The effects of state on the behavioural decisions and survival in the house sparrow

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PhD Thesis

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Female house sparrow — Photo by Á.Z.Lendvai

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Chapter I.   Introduction

BEHAVIOURAL DECISIONS

Animals, during their lives, are almost constantly faced with behavioural decisions. For instance, in a given time, should an animal forage or rest? If foraging, where should it go to eat? What type of food to pursue? Feed alone or join others? Which mate to choose? Fight rivals or run away? How many offspring to produce? Whether to care for the young or desert? One central goal of behavioural studies is to study what are the factors that influence these behavioural decisions. Since the situations in which individuals have to make a decision cover virtually all aspects of behaviour, in the past decades new fields emerged to deal with different sets of questions. For example, individual decisions during the foraging are analysed by the Optimal Foraging Theory (Stephens & Krebs 1986), Game Theory is extensively used in the examination of the social decisions, i.e. when the outcome of the individuals' choice depends on the behaviour of their companions (Maynard Smith 1982) and strategic decisions over the lifetime of the organisms are discussed by the Life History Theory (Stearns 1992). Behavioural Ecology, by integrating the ideas of evolution, ecology and behavioural studies, provides a common, general framework for all these analyses (Krebs & Davies 1997) in order to seek the adaptive value of behaviour; i.e. to investigate what the fitness consequences are of a certain behavioural decision.

There are two important constraints which characterises behavioural decisions. First, time and energy cannot be allocated simultaneously to all behaviours, e.g. an individual can either feed or rest or mate, but cannot do them at the same time. Even if the concurrent behaviours are not completely incompatible, the efficiency of a given action is generally lower if it is performed together with another action than if it is performed in isolation (Futuyuma & Moreno 1988, Leigh 1990). The second characteristic arises from the observation that most behavioural decisions have some benefits and costs. A classical example may be the courting behaviour of the male Túngara frogs (*Physalaemus pustulosus*). In this species, males attract their mate by acoustic calls. It is undoubtedly advantageous for a male to signal his presence and willingness to mate for the possible partners. Nevertheless, the males' croaking attracts not only the female frogs but also the predatory bats (*Trachops cirrhosus*), which represents a cost of this signalling behaviour (Tuttle & Ryan 1981).

These two constraints stand for the concept of trade-offs: the benefits from performing a behaviour can only be gained at the expense of either another behaviour or some direct cost, e.g. increased mortality in the example above. Trade-offs thus form a central pillar in the evolutionary approach to behaviour. One of the most widely applied tools in Behavioural Ecology to analyse trade-offs is the use of optimality models (Krebs & McCleery 1984). The argument of using optimality models is that when the benefits are traded off against the costs of a behavioural option, natural selection favours the behavioural responses which best promote an individual's propagation of copies of its genes into future generations (MacArthur & Pianka 1966, Alexander 1996, Krebs & Davies 1997).

THE ROLE OF STATE IN BEHAVIOURAL DECISIONS

Using the approach based on the analysis of costs and benefits, optimality models have been used to analyse the decisions of individuals which may be influenced by a wide array of ecological factors. However, even under the same environmental circumstances not all individuals behave in the same way. Consequently, much unexplained variation can be seen in the empirical studies of animal behaviour, and the existence of this variance has been often neglected as meaningful variation or was explained by environmental 'noise' and measurement errors. For example, in one of his seminal papers, Lack (1947) proposed that in a population 'the average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and at the season in question' and therefore 'natural selection eliminates a disproportionately large number of young in those clutches which are higher than the average'. Hence, according to Lack's hypothesis, in a given population the average clutch size is which produce the most surviving offspring. In most field studies however, discrepancies have been found between the most productive clutch size (the 'Lack optimum'), and the average or modal clutch sizes (Perrins 1965, Klomp 1970, Stearns 1976). Several hypothesis have been suggested to explain this paradox implying the costs associated with brood rearing (i.e. the trade-off between current and future reproduction, with birds producing fewer in the present year while increasing their chances of surviving to reproduce in subsequent years; Williams 1966), the unpredictable environmental fluctuations which may favour a 'bet hedging' strategy resulting in a smaller clutch size (Mountford 1973, Boyce & Perrins 1987, Nur 1987), etc. However, to understand the variation in clutch size, one needs to consider individual differences between the parents, which is often referred to as 'individual quality' (or 'parental quality' in the present context).

In fact, individuals differ in their ability to rear their young, and therefore, there is an optimum level of parental investment for each individual (Högsted 1980, Pettifor *et al.*1988). The consequences of this intrinsic individual variation in animal decisions has become the subject of scientific interest in the past two decades (Clark 1993).

Individuals at any given time are likely to differ in a set of variables that are usually referred to as 'state'. Such variables may include age, body size, body temperature, energy levels, parasite load, immune function, etc. The costs and benefits of a given behavioural decision may depend on these state variables. As a result, natural selection should favour those individuals that base their actual behavioural decisions on their current state. In line with this intuitive notion, recent theoretical models based on optimisation showed that the state of animals have a major role in the decisions of individuals (Houston & McNamara 1999). Recent empirical evidences corroborate the main assumptions and many predictions of these theoretical models, showing that individuals indeed make state-dependent decisions (Thomas 1999, Godfrey & Bryant 2000, Thomas 2000, Banks 2001, Bilde *et al.* 2002, Spencer & Bryant 2002, Thomas & Cuthill 2002, Jakob 2004).

An organism's state in a given time may be characterised by several state variables, and one should establish what are the important components of an individual's state. Fortunately, in most cases the context in which the animal is confronted with a certain behavioural decision determines the relevant state variables. For example, an obvious element to consider in foraging decisions is the level of energy reserves (also often referred to as 'body-state', or 'body condition' in empirical studies). If an animal has low energy levels, its behaviour must tackle this situation, otherwise it may jeopardise starvation. For instance, hungry whirligig beetles (*Dineutes assimilis*) are more willing to take the riskier position at the edge of the group than the satiated individuals (Romey 1995). The energetic state of an organism may have a major role in the decision making, therefore I address the role of energy reserves in behavioural decisions in *Chapter III & Chapter IV*.

Social Foraging as a Model System to Study Social Behaviour

The role of state variables have been documented in the decisions of solitary animals (Thomas 1999, Thomas & Cuthill 2002, Spencer & Bryant 2002). In this Thesis, my principal aim is to extend our knowledge on state-dependent behaviour towards social behavioural strategies. The animal's behavioural strategy is a rule that specifies how the organism deals with every possible circumstance (Houston & McNamara 1999). One of the best studied social systems,

where individuals use alternative strategies is social foraging (Giraldeau & Caraco 2000). During social foraging, individuals may have to choose between two main options: either searching for food resources on their own ('producing'), or exploiting their flockmates' food discoveries ('scrounging'). These two distinctive alternative behaviours are widespread: the occurrence of the producer-scrounger strategies has been observed in a wide taxonomical range (e.g. in spiders, birds, mammals and humans, Giraldeau & Beauchamp 1999). In most cases, the foraging individuals use these strategies in a flexible way, and often switch between them (Coolen *et al.* 2001).

From an evolutionary perspective, this social foraging system represents a specific case of a more general social phenomenon. The producer-scrounger system is an alternative-option scramble competition, where certain individuals (producers) invest time and energy in creating or guarding some resource, which other individuals (scroungers) may then parasitize (Barnard & Sibly 1981, Parker 1984). A common characteristic of all producer-scrounger type games is that the fitness of scroungers is strongly and negatively frequency dependent; scrounging is only profitable when scroungers are rare (Figure I.1).
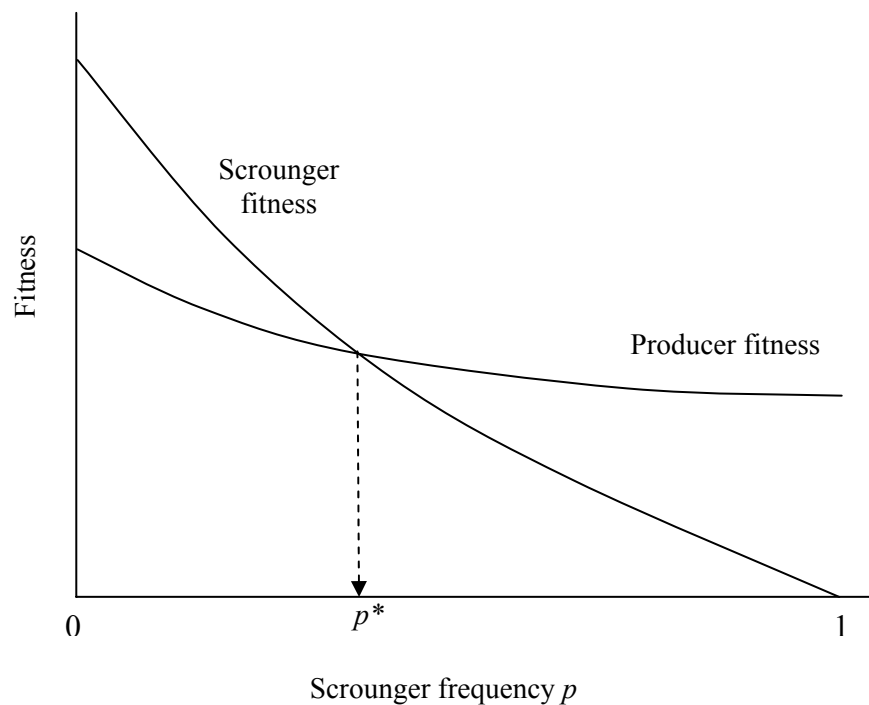
Figure I.1. The producer-scrounger model. The fitness of a scrounger decreases with the frequency of scroungers in the population, *p*. The fitness of producers is less frequency dependent. The equilibrium *p** where the fitness of scroungers is equal to the fitness of producers. (After Barnard & Sibly 1981.)

A vast range of biological phenomena can be modelled by the producer-scrounger game: host-parasite systems, alternative mating strategies ('sneaks/guarders' or 'callers/satellites'; Alcock *et al.* 1977, Thornhill 1979, Dunbar 1982), alternative nesting strategies ('digging' and 'entering' in the parasitoid wasp, *Sphex ichneumoneus*; Brockman *et al.* 1979), food hoarding (Andersson & Krebs 1978), etc. The producer-scrounger system therefore, is an excellent model to study social behavioural decisions.

Early studies of social foraging (both theoretical and empirical) focused on the conditions of the stability of the producer-scrounger system (e.g. stable proportion of scrounging), and these investigations characterized individuals with identical phenotypic attributes. Consequently, less is known about the factors that determine the strategies followed by individuals in a particular situation, i.e. the focus of this Thesis.

EVOLUTIONARY CONSEQUENCES OF STATE-DEPENDENT BEHAVIOUR

The state-dependent approach to behaviour lies on the assumption that the state is a 'set of the values of factors relevant to the animal's fitness which are altered by its behaviour' (Krebs & McCleery 1984). In other words, the statement above suggests a framework, in which the animals make state-dependent decisions, and these decisions in turn, have consequences on their state (Figure I.2). If, for example, an animal's energy levels are low, it may start feeding which would reduce its energy deficit, hence it may control its own state by means of behaviour (McFarland 1971, Krebs & McCleery 1984, Houston & McNamara 1999).

However, animals have only partial control on their state. In nature, several unpredictable environmental effects (weather, diseases, etc.) may cause changes in the animal's state. These effects are integrated by means of some physiological process (e.g. involving changes in hormone levels) and the subsequent behavioural decisions are based on the new state of the organism. An essential feature of this framework is that the relevant behavioural action has some genetic basis and is related to the fitness, otherwise the natural selection could not act on behaviour and thus the animal may behave in any way without evolutionary consequences.
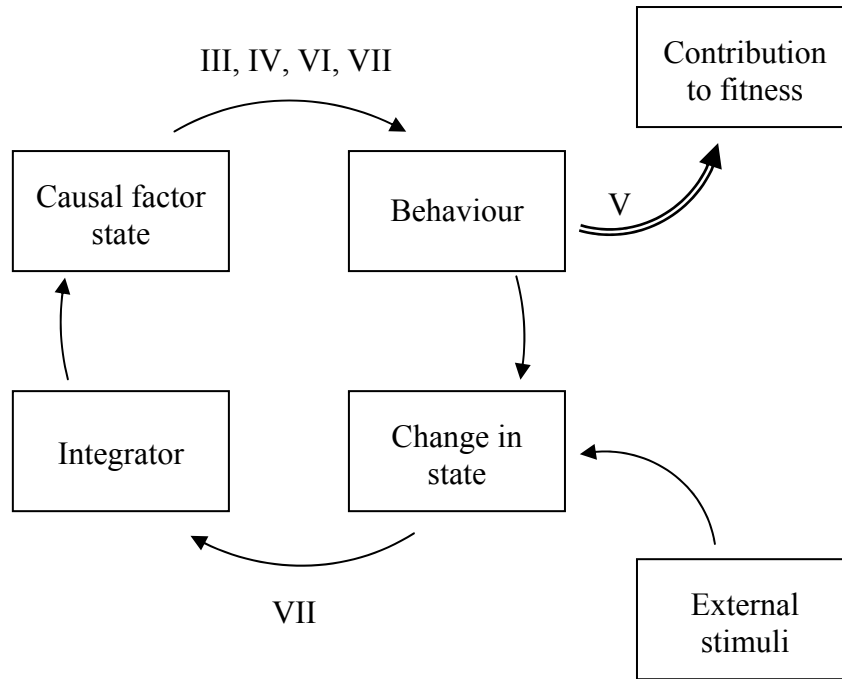
Figure I.2. Feedback system of the relationships between state and behaviour. Numbers on the arrows indicate the chapters of this Thesis, which deal with a particular relationship of this framework. See also the text for further explanation. (Modified after Krebs & McCleery 1984.)

For instance, we may illustrate the selective advantage of the state-dependent decisions by a simple model (Houston & McNamara 1999). This model analyse the hypothetical foraging behaviour of an animal, which attempts to survive a given period of time, e.g. the winter. The animal has two choices about foraging. Either it chooses option 1, say, a feeding site, which is safe from predators but the net rate of energetic gain is low, or it chooses option 2, which involves a risk of predation but gives a higher net rate of energy gain. The best strategy minimizes mortality, i.e. gives the highest probability to survive the given period (Figure I.3).
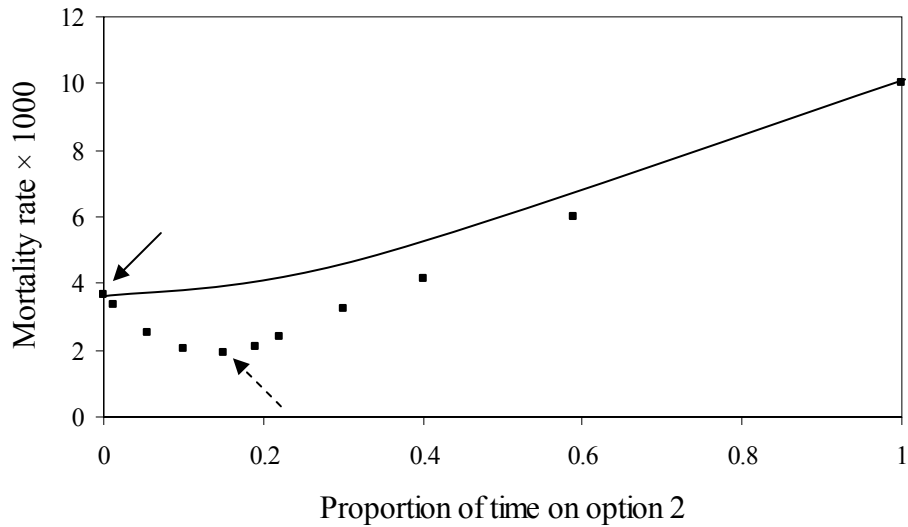
Figure I.3. Selective advantage of state-dependent strategies. The figure shows equilibrium mortality rates as a function of the proportion of time spent on option 2. The solid line gives mortality rates when behaviour does not depend on state. Squares represents the mortality resulting from the state-dependent strategies. The upper arrow shows the best non-state dependent strategy. The lower dashed arrow shows the best state-dependent strategy (After Houston & McNamara 1999.)

Without going into the details of the parameterisation, it will suffice here to emphasize the conclusions of the model. It can be seen in Figure I.3. that for any proportion of time spent in option 2, the state-dependent strategy achieves lower mortality than the non state-dependent strategy. Furthermore, the optimal state-dependent strategy has a much lower mortality than the optimal non-state dependent strategy (indicated by arrows on Figure I.3). Consequently, the individuals making state-dependent decisions should have a selective advantage. In *Chapter V*, I investigate the ultimate fitness consequences of the state, by analysing the relationship between a state variable and the survival probability.

DOMINANCE

Animals often compete for scarce resources, such as mate, food or safe refuge. Some components of the animals' state (like size, strength, aggressiveness) may influence their ability to compete for the limited resources. These differences then can generate dominance relationships between pairs of individuals, thus finally leading to the establishment of dominance hierarchy in groups of animals. Dominant individuals (those who are high in the hierarchy) often have an advantage over subordinates (who have low position in the hierarchy) in acquiring limited resources (Huntingford & Turner 1987). For example, in the

Willow tit (*Parus montanus*) dominant individuals obtain safer feeding sites than subordinate birds (Ekman & Askenmo 1984, Ekman 1987), and dominant male Yellow-rumped cacique orioles (*Cacicus cela*) monopolize the females when they can be fertilised (Robinson 1986). Besides the numerous benefits of being dominant, it also bears costs as well. Dominant individuals may be more often involved in aggressive interactions than subordinates (Balph 1977, Kikkawa 1980) resulting in higher probability of injuries. The need to be constantly prepared for fight rivals entails energetic costs. Accordingly, metabolic costs of dominant individuals are found to be positively correlated with social rank in birds and in fish (Hogstad 1987, Metcalde *et al.* 1995). Although the costs and benefits of the social dominance have been studied, we know much less about how these dominance effects interact with other state variables. I address this issue in *Chapter IV*.

Various selection forces may determine whether the internal state of an animal should be detectable to others or not. In several cases, the internal state of an organism remains unknown for others, either because the animal would not benefit from advertising it, or let it know for others may be harmful (e.g. signalling poor condition in the presence of a predator). However, there are situations when it is advantageous for the animals to indicate their state. For example, in competitive situations, when the outcome of the contest may be predicted (e.g. on the basis of size or weaponry), all participants may benefit from assessing the opponent's winning chances as they may avoid to be unnecessarily involved in escalated fights (Maynard-Smith & Parker 1976, Hammerstein & Parker 1982). Yet, the probability of winning an aggressive encounter may depend on a number of state variables, including for instance age (Packer 1979, Creel *et al.* 1992), hunger (Hazlet *et al.* 1975, Andersson & Åhlund 1991). The status signalling hypothesis proposes that individual variation in conspicuous colour traits reflects the ability to win agonistic encounters, thus they may serve as signals of the dominance status (Rohwer 1975). Signalling status may be particularly beneficial for group living animals, if the groups are variable with regard to membership, because signalling may reduce the cost of asserting status each time a new member joined the group. The classical textbook example of status signalling is the case of Harris' sparrows (*Zonotrichia querula*). Individuals of Harris' sparrows vary greatly in the amount of black coloration on their throats and crowns. Rohwer (1975) reported that individuals with more black consistently won aggressive interactions with individuals having less black. After the pioneering studies of Rohwer, the status signalling hypothesis was extensively studied in birds, and several studies have documented that conspicuous plumage ornaments may signal dominance status (e.g. in the great tits (*Parus major*) Jarvi & Bakken 1984), in the pine

siskins (*Carduelis pinus)* Senar *et al.* 1993, in the house sparrow (*Passer domesticus*) Møller 1987, Liker & Barta 2001, Hein *et al.* 2003). Very often, animals possess several striking morphological features that may be signals of fighting ability or dominance status (e.g. different colourful patches, and/or a crest, comb, horn, antlers, etc.). The coexistence of several traits raise the possibility that these traits may function as multiple signals. The idea of multiple signals has received increased attention in recent years in the context of mate choice.

Different hypotheses have been put forward why should animals, use multiple cues instead of only one cue. These hypotheses may be grouped into three main category on the basis of the relationship between the use of multiple cues and its fitness consequences (Candolin 2003). First, most hypothesis deal with the scenario under which the use of multiple cues is adaptive and increases fitness by reducing the costs of assessing the quality of the partner, or by reducing the errors during assessment. Multiple cues may be either 'multiple messages', with different signals giving information about different qualities of the signaller (Møller & Pomiankowski 1993, Johnstone 1996); or may serve as 'backup signals', which allow a more accurate assessment of mate quality as each signal reflects the same quality with some error (Møller & Pomiankowski 1993, Johnstone 1996). The 'backup signals' hypothesis differs from the 'multiple messages' hypothesis in that different signals reflect the same aspect of quality instead of different aspects. Second, the use of multiple cues may have no influence on fitness, but may include preferences that are remnants from past selection or have arisen in another context and are exploited by the signaller (Holland & Rice 1998). Finally, using multiple cues may have been evolved during sexual conflict. As a result, multiple cues may be even maladaptive and decrease fitness of the receiver, if the signaller manipulates mating resistance of the receiver by taking advantage of pre-existing sensory biases (Holland & Rice 1998). Although these hypotheses were proposed in the context of mate choice, most of them is applicable to status signalling as well, since in agonistic interactions individuals may also benefit from using multiple cues in the assessment of the fighting ability of their opponent. In *Chapter VI*, I investigate whether different plumage patterns may be related to different aspects of dominance status.

THE PROXIMATE BACKGROUND OF STATE-DEPENDENT DECISIONS

A major challenge in modern behavioural ecology is to understand the mechanistic, or proximate basis of behaviour. As we have seen, various aspects of state can affect behavioural decisions in animals, but our knowledge is still scanty about the way these variables are

represented in the organism (Houston & McNamara 1999). Hormonal state of the individuals may be such an important cue by which environmental and physiological stimuli are assessed and integrated in decision making (Cuthill & Houston 1997, Sinervo & Svensson 1998). For instance, in response to various environmental stimuli, the levels of several hormones change in a dynamic way in the organism, thus the circulating hormone concentrations within an individual might reflect its physiological response to the environmental stimuli (Nelson 2005). Thus the hormonal state of an individual may be seen as an internal representation of a given external environmental stimuli. In *Chapter VII*, I investigate the process of the internal hormonal perception of an environmental stressor, and on how it influences the behaviour.

Chapter II.   Thesis objectives

THESIS OBJECTIVES

In this Thesis I focus on four aspects of state-dependent behaviour by investigating the house sparrow.

(1)   I seek experimental evidence that, according to recent theoretical models, individuals make state-dependent decisions.

(2)   I examine the survival consequences of a state variable.

(3)   I investigate the relationship between the signals of dominance and different aspects of aggressive behaviour.

(4)   I study how behavioural actions and ecological circumstances influence the physiological response to an environmental stimulus, and how this physiological response influences the behaviour.

THE EFFECTS OF STATE VARIABLES ON THE SOCIAL BEHAVIOUR

In *Chapter III & Chapter IV*, I investigate the relationship between the internal state (the level of energy reserves) and the frequency of scrounging (exploiting others' food findings) in captive flocks of house sparrows. In *Chapter III*, using experimental manipulations of energy expenditure, and behavioural observation of the birds, I test the specific prediction of Barta & Giraldeau's (2000) model that early in the morning, individuals with low energy reserves should prefer the use of scrounging. I also investigate that scrounging is risk-averse tactic, i.e. it provides more reliable food gain than producing. In *Chapter IV*, I study how the effects of energy reserves on the use of scrounging are modulated by the effects of social dominance. To investigate this question, I use an identical experimental setup as in *Chapter III*, but I study individuals in two different dominance groups.

SURVIVAL CONSEQUENCES OF A STATE VARIABLE

In *Chapter V*, I study whether the quality of the primary flight feathers of wild house sparrows is related to their short-term survival probability. To address this question, I captured individuals of a free living house sparrow population before the onset of breeding season, and

measured the quality of their flight feathers from close-up photographs. Thereafter in regular time periods, I conducted behavioural observations to determine their presence or absence in the study area. Based on these observations I analyse whether their apparent survival during the breeding season is related to the quality of their flight feathers.

STATUS SIGNALLING AND FIGHTING BEHAVIOUR

In *Chapter VI*, I investigate whether there are multiple status signals in male house sparrows, i.e. whether different plumage traits may convey different information about the sparrows' fighting behaviour. Specifically, I investigate the role of the wingbars and wing displays in aggressive interactions in winter flocks of house sparrows. Specifically I addresse two questions. First, I ask whether males with larger and/or more conspicuous wingbars are more successful in social competition among conspecifics. Second, I ask whether the wing displays are related to different aspects of fighting behaviour. To test these questions, I measured the bib and the wingbars of male house sparrows and then I conducted behavioural observations on their fighting behaviour in captive flocks.

PHYSIOLOGICAL RESPONSE TO AN ENVIRONMENTAL STIMULUS

In *Chapter VII*, my goal is to study how animals may integrate the effects of both their behavioural activity (e.g. parental behaviour) and the environmental circumstances (e.g. the breeding season) and by what kind of physiological reaction should they respond to these effects. Specifically, I test two hypotheses that have been proposed to explain the individual differences in the hormonal response to an unpredictable environmental factor (stress). I investigate whether the amount of parental investment and the probability of renesting influences the hormonal response to stress, and whether this hormonal response to stress influences behaviour (return to the nest after capture). To test these hypotheses, I studied a free living, breeding population of house sparrows. I captured the parents tending large chicks and collected a small amount of blood to measure their hormone concentrations.

THE HOUSE SPARROW AS A MODEL SPECIES

My investigations were carried out in the house sparrow, a small (14 cm, 28 g), sexually dimorphic, highly gregarious passerine bird. In this species, males have a characteristic black

throat patch (bib), the size of which is highly variable among individuals (Møller 1987). In breeding plumage, males are colourful, having grey crown, light cheek and chestnut nape; females are brownish buff-coloured. One of the striking characteristics of this species is its exceptional skills in adapting to new environments. Most populations live near humans, which provides a ready source of food (including human food waste) and nesting sites, most often beneath gutters, roof tiles, eaves, holes in wood siding. However, as a member of the family of Old World Weaver Finches (*Passeridae*), the house sparrow readily builds bowl-like nests in open trees; these nests may contain a narrow entrance tunnel that leads to a nest chamber. Sparrows can adapt to the most extreme conditions, as may be illustrated by those birds that bred in a colliery over 200 m below ground level, being fed by the miners (Summers-Smith 1963).

The house sparrow is a prolific breeder: depending on the breeding conditions, it may raise up to 5 clutches of 2-7 chicks in one breeding season (Summers-Smith 1963). Eggs are incubated for 10-14 days, and nestlings are fully feathered in just 15-17 days. This high productivity makes them very effective invaders all over the world. Although the Falklands may have been colonised by house sparrows 'hitchhiking' aboard a fleet of whalers from Uruguay, the appearance of the species in most areas outside Europe was due to an artificial introduction by humans. For instance, the first sparrows were released in the United States in 1850, but at the end of the 19th century, it was already treated as a common pest, and only in Indiana, the eradication of almost half a million sparrows was insufficient to stop its spread across the state.

The highly social nature, the ability to accept new environments and the flexibility of breeding behaviour makes the house sparrow an outstanding model species to study the research questions of this Thesis. First, the use of the social foraging strategies in the flocks of house sparrows is widespread and easily observable; the producer-scrounger strategies were first documented on a captive flock of house sparrows (Barnard & Sibly 1981). In fact, the wild-caught house sparrows can be easily kept in captivity, and their natural behaviour can be easily observed shortly after the capture (Summers-Smith 1963). Second, the house sparrow has one of the best studied system of status signalling. There is hardly another animal species in which a single trait were the subject of so many investigations as it was in the case of the bib of male house sparrows. Third, the reproductive behaviour of the house sparrow is quite plastic, thus can be easily manipulated by means of manipulation of the clutch size (Seel 1969, Hegner & Wingfield 1987, Chastel & Kersten 2002, Bonneaud *et al.* 2003). Finally, the highly resident nature of the house sparrow (Summers-Smith 1963) makes it an ideal subject

for survival analyses, as the survival is weakly confounded by the migration (Ringsby *et al.* 1999), which is the case for many bird and mammal species.

The investigations presented in this Thesis fit well in the line of studies carried out by our research group. For example, Liker & Barta (2001) studied the aggressive behaviour in captive flocks and found that both sexes were involved frequently in aggressive encounters, and there were no difference in their mean dominance rank. Liker & Barta (2002) studied the relationship between dominance and the social foraging tactic use and found that dominant sparrows used scrounging more than subordinates. Barta *et al.* (2004) investigated the effects of predation risk on the social foraging tactic use in tree sparrows (*Passer montanus*), and showed that increased predation risk affected the scrounging frequency.

GENERAL METHODS

In this Thesis I conducted experimental manipulations and observations of house sparrows, both in aviaries on captive birds and in the field. During these investigations I used standard methods, details of which can be found in each chapter. All of the studies presented here were carried out in cooperation with other students or researchers. For all studies, I participated in all stages of the work, from designing the research, through the data collection and analysis until the preparation of the manuscript.

Chapter III.   The effects of energy reserves on social foraging: hungry sparrows scrounge more

ABSTRACT Animals often use alternative strategies when they compete for resources, but it is unclear in most cases what factors determine the actual tactic followed by individuals. Although recent models suggest that the internal state of animals may be particularly important in tactic choice, the effects of state variables on the use of alternative behavioural forms have rarely been demonstrated. In this study, using experimental wind exposure to increase overnight energy expenditures, we show that flock-feeding house sparrows (*Passer domesticus*) with lowered energy reserves increase their use of scrounging (exploiting others' food findings) during their first feed of the day. This result is in accordance with the prediction of a state-dependent model of use of social foraging tactics. We also show that scrounging provides less variable feeding rates and patch finding times than the alternative tactic. These latter results support the theoretical assumption that scrounging is a risk-averse tactic, i.e. it reduces the risk of immediate starvation. As the level of energy reserves predicts the use of social foraging tactics, we propose that selection should favour individuals that monitor the internal state of flock mates and use this information to adjust their own tactic choice.

INTRODUCTION

Animals often follow alternative behavioural tactics when they compete for resources such as mates or food (Maynard Smith 1982; Gross 1996; Giraldeau & Caraco 2000). Although the evolutionary outcomes of behavioural polymorphism can be explained by theoretical models (Maynard Smith 1982; Gross 1996; Houston & McNamara 1999; Giraldeau & Caraco 2000), we know less about what factors actually determine the tactic followed by an individual in a particular situation. Recent models suggest that the state of individuals, such as age, size, level of energy reserves or parasite load can effectively influence what actions are available to them and how these actions affect their fitness (Gross 1996; Houston & McNamara 1999). Consequently, the internal state of animals can significantly determine their choice between alternative behavioural tactics (Houston & McNamara 1987, 1988, 1999). Experimental tests of the effects of state variables on tactic use, however, are scarce.

Social foraging is one of the best-studied systems where individuals use alternative tactics (Giraldeau & Caraco 2000). For instance, in flock-feeding birds it is frequently observed that some individuals (producers) actively search for food patches whereas others (scroungers) wait for producers to discover a patch and then feed from it (Barnard & Sibly 1981; Giraldeau & Caraco 2000). It has been shown that individuals of many species flexibly use these tactics, i.e. birds may frequently switch between producing and scrounging (e.g. Koops & Giraldeau 1996; Coolen *et al.* 2001; Liker & Barta 2002). Although the results of several studies suggest that the frequency of scrounging may be related to ecological factors (e.g. food distribution, Koops & Giraldeau 1996; predation risk, Barta *et al.* 2004) and the birds' phenotypes (e.g. age, Steele & Hockey 1995; dominance rank, Liker & Barta 2002), the effects of quickly changing state variables on tactic use are poorly understood.

It is widely accepted that the level of energy reserves might be a particularly important state variable that can affect the use of social foraging tactics. In a state-dependent dynamic game model, Barta & Giraldeau (2000) investigated the effects of energy reserves on the frequency of scrounging. This model, in which the effects of the individuals' dominance ranks were not considered, predicts that when an individual faces an energy shortfall (i.e. when its energy reserves are near to its lower lethal boundary) it is optimal to be risk-averse, i.e. to follow a tactic that minimizes the risk of immediate starvation by providing a small but reliable amount of food. Risk-sensitive models of social foraging propose that scrounging is a risk-averse tactic, because individuals can decrease the variance in their food intake by

increasing the use of scrounging (Caraco & Giraldeau 1991; Barta & Giraldeau 2000). Consequently, Barta & Giraldeau's (2000) model predicts that, early in the morning, birds with low energy reserves will increase the use of scrounging, whereas individuals with high reserves will more often be producers. Note that this prediction is different from the energy budget rule (Stephens 1981) which does not consider the possibility of immediate starvation and predicts risk-prone behaviour if the animal cannot meet its daily energy requirement (i.e. it has low reserves).

In this study we investigated the effects of energy reserves on the use of social foraging tactics in house sparrow (*Passer domesticus*) flocks. Sparrows usually feed in flocks and use both producer and scrounger tactics to find their food (Barnard & Sibly 1981; Johnson *et al.* 2001; Liker & Barta 2002). To investigate the effects of energy reserves we experimentally manipulated the birds' overnight energy expenditure by simulating nocturnal wind exposure. We tested the specific prediction of Barta & Giraldeau's (2000) model that individuals with lowered energy reserves should use scrounging more frequently than control birds early in the morning. Furthermore, we investigated one of the basic assumptions of the model, namely that scrounging is risk-averse, i.e. it provides more reliable rewards than producing for individuals trying to avoid starvation early in the day.

METHODS

Study subjects

We captured 88 house sparrows with mist nets between 8 November 2002 and 10 February 2003 in Budapest and then formed four flocks each consisting of 22 individuals. Four birds died before the experiments for unknown reasons (we found no evidence for physical injuries or infections on dead birds). Wild-captured birds may die in captivity because some of them may be more susceptible to handling or a changing and potentially stressful environment than others (Gonzalez *et al.* 1999). Nevertheless, the survival of birds in our study flocks during the approximately one month of captivity was high (95.5 %) as compared to other studies on captive house sparrows (e.g. 63% during three months: Gonzalez *et al.* 1999; 64% during two weeks Gill & Paperna 2005). After the death of the four birds, our flocks included 19, 22, 22 and 21 individuals, respectively, and these flock sizes did not change further. The sex ratio in the flocks was approximately balanced (10:9, 13:9, 11:11 and 12:9 males:females,

respectively). After capture we measured body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm), and ringed all birds with a numbered metal ring and three colour rings. We also marked the individuals with small dye spots on their crown or tail feathers to facilitate quick individual recognition during the observations.

After the measurements the birds were taken to a 2 (W) × 3 (L) × 2 m (H) 'acclimatizing' aviary, where they were kept for at least one week to become familiar with the experimental environment. The flocks were then transferred to a 3 (W) × 4 (L) × 2 m (H) 'test' aviary, while another flock was captured and placed in the acclimatizing aviary. All observations (i.e. data collection on fighting behaviour and testing foraging tactic use) were performed in the test aviary, where the birds spent two weeks. The two aviaries were separated so that individuals of different flocks could not interfere with each other.

Both aviaries were lit by artificial light with 9:15 hr light:dark periods and contained artificial roosting trees and several small (10 × 10 × 10 cm) boxes for sleeping and resting. The aviaries also contained two water dishes, two sand dishes and one dish with pieces of fine gravel to facilitate digestion. Feeding took place on a 1.2 × 1.2 m plywood board ('grid' henceforth) that contained a 12 × 12 grid of 144 equidistant wells (diameter: 2.5 cm, depth: 1.2 cm) for presenting food. Water and food were provided *ad libitum* during the acclimatization and between the observations. Food consisted of millet, oat, wheat, hemp and sunflower seeds. In addition, multi-vitamin droplets were added to the water. Birds apparently became familiar with the aviary during the acclimatization period and subsequent observations on fighting behaviour (see below), and they have learned to use the grid actively for searching for food by the time of the experimental testing of foraging behaviour. The birds were provided with millet, oat, wheat, hemp and sunflower seeds *ad libitum* during the acclimatization period and between observations. In addition, multi-vitamin droplets were added to their water. The birds apparently became familiar with the aviaries during the acclimatization period and subsequent observations on fighting behaviour (see below), and they had learned to use the grid actively to search for food by the time of the experimental testing of foraging behaviour.

After the experiment, the birds were released at the site of capture. Released birds were in good condition and appeared to re-establish themselves in the local colony, as we often re-encountered them at the capture sites (ÁZL personal observation; Liker & Barta 2001). The study was licensed by the Duna-Ipoly National Park (847/3/2003).

Experimental protocol

The experiment consisted of two parts for each flock. First, because scrounging sparrows are often aggressive against flock mates and dominance status influences the foraging tactics of individuals (Liker & Barta 2002), we attempted to reduce dominance effects by using 'middle-ranked' individuals in the experiments. To do so, we observed fighting behaviour for one week in each flock. Fighting observations were only recorded when the birds were feeding on the grid. During the observations we recorded 1695 fights between pairs of individuals (mean ± SE: 423 ± 48 fights per flock). For each individual in a flock, we determined fighting success (number of fights won per total number of fights in which an individual was involved; for more details see Liker & Barta 2001, 2002). We ranked individuals within each flock on the basis of their fighting success (as fighting success strongly correlates with dominance rank, Liker & Barta 2001) and selected the ten middle-ranked individuals in each flock (starting from rank 7 in the flocks with 22 birds, and from rank 6 in the flocks with 19 and 21 birds). We then used the 10 selected birds per flock as the subjects of the manipulation (below).

In the second part of the experiment we manipulated the middle-ranked birds' overnight energy expenditure and then observed their foraging behaviour during their first foraging next morning. In the evening before the foraging observations, we captured all birds and removed all food items from the aviary. High and low-ranked birds were immediately released back to the aviary to form the 'core flock' (*sensu* Giraldeau *et al.* 1994). After measuring the body mass (± 0.1 g) of the middle-ranked birds we individually housed them in cages measuring 0.3 (L) × 0.4 (W) × 0.6 m (H). Half of these birds were randomly assigned to the manipulation, whereas the remainder were controls (i.e. 5:5 individuals in each flock). To manipulate overnight energy expenditure we placed electric fans in front of the cages of each manipulated bird to simulate wind exposure, whereas controls were kept in the cages without wind exposure. Fans operated throughout the night. Ambient temperature during the treatments ranged from 12 to16 °C. To prevent air flow across the cages, we placed plastic sheets (0.7 × 0.5 m) between them. In addition, we placed two 1.5 × 1 m plastic sheets on both sides of each fan and one sheet above these, to avoid air turbulence in the room as much as possible. All cages were located within the same room, so the noise disturbance was similar for all birds. Wind exposure significantly reduces surface body temperature and increases metabolic rate in small passerines (Bakken & Lee 1992; Wolf & Walsberg 1996; Zerba *et al.* 1999), and has been successfully used to manipulate overnight energy expenditure (Witter *et*

al. 1994; Cuthill *et al.* 2000). One might argue that restricted access to food could be a more effective means of reducing reserves. Food deprivation would, however, not only decrease the birds' energy reserves but also change their estimation of food variability and predictability, both of which are considered to affect foraging behaviour (Cuthill & Houston 1997; Houston & McNamara 1999; Cuthill *et al.* 2000). To avoid these confounding changes in foraging we manipulated overnight wind exposure only.

The next morning, one hour before lights on, the birds were removed from their cages and their body mass was measured again. They were then released back to the core flock in the aviary and were left there undisturbed for at least 30 min to reassure themselves. At lights on, we placed millet seeds in 12 randomly chosen wells on the grid (approximately 120 seeds per well). After the provision of food, we started to record the behaviour of the birds with two synchronized digital video cameras through one way windows approximately 2 m from the grid. One video camera was fixed on a tripod and filmed the whole grid, while the other camera was controlled by the observer and was used to take close-up pictures of the individuals on the grid so that their individual markings were unambiguously recognizable. Because the cameras were synchronized and the wells were numbered to recognize position, we could use close-up recordings to identify individuals on the other ('whole-grid') records which were used to analyse behaviour. Feeding trials lasted 5 min, during which seed clumps were usually depleted and the birds left the grid.

Data processing and statistical analyses

We analysed the foraging behaviour of 40 middle-ranked sparrows (20 experimental and 20 control) from the four flocks. We followed each experimental and control bird throughout the trial on the whole-grid video record and coded their behaviour. We also recorded the time when the birds arrived on the grid, and their time spent on the grid.

Feeding events were divided into two types, finding and joining. These terms were used instead of producing and scrounging, respectively, because we recorded actual feeding events and not directly observed tactic use, i.e. whether a bird was searching as a producer or a scrounger (Mottley & Giraldeau 2000; Coolen *et al.* 2001; Liker & Barta 2002). In 'finding' events a bird discovered an unoccupied well (i.e. no other birds within 10 cm of the well) and fed from it. In 'joining' events the well from which the focal bird fed was occupied by another feeding bird at the moment of the arrival of the focal individual. We calculated joining proportion as the number of all joining events divided by the total number of feeding events

(i.e. number of finding plus joining events) for each focal bird during the trial. This proportion was used as a surrogate of scrounger tactic use. Note that one bird left the grid without feeding; thus this individual was omitted from the analysis of joining proportions.

We also recorded joining attempts, i.e. the number of unsuccessful attempts to obtain food either by attacking foraging individuals or 'stealing' food items by quick pecks from an occupied well. Furthermore, we recorded the number of food searching attempts: we defined birds' behaviour as an attempt at food searching when they clearly looked into a well, e.g. with quick glances into the well with characteristic side-turned head position, or by popping the head into the hole. Similarly to joining proportion, we calculated joining attempt proportion, which was the number of joining attempts divided by the total number of attempts (i.e. joining attempts plus food searching attempts). Finally, we measured overall feeding rate as the total number of pecks divided by the time spent on the grid. This measure of feeding rate included pecks from both found and joined patches.

To compare the variability and success of the two feeding tactics, we recorded the following variables for each feeding event: (1) the tactic by which the food patch (i.e. well) was discovered, (2) patch-finding time as the time elapsed from leaving the previous well from which the bird fed until the start of the given feeding event. In the case of the first well, this value was the time elapsed from arrival at the grid until the first successful feeding event. We also measured (3) the time spent in the patches, i.e. the time elapsed from acquiring the well containing food until leaving it, and (4) the number of food items eaten from the well. From these variables we calculated the patch feeding rate, i.e. the number of pecks from the given patch divided by the patch finding time plus the time spent in that patch (Stephens & Krebs 1986). Note that this calculation assumes that time spent searching between patches can be clearly assigned to joining or finding, i.e. the birds do not change tactic during a search.

We estimated the within-individual variability of patch feeding rates for each tactic as absolute differences from the average patch feeding rates, where average patch feeding rates were calculated within individuals for each tactic separately. The variability in patch finding times was similarly estimated. Differences were log transformed and analysed by parametric tests. To compare the success of the different tactics we compared the within-individual average patch feeding rates between tactics.

Biometric variables were analysed by a MANOVA model with treatment as a fixed factor and flock as a random factor. We used the same model structure in an ANOVA model to analyse changes in body mass. Foraging behaviour data were analysed by linear mixed effect models ('lme' function of the 'nlme' package of the R statistical computing

environment; Pinheiro & Bates 2000) with flock as the random factor. Where distributional assumptions of 'lme' did not hold we used 'glm' with binomial error. The effect of flock was, however, non-significant in all cases; therefore we do not present statistical results for flock effects. Two-tailed probabilities and mean ± SEs are given. We used the R statistical computing environment (R Development Core Team 2003) and SPSS for Windows v. 8.0 for statistical analyses.

RESULTS

Body mass change

Individuals in the wind-exposed and control groups did not differ either in their body size measured at capture (tarsus length, wing length and body mass; MANOVA, treatment: Wilk's $\lambda = 0.965$, d.f. = 33, $p = 0.752$) or in fighting success (ANOVA, treatment: $F_{1, 35} = 0.194$, $p = 0.663$). There was also no difference between the two groups in the premanipulation (evening) body mass ($F_{1,35} = 1.501$, $p = 0.312$). However, the overnight decrease in body mass during the night of treatment was greater in wind-exposed than in control groups ($F_{1,35} = 8.019$, $p = 0.008$, Figure III.1).
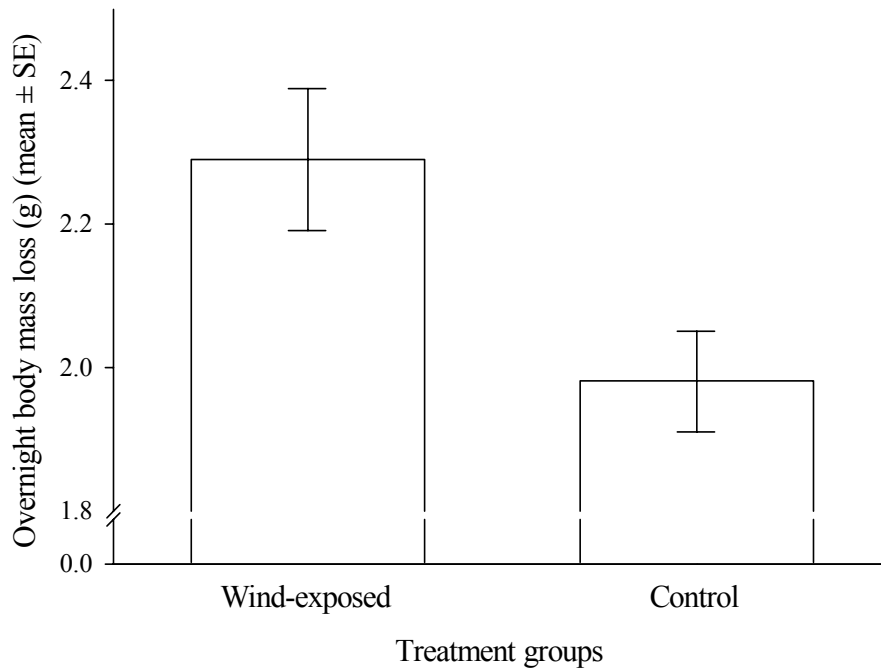
Figure III.1. Overnight body mass loss of house sparrows in the wind-exposed and control groups (N = 20 individuals in both groups).

Foraging behaviour

Birds in the wind-exposed group used joining to a higher degree than birds in the control group (wind-exposed: 0.69 ± 0.05, control: 0.34 ± 0.05; $F_{1,34} = 13.288$, $p = 0.001$, Figure III.2). Joining attempt proportion was also higher in the wind-exposed group than in the control group (wind-exposed: 0.15 ± 0.03, control: 0.12 ± 0.04; 'glm' with binomial error distribution: $F_{1,34} = 10.102$, $p = 0.001$). Tactic use was unrelated to the pre-manipulation fighting success, indicating that we successfully removed the effects of dominance by selecting middle-ranked individuals (ANOVA, fighting success included as covariate: $F_{1,33} = 0.012$, $p = 0.915$).
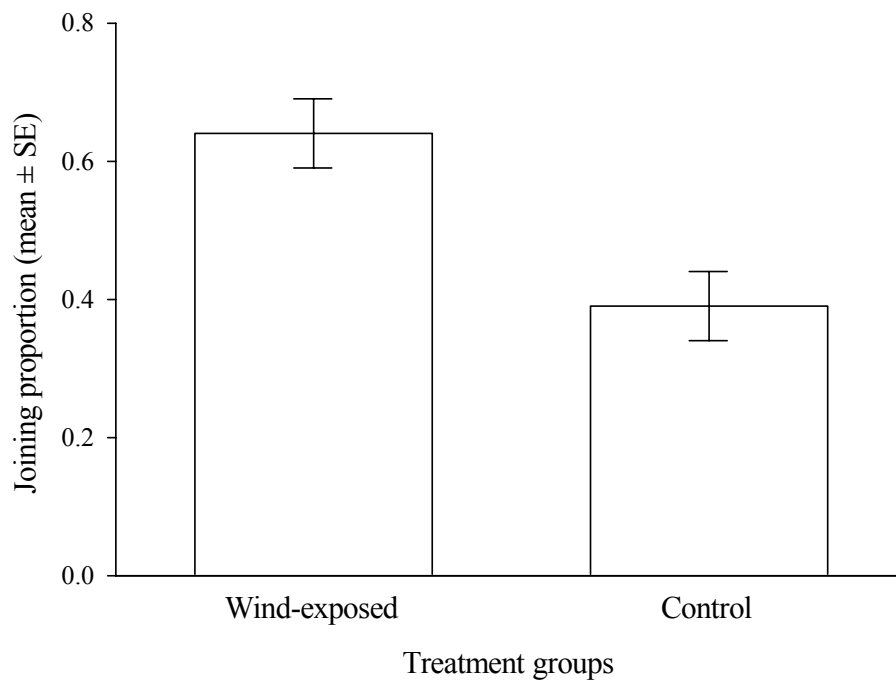
Figure III.2. The effect of treatment on foraging tactic use as expressed by the proportion of joining events (for definition of joining, see text). There were 19 individuals in the wind-exposed group and 20 in the control group.

Variability and success of foraging strategies

Within-individual variability of patch feeding rates differed between foraging tactics, with joining having a smaller variance than finding (joining: 0.11 ± 0.02, finding: 0.15 ± 0.02; $F_{1,24}$ = 5.073, p =0.034, Figure III.3a). The variability of patch finding time was also smaller for joining than for finding (joining: $4.01 +$ SE 1.00 -SE 0.83, finding: $6.35 +$ SE 1.10 -SE 0.96; $F_{1,23}$ = 4.429, $p = 0.046$, Figure III.3b). On the other hand, there was no significant difference between joining and finding either in average patch feeding rate (joining: $0.32 +$ SE 0.04 -SE 0.03, finding: $0.30 +$ SE 0.03 -SE 0.02; $F_{1,33}$ = 0.372, $p = 0.546$) or average patch finding time (joining: $7.24 +$ SE 0.97 -SE 0.86, finding: $8.31 +$ SE 0.86 -SE 0.78; $F_{1,33}$ = 1.198, $p = 0.282$).
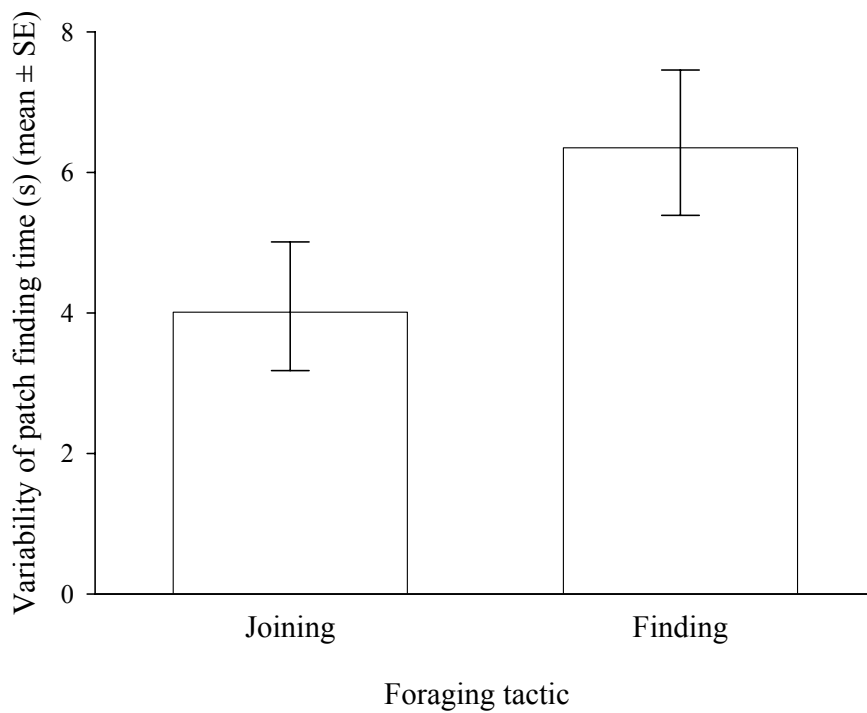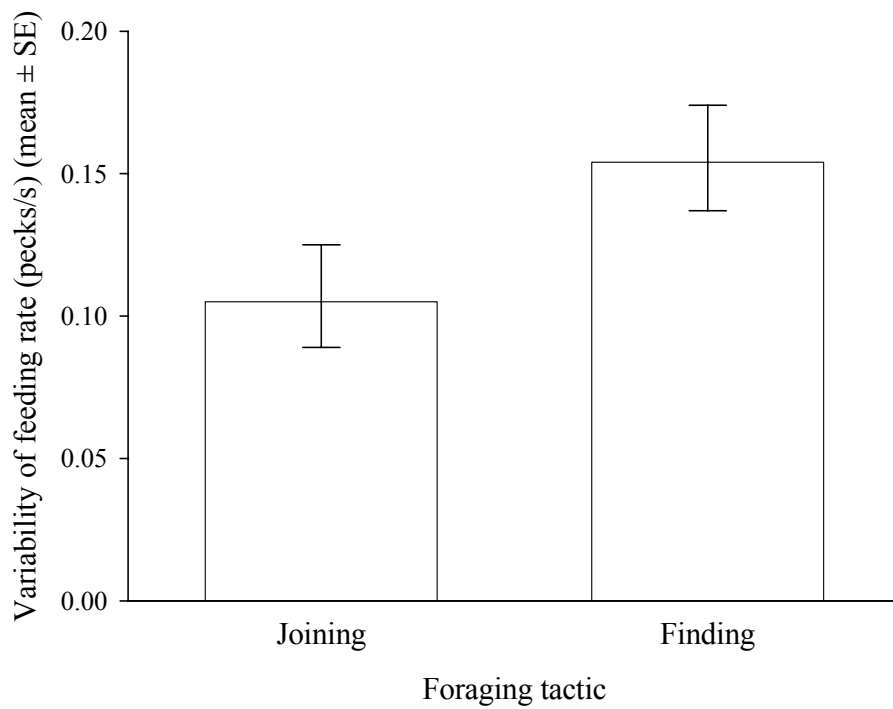
Figure III.3. Within-individual variability of (a) patch feeding rates (pecks/s) and (b) patch finding times (s) for different foraging tactics. Variability is measured as the absolute difference from within-individual averages.

DISCUSSION

In this study we experimentally investigated how the level of energy reserves influences the individual's choice of alternative social foraging tactics. We found that birds exposed to overnight wind responded strongly: they almost doubled the use of joining during their first feeding of the day compared with control birds. This suggests that individuals with lowered energy reserves scrounge more in the morning. Hence, this result provides strong support for the idea that internal state variables (such as energy reserves) play a significant role in decision making about alternative tactic use not only in solitary individuals (see for example Thomas 2002a,b; Thomas & Cuthill 2002) but in a social context too. These results underline the importance of the risk of starvation in the animals' foraging decisions. We also showed that variability in both patch feeding rates and patch finding time was smaller for patches discovered by joining than by finding which supports the idea that scrounging is a risk-averse foraging option compared with producing. Altogether, these findings are in accordance with both an assumption and a major prediction of the state-dependent dynamic game model presented by Barta & Giraldeau (2000).

The effect of energy reserves on social foraging tactic use has been investigated in small laboratory flocks of European starlings (*Sturnus vulgaris*, Koops & Giraldeau 1996) and nutmeg mannikins (*Lonchura punctulata*, Wu & Giraldeau 2004). By reducing the birds' food intake before the experiments, these investigators found small (non significant) effects of food deprivation on the use of joining (starlings responded with a small increase whereas mannikins used joining less). These small effects might be explained by the fact that the birds were allowed to accommodate to food deprivation. Thus, birds expecting a shorter foraging period might pre-emptively feed more before the tests, i.e. their reserves might not change as much as could be expected by the length of food deprivation periods.

Despite the significant differences we detected between the foraging tactics in variability of both patch feeding rate and search time, we found no difference in the average success of the tactics as measured by average patch feeding rate and average patch finding time. As joining provided a similar reward to finding, the two experimental groups did not differ in the overall feeding rate and food intake, even though birds in the wind-exposed group used joining to a much greater extent than control birds. This pattern indicates that by using scrounging, sparrows with low energy reserves may reduce the variance of their food intake without considerably diminishing their energy intake.

If the two alternatives provide similar rewards and scrounging may reduce intake variance, then the use of scrounging would usually be profitable for all group members. Note, however, that the payoff of scrounging is negatively frequency-dependent (i.e. as the frequency of scrounging increases in the group, its payoff decreases relative to the payoff of producing; Barnard & Sibly 1981) which prevents the very frequent use of scrounging. As minimizing intake variance may be crucial only for birds with low energy reserves, birds with higher reserves may be 'constrained' to use producing (*sensu* phenotype limited games, Parker 1982). It is also noteworthy that house sparrows often fight aggressively for food patches (finding events were always without aggression, whereas in 44% of joining events birds seized the food patch aggressively); thus scrounging may imply a cost of injury (Liker & Barta 2002). Birds whose energy reserves are far from the critical level can avoid such costs by playing producer. It is still unclear what keeps this producer-scrounger game at equilibrium. Our results clearly show that energy considerations must play a crucial role, but the fact that sparrows frequently fight for food indicates that the costs of aggression may also be important. Future studies, in which both energy reserves and dominance are carefully controlled, should clarify this issue further.

We obtained the present results in flocks where only a few individuals suffered relatively large reductions in their energy reserves. It is at present unclear whether variance reduction in food intake by scrounging also occurs in flocks where the energy reserves of most or all individuals are heavily reduced over night, e.g. as may be the case in winter flocks of small birds. Variation in morning energy reserves may be considerable in wild birds (e.g. Broggi *et al.* 2003) because flock members may differ both in their evening energy reserves (i.e. in their starting point before nights) and also in the quality of their roosting sites, which influence the rate of energy loss. Our results apply to middle-ranked birds; thus the effects of energy reserves on tactic use among high- and low-ranked birds remain unknown.

Because in social foraging situations each individual's payoff depends on their companions' behaviour (Maynard Smith 1982; Giraldeau & Caraco 2000), natural selection should favour individuals that are able to respond quickly to changes in their flock mates' behaviour by adjusting their own behaviour. To accomplish this efficiently, individuals are expected to monitor the behaviour of others in the flock. For example, in common cranes (Grus grus), where individuals often exploit their flock mates' food discoveries, aggressors increase their vigilance behaviour before attacking a flock mate and hence probably monitor the feeding success of their neighbours. As a consequence, these birds usurp the food resources of those flock mates whose intake rate is higher than average, thereby achieving an

immediate increase in their own feeding rate (Bautista *et al.* 1998). Birds might use cues other than flock mates' behaviour, i.e. monitoring level of energy reserves of others might be a useful predictor of their social behaviour even before foraging. For example, in birds, body mass is known to affect flight performance (Witter *et al.* 1994), thus individuals may use this information to assess the energetic state of their companions.

To summarize, our study provides the first robust empirical evidence that energy reserves may play a significant role in the choice between alternative social foraging tactics. In dominance-based social systems, we recommend further studies to investigate the mutual effects of energy reserves and dominance.

Chapter IV. The effects of energy reserves and dominance on the use of social foraging strategies in the house sparrow

ABSTRACT In social animals, dominance rank often influences the individuals' behaviour, but in most cases it is unknown how dominance modulates the effects of other phenotypic traits. We investigated the mutual effects of social dominance and the amount of energy reserves on the use of social foraging strategies in captive flocks of house sparrows, *Passer domesticus*. We used experimental wind exposure to manipulate overnight energy expenditure of dominant and subordinate individuals. We found that in response to the experimental treatment dominants significantly used scrounging (exploiting others' food finding) more, whereas subordinates responded to the treatment by a moderate and non-significant increase in scrounging. Individual variability in the frequency of scrounging was higher in subordinates than in dominants and this difference between the dominance groups was unaffected by the treatment. These results suggest that individuals of different dominance status play different strategies: to cope with an energetically challenging situation, dominants behave rather uniformly by increasing further their preference for scrounging, while subordinates do not alter their tactic choice, but may rely on using scrounging opportunistically.

INTRODUCTION

Dominance is an important phenotypic attribute of group living animals: dominant individuals often have superior access to scarce resources, such as mate, food or safe refuges (Huntingford & Turner 1987). This preferential access usually increases the dominants' gain from a given strategy and may constrain the subordinate individuals to use alternative strategies (Gross 1996). Although there is considerable evidence for these dominance effects, our knowledge is still scarce about how these effects interact with other phenotypic attributes.

Another crucial phenotypic characteristic that plays a major role in animals' decision making is the amount of energy reserves. In contrast to dominance rank, which remains relatively stable across longer periods (weeks or even years), the level of energy reserves may show significant daily variation (Broggi *et al.* 2003). Thus, as the level of energy reserves changes during the day, the animal's dominance status and actual physical state may favour different behavioural responses: for example, low levels of energy reserves would favour the use of a particular foraging tactic while the dominance status of the individual may favour another one. How should then an animal adjust its strategy to such multiple demands of its phenotypic state?

This question has been rarely investigated in a social context, i.e. when the payoff from an individual's decision depends also on the behaviour of its companions. In the present study, we investigate how dominance rank modulates the effects of the amount of energy reserves in social strategy use of house sparrows (Passer domesticus). Social foraging is one of the best studied systems, where animals may use distinct alternative tactics in a group of interacting individuals. Individuals may either search for food on their own ('producing'), or join their feeding companions and exploit their food discoveries ('scrounging'). It has been shown that individuals of many species use these tactics in a flexible way: for instance, birds may frequently switch between producing and scrounging according to the actual ecological conditions or to their own internal state (e.g. Koops & Giraldeau 1996, Coolen 2002, Liker & Barta 2002, Barta *et al.* 2004, *Chapter III*).

Previously, we have shown that social foraging tactic use is related to dominance rank in the house sparrow; dominant individuals use scrounging more than do subordinates (Liker & Barta 2002). Moreover, in a recent experiment, we have demonstrated that the level of energy reserves also influences tactic choice: individuals with lowered energy reserves used scrounging in a higher proportion than individuals with higher levels of reserves

(*Chapter III*). However, in the latter study we controlled for the effects of dominance and investigated only the behaviour of middle-ranked birds. In the present study, we analysed the mutual effects of dominance rank and energy reserves: by using experimental manipulation we investigated the effects of energy reserves on the social foraging behaviour within high and low ranking individuals.

METHODS

Study Subjects

We used the same 78 house sparrows that were captured between 8 November 2002 and 10 February 2003 and formed the four flocks in the experiment described in *Chapter III*. Therefore, housing conditions were identical to that of the *Chapter III*.

Experimental Protocol

We used the same experimental protocol as in *Chapter III*, so a more detailed description can be found there. Here, I only present the essential elements of the experimental protocol.

The experiment consisted of two parts for each flock. First, as we intended to study the effect of energy reserves in dominant and subordinate birds, we categorised birds into dominance groups according to their success in aggressive interactions. We ranked individuals within each flock based on their fighting success and divided them into three dominance categories: dominants, subordinates and middle-ranked birds. Dominants were the 6 highest ranked individuals in flocks with 22 birds, and the 5 highest ranked individuals in flock with 21 and 19 birds. Similarly, individuals with the 6 lowest ranks were considered as subordinates in the flocks with 22 birds, and 5 and 4 individuals with the lowest ranks in flocks with 21 and 19 ranks, respectively. Then we used the dominants and the subordinates in each flock as the subjects of the manipulation (see below).

In the second part of the experiment, we manipulated the overnight energetic expenditure of dominant and subordinate birds, and then observed their foraging behaviour during their first foraging next morning. In the evening prior to the foraging observations, we captured all birds and removed all food items from the aviary. Middle-ranked birds were immediately released back to the aviary to form the 'core flock' (*sensu* Giraldeau *et al.* 1994). After measuring the body mass (± 0.1 g) of the dominants and subordinates we individually

housed them in cages. Half of the dominants and also half of the subordinates were randomly assigned to the manipulation, whereas the remainder were controls. In flocks with 5 individuals, we randomly allocated the fifth bird to the manipulation or the control treatment.

To manipulate overnight energy expenditure, we used the same manipulation as in *Chapter III*, i.e. throughout the night, we used electric fans to simulate wind exposure, whereas controls were kept in the cages without wind exposure.

The next morning, one hour before lights on, the birds were removed from their cages and their body mass was measured again. Then they were released back to the core flock in the aviary and were left there undisturbed for at least 30 min to reassure themselves. At lights on, we placed millet seeds in 12 randomly chosen wells on the grid (approximately 120 seeds per wells). After the provision of food, we started to record the behaviour of the birds with two synchronized digital video cameras through one-way windows approximately 2 m from the grid (see *Chapter III*. for more details). All individuals fed during the observations, thus the presence of dominants did not hold back the subordinates from feeding. Video recordings were used to analyse behaviour. Feeding trials lasted 5 min, during which seed clumps were usually depleted and the birds left the grid. After the trials, food containers were replenished *ad libitum*.

Data Processing and Statistical Analyses

We analysed the foraging behaviour of the 22 dominant and 22 subordinate sparrows from the four flocks (11 experimental and 11 control birds in both dominance categories). We followed each experimental and control bird throughout the trial on the video recordings and coded their behaviour. We also recorded the time when the birds arrived on the grid, and their time spent on the grid. The behaviour of unmanipulated middle ranking individuals (the 'core flock') was not analysed (see also Giraldeau *et al.* 1994). Although each individual's behaviour is dependent on the other birds in the flock, the presence of the core flock individuals resolves the relationships between the experimental individuals, preserving so the statistical independence of data points.

Feeding events were divided into two types, finding and joining. In finding events a bird discovered an unoccupied well (i.e. no other birds within 10 cm of the well) and fed from it. In joining events the well from which the focal bird fed was occupied by another feeding bird at the moment of the arrival of the focal individual. We calculated joining proportion as the number of all joining events divided by the total number of feeding events (i.e. number of

finding plus joining) of each focal bird during the trial. This proportion was used as a surrogate of scrounger tactic use (Beauchamp 2001, Barta *et al.* 2004). We measured the variability of joining proportion in each treatment group for both dominance ranks. To do this, we calculated the absolute differences of individuals from the median joining proportion within the four categories (i.e. for the two dominance × two treatment groups separately). We also measured the proportion of all joining attempts: in this case we divided the number of successful plus unsuccessful joining attempts by all food searching attempts (i.e. finding plus unsuccessful searching). Finally, we measured overall food intake as the total number of pecks during the trial, and overall feeding rate as the total number of pecks divided by the time spent on the grid. These measures of overall food intake and feeding rate included pecks from both found and joined patches.

We analysed our data by linear mixed effects models, with flock as a random factor. The effect of flock was, however, non-significant in most cases; therefore we do not present statistical results for non-significant flock effects. Two-tailed probabilities and mean ± SEs are given throughout the paper. We used SPSS 11.0 for statistical analyses.

RESULTS

Overnight Body Mass Change

Neither dominance groups, nor treatment groups differed in body size measured at capture (body size measured as tarsus length and wing length; MANOVA, dominance group: Wilk's λ = 0.975, d.f. = 37, p = 0.625, treatment: Wilk's λ = 0.992, d.f. = 37, p = 0.868). There was also no difference between dominance and treatment groups in the pre-manipulation (evening) body mass (dominance group: $F_{1,38}$ = 0.093, p = 0.763, treatment: $F_{1,38}$ = 2.264, p = 0.141). The overnight decrease in body mass during the night of treatment differed between flocks ($F_{3,37}$ = 9.805, p < 0.001). However, as expected, it was greater in wind-exposed than in control groups, whereas it was similar in high and low ranked birds, with no interaction between dominance and treatment (dominance group: $F_{1,37}$ = 1.148, p = 0.291, treatment: $F_{1,37}$ = 5.677, p = 0.022, dominance group*treatment interaction: $F_{1,37}$ = 0.162, p = 0.690; Figure IV.1).
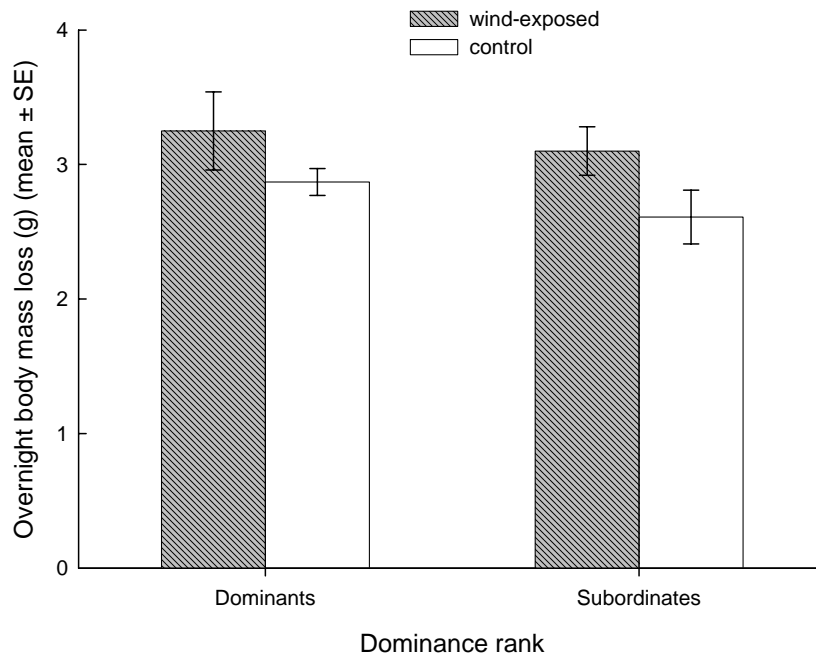
Figure IV.1. Overnight body mass loss (g) of house across dominance groups and treatments (N = 44 individuals, with 11 wind-exposed and control individuals in both the dominant and subordinate groups).

This overnight decrease was on average 10.3 ±0.36 % of their evening body mass, but, only the flock and the experimental treatment had an influence on the percentage of body mass lost (flock: $F_{3,37}$ = 13.4944, p < 0.001, dominance group: $F_{1,37}$ = 1.274, p = 0.266, treatment: $F_{1,37}$ = 5.152, p = 0.029, dominance group*treatment interaction: $F_{1,37}$ = 0.576, p = 0.453). Larger birds tended to loose more of their evening body mass than smaller ones, however, the treatment had significant effect on overnight body mass loss even after controlling for body size (flock: $F_{1,36}$ = 14.023, p < 0.001, tarsus: $F_{1,36}$ = 2.885, p = 0.098, dominance group: $F_{1,36}$ = 1.897, p = 0.177, treatment: $F_{1,36}$ = 4.448, p = 0.042, dominance group*treatment interaction: $F_{1,36}$ = 0.496, p = 0.486).

Foraging Behaviour

Birds across the four experimental groups showed a large variability in terms of tactic use: the observed joining proportion ranged from zero to one (Figure IV.2).
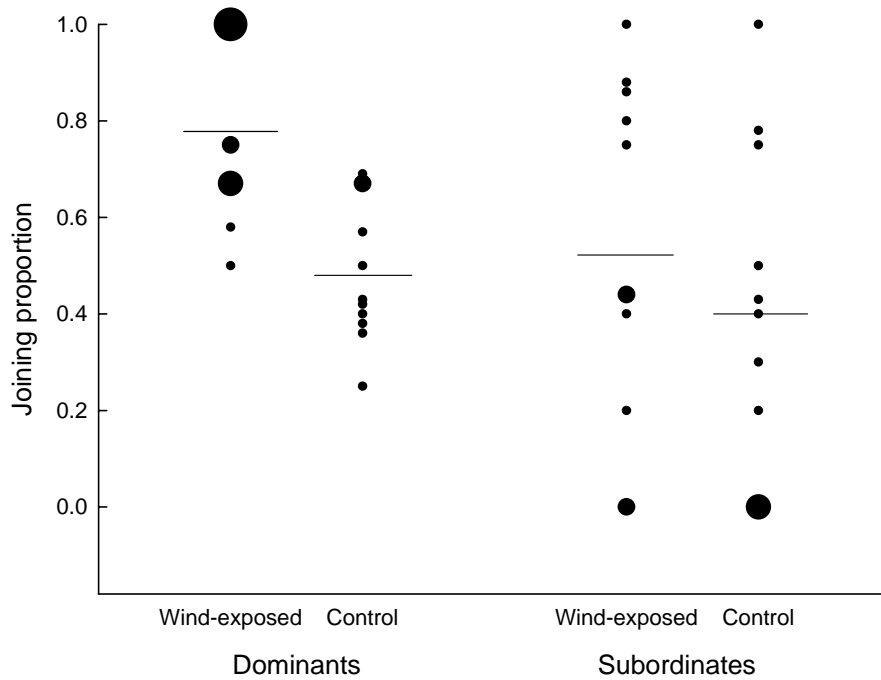
Figure IV.2. The distribution of joining proportion across dominance groups and treatments. The size of the dots indicates the number of individuals (1, 2, 3 or 4) with identical joining proportion values. N = 44 individuals, with 11 wind-exposed and control individuals in both the dominant and subordinate groups. Horizontal lines indicate the means for each group.

Variability in joining proportion was greater in the subordinate groups than in the dominant groups, but the treatment had no influence on the variability (dominance group: $F_{1,37}$ = 10.150, p = 0.003, treatment: $F_{1,37}$ = 0.372, p = 0.546, dominance group*treatment interaction: $F_{1,37}$ = 0.001, p = 0.979; Figure IV.2). Due to this significant heteroscedasticity, we cannot analyse the two dominance groups together, because one of the main assumption of the ANOVA model (the homogeneity of variances) would be violated. Variable transformations do not resolve this heteroscedasticity in the data.

In the dominant group, in response to the wind-exposure, individuals increased their use of joining, whereas in subordinates we found no difference between experimental groups (dominants: treatment, $F_{1,17}$ = 15.398, p = 0.001; subordinates: treatment, $F_{1,17}$ = 0.806, p = 0.382). The treatment had no effect on the joining attempts (dominants: treatment, $F_{1,17}$ = 4.061, p = 0.060; subordinates: treatment, $F_{1,17}$ = 1.502, p = 0.237); however, within the dominant group wind-exposed birds tended to make more attempts for joining than control ones (wind-exposed *vs.* control means with [95% CI]: 0.486 [0.354–0.618] *vs.* 0.323 [0.191–0.455]), whereas in subordinate individuals the difference in joining attempts between wind-exposed and control treatments was smaller (0.348 [0.216–0.480] *vs.* 0.223 [0.090–0.355])

Neither in the dominant nor the subordinate group, experimental treatment affected the number of food patches (i.e. wells) found by the birds (Table IV.1). Furthermore, in neither dominance groups the overall feeding rate, overall food intake nor time spent on the grid differed between experimental treatments (Table IV.1).

Table IV.1. The effect of dominance rank and wind exposure on foraging behaviour (ANOVA, with flock as random factor and treatment as fixed factor)

| | Effect of wind exposure | | | |
| | Dominants | | Subordinates | |
Response variable	$F_{1,17}$	p	$F_{1,17}$	p
Time spent on the grid	0.538	0.473	0.500	0.489
Number of food patches found	0.008	0.932	0.107	0.748
Feeding rate	0.070	0.795	0.806	0.382
Food intake	0.002	0.964	1.699	0.210

Non-significant flock effects are not shown in the table.

DISCUSSION

In this study we investigated the mutual effects of dominance rank and energy reserves on social foraging behaviour. We found that in response to the wind exposure, both dominance groups tended to increase the proportion of joining. However, this increase was only significant in the dominant group. Moreover, the increase in the proportion of joining was 2.5 times greater in the dominant group than in subordinate one.

This difference between the dominance groups may have several explanations. First, it could be a consequence of a higher effect of the wind exposure on the dominant individuals. Yet, we have found no effect of dominance in the overnight body mass loss after the wind exposure, moreover the mean difference between wind-exposed and control individuals was even slightly greater in subordinates (0.49g) than in dominants (0.38g). Second, reducing energy reserves would increase the use of scrounging in both dominance groups but subordinate sparrows could not realise this because of the increased scrounging activity of dominants. Note that the payoff from scrounging is frequency dependent, i.e. its frequency in a group cannot be increased beyond a certain point (Barnard & Sibly 1981, Giraldeau & Livoreil 1998). However, this explanation is also unlikely, because beside the frequency of successful joining, wind-exposed subordinates did not increase the frequency of their joining attempts either.

A more likely explanation for the different effect of wind exposure may be that individuals of different dominance rank play different strategies, i.e. the same change in their energy reserve generates different behavioural reactions in terms of tactic use in high and low ranked birds. Dominant individuals in response to the wind exposure showed a marginally non-significant trend to initiate more joining and realized significantly higher number of successful joining. These results suggest that when energy reserves of dominant individuals are low, they both raise their preference for joining and they also become more successful. This is not surprising, since house sparrows are often aggressive when scrounging (Johnston 1969, Liker & Barta 2002), and hungry sparrows may be more motivated along with more successful in fights than their more satiated companions (Andersson & Åhlund 1991). In contrast, within the subordinate group, we found only a moderate and non-significant difference between the treatment groups in either the proportion of all joining attempts and the proportion of successful joining events. The latter result suggests that subordinates are not simply less successful in joining than dominants, but their behavioural response to the change in level of energy reserves is different from that of the dominants. This might be explained by the fact that being subordinate reduces remarkably the chance of successfully supplanting other sparrows from a discovered patch (e.g. Wiley 1991). Hence, energetically stressed subordinates, instead of increasing the use of scrounging, must rely some other means to cope with this situation.

Another indication for the dissimilarity in strategy use between the dominant and subordinate birds is the difference in the variability of the joining proportions between the high and low ranking individuals. Note that this difference was unaltered by the experimental treatments, i.e. this heterogeneity in the variability of tactic use was only explained by the differences in dominance rank. But why does this variability differ between dominant and subordinate individuals? It might be possible that subordinates found less food patches, and consequently the calculation of their joining proportion has higher error. Although subordinates tended to find less patches than dominants, this explanation is unlikely, because the difference in the number of food patches was small and non-significant (mean ± SE: dominants = 7.61 ± 0.70, subordinates = 5.90 ± 0.71). Furthermore, the difference in the variance of joining proportion between dominant groups remained significant after controlling for the number of food patches found (results not shown).

The difference in the variance of joining proportion more likely indicates that individual differences in tactic use are greater in subordinates than in dominants. Dominants use joining frequently (Liker & Barta 2002), but when their energy reserves fall, they can still

increase their use of joining, mainly by using aggression. Since dominant birds have a clear advantage in aggressive interactions (i.e. win more fights), they can secure the rise of their scrounging use; for some individuals it may be even possible to use scrounging exclusively (e.g. see the four individuals with the highest joining proportion in the wind-exposed dominant group in Figure IV.2). On the other hand, subordinates may be predisposed to use mainly producing (Barta & Giraldeau 1998), but they may follow an opportunistic strategy: they may scrounge whenever they have a possibility to do so. For example, since house sparrows aggressively defend food patches, attempting a scrounging from a high ranking individual would entail the costs of time, energy and the risk of injury for a subordinate bird. Consequently, tactic choice of subordinates may be more context-dependent than that of dominants, i.e. it may be more influenced by the actual circumstances (e.g. by the dominance rank of the surrounding patch-owners). Due to this context-dependence, some "lucky" subordinate individuals may eventually scrounge frequently, while others may lack the opportunities and use mainly producing.

In both dominance groups neither feeding rate nor overall food intake differed between the treatment groups. It is consistent with our previous studies, where we found that tactic use was unrelated to the food reward (i.e. feeding rate; Liker & Barta 2002, *Chapter III*). Note however, that we investigated only the birds' first foraging during the day, where food resources were depleted quickly. In a natural environment individuals feed many times in a day, thus they may recover their body mass later on. Recent dynamic models suggest that early in the morning birds tend to maximise their immediate survival prospects, and mass gain becomes more important later in the day (Barta & Giraldeau 2000). As a result, by determining the level of scrounging use, animals may principally regulate the risk of an energetic shortfall and trade it off against the costs of scrounging (e.g. energetic costs, risk of injury, etc.).

To summarise, our study provided the first experimental investigation on the mutual effects of multiple state variables on the social foraging tactic use. We demonstrated that the effects of dominance modulate the effects of energy reserves: it reinforces a preference for scrounging in high ranking individuals, whereas it only generates a weak preference for scrounging in subordinate birds. Thus dominance status may determine what behavioural alternatives are available for the animals in an energetically challenging situation. If dominant individuals have a wider scale of available behavioural actions in such situations, they may have an advantage in choosing the optimal strategy. This interesting benefit of being dominant would be worth investigating further in the future.

Chapter V. Feather quality and survival in the house sparrow

ABSTRACT Feathers, being the tools of flight, are crucial morphological features for birds. The quality of flight feathers have a major influence on the flight performance and the energy expenditure of the flight, still few studies have examined the fitness consequences of the feather quality. In this study, we investigated whether biometrical variables (body size, body mass and the size of the bib in males) are related to two aspects of feather quality of free living house sparrows. We also analysed the relationship between feather quality and the apparent survival during six months from spring to autumn, until the period of moulting. Feather quality was characterised by the diameter of the rachis (a presumed measure of feather rigidity determined during the process of feather formation) and by the degree of feather wear (a measure of the continuous feather abrasion after the moult). Both variables were measured from close-up photographs taken on the primary flight feathers. The effects of feather quality on the survival were analysed as individual covariates in a capture-recapture model. Feather wear was not related to rachis diameter, but it was positively correlated with bib size in males. The survival modelling showed that rachis diameter, but not the degree of feather wear influenced the survival. Individuals with thick rachis survived better during the study period than individuals with thin rachis. These results indicate that the quality of flight feathers may have fitness consequences, although different components of feather quality may contribute to the fitness in a different manner.

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INTRODUCTION

The body of all birds is covered by feathers. Feathers not only determine the birds appearance, but also insulate the body and are the tools of flight. The efficiency of insulation and flight are strongly influenced by the quality of the feathers; reduced feather quality brings about an increased heat loss (Wolf & Walsberg 2000) and lower flight performance (Swaddle & Witter 1997). The feathers abrade continuously after their formation, thus all birds have to renew them regularly in the process of moult. However, the moult, being a major time- and energy-consuming process, cannot occur at any time of year, it must be properly timed (Barta *et al.* 2006). The state of the worn feathers can only be restored during the subsequent moult. But even then, there are constraints for producing high-quality feathers. The renewal of the feathers requires substantial amount of energy and limited resources, such as proteins (Murphy 1996). For example, in the house sparrow (*Passer domesticus*), the rate of the whole-body protein synthesis is significantly increased during the annual moult, showing the extensive energetic costs of feather formation (Murphy & Taruscio 1995). As a consequence, the individual's state before and during the moult have a great impact on the quality of the feathers produced.

Although the state of flight feathers is a good indicator of individual quality, that has been recently recognized by the avian clinical practice (Ritchie *et al.* 1994), very few studies have addressed the question how these traits are related to the fitness components. Due to the fundamental importance of feather quality on energy consumption and flight performance, theoretical models suggest that feather quality should affect individual survival (Barta *et al.* 2006). However, empirical studies on the survival costs of feather quality are scanty. Furthermore, our understanding is still rudimentary about which aspects of feather quality may affect survival.

In this study, we investigated the individual quality of primary flight feathers in a free-living marked population of house sparrows. We measured two components of flight feathers: (1) the quality of feathers that was determined during the moult and (2) the degree of feather wear. We investigated the relationship between these measures of feather quality and any other aspects of individual state (i.e. body size, body mass and the size of the bib in the males, a sexually selected trait). We also analysed whether the two components of feather quality affected survival during the breeding season until the period of the next moult. To examine this question, we used capture-recapture modelling, by which the survival and recapture

probabilities may be estimated separately, and a number of biological phenomena, such as temporary emigration may be controlled for, which would otherwise severely bias survival estimates.

METHODS

General

Fieldwork was carried out between 25 March and 24 September 2003, at the National Horserace Ltd.'s farm, Dunakeszi, Hungary (Appendix 1). House sparrows were caught by mist-nets throughout the study. Individuals were ringed with a numbered aluminium ring and a unique combination of three colour plastic rings. At capture we measured body mass ($\pm$ 0.1 g), tarsus ($\pm$ 0.1 mm) and wing length ($\pm$ 1 mm). We also measured the length and width of the males' throat patch (bib) ($\pm$ 1 mm). Bib area was calculated according to Veiga (1993).

Feather Measurements

From 25 March to 25 April, to measure feather quality we took close-up photographs from the primary wing feathers on both wings, because the primaries are thought to have the strongest effect on flight ability (Jenni & Winkler, 1994). Using the photographs, we measured two aspects of feather quality (Appendix 2). First, to obtain a measure of the feather quality that was determined during process of feather formation, we measured the diameter of the rachis of each primary feather. The width of the rachis depends on the structure and quantity of keratin deposited to the new feathers during the moult and it determines the rigidity of the feathers (Dawson *et al.* 2000). For each primary feather, the rachis diameter was measured to the nearest 0.1 mm along a perpendicular line to the axis of the rachis at the bottom tip of the corresponding primary cover feather. Second, to measure feather wear, we scored each primary from 0 to 4 according to the degree of feather abrasion along the edge of the feather tips, a method similar to that of other investigations of feather wear (e.g. Merilä & Hemborg 2000). Here, 0 indicates an intact feather edge and 4 indicates very worn feather edge. Both measures of feather quality were highly repeatable (all *R* values > 0.8581, all *p* values < 0.005). For both rachis diameter and feather wear, we measured 9 primaries on both wings, and we used the means of the individual feather measurements in our analyses. Both variables were normally distributed, and we analysed them in parametric tests. Neither rachis diameter

nor feather wear changed during the period when we took the photographs (rachis: $r = -0.036$, $p > 0.7$; feather wear: $r = 0.008$, $p > 0.9$, $N = 73$ birds).

Marking and Recapture

We used capture-recapture analyses to estimate survival. After the initial capture, we used two methods to re-encounter individuals: we recaptured birds using mist-nets and we used field observations of colour ringed individuals. Recaptures and resightings were carried out on a monthly base in 6 recapture sessions from April to September 2003. At the end of each month we captured and observed the birds during a 3-5 day period. Recapture sessions were considered as one encounter occasion, and we had 7 occasions, until September, as house sparrows usually moult in September-October (Svensson 1994).

Statistical Analyses

The relationship between different aspects of feather quality and biometric variables were analysed in linear regression models. The relationship between survival probabilities and feather quality was modelled using capture-recapture data (Burnham *et al.* 1987). Both resighting and physical capture was considered as recapture in the analyses. We used Program MARK (White & Burnham 1999) for the analyses of survival (Φ) and recapture (p) probabilities. Modelling procedure was begun from the fully parameterized Cormack-Jolly-Seber (CJS) model (Clobert & Lebreton 1987). Afterwards, we gradually decreased the dimensionality of the models toward a more parsimonious structure by removing interaction terms and factors (Lebreton *et al.* 1992). Model selection was undertaken on the basis of a second order variation of Akaike's Information Criterion (AICc) which accounts for moderate sample sizes (Hurvich & Tsai 1989).

Goodness-of-fit (GOF) tests for the CJS model were performed by the program U-CARE (Choquet *et al.* 2003). U-CARE performs χ^2 statistics to test the assumptions of the CJS model. These GOF tests (TEST2 & TEST3) are the same as tests in RELEASE (Burnham *et al.* 1987), and we used their overall result to test the fit to the CJS model. We also tested two frequent reasons for the possible lack of fit in the general model. Specifically, we analysed (i) the effects of 'transient' individuals in the data sample, i.e. newly marked individuals that were never seen again after their initial capture, probably because they undertook temporary or permanent emigration or they were only in transit among resident

birds in the study population (Pradel *et al.* 1997). On the other hand, we also tested (ii) the short-term deviations from the homogeneity of the recapture probabilities, i.e. the difference in the probability of being recaptured between the animals captured and not captured at the previous occasion ('trap dependence', Pradel 1993). To test the latter two effects, we used the *z* statistic for transience and for trap dependence in the program U-CARE (Choquet *et al.* 2003).

The effects of feather quality on the survival probability were analysed using individual covariates in Program MARK (White & Burnham 1999, Pollock 2002). First, the best fitting model without covariates were selected and subsequently the individual covariates were added to this model. To test the effects of individual covariates we compared these models (i.e. the best fitting 'constant' model without individual covariates and the models including feather wear or rachis diameter as individual covariates). Model comparisions were performed on the basis of the difference in the Akaike's Information Criterion between the candidate models (ΔAICc). For completeness, we also report the results of Likelihood Ratio Tests (LRT) between the 'constant' and the 'covariate' models. LRTs provide χ^2- tests for the differences in deviances between two models (Lebreton *et al.* 1992).

We use the model notation suggested by Lebreton *et al.* (1992). The asterisk (*) between two factors (e.g. sex and time, s*t) is a shorthand for the main effects and their interaction (i.e. sex and time dependence and sex*time interaction), whereas the plus sign (+) represents an additive model structure (i.e. s+t stands for the main effects of sex and time).

RESULTS

Feather Quality and Body Size

Neither rachis diameter nor feather wear differed between the sexes (Wilk's λ = 0.995, *p* > 0.8, *N* = 73 birds). The degree of feather wear was not related to the rachis diameter (*r* = 0.127, *p* > 0.2).

In females, neither rachis diameter, nor feather wear was related to the measures of body size (Table V.1a). In males, the best predictor of feather wear was the bib size, moreover, shorter wings tended to be more worn, but tarsus and mass was not related to the degree of feather wear (Table V.1b).

Table V.1a. Multiple regression analysis of the relationship between measures of body size, body mass and two aspects of feather quality (rachis diameter and feather wear) in female house sparrows. $N = 35$ females.

	Wing length		Tarsus length		Body mass	
	β	p	β	p	β	p
Rachis diameter	0.247	> 0.2	0.158	> 0.3	−0.268	> 0.1
Feather wear	−0.049	> 0.7	0.173	>0.3	0.294	> 0.1

Table V.1b. Multiple regression analysis of the relationship between measures of body size, body mass, bib size and two aspects of feather quality (rachis diameter and feather wear) in male house sparrows. N = 33 males.

	Wing length		Tarsus length		Body mass		Bib size	
	β	p	β	p	β	p	β	p
Rachis diameter	−0.194	> 0.4	0.116	> 0.6	0.151	> 0.5	−0.042	> 0.8
Feather wear	−0.359	0.086	0.348	>0.1	0.046	> 0.8	0.373	0.038

Survival

The general Cormack-Jolly-Seber did not fit the data, and this lack of fit was due to a transient effect ($z = 1.78$, $p = 0.04$) and trap dependence ($z = -3.12$, $p = 0.002$). To deal with these effects, we created a new global starting model with two-level dummy age-class model structure in both the survival and the recapture probability: $\Phi_{a2+s*t}\ p_{m+s*t}$, where the subscript 'a2' in the survival parameter denotes the two age-classes, which accounts for transient effects (Pradel *et al.* 1997), whereas the subscript 'm' denotes that the model accounts for the heterogeneity in recapture probability (Pradel 1993). Subscripts 's' and 't' stand for sex and time-dependence, respectively for both the survival and recapture probability. Using this model structure, we can derive unbiased estimates of survival and recapture probability.

Modelling of the recapture parameter showed that recapture rate varies over the study period, but it does not differ between the sexes (Table V.2). Survival was constant during the study period, and did not differ between the sexes. Nevertheless, the model with rachis diameter explained best the data, significantly better than the constant model (ΔAICc = 2.12, Likelihood Ratio Test: $\chi^2_1 = 4.316$, $p = 0.038$; Table V.2), whereas the model including feather wear was less supported than the constant model (ΔAICc = −1.12, Likelihood Ratio Test: $\chi^2_1 = 1.078$, $p = 0.299$; Table V.2). Parameter estimates of models with individual covariates showed that there was a positive relationship between rachis diameter and survival probability (intercept, $\beta = -\ 802.11$ ($\pm$ 8.17 SE), slope, $\beta = 154.92$ ($\pm$ 2.43 SE)), whereas

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individuals with more worn feathers had lower survival than those with less worn feathers (intercept, $\beta = -5.47$ (± 9.45 SE), slope, $\beta = 11.23$ (± 14.14 SE)).

Table V.2. Akaike's Information Criterion (AICc), number of parameters (NP) and Deviance for candidate models of the survival and recapture probabilities in the house sparrows. Modelling procedure began with the recapture probability, then the model with the lowest AICc value was selected for modelling the survival probability. The best model is shown in bold. Model notation: a2: two level age-class for transients, s: sex, t: time, m: short-time trap dependence

Models	AICc	NP	Deviance
Modelling recapture probability			
(1) $\Phi_{a2+s*t}\ p_{m+s*t}$	467.40	23	415.13
(2) $\Phi_{a2+s*t}\ p_{m+s+t}$	461.86	18	422.08
(3) $\Phi_{a2+s*t}\ p_{m+t}$	460.84	17	423.48
(4)[a] $\Phi_{a2+s*t}\ p_{m}$	467.71	12	442.05
Modelling survival probability			
(5) $\Phi_{a2+s+t}\ p_{m+t}$	452.33	13	424.37
(6) $\Phi_{a2+t}\ p_{m+t}$	451.00	12	425.33
(7)[b] $\Phi_{a2}\ p_{m+t}$	443.21	8	426.46
Modelling the effect of feather quality on survival probability			
(8) $\Phi_{a2+\ feather\ wear}\ p_{m+t}$	444.33	9	425.38
(9) $\Phi_{a2+\ rachis}\ p_{m+t}$	**441.09**	**9**	**422.14**

[a] Note that 'm' cannot be removed from the model structure, because it accounts for trap dependence
[b] Note that 'a2' cannot be removed from the model structure, because it accounts for transient effects

DISCUSSION

Our study provided three key results that may contribute to our understanding of the adaptive significance of feather quality. First, we found that feather wear was not related to rachis diameter. This result may be surprising at first, because it suggests that the degree of feather abrasion is not primarily determined by feather rigidity. Previous studies have pointed out that individual differences in activity or habitat use may affect the degree of feather abrasion (Willoughby 1991). The idea that feather wear may be predominantly influenced by individual differences in behaviour, is supported by our second main result. Namely, we found a positive relationship between the males' bib size and the degree of feather wear. Bib size was the only predictor of feather wear in males, and in females we found no correlates of feather wear. Bib size is a signal of dominance status (e.g. Møller 1987, Liker & Barta 2001, *Chapter VI*), and an important determinant of lifetime reproductive success (Jensen *et al.*

2004), thus may genuinely reflect individual differences in activity or habitat use. But how these differences would be related to the feather wear?

After moulting, the bib is partially covered by white tips on the bib feathers (Svensson 1994). To acquire breeding coloration, males actively abrade their white feather tips mainly by dust bathing and preening. Large-badged males abrade more their feathers than small-badged ones (Møller & Erritzøe 1992). Although the goal of the latter behaviour is to reveal the black parts of the bib feathers, a possible side effect of frequent preening and dust bathing may be a more intensive feather wear on the flight feathers too. Alternatively, the relationship between the bib and the feather wear may be determined during the moult. During the moult, elevated levels of testosterone are needed to create the bib, a secondary sexual character (Evans *et al.* 2000). However, the testosterone seem to counteract feather development; for instance, in European starlings experimental administration of testosterone led to a delayed moulting and to the production of feathers of low mass (Dawson 2004). Moreover, the black bib of the males is a melanin-based ornament, whereas the melanin deposited to the feathers influence their durability (Bergman1982, Bonser 1995). As the melanin synthesis capacity of individuals is limited, it may be possible that the flight feathers and the bib are 'competing' to some degree for the melanin. It is noteworthy however, that the rachis diameter, a more direct measure of the feather rigidity and durability (Dawson *et al.* 2000) was not related to bib size, underlining the importance of post-moulting behavioural differences in the process of feather wear.

Finally, we found that rachis diameter but not feather wear influenced strongly the survival during the breeding season, when the mortality of house sparrows is the greatest in the year (Summers-Smith 1988, Lendvai Á.Z. unpublished data) . Although we do not know the actual mechanism by which feather quality acts on survival, the central pillar in this system should be the alteration of flight performance. Reduced flight performance may impinge on survival in at least two ways. First, weak flight performance may diminish the probability to escape from predators (Swaddle *et al.* 1996), and also may cause increased flight metabolism (Murphy 1996, Chai 1997, Hedenström & Sunada 1999). Whatever may be the cause, the effects of feather rigidity seems more important than damages on the feather edge. One must bear in mind however, that we only investigated survival until the moulting period. The repercussions of even minor discontinuities in the structure of the feather webs may be multiplied during moult, when due to the loss and regrowth of the worn feathers, the flight performance considerably drops off (Swaddle *et al.* 1996, Swaddle & Witter 1997). For instance, in the Collared Flycatcher (*Ficedula albicollis*), individuals with lesser degree of

feather wear were more likely to return to their breeding site after the winter. In this study however, the survival is clearly confounded by the recapture probability and eventually by other factors.

Taken together, our study provided one of the first evidences that the quality of flight feathers, which is determined during the moult may affect survival and that different aspects of the feather quality may have different relationships with survival and sexual signals. Future studies should investigate survival during the whole year including the moult, and should also examine the direct consequences of feather quality on the behaviour (Barta *et al.* 2006).

Chapter VI.   Multiple cues in status signalling: the role of wingbars in aggressive interactions of male house sparrows

ABSTRACT During aggressive interactions animals may signal their competitive ability by various ornaments referred to as badges of status. The use of a single badge predicting dominance rank occurs in many vertebrate species. However, animals often display multiple ornaments that may convey information about either different or the same aspects of the signaller's quality, or alternatively, may serve as signal amplifiers. We observed the fighting behaviour of male house sparrows in two captive flocks to investigate whether they may use multiple cues in status signalling during aggressive interactions. Beside the status-signalling bib, male sparrows possess a conspicuous white wingbar that they often display upon aggressive encounters. We tested whether bib size and the wingbar's conspicuousness (i.e. its achromatic contrast with the neighbouring dark feathers) or its area predicted success in various aspects of fighting. We found that bib size strongly predicted overall fighting success (i.e. proportion of fights won) and defence success (i.e. proportion of successful defences out of all attacks received). Wingbar conspicuousness was positively related to defence success after controlling for the effect of bib size in multivariate analyses. Furthermore, displaying the wings also tended to improve the birds' success in defence but not in attack. Wingbar area was unrelated to any measured aspect of fighting ability. We suggest that bib size and wingbar conspicuousness may convey multiple messages on fighting abilities, specifically on overall aggressiveness and defending potential, respectively. Alternatively, wingbars may serve as amplifiers for the wing displays of aggressive motivation. Thus, male sparrows may use multiple cues in assessing the competitive ability of opponents during social interactions.

INTRODUCTION

The status signalling hypothesis (Rohwer 1975) proposes that conspicuous colour traits have evolved to signal differences in the ability to win agonistic contests. Signalling fighting abilities or aggressiveness should be advantageous for all participants, as they may assess the expected outcome of the fight and may therefore avoid costly and unnecessary interactions (Rohwer 1975). Several studies have found a relationship between coloration and dominance status in diverse vertebrate species including birds (reviewed by Senar 1999) and lizards (reviewed by Whiting *et al.* 2003). Such colour traits were termed 'badges of status' as they were considered uncostly to produce and potentially open to cheating. However, increasing evidence suggests that certain colour badges are costly to produce and/or to maintain (Gonzalez *et al.* 2001, 2002, Jawor & Breitwisch 2003, McGraw *et al.* 2003, Török *et al.* 2003) such that it may only pay high-quality (Johnstone 1995) or highly motivated (Enquist 1985) individuals to signal high status. Although animals often exhibit several conspicuous ornaments, however, previous studies have almost exclusively focused on single badges of status.

Multiple ornaments have received increasing research interest rather in the context of sexual signalling and mate choice (reviewed by Candolin 2003). Most of these studies found multiple ornaments to function either as 'multiple messages' that reflect different aspects of individual quality or as 'backup signals' that allow a more accurate assessment of a single aspect of quality (Candolin 2003). Evidence also increases for 'uninformative cues' that do not indicate qualities *per se* but facilitate the detection and assessment of an indicator trait (Candolin 2003). Such interactions among cues of individual quality may also be advantageous during status signalling in competition for resources other than mates, such as for food in wintering flocks of birds. Although a few studies raised the possibility of multiple status signals (Balph *et al.* 1979; Zucker 1994; but see Zucker & Murray 1996), these were not of strong support and left the topic open for debate.

One of the best studied species with a status signalling system is the house sparrow (*Passer domesticus*). In winter flocks of house sparrows, the size of males' black throat patch (the bib) predicts their dominance rank (Møller 1987; Solberg & Ringsby 1997; Liker & Barta 2001; Gonzalez *et al.* 2002; Hein *et al.* 2003). Beside the bib, however, male sparrows exhibit several other contrastingly coloured plumage patches, including a conspicuous wingbar formed by light tips on the median coverts. The wingbars may be flashed by slightly

spreading the wings, or totally hidden by ruffling the flank feathers. When competing for food, sparrows frequently use a threatening position (wing display henceforward) in which they spread and wiggle their wings (Perrins 1998) that appears to emphasize the wingbars. This behaviour suggests that wingbars may be involved in assessing the opponents during aggressive interactions.

Many other bird species also exhibit light wing patterns (Price & Pavelka 1996), and several functions have been found for such ornaments in various taxa, from distracting prey (Jablonski 1996) or predators (Brooke 1998) through facilitating flock cohesion (Beauchamp & Heeb 2001) to sexual selection by female choice (Senar *et al.* 2005). Displaying the wings during aggressive encounters is also widespread among birds (Perrins 1998; Hurd & Enquist 2001), and some studies on various avian species have suggested that white wingbars might signal individual quality in intra-sexual competition in males (Jablonski & Matyjasiak 2002; Török *et al.* 2003) and females (Ruusila *et al.* 2001). However, the function of the wingbars has not been tested in house sparrows.

In this study we investigated the role of the wingbars and wing displays in aggressive interactions among male house sparrows. Specifically, we asked whether these traits may act as multiple cues in status signalling, that is, do they in addition to bib size predict any aspect of fighting success. First, we tested whether males with larger and/or more conspicuous wingbars are more successful in social competition among conspecifics in winter flocks. Second, we examined whether the use of wing display is related to success in different aspects of fighting behaviour.

METHODS

Study Subjects

We captured 28 house sparrows using mist nets in November 2003 in the Budapest Zoo, Hungary. After capture we immediately measured body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm), and ringed all birds with a numbered metal ring and an individual combination of three colour rings. We then formed two mixed-sex flocks consisting 15 and 13 individuals, respectively (male:female ratios were 9:6 and 10:3). House sparrows live in mixed-sex flocks year-round, and sexes do not differ in dominance rank or aggressiveness (Hein *et al.* 2003, Liker & Barta 2001). Flocks were housed in two indoor aviaries measuring

3 m (W) × 4 m (L) × 2 m (H) and 2 m (W) × 3 m (L) × 2 m (H), separated so that individuals of different flocks could not interfere with each other. Both aviaries were lit by artificial light (9L:15D) and contained a feeding board for presenting food, artificial roosting trees and small boxes for sleeping and resting. Food, water, sand and fine gravel (to facilitate digestion) were provided *ad libitum*. Food consisted of a mixture of seeds and occasionally mealworms. After the study we released the birds at the site of capture. Released birds were in good condition and apparently re-established themselves in the local population, as we often re-encountered them after the release (pers. obs.). The study was licensed by the Duna-Ipoly National Park (847/3/2003).

Aggressive Interactions

Behavioural observations were conducted between November 2003 and February 2004. During the observations we recorded aggressive encounters between pairs of individuals when both participants were identified and the outcome of the contest was straightforward. We recorded 1050 dyadic fights in which one or both participants were males. An individual was considered to win a fight if it clearly supplanted the opponent. For each male we calculated overall fighting success, i.e. the number of wins divided by the total number of aggressive encounters which the focal bird was involved in (a measure that strongly correlates with dominance rank; Liker & Barta 2001). Then we calculated two additional components of fighting success: (1) attack success, i.e. the proportion of successful attacks out of all attacks launched by the focal bird, and (2) defence success, i.e. the proportion of successful defences out of all attacks received by the focal bird. Measuring success between opponents in established flocks is a standard method to test the relationship between candidate status signalling traits and fighting ability or aggressiveness of individuals (e.g. Møller 1987; Solberg & Ringsby 1997; Liker & Barta 2001; Hein *et al.* 2003).

To study wing displays we videorecorded the birds' behaviour in each flock on two occasions during the first feeding in the morning. Before the recordings we placed six clumps of millet seeds on the feeding board. Trials lasted until the food clumps were depleted and the birds left the feeding board. We analysed a total of 32 min video recordings for the two flocks. In these recordings, we identified 116 aggressive interactions in which one or both participants were males. For these interactions we recorded the aggressor and the winner, and noted whether participants used wing display. We defined wing display as flapping or wobbling the wings towards the opponent during fights (we excluded wing movements

associated with flight). For all males (N = 19) we calculated attack success and defence success (as above) separately for interactions with and without wing display.

Measuring Coloration

Before releasing the birds we took digital photographs from each male to measure their bib size and the conspicuousness and area of their wingbars (Appendix 3). Birds were held in standard position and were photographed in a standardized set-up with constant lighting conditions. Bibs were photographed with the birds' beak held perpendicular to body axis so that we could measure the so-called visible bib (Gonzalez *et al.* 2001). Wingbars were photographed on the left wings flattened. Photos were converted to grey-scale and measured using the Scion Image software (Scion Corporation 1998). We selected the area of bib or wingbar using the 'density slice' and 'wand tool' functions. Areas were measured in pixels and converted to cm^2 using a measured standard in the photos. Brightness of the wingbar was measured as the mean density of the pixels constituting the wingbar on the photos (the lighter the pixel, the smaller the density value). We also measured the mean density of the area of brown lesser coverts above the wingbar. This area may serve as a natural background or 'standard' against which birds see and judge wingbars, since during threat displays sparrows rotate their wings so that lesser coverts point towards the opponent (Perrins 1998; pers. obs.). We calculated wingbar conspicuousness by subtracting wingbar density from lesser coverts density, and used this variable as a measure of wingbar conspicuousness (greater values may be interpreted as greater achromatic contrast between the wingbar and the lesser coverts). We preferred wingbar conspicuousness over wingbar brightness because conspicuousness depends not only on the brightness of the plumage patch but also on its visual environment, and within-animal contrast may be a more objective measure of conspicuousness in most natural habitats of sparrows (Endler 1990).

We tested the reliability of our colour measurements in several ways. First, we measured each photograph twice and calculated the repeatability of measurements (Lessels & Boag 1987). Repeatability proved very high for bib size (r = 0.97, $F_{18,19}$ = 64.3, p < 0.001), wingbar area (r = 0.78, $F_{18,19}$ = 8.1, p < 0.001) and wingbar conspicuousness (r = 0.90, $F_{18,19}$ = 19.7, p < 0.001; see also Bókony *et al.* 2003 for further justification of area measurements from photos). Second, to validate our method using grey-scale density values as a proxy for wingbar conspicuousness, we plucked the 2-5th median coverts with white tips from 25 male sparrows captured at a different site, and measured their reflectances using an USB2000

spectroradiometer with a Mini-DT deuterium-halogen light source (Ocean Optics Europe; methods as in Cuthill *et al.* 1999). Since these feathers did not reflect in the UV, we calculated total reflectance for the 400-700 nm range of the spectra as an objective measure of wingbar brightness (Marchetti 1993; McNaught & Owens 2002). Before plucking the feathers, we took photographs of the birds' wingbars and measured the density values of these as described above. Wingbar density correlated significantly with total reflectance ($r = -0.49$, $p = 0.013$, $N = 25$; note that a negative correlation is expected since the greater the brightness, the less the density value).

Statistical Procedure

To explore the relationships between colour traits and measures of fighting ability in males, we used general linear models with flock as a random factor and bib size, wingbar area and wingbar conspicuousness as covariates. Dependent variables (fighting success, attack success and defence success) were arcsine square-root transformed before the analyses. We used stepwise backward elimination of non-significant effects, by removing the predictor with the largest *p*-value in each step. We do not report flock effects since these were non-significant in all models, and there were no significant interactions between the flock factor and other predictor variables. Since tarsus and wing length and body mass were unrelated to measures of both coloration and fighting ability in our sample (results not shown) and also in other studies (e.g. Møller 1987; Liker & Barta 2001), we did not control for these biometrical variables in the analyses.

Since the power of our tests was low due to small sample sizes, we did not use any corrections of significance levels for multiple comparisons, as these would only exacerbate the problem of low power by increasing the risk of neglecting existent small effects (Nakawaga 2004). Instead, to prevent our conclusions from being based purely on the significance of each test, we also evaluated our results using a different analytical approach, the information-theoretic model comparison (Anderson *et al.* 2000), where inference is based on the entire model set. We evaluated all possible subsets of the three initial GLM models based on the second-order Akaike's information criterion corrected for small sample size (AICc). As no single model was highly superior compared with the others in our model sets, we performed model-averaging (Anderson *et al.* 2000) where model coefficients were weighted using Akaike weights. We also examined the relative importance of predictors by summing the Akaike weights for each predictor across all sub-models that contained that

predictor. Then we compared the final sets of predictor variables selected in each approach (i.e. stepwise GLM and AICc-based model-averaging).

We analyzed the data on display behaviour using the independent sample derived from video recordings. Here we used non-parametric tests because the distribution of these variables did not allow for parametric tests. Using Wilcoxon matched-pairs signed-ranks tests we tested whether the males' attack success and defence success was greater when displaying than when not displaying. Since the power of these tests were low due to the small number of males performing attacks and defences both with and without wing display in our sample, we also checked for the associations between success and display using fights as data points in χ^2-tests. Since these data points are not independent (each male participated in several fights), in this latter case we used a full permutation procedure to calculate the exact level of significance for the tested associations.

All statistical tests were two-tailed with a 95% confidence level. We used the **R** statistical computing environment (R Development Core Team 2003) and SPSS for Windows 12.0 for statistical analyses.

RESULTS

Wingbar area and wingbar conspicuousness were not correlated (Pearson correlation, $r = -0.05$, $p = 0.828$, $N = 19$). Bib size was not correlated with wingbar area ($r = 0.37$, $p = 0.120$, $N = 19$) or wingbar conspicuousness ($r = 0.24$, $p = 0.324$, $N = 19$). Defence success and attack success were significantly correlated ($r = 0.68$, $p = 0.001$, $N = 19$).

Coloration and Fighting Ability

Bib size was the strongest predictor for each measure of fighting ability both in stepwise GLMs (Table VI.1) and AICc-based model comparison (Table VI.2, Table VI.3). For fighting success and defence success, both the final GLM (Table VI.1) and the models with the lowest AICc included bib size (Table VI.2). For attack success, the best model contained bib size again, but its relative importance was similar to that of the other coloration variables (Table VI.3), and its effect was non-significant in GLM (Table VI.1).

Table VI.1. Relationships of plumage colour traits with measures of fighting ability in male house sparrows using stepwise GLMs. Predictor variables are bib size (B), wingbar conspicuousness (C), and wingbar area (A). Asterisks (*) indicate predictors included in the final models. For these variables, regression coefficients (b) ± SE and effect sizes (η^2) are given for the final models. For predictors not included in the final models, estimates are given for the initial models.

Predictor	Fighting success[a]		Attack success		Defence success[b]	
	$b \pm$ SE	η^2	$b \pm$ SE	η^2	$b \pm$ SE	η^2
B	0.10 ± 0.04	0.274*	0.04 ± 0.04	0.055	0.09 ± 0.03	0.416*
C	0.01 ± 0.01	0.189	0.01 ± 0.01	0.098	0.01 ± 0.004	0.381*
A	-0.01 ± 0.24	< 0.001	0.01 ± 0.24	< 0.001	-0.20 ± 0.16	0.096

[a] Final model: $F_{1,17} = 6.42$, $p = 0.021$.
[b] Final model: $F_{2,16} = 13.97$, $p < 0.001$.

Wingbar conspicuousness was significantly related to defence success only; both the final GLM (Table VI.1) and the model with the lowest AICc (Table VI.2) for defence success included wingbar conspicuousness in addition to bib size. Both traits were of similar importance in explaining defence success, as indicated either by effect size in GLM (Table VI.1) or the sum of Akaike weights (Table VI.3).

Wingbar area was not related to any measures of fighting ability in GLMs (Table VI.1) and proved of minor importance in AICc-based model selection (Table VI.3).

Wing Displays

In the video samples, defence success tended to be greater when the defender's wingbar was displayed than when it was not (Wilcoxon matched-pairs signed-ranks tests, $Z = -1.49$, $p = 0.068$, $N = 8$ males, Figure VI.1), while attack success was not improved by wing displaying ($Z < 0.001$, $p > 0.999$, $N = 7$ males). When we used fights as data points, success was significantly associated with the use of wing display in defences ($\chi^2_1 = 16.36$, $N = 63$ defences, exact $p < 0.001$) but not in attacks ($\chi^2_1 = 1.06$, $N = 91$ attacks, exact $p = 0.388$).

Table VI.2. Results of AICc-based model selection: AICc values, number of estimated parameters (K), AICc differences between the best model and each candidate model (Δ_i), and Akaike weights (ω_i) of the candidate models are given for measures of fighting ability. Predictor variables are bib size (B), wingbar conspicuousness (C), wingbar area (A), and flock (F).

Dependent	Model	Predictors	AICc	K	Δ_i	ω_i
Fighting success	1	B	1.04	3	0.00	0.41
	2	B+C	1.98	4	0.94	0.26
	3	C	3.15	3	2.10	0.14
	4	B+A	4.23	4	3.19	0.08
	5	A+C	5.72	4	4.67	0.04
	6	B+A+C	5.74	5	4.70	0.04
	7	A	6.99	3	5.94	0.02
	8	B+F	15.01	4	13.97	0.00
	9	A+F	16.56	4	15.52	0.00
	10	B+A+F	19.66	5	18.62	0.00
	11	C+F	20.69	4	19.65	0.00
	12	B+C+F	24.77	5	23.73	0.00
	13	A+C+F	24.91	5	23.87	0.00
	14	B+A+C+F	30.18	6	29.14	0.00
Attack success	1	B	0.27	3	0.00	0.36
	2	C	1.08	3	0.81	0.24
	3	A	1.74	3	1.47	0.17
	4	B+C	3.12	4	2.85	0.09
	5	B+A	3.53	4	3.26	0.07
	6	A+C	4.08	4	3.81	0.05
	7	B+A+C	6.87	5	6.60	0.01
	8	A+F	12.08	4	11.80	0.00
	9	B+F	13.93	4	13.65	0.00
	10	C+F	17.81	4	17.54	0.00
	11	B+A+F	18.72	5	18.45	0.00
	12	A+C+F	22.59	5	22.31	0.00
	13	B+C+F	25.06	5	24.78	0.00
	14	B+A+C+F	30.49	6	30.22	0.00
Defence success	1	B+C	-13.83	4	0.00	0.71
	2	B+A+C	-11.59	5	2.24	0.23
	3	B	-6.85	3	6.98	0.02
	4	B+A	-6.58	4	7.25	0.02
	5	C	-5.21	3	8.62	0.01
	6	A+C	-2.02	4	11.82	0.00
	7	B+F	6.90	4	20.73	0.00
	8	B+A+F	10.20	5	24.03	0.00
	9	C+F	11.73	4	25.56	0.00
	10	B+C+F	11.75	5	25.58	0.00
	11	A	11.99	3	25.82	0.00
	12	A+F	12.49	4	26.33	0.00
	13	B+A+C+F	16.51	6	30.34	0.00
	14	A+C+F	16.97	5	30.80	0.00
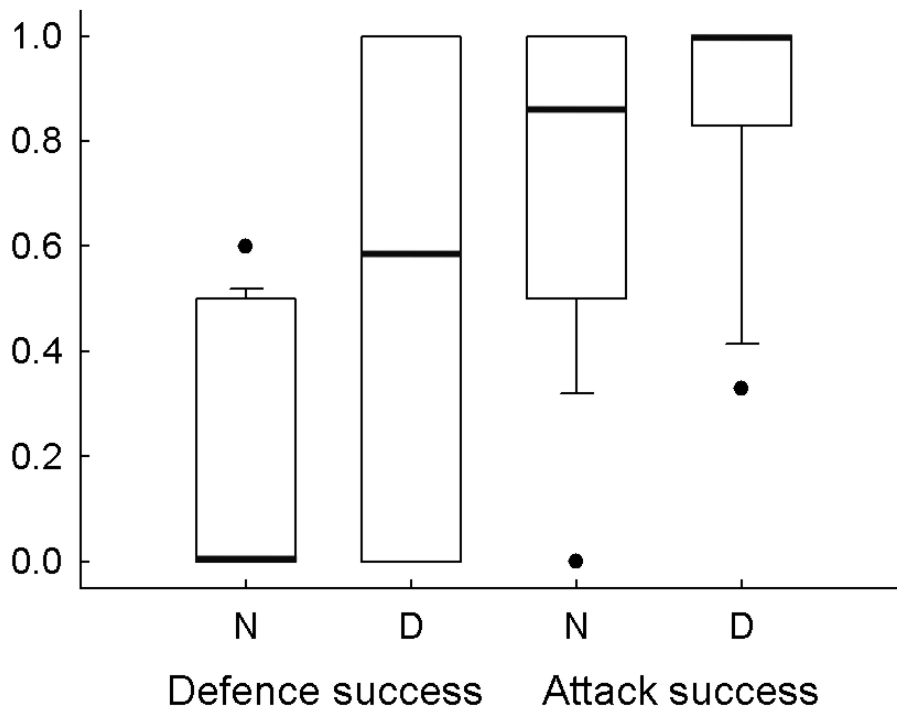
Figure VI.1. Defence success and attack success of male house sparrows in aggressive interactions without wing display (N) and with wing display (D). Box plots show the medians (horizontal bar), 25th and 75th percentiles (top and bottom of box, respectively), 10th and 90th percentiles (whiskers) and outliers (dots).

Table VI.3. Model-averaged regression coefficients (*b*) and their unconditional standard errors (SE) for bib size (B), wingbar conspicuousness (C), and wingbar area (A) in relation to measures of fighting ability. Coefficients of a given predictor were weighted using the Akaike weight of each candidate model containing that predictor. Σ shows the sum of Akaike weights for each predictor across all models that contain that predictor, reflecting the relative importance of predictors in explaining variation in the dependent variable. The effect of flock as a random factor was not estimated.

Predictor	Fighting success		Attack success		Defence success	
	Σ	$b \pm SE$	Σ	$b \pm SE$	Σ	$b \pm SE$
B	0.79	0.08 ± 0.17	0.53	0.03 ± 0.10	0.99	0.09 ± 0.09
C	0.48	0.01 ± 0.05	0.39	0.00 ± 0.03	0.96	0.01 ± 0.07
A	0.18	0.01 ± 0.11	0.31	0.02 ± 0.13	0.25	-0.05 ± 0.10

DISCUSSION

In this study we demonstrated that male house sparrows may use multiple cues in status signalling during social competition. First, we found that bib size of males was related to their fighting success. This finding agrees with other observations and experimental studies showing that bib size functions as a status signal during aggressive interactions of sparrows (Møller 1987; Solberg & Ringsby 1997; Liker & Barta 2001; Gonzalez *et al.* 2002; Hein *et al.*

2003). Second, we showed that beside bib size, the conspicuousness of the wingbar also explained a significant proportion of variation in defence success. This relationship was independent of the effects of bib size because (1) wingbar conspicuousness was unrelated to bib size in our sample, and (2) we controlled for the effects of bib size in multivariate analyses. Furthermore, we found that using the wing displays also tended to improve the sparrows' success in defence but not in attack. Thus, our results suggest that conspicuous wingbars may function in aggressive interactions of male sparrows by increasing the defence success of their bearer.

Since bib size and wingbar conspicuousness were not correlated, it is unlikely that the wingbar is merely a backup signal that serves to reinforce the signal of the bib. Furthermore, wingbar conspicuousness was related to defence but not overall fighting success, suggesting that bibs and wingbars may signal slightly different aspects of fighting ability. Namely, bib size may be important for assessing the opponents' overall aggressiveness or fighting ability (including both attacks and defences), whereas wingbar conspicuousness may specifically signal their ability to defend their already occupied resources (e.g. a food patch or resting site). This defending potential may in some way differ from overall fighting ability. For example in great tits (*Parus major*), males selected for 'fast' exploratory behaviour attack their opponents more vigorously, but 'slow' individuals use more threat displays and they recover sooner after a defeat (Groothuis & Carere 2004), suggesting that attack and defence may involve different behavioural mechanisms. Under this scenario, bib size and wingbar conspicuousness may act as 'multiple badges of status' in sparrows.

Alternatively, wingbars may not signal specific information about defending potential, but may serve as signal amplifiers (Hasson 1989; Candolin 2003) to facilitate the detection and/or assessment of the birds' wing displays. Avian wing displays probably signal aggressive motivation or willingness to escalate fights (Hurd & Enquist 2001). Since sparrows can regulate the visibility of their wingbars either by exposing them in wing display or by hiding them with the neighbouring feathers, wingbars may function as 'coverable badges' (Hansen & Rohwer 1986) that are exposed when birds are highly motivated to defend their resources but not displayed when birds are not willing to engage in an escalated fight. Although sparrows use the wing display during both launching and withstanding attacks, it may be especially useful during defence because the level of motivation may be more variable among defenders than among attackers. Attackers may usually be willing to fight (otherwise they would not attack), and accordingly, the majority of attacks result in wins in sparrows (Jawor 2000; this study: Figure VI.1). Contrarily, defenders cannot help being attacked, and they should only

risk fighting if they are motivated enough to defend their resources. This may explain our finding that wing displays increase defence success but do not affect attack success in sparrows. Birds may uncover their wingbars to amplify the signal of wing display, with more conspicuous badges being more effective threats (Hansen & Rohwer 1986).

We have found that the conspicuousness but not the area of wingbars was associated with defence success. This may reflect the fact that different characteristics of an ornament may differ in developmental constraints and/or selection pressures (Badyaev *et al.* 2001). For example, different aspects of a single plumage ornament in house finches (the hue of the red breast patch, its area and the symmetry of both) are partially independent of each other and differ both in proximate control and in fitness consequences (Badyaev *et al.* 2001). In sparrows, it is also possible that wingbar conspicuousness is a more reliable signal of defending ability or is more effective in amplifying rapid wing displays than the area of the wingbars (Endler 1990; Marchetti 1993).

In sum, we have found that in addition to the well known bib size, the conspicuousness of the wingbar also relates to success in social competition in male house sparrows. Wingbar conspicuousness is specifically related to defence success, which is also improved by actively displaying the wingbars. We propose that the bib and the wingbar may convey multiple messages on aspects of fighting abilities or, alternatively, wingbars may serve as amplifiers for aggressive wing displays. Although an observational study with small sample size, this is the first one to demonstrate a possible use of colour traits as multiple cues in non-sexual status signalling.

Chapter VII. Modulation of the adrenocortical response to stress: a test of the hypotheses in the house sparrow

ABSTRACT Individuals often vary in the magnitude of their hormonal response to stressful situations. Two main hypotheses have been proposed to account for this variance. The first hypothesis suggests that individuals with high level of parental effort should suppress their hormonal response to stress in order to avoid the abandonment of the nest. The second hypothesis suggests that as individuals with low chances to renest should invest more in the current reproductive episode, they are expected to suppress their stress response. We simultaneously tested these ideas in a free living population of house sparrows (*Passer domesticus*) by capturing the breeding birds and measuring their basal and stress-induced corticosterone levels. We showed that sparrows tending experimentally enlarged broods had weaker adrenocortical response to stress than parents tending reduced broods. The baseline corticosterone levels and also the magnitude of the stress response decreased over the breeding season in the birds' first breeding attempt but remained constant during their second breeding attempt. The same seasonal pattern was observed during the time span when the breeding activity of parents tending their first and their second brood overlapped. Within individual variability in the stress response was significantly explained by the differences in the brood size manipulations the birds received in their two consecutive breeding attempts. These results are in accordance with both hypotheses and provide strong support for the idea that individuals may adaptively and actively modulate their hormonal response to stress.

Ádám Z. Lendvai, Mathieu Giraudeau & Olivier Chastel. – *Manuscript*.

INTRODUCTION

A key concept in life-history theory is that energy allocated to the current reproductive event can only be increased at the expense of survival and hence future reproduction (Stearns 1992). This trade-off reflects the 'cost of reproduction' (Williams 1966) which is a fundamental component determining the level of 'parental investment' (Trivers 1972). Parental investment however, depends not only on its costs but also on the benefits from the current reproduction, e.g. the value of the offspring. Although these factors have been shown to shape the animals' reproductive decisions, our knowledge is still scarce about the actual mechanisms by which these costs and benefits are assessed and integrated within the animals.

Recent theoretical models of resource allocation have shown that the life-history decisions may be influenced by the physiological state of individuals (McNamara & Houston 1996, Houston & McNamara 1999). Endocrine hormones play a major role in the mediation of decision-making on life-history trade offs. For instance, stressful situations, i.e. unpredictable or uncontrollable evocative stimuli induce a rapid elevation in circulating glucocorticoids, which promote the mobilisation of energy resources and the occurrence of those behavioural forms that enhance the immediate survival, but it may also compromise reproductive and parental behaviour in a longer term. This adrenocortical response to stress is thought to be adaptive, because it may interrupt the current reproductive episode of an individual and promote its survival for future reproduction (Wingfield & Sapolsky 2003). The glucocorticoid levels therefore seem to have a role in mediating an important life-history trade-off. In line with this idea, individuals of several species have been found to modulate their adrenocortical response to stress in function of the costs and benefits associated with their reproductive status. To explain the adaptive significance of the modulation of stress responses, it has been proposed that individuals may suppress their adrenocortical response to stress when the value of their offspring is high. This idea has been postulated in two hypotheses.

First, the 'parental care hypothesis' suggests that the extent of parental investment is related to the adrenocortical response to stress, i.e. in the critical periods of parental care, individuals providing more parental care suppress their stress response compared with individuals that provide less parental care (Wingfield *et al.* 1995). Accordingly, breeding female marine turtles exhibited lower increase of corticosterone than both non-breeding and pre-breeding counterparts (Jessop 2001). Second, the 'short season hypothesis' proposes, that

when the breeding period is brief, and the probability of renesting in the current season is low, individuals should down-regulate their response to stress, otherwise they may risk a complete reproductive failure for a given year (Wingfield *et al.* 1995). For instance, individuals of Pied flycatchers (*Ficedula hypoleuca*) breeding in a temperate zone in southern Sweden had higher levels of corticosterone in response to capture stress than individuals breeding in a sub-arctic site in Swedish Lapland (Silverin & Wingfield 1998). These studies, however, did not use experimental manipulations, but compared different populations or individuals in different breeding stages which may have confounded the results, and therefore the topic was left open for debate.

In this study we tested simultaneously these two hypotheses by examining the corticosterone response to capture/restraint stress in one breeding population of house sparrows (*Passer domesticus*), a highly suitable species to investigate the modulation of the stress response. First, the parental effort of house sparrows can be easily manipulated by the alteration of the nestling number (Seel 1969, Hegner & Wingfield 1987, Chastel & Kersten 2002, Bonneaud *et al.* 2003). Therefore, to experimentally test the 'parental care hypothesis', we manipulated the brood size of parents by adding or subtracting two chicks, and compared the response to capture/restraint stress between the experimental groups. According to the 'parental care hypothesis', we predicted that the rise in corticosterone levels in response to stress would be weaker in birds with increased parental effort than in birds with reduced parental effort. Second, in the study population, there is considerable individual variation in the onset of breeding: there are birds that start breeding early in the season and may have up to three subsequent clutches, whereas an important proportion of the population start the reproduction later and have only one breeding attempt (Chastel *et al.* 2003). As the probability of renesting decreases over the breeding season, we used the date of breeding as a surrogate measure to test the 'short season hypothesis'. To date, no study has controlled for the effects of different breeding stages of individuals within a breeding season. In the present study we only use parents tending large chicks, i.e. a period when the parents are close to fledge their young and renest or finish the reproduction. Specifically, we predicted that individuals breeding at the beginning of the season (high renesting probability) would have a stronger adrenocortical response to capture/restraint stress than those that bred later (low renesting probability).

METHODS

Study Species and Population

The study was carried out between March and July 2005, in a free living population of house sparrows (*Passer domesticus*) in Chizé (46°09' N, 0°24' W), France, where most individuals bred in nest boxes fixed to the walls of buildings (Chastel *et al.* 2003). During the pre-breeding period a large proportion of the breeding population were captured by mist nests and ringed with a numbered metal ring and a unique combination of three colour rings. Nest boxes were checked at least every third day to determine laying date and clutch size. House sparrows lay one egg per day (Summers-Smith 1963), thus if two or three eggs were found in the nest box, the date of clutch initiation was derived by subtracting one or two days respectively from the date when the eggs were first seen. From the ninth day after the clutch completion, nest boxes were checked daily to determine the date of hatching and the number of hatchlings.

Brood Size Manipulation

To manipulate breeding effort of the parents, we modified their brood size as follows. When nestlings were 2 days old, two randomly chosen chicks were transferred between two synchronous broods, thus we had an enlarged and a reduced brood in each manipulation block. The clutches for which no other synchronous clutch was available were not manipulated. Due to the moderate number of available clutches, we did not use a control group. This was a trade-off between maximising the sample sizes of the manipulated broods and testing the effects of changes in the brood composition. An identical design was used by Chastel & Kersten (2002). The after-manipulation brood sizes ranged 2-7 nestlings that matched the natural brood size range found in this population in the year of the study.

Capture and Blood Collection

To study the stress response of the individuals, we used the standard capture-handling-restraint protocol (Wingfield 1994), which has been used across a wide range of bird species. Breeding sparrows were captured in their nest box using a wire trap, when the nestlings were 10-12 days old. Immediately after capture, a small sample of blood (50-100 µl) was collected

in heparinized micro tubes from the brachial vein following puncture with a 27-gauge needle (Appendix 4). To control for the possible effects of handling time we measured the time elapsed from the moment when the nest box trap was released until the end of the first blood collection for each individual. Mean handling time was 2:37 ± 0:02 (SE) min, maximum 3:09 min. Corticosterone levels measured at the initial bleeding were not related to handling time ($r = 0.206$, $p = 0.112$, $N= 61$). Therefore we assume that the corticosterone levels measured at capture were representative of the circulating baseline hormone levels prior the capture. We found no significant linear or curve-linear relationship between the corticosterone levels from the first bleeding and time of day when the blood sample was taken.

After the initial blood sampling, the birds were immediately placed in a cloth bag, and 30 min later the bleeding procedure was repeated. The time elapsed between the two bleedings were also recorded. After the second blood sampling, we measured the tarsus length (± 0.1mm) and body mass (± 0.1g) for all birds. After the measurements, birds were released in a standard location of the study site. After the release, we measured the time elapsed until they returned to their nest box and resumed breeding activities (Appendix 5). The blood samples were centrifuged (4500 rpm, 6 min) as soon as possible, and were stored at –20°C until hormone analyses.

Corticosterone Assay

Plasma titres of corticosterone were determined by radioimmunassay at the Centre d'Etudes Biologiques de Chizé following the procedure detailed in Lormée *et al.* (2003). Corticosterone was extracted from a 50 μl plasma sample and determined in duplicates were run in one assay (coefficient of intra-assay variation was 4.3 %).

Data Processing and Analysis

Baseline and maximum corticosterone levels were ln-transformed to obtain normal distributions. First, we tested whether the capture-restraint protocol induced changes in the corticosterone levels of the sparrows, using a general linear model with two-level repeated measures (i.e. the initial and the 30-min sampling). Second, we analysed the between-individual differences in baseline level of corticosterone and the magnitude of their response to stress. Response to stress was characterised by the rate of increase from baseline to maximum corticosterone levels per minutes (ng/ml/min) (Silverin *et al.* 1997, Lindström *et al.*

2005). This measure of stress response was highly correlated with the maximum levels of corticosterone ($r = 0.920$, $p < 0.0001$), and the statistical analyses of these variables gave nearly identical results, hence we do not repeat results on maximum corticosterone levels. To analyse seasonal changes in both the baseline and the stress-induced hormone levels, we used the date of capture and blood sampling as the independent variable.

Seventy percent of the individuals were captured only in their first or only in their second brood, hence the two breeding attempts were analysed separately. Parents tending their third brood were not captured. The inter-individual differences in the effects of manipulations were analysed only in individuals captured in manipulated broods.

We also made two comparisons between the breeding attempts. First, we compared the stress response of 'early' and 'late' breeders. Late breeders were defined as individuals starting their first reproductive attempt when others (early breeders) had been already tending their second broods (Chastel *et al.* 2003). Therefore, early and late breeders were compared in a time span where their breeding activity overlapped, i.e. from the earliest second clutch initiation until the last initiation of first clutch (from 15 May until 13 June, Figure VII.1). Second, for those individuals that were sampled in both their first and the second brood, we also performed within-individual comparisons to investigate whether the variation in their physiological response to stress was a function of the differences between the manipulations they received in their first and the second breeding attempt. We created three categories: (1) where the brood size manipulation induced greater parental effort in the first brood compared with the second brood (i.e. the first brood was enlarged and the second was either unmanipulated or reduced); (2) where the individual either received the same type of manipulation or were left unmanipulated in both breeding attempts; (3) where the brood size manipulation induced lesser parental effort in the first brood compared with the second brood (i.e. the first brood was reduced and the second was either unmanipulated or enlarged).

In the nests where both male and female parent were captured, we found no relationship between the baseline corticosterone levels or the rate of increase in corticosterone levels of the two parents (all p values > 0.1), indicating that these variables reflect individual variation in the physiological response to the manipulation. Hence, we used males and females as independent data points in our analyses.

Body condition was expressed as the residual mass from a linear regression with tarsus length as independent variable. Dates are presented as the number of days elapsed from the initiation of the first clutch in the population (15 April). Two-tailed probabilities and mean ± SEs are given throughout the paper. We used SPSS 11.0 for statistical analyses.

RESULTS

The Study Population

Sparrows reproduced in the breeding season in three overlapping waves of breeding attempts (Figure VII.1).
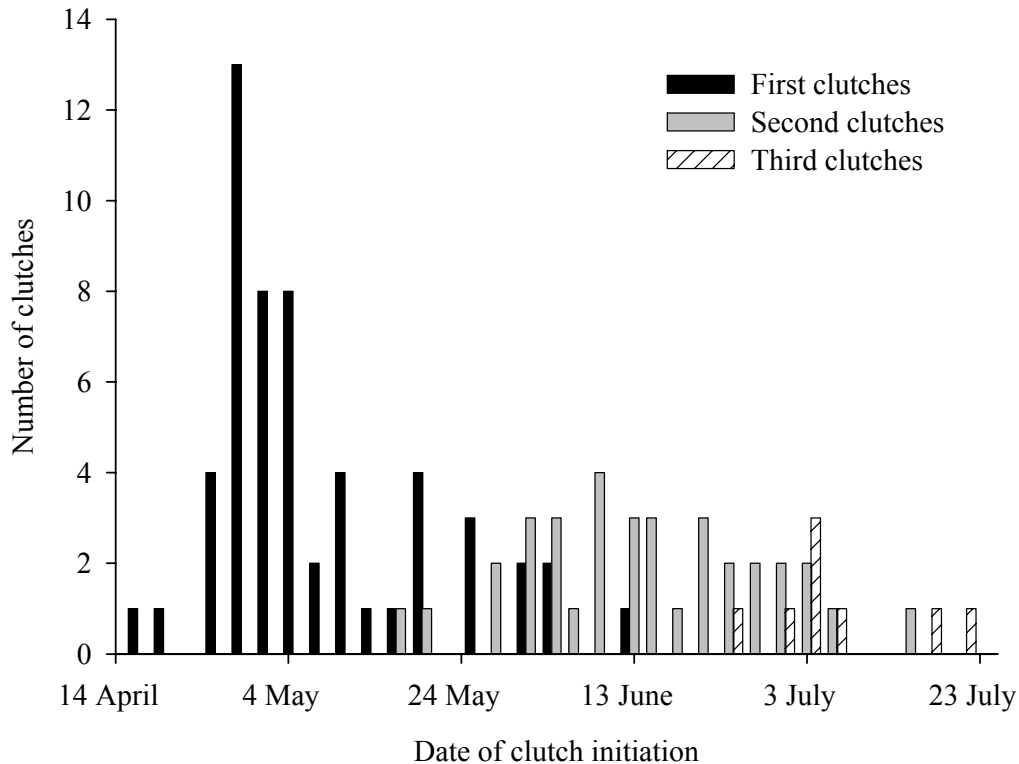
Figure VII.1. Number of clutches initiated by house sparrows in 2005 in 3-day periods during the breeding season.

The first wave of clutches was produced from mid-April onwards. By mid-May, some birds initiated their second clutches, while others started their first breeding attempt. Most birds in the population were colour-ringed, hence regular observations of marked individuals and checking of nest boxes confirmed that birds initiating their first clutch had not bred elsewhere. After the first clutch, 54 % of the individuals did not lay a second clutch, and finished the reproduction. The probability of starting a second clutch decreased significantly with the date of the first clutch initiation (binary logistic regression, $B = -0.044$, $p = 0.017$). From the end of June, 15 % of the birds that had a second clutch laid a third clutch, while most birds in the population had finished the reproduction. The probability of having a third clutch depended

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also on the date of starting the second clutch (binary logistic regression, $B = -0.210$, $p = 0.006$).

Baseline Hormone Levels and Body Condition

Baseline corticosterone levels decreased during the season in the first, but not in the second breeding attempt (first breeding attempt, $r = -0.418$, $p = 0.005$, $N = 44$; second breeding attempt, $r = -0.048$, $p = 0.786$, $N = 34$; Figure VII. 2).
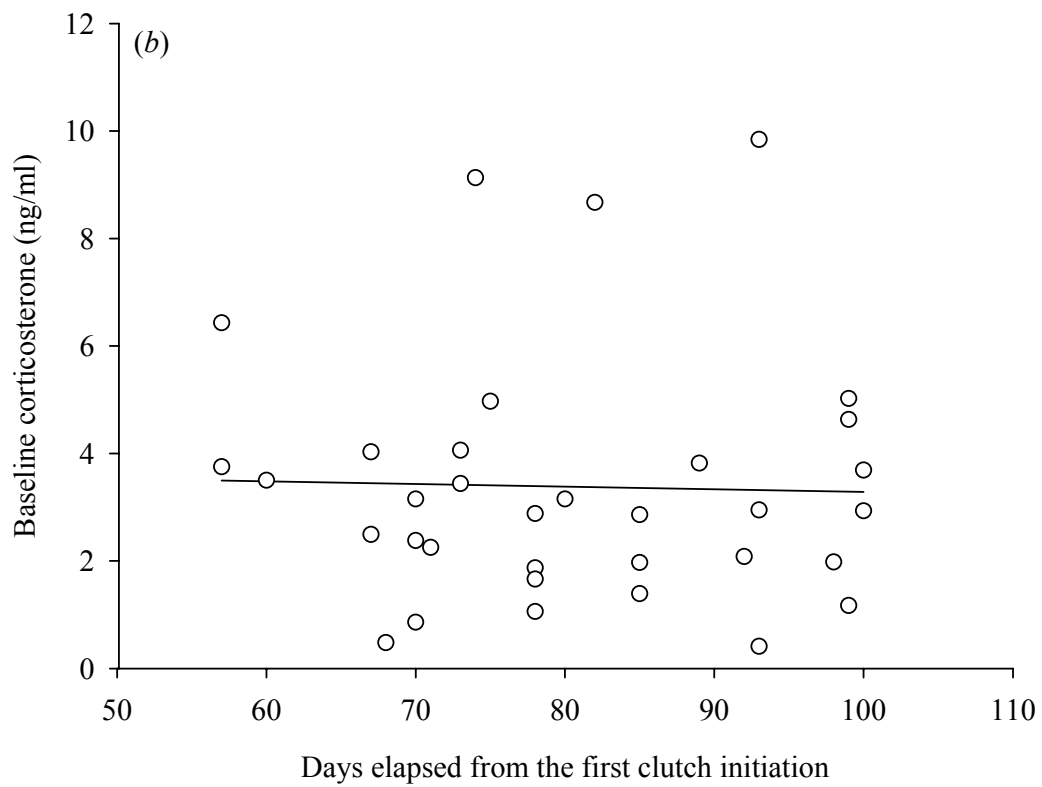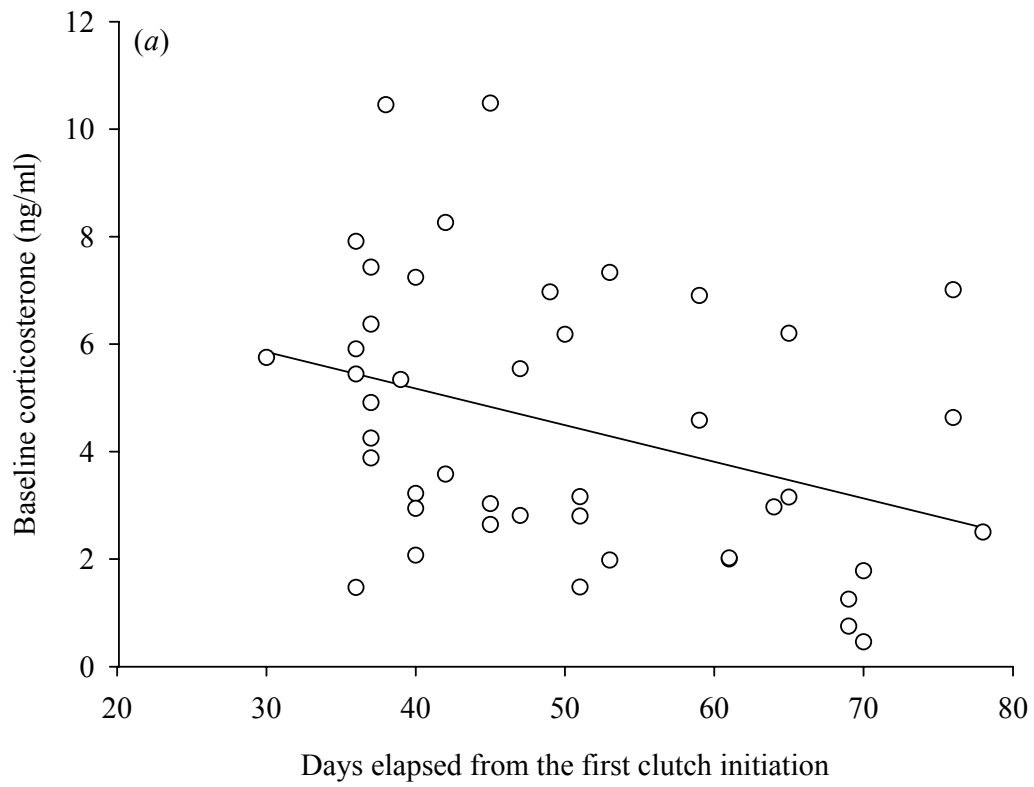
Figure VII.2. Seasonal change in the baseline corticosterone levels in the (a) first breeding attempt and in the (b) second breeding attempt.

Manipulation groups did not differ in the baseline corticosterone levels, even after controlling for the seasonal effects (first breeding attempt, $F_{1,28}$ = 0.153, p = 0.699; second breeding attempt, manipulation: $F_{1,21}$ = 2.574, p = 0.124). Body condition did not differ between the manipulation groups and the sexes either in the first or in the second breeding attempt (first breeding attempt, manipulation: $F_{1,26}$ = 1.047, p = 0.316, sex: $F_{1,26}$ = 0.845, p = 0.366, interaction: $F_{1,26}$ = 1.614, p = 0.215; second breeding attempt, manipulation: $F_{1,23}$ = 0.209, p = 0.652, sex: $F_{1,23}$ = 1.396, p = 0.252, interaction: $F_{1,23}$ = 1.038, p = 0.321). Body condition was related to the baseline corticosterone levels in both breeding attempts although in the opposite direction (first breeding attempt, r = 0.440, p = 0.008, N = 42; second breeding attempt, manipulation: r = –0.349, p = 0.050, N = 32).

Adrenocortical Response to Stress

Circulating plasma levels of corticosterone increased markedly following capture, handling and restraint (GLM repeated measures, first breeding attempt, $F_{1,43}$ = 536.559, p < 0.001; second breeding attempt, $F_{1,31}$ = 320.567, p <0.001). The rate of increase in corticosterone levels was not dependent on the baseline corticosterone levels (first breeding attempt, r = 0.138, p = 0.371, N = 44; second breeding attempt, r = –0.084, p = 0.646, N = 32) and the body condition (first breeding attempt, r = –0.026, p = 0.871, N = 42; second breeding attempt, r = 0.107, p = 0.561, N = 32). The rate of corticosterone increase was not different between the sexes (first breeding attempt, $F_{1,42}$ = 0.143, p = 0.707; second breeding attempt, $F_{1,30}$ = 0.375, p = 0.545).

The Effects of Season and the Manipulation

During the first breeding attempt, the magnitude of stress response decreased over the season and this decrease was also significant after controlling for the baseline corticosterone levels, indicating that the decrease in the rate of corticosterone increase was not merely a by-product of the similar decrease in the baseline corticosterone levels (season: $F_{1,41}$ = 11.280, p = 0.002, baseline corticosterone: $F_{1,41}$ = 1.019, p = 0.319; Figure VII.3a).
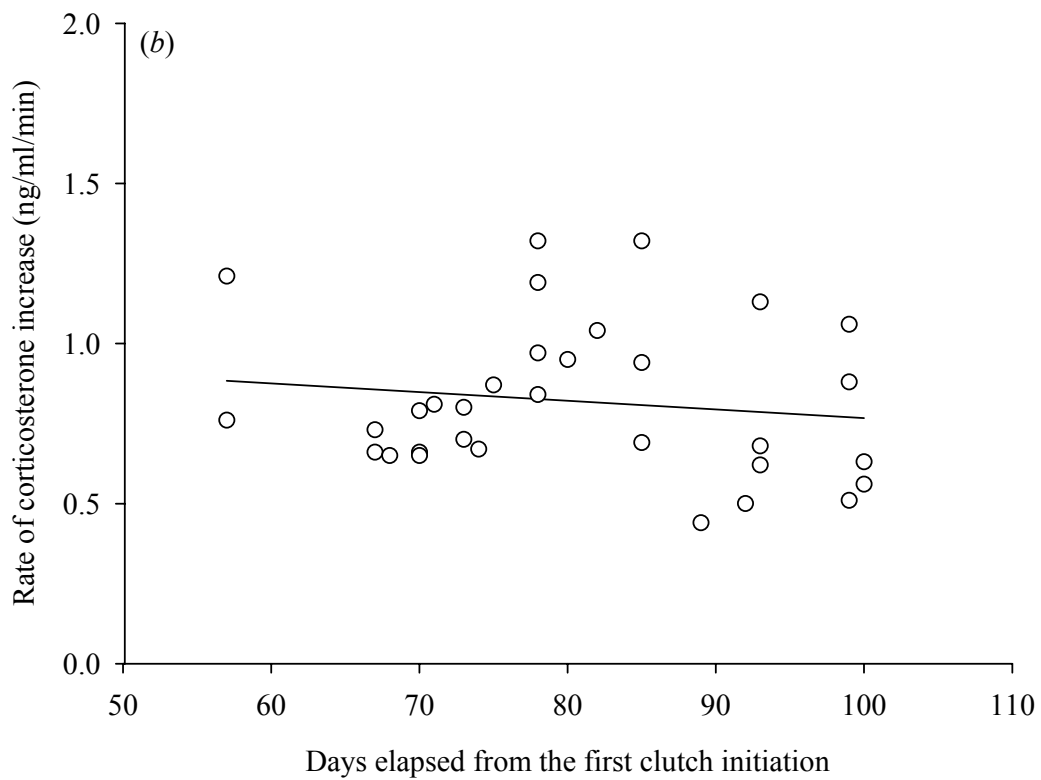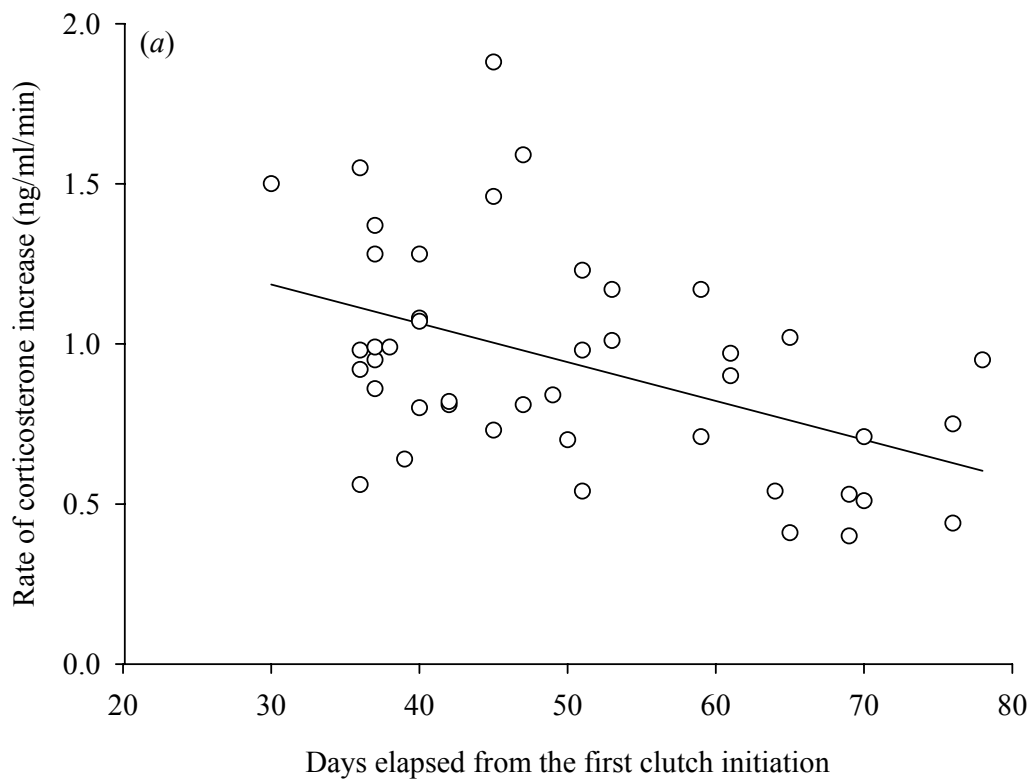
Figure VII.3. Seasonal change in the rate of corticosterone increase in the (a) first breeding attempt and in the (b) second breeding attempt.

In the second breeding attempt, the rate of increase in corticosterone levels was also independent from baseline corticosterone levels, but did not change over the season (season: $F_{1,29} = 0.621$, $p = 0.437$, baseline corticosterone: $F_{1,29} = 0.213$, $p = 0.648$, Figure VII.3b).

In both breeding attempts, individuals tending reduced broods had higher stress response than individuals tending enlarged broods, and this difference remained significant after statistically removing the effect of the season (first breeding attempt, $F_{1,29} = 6.163$, $p = 0.019$; second breeding attempt, $F_{1,20} = 10.940$, $p = 0.004$; Figure VII.4).
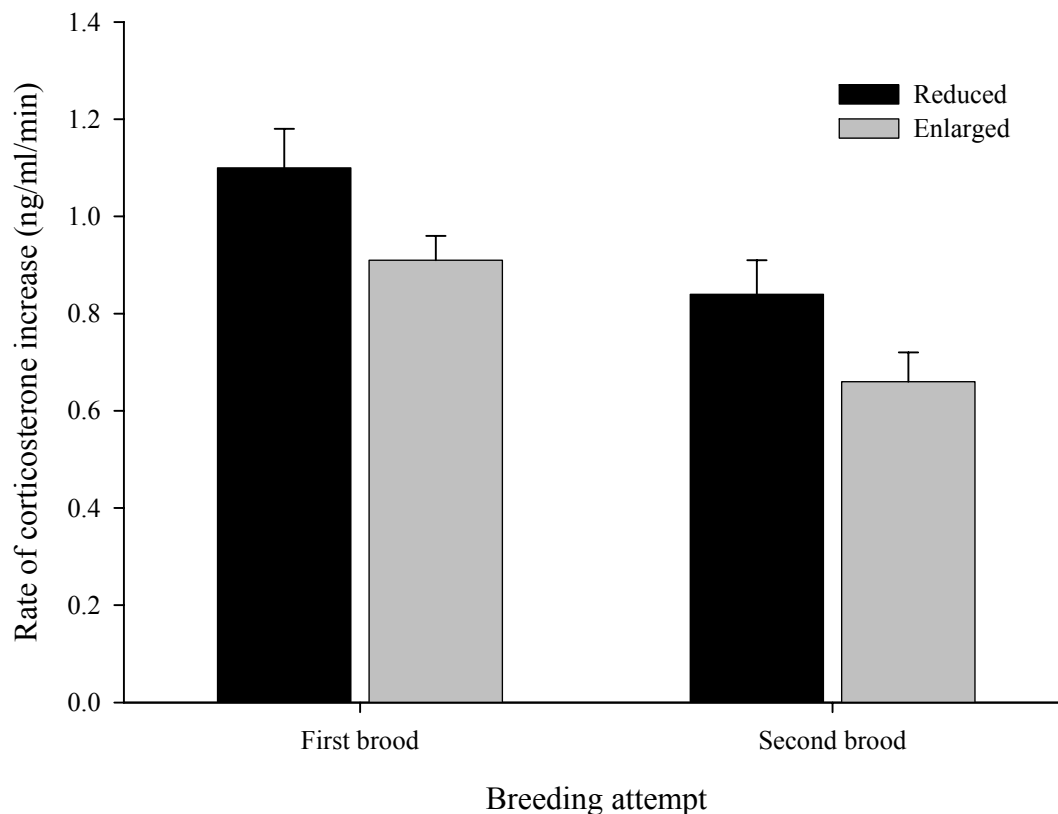
Figure VII.4. Rate of corticosterone increase in function of the brood size manipulation in the (a) first and in the (b) second breeding attempt.

We found no interaction between the brood size manipulation and the season in either breeding attempt (first breeding attempt, $F_{1,28} = 0.727$, $p = 0.401$; second breeding attempt, $F_{1,19} = 0.809$, $p = 0.380$).

Within-individual Comparisons

We compared the stress response in the first and second breeding attempt for those individuals that were sampled in both occasions. We investigated whether the difference in

the stress response in the first and the second breeding attempt was related to the difference in the brood size manipulation that individuals received for their first and second brood. A general linear model with repeated measures showed that there was significant change in the stress response of individuals between their first and second breeding attempt ($F_{1,12} = 12.692$, $p = 0.004$), and this change was related to the differences in manipulation ($F_{2,12} = 9.318$, $p = 0.004$; Figure VII.5).
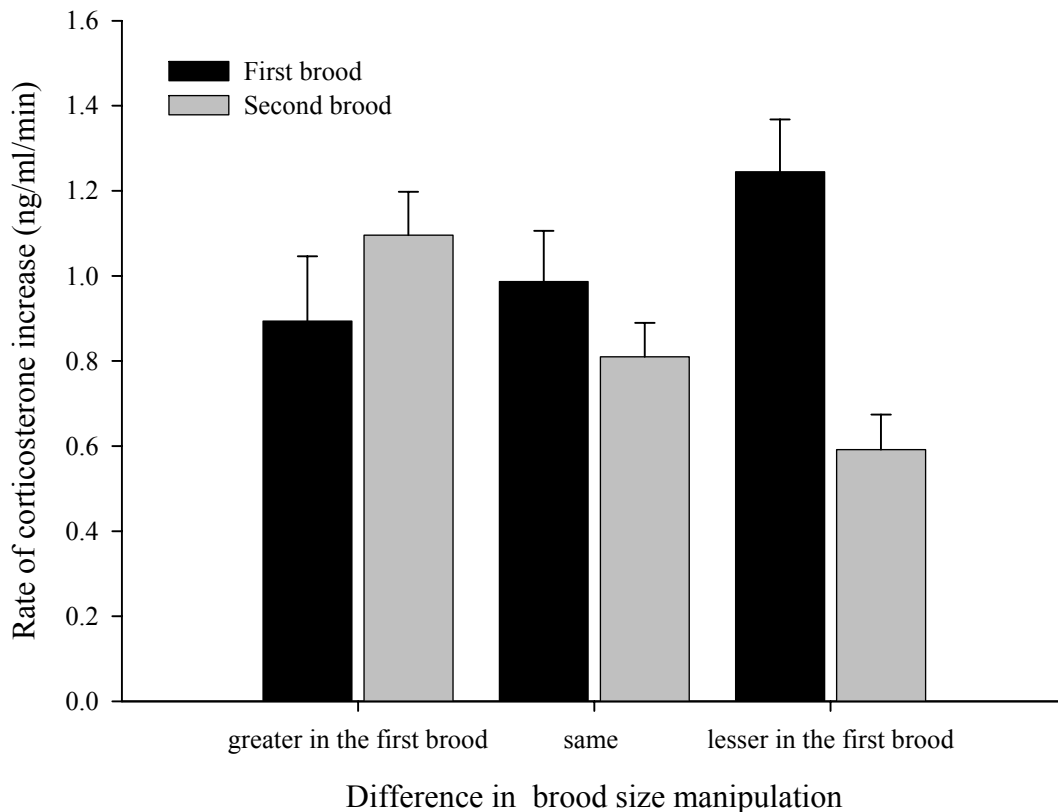
Figure VII.5. Within-individual comparisons of the adrenocortical response to stress as a function of the difference between the brood size manipulations received in the first and in the second breeding attempt. The parental effort induced by the manipulation was either (1) 'greater in the first brood' (on the left side of the figure) if the first brood was enlarged and the second was either unmanipulated or reduced; (2) 'same' (in the middle of the figure) if the individual either received the same type of manipulation or were left unmanipulated in both breeding attempts; (3) 'lesser in the first brood' (on the right side of the figure) if the first brood was reduced and the second was either unmanipulated or enlarged.

In this model we also controlled for the date of the first breeding ($F_{1,12} = 1.518$, $p = 0.214$) and the number of days elapsed between the two captures ($F_{1,12} = 0.219$, $p = 0.648$).

Comparison of Early and Late Breeders

To distinguish between seasonal effects and the individual differences in the adrenocortical response to stress, we compared the stress response of the early breeders tending their second brood and the late breeders tending their first brood, in the same time span.

Table VII.1. Comparison of the stress response of individuals reproducing for the first or for the second time in 2005 over the same time span. The table shows the results of a GLM model with the rate of corticosterone increase (ng/ml/min) as dependent variable. Significant effects are shown in bold.

Source of variation	$F_{1,16}$	p
Season	**5.245**	**0.036**
Manipulation	**5.784**	**0.029**
Breeding attempt	0.026	0.874
Breeding attempt * manipulation	0.011	0.919
Breeding attempt * date of capture	**4.808**	**0.043**

During this limited time span, the effects of season and manipulation on the response to stress were still significant (Table VII.1). The magnitude of stress response did not differ between early and late breeders; however, it decreased over the season in the late breeders while it increased slightly in early breeders resulting in a significant interaction between breeding attempt and the date of capture (Table VII.1, Figure VII.6).

Return to the Nest

In the first breeding attempt, individuals with higher response to stress returned sooner to their nest than birds with lower stress response ($r = -0.331$, $p = 0.039$, $N = 39$). Accordingly, the manipulation affected the return rate inversely as was found in the stress response: individuals with reduced broods returned sooner to their nest than individuals tending enlarged broods, although seasonal effects on return time were not significant (season: $F_{1,29} = 2.312$, $p = 0.140$, manipulation: $F_{1,29} = 4.485$, $p = 0.044$). Nevertheless, in the second breeding attempt, the rate of corticosterone increase was unrelated to the return time ($r = -0.213$, $p = 0.242$, $N = 32$), and the return time was also unaffected by the season and the manipulation (season: $F_{1,21} = 0.007$, $p = 0.933$, manipulation: $F_{1,21} = 0.762$, $p = 0.323$).
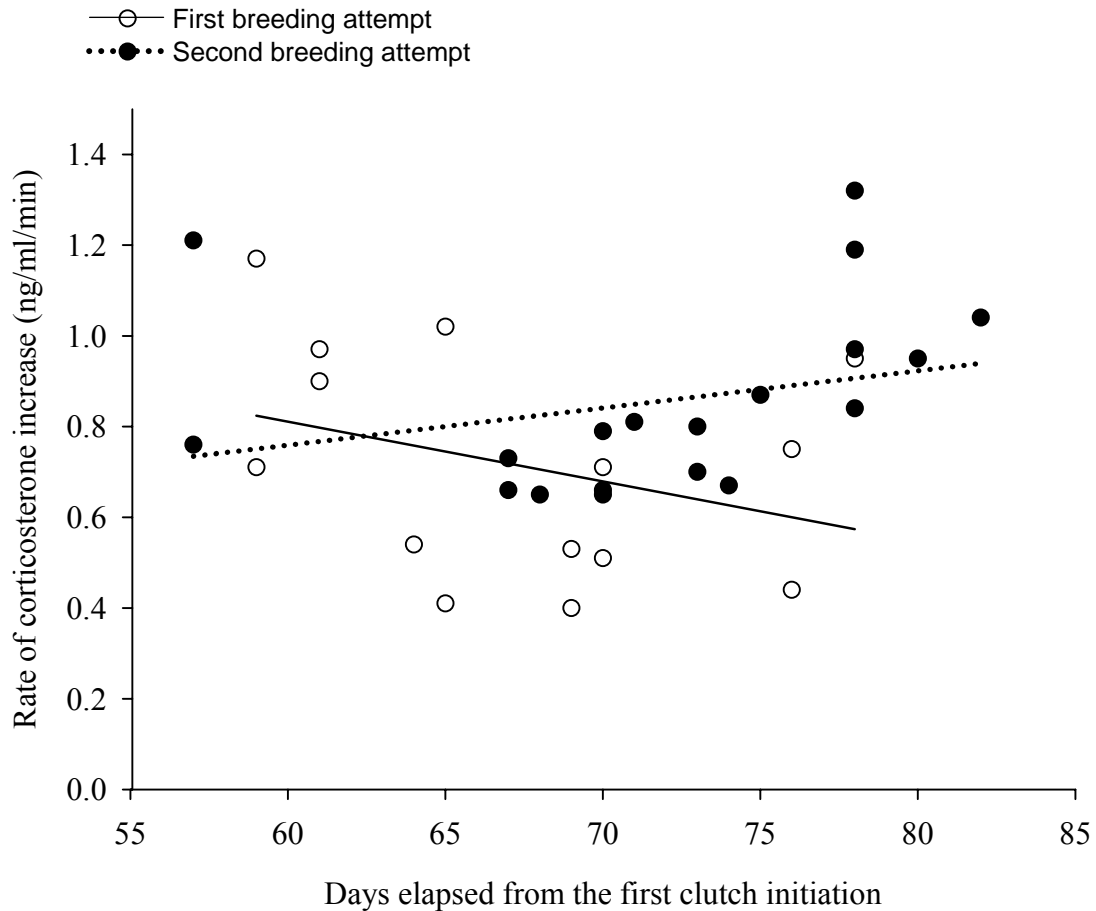
Figure VII.6. Comparison of the adrenocortical response to stress between individuals reproducing for the first or for the second time in 2005 during the time span when they breed simultaneously. The stress response is expressed as the rate of corticosterone increase.

DISCUSSION

In this study we investigated two major hypotheses that have been proposed to explain the adaptive value of the variation in the adrenocortical response to stress.

We experimentally tested the hypothesis that the extent of parental investment is inversely related to the hormonal response to stress, we got that the strength of the rise in plasma concentrations of corticosterone in response to acute stress is lower in individuals investing more in their current offspring than in individuals with less parental investment (Wingfield *et al.* 1995, O'Reilly & Wingfield 2001). To the best of our knowledge this study is the first experimental test of this hypothesis. Moreover, an essential, yet untested underlining assumption of the hypotheses on the adaptive stress responses is that individuals are able to flexibly 'modulate' their hormonal response to stress in function of the environmental, ecological conditions. Our results lend robust support for the parental care

hypothesis and also corroborate the assumption that the same individuals may react with different physiological response to stress according to the actual costs and benefits of their reproductive decision.

First, we found that in both breeding attempts, birds tending enlarged broods raised their circulating corticosterone levels to a smaller degree than those that tended reduced broods. Second, we found that individuals responded in different way to a standardized stress protocol in their two consecutive breeding attempts; and the difference was explained by the different types of manipulation they received. In short, the rise in corticosterone was weaker in that breeding attempt when their parental effort was experimentally increased compared with the other breeding attempt.

It is also remarkable that within the individuals there was a significant effect of the breeding attempts: the stress response was weaker in the second attempt than in the first one. Two main reasons may account for these results. First, one may argue that the sparrows habituated to some degree to the capture stress and therefore showed weaker physiological response to stress in the second breeding attempt. This explanation is, however, unlikely because the stress response of the birds sampled for the first time in the second breeding attempt was not different from the birds sampled for the second time ($p = 0.595$ after controlling for the effects of season and the manipulation). Moreover, most birds were captured and sometimes recaptured before the onset of breeding. Although during the early captures, birds were not bled, they experienced similar capture and handling as during the stress protocol. A more likely explanation is based on the life-history theory and is in accord with the parental care hypothesis. Life history theory predicts that parental investment may be greater in the last brood than previous broods in the season, since the residual reproductive value of an individual decreases at the end of the current reproductive period because of the uncertainty to survive until the next breeding season. Our results seem to show an additive effect of the 'terminal investment' and the experimental manipulations; the within-individual difference in the stress response was the greatest if the birds had the higher workload in the second attempt.

The second hypotheses proposes that along with the decreasing probability for renesting in the breeding season, individuals are expected to down-regulate their adrenocortical response to stress, in order to reduce the chance of nest abandonment, and thus to avoid a complete reproductive failure, i.e. the loss of their young. In accordance with this idea, we found that among birds tending their first brood, individuals in the beginning of the reproductive season showed higher response to capture and handling stress than individuals

later in the season. Were these late breeding birds really constrained by time? We found that about half of the individuals had only one breeding attempt; moreover, the probability of starting a second clutch was significantly greater for individuals that began the reproduction early. Accordingly, it seems that the convenient circumstances for breeding are limited indeed for some individuals, and by giving up too easily their young, these individuals would risk of producing no offspring in a given year. Missing a year of reproduction may have serious fitness consequences for a short-lived animal, such as the house sparrow. In this species, with a modal life span of two years, the most important component determining the lifetime reproductive success is the number of successful broods produced per year (Jensen *et al.* 2004). Long lived species, on the other hand, are often found to maintain robust stress responses during breeding, probably to ensure the opportunity for future reproduction (Chastel *et al.* 2005).

Contrary to the first breeding attempt, birds tending their second brood showed similar corticosterone response to stress, irrespective to the date of laying. Although the probability of laying a third clutch was also related to the date of the second breeding attempt, only a low proportion (15 %) of these birds started a new clutch, hence the individual differences in the future breeding opportunities may be smaller in the second breeding attempt compared with the first breeding. Moreover, the third clutch is generally less productive than the second one (e.g. McGillivray 1983). According to the latter two arguments, individuals may base their reproductive decisions on the value of the second brood, rather than the possibilities of future breeding and therefore the timing of breeding may have less influence on the response to stress in the second brood than in the first one.

We also found similar seasonal patterns in the basal corticosterone levels: it decreased with the date in the first breeding attempt, whereas it was unrelated to the date in the second breeding attempt. These results might be interpreted as part of an intrinsic seasonal change in both the baseline hormone levels and the endocrine responsiveness to stress, which would be steeper at the beginning of the reproductive season. In fact, several endocrine, metabolic or neural processes undergo changes during the annual cycle (Nelson *et al.* 2002). For example, in the house sparrow, corticosterone levels, plasma concentrations of corticosteroid binding globulin (CBG) and corticosteroid receptors in the brain changed between different periods of the year resulting together a more pronounced corticosterone response to stress in the nesting than in the post-breeding period (Breuner & Orchinik 2001). To separate the effects of the season *per se* (i.e. some environmental variable acting as a common stimulus on the physiology of the birds, such as the day length, ambient temperature, etc.) and the individual

differences in the hormonal response to stress, we compared the stress response of the early breeders tending their second brood and the late breeders tending their first brood, in a time span when their breeding activity overlapped. The seasonal pattern of the stress response differed significantly between the two breeding attempts. This result supports further the idea that the responsiveness to the stressors depends not only on the environmental factors, but also on the individual differences, for instance in the recent breeding history or the prospects for renesting.

Another attribute which is often associated with the timing of the reproduction is the 'quality' of the individuals. High quality individuals are thought to breed early (e.g. Cobley *et al.* 1998, Chastel *et al.* 2003, Ardia 2005) and individuals of high quality may be better able to mount an intensive stress response. Since a major function of glucocorticoids is to mobilize energy resources in homeostatic perturbations (Wingfield & Sapolsky 2003), individuals of high quality might be better able to cope with energetically challenging situations. Most interestingly, the corticosterone response to stress was negatively related to the time the birds took to return to their nest in the first breeding attempt. Hence, early breeding individuals, potentially of high quality may bear the costs of an elevated hormonal response, but they also may have the capacity either to clear or resist to the effects of corticosterone. To separate the effects of individual quality and the effects of short season, more sophisticated experimental designs are required involving the manipulations of the renesting probability in the population.

Chapter VIII.   Conclusions

DO HOUSE SPARROWS MAKE STATE-DEPENDENT FORAGING DECISIONS?

Two theoretical keystones of the evolutionary approach to the study of behaviour are that animals individually optimise their behaviour and that the internal state plays a pivotal role in the process of individual optimisation. Based on this idea, theoretical models have recently investigated various fields of animal behaviour and produced testable predictions about the expected behavioural choices of animals. My first aim in this Thesis was to experimentally test the realism one of these mathematical models in a biologically reasonable situation. In *Chapter III*, I tested an important prediction and one main assumption of the model of Barta & Giraldeau (2000). I showed that individuals with experimentally lowered energy reserves scrounge more and that scrounging is a risk-averse tactic. These results are consistent with both the assumption of many models of social foraging (i.e. that scrounging is a risk-averse tactic; Caraco & Giraldeau 1991, Barta and Giraldeau 2000, Giraldeau & Caraco 2000), and the prediction of the state-dependent dynamic model of Barta & Giraldeau (2000). These results demonstrate that the effects predicted by the model are detectable in a real social system. Recent empirical studies have shown that solitary individuals may make state-dependent decisions e.g. about reproductive effort (Spencer & Bryant 2001), singing behaviour (Thomas 1999, Thomas & Cuthill 2002), nest site selection (Bilde *et al.* 2002). My results extend our knowledge towards the social systems.

One may reason however, that evidence for state-dependent behaviour and our results makes intuitive sense. It has been long known that hungry animals are often more motivated and more aggressive than satiated ones (e.g. Gardner 1964, Hazlet *et al.* 1975, Andersson & Åhlund 1991). Although this is a widely accepted notion, we poorly understand the biological basis of this paradoxical behaviour (i.e. using the energy-consuming aggression in a bad state). Most often, the reasoning to explain this phenomenon is that the value of a resource is more valuable for a hungry animal (Enquist & Leimar 1987). However, the results of *Chapter III* demonstrate that mainly by using aggression, house sparrows could increase their use of scrounging; and scrounging has lower variance in food intake, i.e. it is a risk-averse tactic which is advantageous for individuals with low reserves. This link could have hardly been suggested by intuition. State-dependent models of behaviour provide a firm

mathematical background to the analysis of behaviour, and experimental tests of such models may contribute to a better understanding of many biological phenomena.

Chapter III and *Chapter IV* evoke that the risk of starvation plays an important role in the foraging decisions of animals. The risk of starvation is a genuine danger for wild animals, though it is not likely that the sparrows in our experiments faced a real threat of immediate starvation, since they were all agile and active, and did not show any indication of being literally about to starve to death. These results suggest that animals may be very sensitive to even minor risks of starvation. Clinical studies have shown that prolonged food deprivation may cause irreversible damage in the organisms which may later be lethal (e.g. Rodríguez *et al.* 2005). In a state-dependent context, animals are expected to avoid this critical level of energy reserves, even if it does not trigger the immediate death of the organism, as simplified by the zero energetic level used in the mathematical models. The important message here is that being close to a critical level of internal state influence the behaviour of animals as suggested by the theoretical models.

During aggressive scrounging, animals may have also to cope with another risk, namely the risk of injuries. Recently, a state-dependent model was proposed to analyse social foraging behaviour of common cranes (*Grus grus*) in a dominance based system, where both the risk of injuries and the food intake rate was considered (Stillman *et al.* 2002). The authors suggested that animals minimize their risk of injury when feeding conditions are good, but maximize their intake rate when feeding conditions are poor, even though this may increase their chances of injury. Their model assume that 'as fighting is more risky than searching independently, searching for food and avoiding competitors are the default behaviours. This means that at the start of simulations all animals avoid dominant competitors and do not fight, and resort to fighting only if their intake rate is below the target' (Stillman *et al.* 2002). Since the actual risk of injuries are unknown for the house sparrows, I can only speculate about its effects. The view outlined by Stillman *et al.* seem to agree with my observations. I show in *Chapter III*, that individuals with lowered energy reserves prefer the low-variance option of food intake (i.e. scrounging), although the food reward (i.e. the intake rate) was similar in both experimental groups. This result suggest that only on the basis of food intake rate and its variance, the scrounging option may be favourable for all members of a foraging group. Beyond the frequency-dependence of scrounging (Figure I.1), the risk of injuries and the loss of feeding time due to the aggressive interactions may be another plausible cost which prevents the very frequent use of scrounging of all foragers in the group. Probably the risk of injury is related to the fighting ability (i.e. dominance rank), therefore the costs of scrounging

for dominant individuals are smaller than for other flock members. As a result, dominant may use scrounging very often, and according to the assumptions of Stillman *et al.* (2002), few birds may challenge them. *Chapter IV* is in agreement with this idea, because dominants used scrounging very frequently, and the dominants with experimentally lowered energy reserves used scrounging even more, probably at the cost of increased risk of injuries. In this view, scrounging is a risk-averse tactic in terms of food intake variance, but is a risk-prone tactic in the terms of injuries (at least in when associated with aggression) and individuals should balance between the costs and benefits associated with scrounging. Future models should incorporate the effects of both starvation and possible injuries, while empirical studies should measure the energetic costs of fighting.

IS THERE MEASURABLE FITNESS CONSEQUENCES OF THE STATE OF FLIGHT FEATHERS IN THE HOUSE SPARROW?

In *Chapter V*, I showed that at least one component of the quality (i.e. the state) of the primary flight feathers affects survival probabilities in the house sparrow: individuals with a thicker rachis survived better until the next fall than those with a thinner rachis. Since I investigated only the relationship between the state variable and its ultimate consequences in terms of survival, I cannot identify what were the causal link between the feather quality and survival. But the mere fact, that this relationship does exist, provides evidence that the actual value of state variables have an aftermath on fitness. The effects of the feather quality on the behaviour and the survival may be straight. For example, the feather quality may determine the flight performance, which may have a direct repercussion on the survival through the predation. However, according to the recent theoretical models (Barta *et al.* 2006), this pathway may be more complex: as the quality of flight feathers alters the energy expenditure of the birds, the quality of their feathers may also influence the energy allocation, e.g. the energy allocated to reproduction, which, in turn may have survival consequences. The important message is that state may alter behavioural actions of an individual, and natural selection may act on these behavioural actions.

DO HOUSE SPARROWS BEAR MULTIPLE STATUS SIGNALS?

In *Chapter III*, I suggested that in particular situations, individuals should scrutinize the state of their companions (e.g. their body condition) in order to forecast their expected behaviour.

In *Chapter VI* however, I investigated a situation, where individuals actively advertise their state, namely their dominance status. Dominance status is the outcome of repeated pairwise interactions, and thus reflects the overall ability of an individual to acquire and defend resources. To acquire and defend, however, does not necessarily demand the same skills, and motivational state may differentially affect these behaviours. In *Chapter VI,* I showed that house sparrows possess multiple correlates of dominance status: the size of their bib is related to overall fighting ability, whereas the conspicuousness of wingbars is related to success in defence, and these two morphological traits are not correlated. These results are consistent with the 'multiple messages' hypothesis of multiple ornaments theory (Møller & Pomiankowski 1993; Johnstone 1997, reviewed by Candolin 2003), which was proposed in the context of mate selection, but it can be also applied to status signalling. The hypothesis suggests that different signals have evolved because they convey information about different and specific aspects of the quality of the partner (here the opponent). For example, in the greenfinch (*Carduelis chloris*), the brightness of yellow wing patches reflects age, whereas yellow tail patches reflect the ability to resist parasites (Lindström & Lundström 2000). In the context of aggressive behaviour, the ability to defend already obtained resources may be a specific component of competitive ability, and wingbars may be used to signal this information. The sparrows can control the visibility of their wingbars on a wide scale: they may even hide them by their cover feathers or they may actively flash them in the wing displays, whereas there are much smaller variation in the visibility of the bib. As noted in *Chapter VI*, this suggests that wingbars are exposed when birds are highly motivated to defend their resources but not displayed when birds are not willing to engage in an escalated fight. As we have seen in the previous section, motivation may be state-dependent and therefore may vary in short-term scales. By regulating the visibility of the wingbars individuals may signal their actual level of motivation. On the other hand, bib size may give information about the overall dominance status, which is a more permanent state of an individual.

HOW DOES PHYSIOLOGICAL STATE CHANGE IN RESPONSE TO AN ENVIRONMENTAL STIMULUS?

Hormones play an important role in decision making. In *Chapter VII*, I demonstrated that individuals may actively control their hormonal levels. Furthermore, I showed that this control is affected by both the value of their offspring (i.e. the number of chicks) and the

future reproductive opportunities (i.e. the timing of breeding). These results are in agreement with two main hypotheses, which proposes that the modulation of hormone levels can be seen as a strategy to maximise individual fitness (Jessop 2001). The latter view of the modulation of hormone levels assumes that the behavioural decisions are mediated by somehow fixed levels of hormones, and these hormone levels should be individually 'manipulated' in order to take into account the actual costs and benefits associated with a trade-off decision. Evidence is also accumulating for complex manipulation of this system, in which not only the hormone levels, but the responsiveness of the organism is also individually modulated, for instance in the European starling, the corticosterone levels and the concentrations of corticosteroid binding globulin interacted to reduce the risk of a corticosterone induced nest abandonment (Love *et al.* 2004). These studies, taken together with my results in *Chapter VII*, reinforces that complex hormone-behaviour interactions are actively and adaptively modulated at the individual level, and hormone levels are not just passively changing in response to seasonal and other ecological factors.

CONCLUDING REMARKS & FUTURE DIRECTIONS

The results of this Thesis reinforced the importance of the individual differences in the study of animal behaviour. These individual differences may be formalized by the definition of state variables and the analysis of their effects on behavioural decisions. Results in *Chapter III* supported the theoretical underpinning of the state-dependent models, namely that state is a critical component in behavioural strategies. *Chapter IV* is ahead of the theory: this is one of the first empirical studies investigating the interaction between different state variables, and currently there is no model of producer-scrounger use which deals with both dominance effects and energy reserves. The results in *Chapter IV* indicate that dominance status may alter the state-dependent decisions, moreover, it may also induce the use of different strategies, i.e. individuals of different dominance status may have to rely on different mechanisms to cope with an energetically challenging situation. *Chapter VI* showed that individuals may potentially use plumage patterns to actively advertise their current state, e.g. their motivation. In fact, during social foraging, individuals use visual displays, such as wing displays to drive out others from a food patch or to hold off those attempting to attack the owner of the resource. Future studies may elucidate the role of aggressive displays in social foraging behaviour.

A recent challenge in behavioural ecology is to understand the mechanistic background of behaviour. Many behavioural, physiological and morphological reactions to external stimuli are mediated by hormones. The perception and the hormonal response to these environmental stimuli also strongly depend on the state of the organism. *Chapter VII* demonstrates the interaction of different ecological factors on the hormonal response to stressful situations. In *Chapter III & IV* we have seen how energetically stressful situations may affect social decisions. Almost nothing is known about the physiological side of these social decisions. Using direct hormonal manipulations, we can mimic the internal representation of an environmental stressor without the stressor itself, and thus we can investigate whether there are causal relationships between hormones and social decisions. By manipulating hormone levels, the perception of an individual about its own state may be temporarily changed and we can study the behavioural consequences of the physiological changes ('phenotypic engineering'; Ketterson & Nolan 1999).

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Summary

The investigation of individual differences is essential to understand animal behaviour. Several behavioural phenomena can only be understood by the analysis of these individual differences. These differences can be defined by using a set of state variables. Recent theoretical models have suggested that these variables play an important role in animals behavioural decisions, but the empirical evidence for these models are scanty. In this Thesis I investigated state-dependent behaviour in the house sparrow (*Passer domesticus*).

In a laboratory experiment (*Chapter III*), I demonstrated that individuals of group foraging house sparrows make state-dependent decisions, as predicted by a dynamic game theoretical model. Individuals with experimentally lowered energy reserves used scrounging (exploiting others' food findings) more. In a second laboratory experiment (*Chapter IV*), I studied how these state-dependent foraging decisions are modulated by another state variable, the dominance status. I found that dominant individuals increased their use of scrounging in response to the experimental manipulations, whereas the foraging behaviour of subordinate sparrows was unaltered by the manipulations. The latter result suggest that individuals of different dominance status respond differently to an energetically challenging situation.

In *Chapter V*, I studied the survival consequences of the state of the flight feathers. I found that individuals with high quality feathers survived better during the study period.

In *Chapter VI*, I investigated different aspects of fighting behaviour and two presumed plumage signal of dominance status. I found that the black throat patch of males was related to their overall fighting success, whereas the conspicuousness of the wingbars was related to their defence success. These results suggest that male sparrows may use multiple cues in assessing the competitive ability of opponents during social interactions.

In *Chapter VII*, I examined the individual differences in the physiological response to stress. I found that individuals tending an experimentally increased brood showed weaker stress response in terms of corticosterone increase than individuals tending experimentally reduced broods. I also found, that renesting probabilities also affected the stress response; individuals with low chances to renest increased their corticosterone levels less than those with better renesting chances. These results suggest that individuals may actively modulate their hormone levels to maximise their fitness.

Taken together, this Thesis supports the biological realism of the theoretical framework proposed to analyse animals' behavioural decisions based on their state. However, the advance of the current models, and further empirical tests are needed to a better understanding of several biological phenomena.

Összefoglaló

Az egyedek közötti különbségek vizsgálata elengedhetetlen az állati viselkedés tanulmányozásához. Számos viselkedési jelenség csak ezen egyedi különbségek elemzésével érthető meg. Ezeket a különbségeket egy sor állapotváltozóval határozhatjuk meg. Bár a közelmúltban megjelent elméleti modellek azt jósolják, hogy az állapotváltozók jelentős szerepet játszhatnak az állatok viselkedési döntéseiben, e modellek empirikus tesztelése alig kezdődött meg. A jelen értekezésben házi verebek (*Passer domesticus*) tanulmányozásával vizsgálom az állapotfüggő viselkedési döntéseket.

Egy laboratóriumi kísérletben (III. Fejezet) kimutattam, hogy a csapatosan táplálkozó házi verebek állapotfüggő döntéseket hoznak, ami összhangban áll egy dinamikus játékelméleti modell egyik fő predikciójával. A kísérletesen csökkentett energia-tartalékkal rendelkező egyedek gyakrabban potyáztak, azaz használták ki a mások által talált táplálékforrásokat. Egy második kísérletben (IV. Fejezet) azt vizsgáltam, hogy a fenti állapotfüggő táplálkozási döntéseket hogyan módosítja egy másik állapotváltozó, a dominancia rang. Ez utóbbi kísérlet megmutatta, hogy a domináns egyedek a kísérletes kezelés hatására gyakrabban potyáztak, míg a szubordináns egyedek viselkedése a manipuláció hatására nem változott szignifikáns mértékben. Ez az eredmény arra enged következtetni, hogy a különböző dominancia rangú egyedek eltérően reagálnak az energetikai szempontból megterhelő helyzetekre.

Az V. fejezetben a szárnytollak (elsőrendű evezőtollak) minőségének túlélésre gyakorolt hatását vizsgáltam. Az elemzések azt mutatták, hogy a jobb minőségű tollakkal rendelkező egyedek nagyobb valószínűséggel élték túl a vizsgálati időszakot.

A VI. Fejezetben az agresszív viselkedés különböző aspektusai és két feltételezett tollazati szignál közötti összefüggést vizsgáltam. A hímek fekete torokfoltja kapcsolatban állt a teljes verekedési sikerrel, míg szárnycsíkjuk feltűnősége a védekezési sikerrel korrelált. Ezek az eredmények azt sugallják, hogy a hím verebek többszörös jelzéseket használhatnak az ellenfelek küzdelmi képességeinek felmérésekor.

A VII. fejezetben a stresszre adott fiziológiás válasz egyedi változatosságát vizsgáltam. Azt találtam, hogy azok az egyedek, amelyek kísérletesen megnövelt fészekaljat neveltek, alacsonyabb stresszválaszt mutattak (kisebb mértékben növelték kortikoszteron szintjüket), mint a csökkentett fészekaljat nevelő egyedek. Másrészt, az újrafészkelés valószínűsége szintén befolyásolta a stresszválaszt: kisebb mértékben növelték kortikoszteron szintjüket azok az egyedek, amelyek újbóli fészkelésére az esély kicsi volt, mint azok, amelyek az ismételt fészkelésre jobb eséllyel bírtak. Ezek

az eredmények azt mutatják, hogy az egyedek rátermettségük maximalizálása érdekében aktívan módosíthatják hormonszintjüket.

Összegezve, a jelen értekezés támogatja annak az elméleti koncepciónak a biológiai realitását, amely az egyedek állapotának vizsgálatát előtérbe helyezi az állatok viselkedési döntéseinek tanulmányozásakor. Mindazonáltal a jelenlegi modellek fejlesztése, valamint további empirikus tesztek szükségesek ahhoz, hogy számos biológiai jelenséget jobban megértsünk.

Appendices

Appendix 1. Observation site for colour ringed sparrows near a barn in the horse-training farm, Dunakeszi, Hungary. Most sparrows bred beneath the roof and some of them in the nest boxes attached to the wall. Although the site seems peaceful, sparrows were often attacked by predators coming from the surroundings, such as sparrowhawk (*Accipiter nisus*) and feral cats (*Felis catus*) – *Chapter V*.

Photo by Á.Z. Lendvai

Appendix 2. Illustration of the measurement of shaft (rachis) diameter and feather wear from photographs. Rachis diameter was measured along a line perpendicular to the axis of the rachis, feather wear was scored on an arbitrary scale. In the right-hand circle, the lower arrow shows an intact part of the feather edge, whereas the two other arrows indicate minor damages on the feather edge. Note the small gap in the first feather (from above) and the unbound outer web in the second feather. – *Chapter V.*
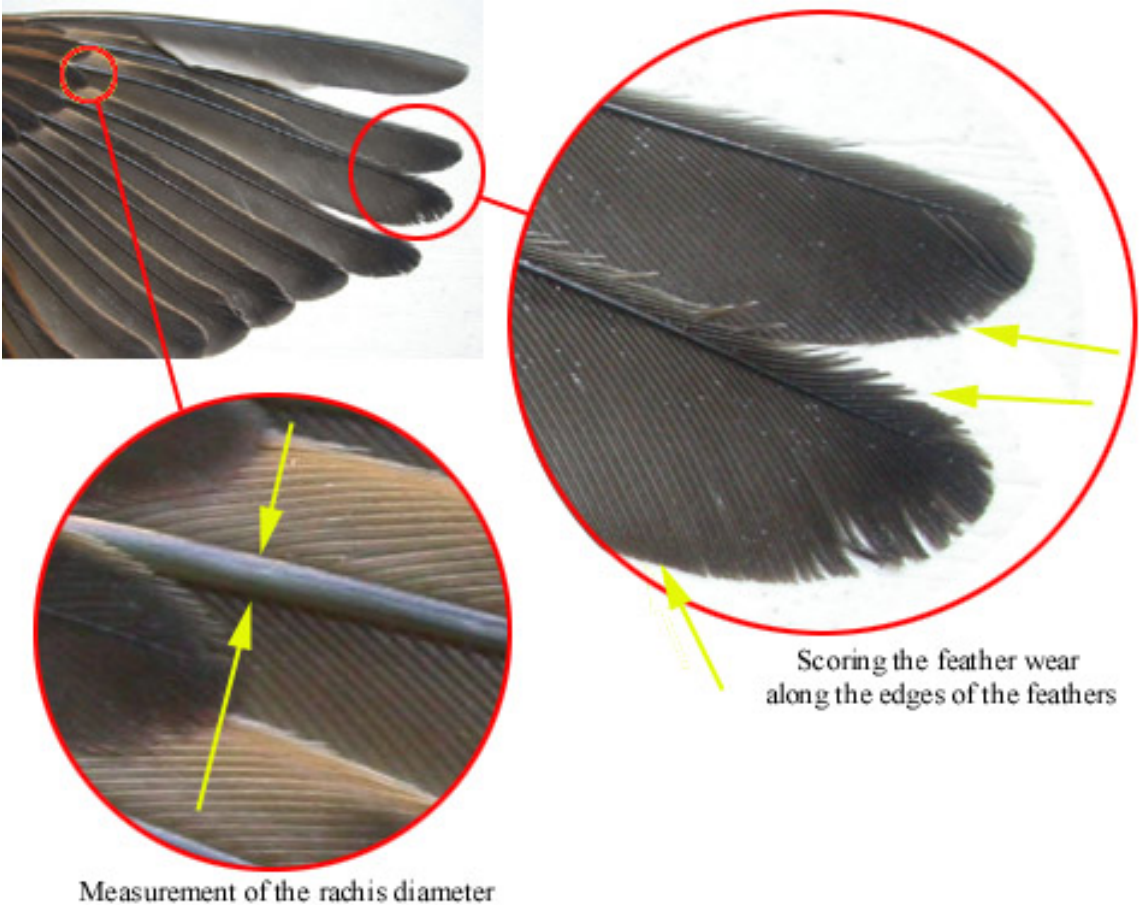

Scoring the feather wear
along the edges of the feathers

Measurement of the rachis diameter

Photo by Á.Z. Lendvai

Appendix 3. Wingbars and bibs in male house sparrows. Note the difference in colour between a conspicuous and a less conspicuous wingbar and the difference in size between a large and a small bib. – *Chapter VI.*

Conspicuous male wing bar

Less conspicuous male wing bar

Large bib

Small bib

Photos by V. Bókony

Appendix 4. Collecting blood sample from a male house sparrow in the laboratory, Chizé, Western France. Immediate bleeding after the capture was essential to measure baseline hormone levels. – *Chapter VII*.

Photo by M. Giraudeau

Appendix 5. Waiting for a sparrow's return to the nest following its release (Chizé, Western France). Although most birds resumed their breeding activity within two hours, some birds could take 5 h 40 min to return to their nest. – *Chapter VII.*

Photo by M. Giraudeau