters or managers (e.g., in red deer: Hartl *et al.* 1991), and finally (iv) it may inadvertently decrease fitness by selectively removing individuals with traits desired by hunters (Harris *et al.* 2002). It is likely that hunting regimes producing sex- and age-specific mortality patterns similar to those occurring naturally, or which maintain demographic structures conducive to natural breeding patterns, will have fewer long-term evolutionary consequences than those producing highly uncharacteristic mortality patterns (see the simulation model by Thelen 1991 and Hundertmark *et al.* 1993).

Among these potential problems, trophy hunting is of special concern. In ungulates, selective hunting pressure via trophy hunting may modify the genetic integrity of populations. Such hunts may unintentionally select against antler or horn size by reducing the life span (and thus the reproductive contribution) of individuals carrying specific alleles. Indeed, horns and antlers are important secondary sexual traits in ungulates. Their size are known to affect individual fitness, especially via their role in male-male fighting for mate access (e.g., in red deer: Kruuk *et al.* 2002; bighorn sheep: Coltman *et al.* 2001; Soay sheep: Preston *et al.* 2003; roe deer: this study). In addition, the size of horns and antlers are highly heritable traits (e.g., Williams *et al.* 1994; Lukefahr & Jacobson 1998; Coltman *et al.* 2003) and it seems that males with the longest horns or antlers may sire offspring of better genetic quality than males with shorter weapons (Coltman *et al.* 2005). As a consequence, the elimination, by selective hunting, of a high proportion of males with large trophies within a population may result in a

selection for shorter antlers or horns, but also, and more importantly, in the elimination of genetic traits favourable to the population, and hence it may have a negative impact on population demographic performance. For example, Ludwig & Hoefs (1995) cited hunting as a possible factor in their finding that Dall sheep *Ovis dalli* in a hunted population had shorter horns than did those in the adjacent unhunted Kluane National Park, despite a similar age distribution. However, where paternities are monopolised by a few highly successful males, artificial human selection is likely to be weaker than where paternities are shared by many males.

Antler size is an important determinant of male access to females and male breeding success in roe deer (Paper 3, 4 and 5). Hence, trophy hunting (e.g., Myrsterud *et al.* 2006) may potentially exert a selection pressure on populations. In addition, antlers have a relatively rapid growth and so males become desirable trophies at a relatively young age. As LBS in bucks seems to be strongly affected by longevity (Paper 2), large-antlered individuals risk being killed before contributing significantly to future generations.

II.7. CONCLUSION

The aim of my study was to provide the first data on male breeding success in roe deer based on molecular analyses and to identify the main local determinants of the variance in individual breeding success among males. My study provides a new example of the great potential of the combined use of molecular analyses, long-term monitoring of populations with individually marked animals, and ecology field studies to investigate issues on mating systems and sexual selection in mammals. This powerful approach allowed me to estimate male breeding success in two roe deer populations in which it would have been impossible to estimate it based on behavioural observations (as has been done by Börger (2006) in an open agricultural landscape), because of the closed forest habitat, and to reveal likely multiple paternity in roe deer. Even for « open-field » roe deer, molecular analyses in conjunction with behavioural observations can be a very useful approach to estimate male breeding success, because continuous observations of animals at night and throughout the rut period is virtually impossible, some fertilised females may fail to give birth, some males may use « sneaky strategies » to mate, multiple paternity can occur (even though it is rare) and females may mate with a male whose territory does not overlap her range. However, genetic paternity analyses are not perfect. To obtain good estimates of male breeding success, it is necessary to sample a large proportion of the population, to minimise as much as possible genotyping

errors and to carefully estimate the number of candidate fathers in the population, which can be costly in terms of time and money. By using molecular analyses to investigate the male mating system and sexual selection in roe deer, I was also able to solve and suggest new interpretations for several debated topics concerning roe deer mating behaviour. My results also provided new evolutionary perspectives to the observations of mating and territorial behaviours previously reported by Bramley (1970), Strandgaard (1972), Johansson (1996), and more recently by Börger (2006) (see also reviews by Hewison *et al.* 1998 and Liberg *et al.* 1998).

II.8. PERSPECTIVES

This thesis opens up new horizons for studies on the male mating system and sexual selection in roe deer and will be useful for setting up future observational and experimental studies, and for improving molecular and paternity analyses in roe deer. I have already alluded to several perspectives in the discussion of my results and the discussion part of my papers. Below, I summarise several of these perspectives and add new suggestions for future research on roe deer.

Concerning the variance in male reproductive success and the determinants of this variance, it could be interesting:

- to further compare the variance in male YBS and LBS and the determinants of this variance between contrasted populations of roe deer: Bogesund and Trois Fontaines, but also Chizé (for which DNA samples are available for about 1500 roe deer but have not yet been genotyped);
- to attempt to include the weaning survival component in the estimates of reproductive success to estimate more accurately individual fitness using LRS;
- to investigate the effects of environmental conditions (e.g., population density, operational sex ratio, climatic conditions, fox predation pressure) on male YBS (e.g., Clutton-Brock *et al.* 1997; Coltman *et al.* 1999; Røed *et al.* 2002), to compare estimates of LRS between cohorts and to investigate early determinants of LRS in males (e.g., Rose *et al.* 1998; Kruuk *et al.* 1999);
- to investigate the effects of phenotypic traits and territory characteristics on variation in male LRS and not only on male YRS;

- to test the effect of body mass and antler size after correction for age and age + body mass respectively;
- to estimate the proportion of the variance in male BS explained by the different factors affecting male BS;
- to test the proposed link between phenotypic quality, territorial status and YBS in both 2-year-old males and old males by combining paternity analyses and intensive field studies during rut;
- to use an experimental approach to further investigate the influence of male density, habitat quality and the abundance of females within a male's territory on male YBS. It could be possible to artificially vary male and female density in a given area through removal, introduction or hunting of specific individuals and to artificially vary habitat quality within a male's territory through changes in forestry and/or agriculture practices from year to year.

Concerning female mate choice, future research should perform detailed investigations of:

- phenotypic cues and/or territory characteristics used by females to choose mates using both experiments (e.g., Carranza 1995; Reby *et al.* 2001) and behavioural observations in the field (e.g., Balmford *et al.* 1992);
- spatial distribution of paternities. In particular, do females mate with their local territorial males?
- female rutting excursions (e.g., duration and distance of excursions, link with the oestrus period, characteristics of the visited male, characteristics of the females performing excursions, proximal and ultimate causes of excursions). In particular, GPS collar technology (e.g., Johnson *et al.* 2002) in combination with behavioural observations and molecular analyses provide a promising approach to track female excursions.

Concerning male mating tactics, it would be interesting:

- to investigate the process of first territory establishment among males (e.g., age of first territory establishment, choice of area, phenotypic characteristics of the youngest males establishing a territory, link between satellite or peripheral mating tactics in sub-adults and the process of first territory establishment; see Paper 2);
- to consider the relationship between phenotypic quality, territoriality and reproductive success in old males (see Discussion of my results);

- to examine reproductive costs and trade-offs between current reproduction and survival or future reproduction (e.g., McElligott & Hayden 2000; see Paper 2);
- to further investigate the male mating system and the variance in male reproductive success in open agricultural landscape habitats, which have been poorly studied up to now (see Hewison *et al.* 1998; Liberg *et al.* 1998; but see Börger 2006).

Concerning molecular and paternity analyses, several aspects should be improved to obtain better estimate of male breeding success in the future in the two study sites and especially at Bogesund:

- the genotyping error rate. It would be clearly important to find solutions to decrease the genotyping error rate (e.g., to replace problematic microsatellite markers with better ones, to spend more time interpreting bands on the auto-radiographs, to systematically re-amplify and re-genotype all samples with poor amplification, stutter bands or artefact peaks), which was quite high in our genotyping database, even though we were particularly careful to keep error rates as low as possible through a combination of specific quality control protocols (see Materials and Methods part of the thesis).
- the proportion of sampled fawns in the population. I had a clear over-estimation of non-breeders in the two studied populations because we did not catch the fawns sired by many males. This could be improved by allocating a greater effort to summer fawn captures in order to maximize the number of fawns caught.
- the estimate of the total number of candidate fathers and mothers in the population each year. The accuracy of the estimate of this user-defined input parameter of CERVUS simulation can influence results of paternity analyses (Marshall 1998). At Bogesund, it would be interesting to estimate the total number of candidate fathers and mothers in the population each year, by using Capture-Mark-Recapture models and by attempting to estimate the number of unmarked animals through behavioural observations.
- the number of fawns for which CERVUS could find the father. It would be interesting to solve paternity assignment uncertainties by genotyping the relevant DNA samples with some new microsatellite markers in order to increase the number of fawns being assigned to a father.

Finally, specifically concerning sexual selection, studies on roe deer and, more widely, other low sexual size dimorphic ungulate species are not as advanced as studies on highly polygynous and dimorphic species such as red deer, bighorn sheep or Soay sheep. Interesting future research perspectives on sexual selection-related areas in roe deer concern, for example, heritability of secondary sexual traits (e.g., Kruuk *et al.* 2002; Coltman 2005), quantitative genetic traits (e.g., Milner *et al.* 1999), links between genes of the major histocompatibility complex (MHC) and phenotypic traits or parasite load (e.g., Ditchkoff *et al.* 2001). It would also be very interesting to compare patterns of opportunity for sexual selection in ungulates, pinnipeds and primates to investigate whether selection pressure is similar in these different groups of mammals including a set of species ranging a wide continuum from monomorphic to highly dimorphic species.

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Roe deer at dusk
(photograph by Olivier Villa)

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Note that references from papers are not listed here but at the end of each paper.

APPENDIX

Appendix 1 : Review of the main published data on male lifetime reproductive success in ungulates.

species		mating system	sexual size dimorphism	reference	method	period	offspring survival component	individuals included	complete cohort	range	mean	SD	variance	I _m
Bighorn sheep	<i>Ovis canadensis</i>	roving	43.40%	Coltman et al. (2002)	MO	6 seasons		all males			0.43	0.91		4.52
Soay sheep	<i>Ovis aries</i>	roving	30.00%	Pemberton et al. (1999)	MO	lifetime	no	all males	no	0 - 19	0.73	1.88	3.5	6.63
					MO	lifetime	no	adults	no	0 - 19	0.31	1.58		26.1
				Coltman et al. (1999)	MO	lifetime	no	all males	yes					3.46
					MO	lifetime	no	successful breeders	yes					1.11
red deer	<i>Cervus elaphus</i>	harem	33.30%	Pemberton et al. (1992)	BO	lifetime	yes	all males	yes	0 - 24	6.38			2.51
				Clutton-Brock et al. (1982)	BO	lifetime	yes	mature males	no	0 - 24	6.38			
				Clutton-Brock et al. (1988)	BO	lifetime	yes	mature males	yes	0 - 32	5.41		41.9	1.43
					BO	lifetime	yes	all males	yes				35.0	2.51
				Clutton-Brock (1987)	BO	lifetime	yes	all males			10.15			1.22
					BO	lifetime	yes	successful breeders						0.96
					BO	lifetime	yes	mature males						1.20
				Marshall (1998)	MO	lifetime	yes	all males	yes					5.97
					MO	lifetime	yes	successful breeders	yes					0.88
					BO	lifetime	yes	all males	yes					9.08
roe deer	<i>Capreolus capreolus</i>	territoriality	7.60%	this study (paper 1)	MO	lifetime	no	mature males	(yes)	0-14	4.54		15.5	0.75
					MO	lifetime	no	successful breeders	(yes)					0.6
fallow deer	<i>Dama dama</i>	lek	26.60%	McElligott and Hayden (2000)	BO	lifetime	no	all males	yes	0 - 171			208.8	
American pronghorn	<i>Antilocarpa americana</i>	harem/territoriality	18.90%	Byers (1994)	BO	lifetime	no	all males?	no?	0 - 25				1.08
					BO	lifetime	yes	all males?	no?	0 - 9				1.87

Note: MO = molecular analyses, BO = behavioural observations of courting and mating. In grey, data used for the comparison of I_m between species in Paper 1.

