COLONISATION D'UN ECOSYSTEME D'EAU DOUCE HETEROGENE PAR UN OISEAU D'EAU HERBIVORE : LE CYGNE TUBERCULE (CYGNUS OLOR) DANS LES ETANGS PISCICOLES DE DOMBES.

Guillaume Gayet

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SCIENCES ET TECHNIQUES DU LANGUEDOC

THESE

pour obtenir le grade de

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Discipline *:* Biologie de l'évolution et écologie

Ecole Doctorale *:* Systèmes Intégrés en Biologie, Agronomie, Géosciences, Hydrosciences, Environnement

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INTRODUCTION

I. Ecosystem dynamics.

Ecosystems are coherent networks where species interact under specific physical and chemical constraints. Animal and plant community structure not only depends upon intrinsic interspecific relationships, but also upon external, abiotic factors, that they can also influence. One main factor responsible for ecosystem temporal dynamics is how new species colonize them. The consequences of such colonization events can be observed at various spatial and temporal scales, as well as at several structural levels (population, community, ecosystem).

1. Disturbance and relative ecosystem equilibrium.

At time t, plant and animal community structures show some consistency. **An ecosystem is considered as being stable if changes over time are few** (« equilibrium stability »), **and if it quickly recovers to initial state after disturbance** (« equilibrium resilience ») (McCann 2000). In response to external factors, even stable ecosystems nonetheless change over time, generally in a slow and gradual manner (Scheffer *et al.* 2001), following successions that eventually lead to a stable community, or climax state (Krebs 2001).

Plant and animal communities therefore are not frozen. Indeed, their two main features are to be dynamic systems and to form heterogeneous systems in space (Sousa 1984). At time t+1, a given ecosystem therefore no longer shows the same structure, even without external agents being at play. An external factor, taking the form of a disturbance, may also have affected the system dynamics, in a more pronounced yet punctual way (Pickett *et al.* 1989).

Disturbance events that partially affect ecosystem dynamics differ very much in their nature (water stress, herbivory, nutrient input …), their intensity, as well as in the scale at which they cause changes. Such disturbance sources may be at the onset of deep community structure changes. They cause species fluxes within ecosystems (e.g. Glenn & Collins 1992 ; Frenot *et al.* 2001), especially so when disturbances are of large magnitude (see Platt & Connell 2003). For example forest fires, decreases in herbivore density in grasslands or water regime management in wetlands can all cause drastic changes within plant communities (Scheffer *et al.* 2001). Species immigration and emigration are among the factors that may enhance such dynamics, as they can both cause or follow disturbance events (Strayer *et al.* 2006).

It is of paramount importance to clearly define the spatial and temporal scales at which changes in ecosystem structure are being observed. Indeed, species colonize habitats and disappear from these at highly variable time scales. A volcano eruption is such a disturbance that most organisms disappear in a few hours (Del Moral & Grishin 1999). At the scale of years, because of global climate warming, Hickling *et al.* (2006) have shown that many UK species now use habitats several tens of kilometers further north and at higher altitude than they did previously.

Depending on the rate at which disturbance occurs and the spatial scale in concern, changes that follow such events may differ considerably (see Romme *et al.* 1998). They can also occur over short spatial and temporal scales in natural environments. In a minute the banks of a river can collapse and create pioneer habitat over a few meters, or a river bed can get obstructed within a few days by beaver *Castor fiber*, which creates favorable new habitats to some wildfowl species like Teal *Anas crecca* upstream (Nummi & Pöysä 1997).

2. Colonization as a major ecosystem disturbance.

Arrival of a foreign species within a given ecosystem is a form of disturbance. This can originate from spontaneous colonization by individuals experiencing favorable environmental conditions, or be due to man introducing individuals beyond the boundaries of their natural habitat range. Global warming hence recently allowed many species colonizing new areas: red fox *Vulpes vulpes* habitat range moved Northwards in Canada, for example (see Walther *et al.* 2002). Introduction by man of a few ruddy ducks *Oxyura jamaicensis* from America lead to the species now being relatively widespread in western Europe (Munoz-Fuentes *et al.* 2006a).

a. The scale at which changes occur.

i. Geographical range.

Depending on whether a species initiates, follows, or is affected by a disturbance event, the observed changes can reach scales up to its geographical range. Indeed, a species geographical range is not a fixed trait, and range contractions and expansions are natural components of animal and plant communities, even if they are sometimes being accelerated by human activity (Lodge 1993). **Changes in geographical range depend upon tight relationships between species-specific factors** (e.g. dispersal rate) **and environmental**

factors (those that limit the distribution of species over time and space, especially) (Brown *et al.* 1996). In North America, range contraction, expansion or stability among ungulates and carnivores following massive and recent arrival of man (Laliberte & Ripple 2004) provide good examples of how variable the response of a species to a given disturbance event can be.

Changes following colonization events can occur over very different scales depending on species dispersal modes. **Secular dispersal** occurs over geological times and is associated with evolutionary processes (e.g. following continent drift). **Diffusion** occurs over generations, so that geographical range then only changes slowly. Lastly, **jump dispersal** occurs over the short term, over areas that the species cannot occupy (Krebs 2001).

ii. Community.

Three stages are distinguished during a species colonization event (Moyle & Light 1996): **arrival** when the species is confronted to environmental resistance, **establishment** which depends upon demographic (extinction versus fertility rates) and biotic resistance of the species (competition, predation, parasitism and food availability), and **integration** following a successful colonization event and will result in a different community because of changes in behavior, niche and interactions among species. Once the population is established, individuals of a species can spread over space and potentially initiate a new colonization event (Hastings 1996).

Changes in interspecific relationships following the arrival of a new species can lead to a switch from an ecological succession to another within the ecosystem. New spaces get created in a given habitat, leading to changes in the composition of communities (Connell & Slatyer 1977). New species can then affect the whole ecosystem through trophic cascades (Pace *et al.* 1999). In a radical way, trout *Salmo trutta* introduction in New Zealand affected the whole aquatic community because of invertebrate consumption by these new fishes: primary production then considerably increased, leading to changes in algae community structure (Townsend 2003). When this is not associated with biological invasions, species can either disappear or remain within colonized ecosystems. In the later case, their populations then enter local communities. Sheatfish *Silurus glanis* hence apparently did not affect native freshwater fish after its introduction in European rivers, except when these were already threatened by human activity (Copp *et al.* 2009). Biological invasion therefore only is a very specific colonization type. Given the large number of covariates that can potentially let a population to decline, caution is required before attributing such declines to the simple arrival of new species (Didham *et al.* 2005).

Colonization of new habitats by a species is considered to be a **biological invasion** when removal of a geographic barrier or limiting biotic factor first allows the species to expand its geographical range, then colonize new habitats, with the new species becoming dominant over native species as the final stage of the process (Valéry *et al.* 2008). Even if invasion is most generally associated with dispersal of foreign species (Wilson *et al.* 2009a), native species can also be associated with biological invasions, especially when human activity may help these both expand their range and colonize new habitats (see Valéry *et al.* 2009). **Biological invasion can have a variety of consequences, some of which being difficult to detect**. In some cases, introduced species hybridize with native species, causing introgression. In Europe, ruddy duck and white-headed duck *Oxyura leucocephala* hybridize, to the point that genetic integrity of the later may be compromised (Munoz-Fuentes *et al.* 2006b). Some species can outcompete native ones, like *Ludwigia uruguayensis* does with European aquatic flora (see Dandelot *et al.* 2005). The ultimate consequence of invasion by a species is the extinction of native ones (Mooney & Cleland 2001). Through predation, rats *Rattus sp.* caused the extinction or the massive decrease of some island bird species (Towns *et al.* 2006 ; Ruffino *et al.* 2009).

It is not always easy today to distinguish the “natural” evolution of an ecosystem from the evolution caused by mankind, as both can co-occur and even interact with each other. **Indeed, human activity can help some pioneer species integrate native communities through environmental changes beneficial to non-native species** (“passenger species”, see MacDougall & Turkington 2005). Massive changes have been recorded in the distribution of wintering wildfowl in eastern Europe, being likely due to the creation of artificial waterbodies that do not freeze over in winter, combined with milder winters during the XXth century (Svazas *et al.* 2001). Further east, drainage of central Asia shallow lakes, combined with the creation of new waterbodies, helped Common Pochard *Aythya ferina* spreading from Eastern Europe over the last century (Cramp *et al.* 1986).

b. Colonization and modern biodiversity conservation issues.

At the end of the XXth century, apparition frequency of new species and the geographic scale at which such colonization occurred were apparently reaching a maximum never recorded in the past. This raises a number of questions relative to ecosystem conservation: wetlands are already profoundly affected by human activities; given their socio-economical as well as ecological roles, it is of crucial importance to assess the consequences of colonization of such systems by new species.

i. Large-scale outcomes.

Conservation of biodiversity requires protecting species as well as ecosystems. During the last century, colonization of new geographic areas by animal and plant species has been a major cause of biodiversity loss at the global scale (Chapin III *et al.* 2000). Among other factors (changes in land use practices, elevated atmospheric CO_2 concentration, climate change or acid rains) Osvaldo *et al.* (2000) consider species introduction as one main potential cause of future biodiversity changes for the coming century. This would lead to homogenization of native communities through genetic, taxonomical as well as functional alterations (Olden *et al.* 2004).

There is today such variability in the possible origin of colonization events that a **specific wording is now being used to qualify such evolutionary processes,** such as “native”, “feral” or “invasive” species… (see Falk-Petersen *et al.* 2006). That people want to associate a particular status to species is most often associated with the need to formalize policies for population management than to assess the role of that species in the ecosystem dynamic processes. Indeed, it is necessary to have knowledge about a species colonization mechanism and possible ultimate development stages to get it a status, yet such knowledge is most often lacking. Knowledge and analytical methods for the study of species distribution are often quite recent, so that caution is required when trying to understand such processes (Brown *et al.* 1996). It is necessary to improve knowledge about the mechanisms that follow species invasions if one wants to assess both their ecological and economical consequences (Lodge 1993). **One of the reasons that may explain the recent interest for such questions is the concomitance of biodiversity conservation issues, socio-economical issues and large-scale animal and plant population fluxes.** This lead to biodiversity monitoring and scientific expertise becoming a double aim since the end of the XXth century. Monitoring aims at providing a dynamic statement about natural heritage (e.g. which are the species that increase ?). On the other hand, scientific expertise aims at understanding interspecific relationships (e.g. does a species decrease because of another ?).

The way people consider colonization events is highly variable, and in most cases highly subjective. In some situations, colonization is considered as a **benefit to ecosystems**, i.e. new species become part of local richness and promote new habitats. Jaksic (1998) thus considers that rabbit *Oryctolagus cuniculus* and hare *Lepus europeaus* had a positive effect once introduced in Chile, as they became prey for local predators, hence reduced predation rate on native species. In Long Point Bay, Canada, introduction of Eurasian water milfoil *Myriophyllum spicatum* and zebra mussel *Dreissena polymorpha*, both considered as being invasive species, had a major effect on macrophyte beds. While *M. spicatum* tends to outcompete native species *D. polymorpha,* which was introduced later, limited *M. spicatum* expansion by filtering the water and reducing water turbidity that benefits this plant. Zebra mussel hence may have allowed partially protecting this ecosystem (Knapton & Petrie 1999). Conversely, if a species threatens what is considered to be the native communities, it will be considered as an **impoverishment factor**.

ii. Issues in wetlands.

Wetlands only cover 1.5 % of the earth area (Fustec & Lefeuvre 2000), so that **preserving wetland animal and plant communities is a worldwide ecological issue**. Indeed, in addition to allow development and maintenance of ecosystems (through the preservation of species restricted to these habitats), wetlands also serve various functions that are beneficial to human activity (Gren *et al.* 1994). Such ecosystems are therefore listed under several international treaties like the Ramsar convention (Secrétariat de la Convention de Ramsar 2006) or the « habitat » directive in the European Union (Directive Habitats – Appendix I). The main threats to such habitats are overexploitation of resources, changes in water regime, climate change, pollution, biological invasions and species extinctions (Brinson & Malvarez 2002). Species introduction has become a common feature in wetlands, leading to changes in community structure and ecosystem processes, with the risk of such aquatic communities gradually becoming more homogeneous (Lodge *et al.* 1998a). In order to develop the most appropriate conservation policies, it is necessary to precisely assess the relative contribution of each of the above threats to wetlands. Some of these can be relatively easily quantified while some others, such as those associated with new species arrival, are more difficult to measure and still require further research.

II. Colonization-induced processes.

An animal or plant community structure mostly depends on the ecological requirements of the species it contains. Eventually, such characteristics determine the spatio-temporal distribution of individuals as well as their interactions. Assessing the relationships between new species and the other biological components of their environment should help better understand the ecological processes that their presence induces.

1. Habitat selection.

There is no ecological system where the individual, population or community can be studied independently from its environment (Begon *et al.* 1990). **It is therefore necessary to understand individual behavior in space and time to assess how they interact with the other elements of the system.** Such studies require investigating habitat selection by these individuals, i.e. how they use a non-random set of habitats within a given space (Morris 2003).

Several theories are necessary to consider if one wants to understand such processes. Among these, **optimal foraging theory** predicts habitat use by foragers. This theory is based on two questions to be answered by the forager: which habitat unit should I use, and for how long ? (Schoener 1971 ; Charnov 1976). Such considerations allow foragers to rank habitat units after their relative profitability. The presence of large herbivores therefore not only depends on the properties of habitat patches they use, but also on the properties of the patches that remain unused (Searle *et al.* 2006). Such a selection process fluctuates over time; the comparison that foragers make depends on both the dynamics of the resources they use and on the rate and level at which these get depleted. Barnacle geese *Branta leucopsis* leave polders for salt marshes in the Netherlands exactly when the production of salt marshes get equivalent to that of polders (in terms of protein resources) at the onset of spring growth period (Prins & Ydenberg 1985). This is exactly what the marginal value theorem (see Charnov 1976) would predict. Similarly, depletion of algae beds and salt marsh vegetation by Brent Geese *Branta bernicla bernicla* in England can explain why they subsequently use cultivated grounds and grasslands (Vickery *et al.* 1995).

The marginal value theorem provides a first framework in which to consider how individual foragers take their decisions. However, Senft *et al.* (1987) recommend to go beyond this for large herbivores, and to **combine this theory with those associated with landscape ecology and hierarchical choices**. Indeed, landscapes should be considered as a whole rather than habitat units in isolation from each other if one wants to understand habitat use patterns by species using large areas (Naugle *et al.* 2001a). This requires more variables than just the resource and its possible depletion to be considered, such as the way habitat units are organized in space. Some passerines (White-crowned Sparrow *Zonotrichia leucophrys*, Vesper Sparrow *Pooecetes gramineus* and Brewer's Sparrow *Spizella breweri*) select mountain grasslands not only after their area but also their isolation within the landscape (Wilson *et al.* 2009b). In waterbird communities, the combined effect of these parameters is well known. Wetland size as well as isolation is for example known to affect richness (Brown & Dinsmore 1986) as well as presence and abundance of these birds (Fairbairn & Dinsmore 2001). Sebastian-Gonzalez *et al.* (2010) have demonstrated that size, connectivity and habitat quality of small reservoirs in southeastern Spain all affect waterbird habitat selection process, especially during the non-breeding period.

Depending on their ecological requirements, not all species are obviously sensible to these habitat size and isolation parameters (number of units, distance, size and derived indices, Wilson *et al.* 2009b). In addition to habitat heterogeneity, habitat selection processes are also affected by many factors depending on the **biology and requirements of the individuals**, such as age, sex, behavior (Manly *et al.* 2002) or life-history traits (Naugle *et al.* 2001b). The size of herbivorous waterbirds as well as their specific food requirements leads to differential selection of habitat units depending on food availability (Durant *et al.* 2004). Ducks can also change their foraging methods depending on food availability in the different habitat units and potential food depletion, so as to maximize their food intake (Guillemain *et al.* 2000).

The spatial distribution of individuals therefore reflects **the species adaptation to its environment** given its energy requirements, predation risk, competition and human-induced disturbance. The species is then absent from unfavorable habitat units (Hanski 1998). The way species alternatively select habitat units is associated with **invasion** (the species immigrates) **and extinction** (it emigrates or the individuals die) processes. The period between colonization and extinction corresponds to when the species is present in a given habitat (Tingley & Beissinger 2009).

Except in birds and some large mammals, **habitat selection processes remain relatively poorly studied** (Krebs 2001). Even if habitat selection studies have developed over the last decades (owing in particular to the improvement of statistical and spatial analytical tools), the interpretation of such work is still constraint by a number of factors. Depending on the scale at which a population is considered (individuals versus population) and the way habitat is described (used or unused versus available), statistical analyses (see Boyce *et al.* 2002, Keating & Cherry 2004) and their interpretation (Manly *et al.* 2002) are strongly limited. Despite some recent progress, waterbird habitat selection therefore still remains poorly understood. Because most of these species are migratory, most studies have been carried out on a part of the annual cycle only. Waterbird ecology thus remains almost unexplored during some seasons like spring, although it is recognized as a crucial period of the year for these birds (Arzel *et al.* 2006). The present studies do not provide a long-term understanding of waterbird spatio-temporal distribution, which would simultaneously consider changes in habitat properties as well as in species ecological requirements over time.

2. From coexistence to competition.

Spatial heterogeneity (e.g. Tilman 1982) and differences between species (Oksanen *et al.* 1979 ; Orians 2000 ; Leyequièn *et al.* 2007) condition their relationships (Case & Gilpin 1974 ; Calsbeek & Sinervo 2002) and their respective ecological niches within ecosystems (Pearman *et al.* 2007). These complex processes allow species using the same resources to **coexist and form population networks**, taking the form of a coherent community that gradually changes over time. **Species assembly theory** aims at explaining potential differences in community structures within a given space (see Weiher 1999). Within this conceptual framework, multiple stable states refer to circumstances where populations have the same access to the community, but where differences in community composition result from differences in colonization events (Young *et al.* 2001). The number of stable states depends on the number of species already present, on connectivity rates within the considered space, on its productivity as well as on its perturbation regime (Chase 2003). When a species is lacking, other ones hence use the space left vacant, suggesting they do have the ability to expand their niche but are constantly limited by the presence of other species (Orians & Willson 1964). Community assembly theory therefore considers community structure in a dynamical manner, where the community is actually considered as a continuous invasion/extinction process (Moyle & Light 1996). Savanna or aquatic herbivore communities are good examples of such processes. In African savannas, plant resources (tree versus grass species, herbaceous versus arborescent stratum), accessibility of this resource (megaherbivores versus mesoherbivores) and the food requirements of herbivores (quantitative versus qualitative diet species) (see McNaughton & Georgiadis 1986) allow a broad range of populations to coexist (from elephant *Loxodonta africana* to dik-dik *Madoqua kirki*). When a species disappears or decrease in numbers, other ones can use a part of the niche left vacant so as to develop or to change their behavior (e.g. in Africa when the decrease in elephant numbers was considered to have allowed other species to develop; Valeix *et al.* 2008). In continental wetlands of Europe and North America, a similar segregation is observed among herbivores, depending on food accessibility and species-specific food requirements (e.g. castor *Castor spp.*, coot *Fulica atra*, swans *Cygnus spp.* and Moose *Alces alces*). Population assembly in such vast communities has however received far less attention than those of terrestrial herbivores.

Relationships between sympatric species can have a positive (mutualism or commensalism) or a negative effect (e.g. competition) for at least one of these. **Competition** occurs when species use the same resource, and that such use is detrimental to one of the species (Krebs 2001) through decreased survival, growth or breeding rate (Begon *et al.* 1990). Ecological similarities between species or the very abundance of resources are among the factors promoting competition: competition will more likely be strong when resources are few (DuBowy 1988). DuBowy (1988) thus suggested that competition among temperate waterbird communities should be stronger in winter, when resources are less abundant. The way two different species select their habitat can be a mean by which competition is reduced. When two species are highly selective, this may explain why competition mostly occurs in intermediate habitats (Orians & Willson 1964).

Competition can take the form of **food depletion** and **interference** between individuals. Interference is different from depletion because it is reversible. Food intake rate recovers as soon as interference stops (e.g. after individual density has decreased), while food stocks do not quickly recover after depletion (Goss-Custard 1980). While **exploitative competition** is related with the way individuals interact for a given resource, **interference competition** includes both negative behavioral interactions and the ways by which a species reduces resource availability for another species (Latham 1999).

When individuals can freely use space with no constraints, and can use habitats where their chances of success are the highest, they are considered to follow an **ideal free distribution** (Fretwell & Lucas 1970) if all individuals get the same food intake rate at equilibrium. Such a distribution can be altered by **territorial behavior**. In such situations, if the first individuals to use a site or the most dominant individuals can monopolize a site to increase their profit (or to get the highest profit), their distribution is said to be **ideal despotic** (Fretwell & Lucas 1970). The ultimate goal of territorial behavior is indeed for an individual to avoid other individuals behaving in the same way in a given area. In such a case, both congeners and individuals from other species can get excluded by non-specific territory defense (Mikami & Kawata 2004). Anatidae commonly behave territorial during the breeding period (e.g. flying steamer duck *Tachyeres patachonicus*; Nuechterlein & Storer 1985, goldeneye *Bucephala clangula*; Savard 1984 or mute swan *Cygnus olor*; Conover & Kania 1994). Under such circumstances, subordinate species can either alter their behavior (they can therefore continue to use the optimal habitat together with the dominant species, but in a different way), still use optimal habitat in the same way but at the cost of negative interactions, or adapt to suboptimal habitat (Murray & Bertram 1971). Territoriality generally leads to increased emigration and mortality in subordinate species (Brown 1969). Passive exclusion behavior, owing to changes in habitat structure, is another form of interference. In African ungulates, Fritz *et al.* (2002) have demonstrated that mesoherbivores (e.g.: African Buffalo *Syncerus caffer*) can be affected by massive food depletion by elephants.

3. Predation as seen in herbivore-plant relationships.

Predation is the relationship by which one organism (the predator) takes all or a part of another organism (the prey), which is used or killed (Begon *et al.* 1990). The relationship between plants and their predators is a special case, as the plant is generally only partially used. On the earth, half of macroscopic species are plants, so a large share of the interactions among ecosystems are actually herbivore-plant relationships. Despite the fact that they are often considered as a loss from the plant to the herbivore (Krebs 2001), the consequences of such relationship can be far more complex.

The outcomes of the relationship between herbivores and plants can occur over highly variable ecological and temporal scales. In some cases herbivores increase fitness (McNaughton 1983) or limit biomass production of plants (Idestam-Almquist 1998, Rodriguez-Perez & Green 2006, Schmieder *et al.* 2006). Mutualism is even suspected between herbivores and some plant species (e.g. Sandsten & Klaassen 2008). At the scale of the community, herbivores can affect plant heterogeneity (see Adler *et al.* 2001, Bakker *et al.* 2003) through the promotion of some species over others (Setälä & Mäkelä 1991 ; Van Donk & Adrie 1996 ; Santamaria 2002 ; Rodriguer-Villafane *et al.* 2007).

Of course, herbivores are only one component of the **complex factors affecting plant development** (Perrow *et al.* 1997) (see figure 1 below). In aquatic environments such factors (nutrients, landscape, hydrology, competition between plants, …) all affect macrophyte beds (listed in Lacoul & Freedman 2006).

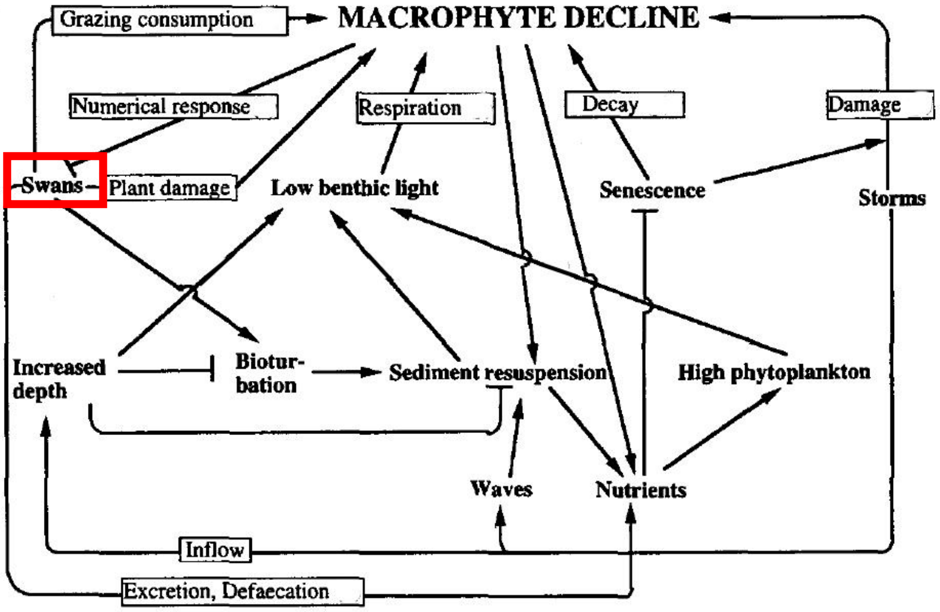

Figure 1: Conceptual model of the role of black swans (*Cygnus atratus*, see *« swans »*) and other non-seasonal factors on aquatic macrophyte biomass decline in shallow lakes. Stimulating effects →; inhibiting effects --|. The effect of detritivores, external nutrients and sediment loads, some elements on nutrient input and interactions in trophic chains that affect phytoplankton are not indicated (after Mitchell & Wass 1996).

In aquatic ecosystems, the effect of herbivores has long been underestimated. The Shelfordian approach considered a minor effect of herbivores on macrophyte communities, which remained the main paradigm for most of the XXth century. It is still common that algae and macrophyte development models lack a « herbivory » variable (e.g. Carr *et al.* 1997), while herbivory is recognized as a limiting factor for macrophytes (Lodge 1991). This is especially the case in aquatic environment where losses due to the foraging activity are additive to the biomass actually ingested by herbivores (Lodge 1991). The consequences of herbivores for aquatic macrophytes have been studied in a variety of contexts: dugong *Dugong dugon* and green turtle *Chelonia mydas* in coastal tropical habitats (Aragones & Marsh 2000), crayfish *Orconectes rusticus* (Lodge & Lorman 1987), herbivorous birds and fishes in shallow lakes (Van Donk & Adrie 1996 ; Marklund *et al.* 2002), which can all considerably decrease the biomass and affect the structure of aquatic macrophyte beds.

Just like competition processes in sympatric species, the outcomes of a predation event by herbivores on a plant community depend on the context in which it occurs. Identifying these relationships and evaluating their consequences requires stratified studies over two gradients: community structure and the general environment in which such systems are.

III. The presence of mute swan in fishponds.

1. The mute swan as a demographically and geographically increasing species.

The mute swan is listed in appendix III of the Bern convention and appendix II of the European Bird Directive. It got protected by the nature protection law in France in 1976. The swan apparently was not among the Holocene French fauna. The species is considered to be non-native, because even if it was previously absent, individuals now breed and form persistent populations (Pascal *et al.* 2003). The present population apparently had two types of origins: introductions by man and increase in the eastern European population associated with range expansion. That the mute swan population increased and colonized new habitats may be due to wetland eutrophication, the creation of new habitats (e.g. reservoirs) and the acquisition of a protection status (Wieloch 1991 ; Kirby *et al.* 1994 ; Fouque *et al.* 2007 ; Ward *et al.* 2007). In any case, no geographic barrier had to be artificially crossed for swan being present in France. Because how much the population will still increase is unknown, **it is difficult to decide if the present population is feral or should be considered a biological invasion.** Conversely, the species in non-native in North America, where it is considered to be invasive (see Perry 2004), despite the fact that its ultimate potential development and the consequences of these birds for the ecosystems are difficult to assess. Mute swan status in North America is quite similar to that of Canada geese *Branta canadensis* in Europe (see DAISIE 2010).

Owing to its range expansion over the last century, mute swan is **a recent element of aquatic ecosystems** in Western Europe, where it could indice major changes. Indeed, this species has multiple relationships with other components of aquatic ecosystems, while its morphology (especially so its large size) provides it a competitive advantage over other waterbirds. The recent presence of swans and the establishment of proper populations raised major concerns about how they could join existing waterbird communities and the extent to which they may deplete aquatic macrophyte beds. In many French regions, mute swan is accused of causing major damages to both natural habitats (Dombes, Brenne, Vendée, Camargue, Somme, Bassin d’Arcachon) and human activities depending on these (vegetable crops in Audomarois, cereals in Seine-Maritime, Eure, Moselle, Côte d’Or, Camargue, aquaculture and hunting in Brenne and Dombes, or leisure activities along the Rhône river).

Concerning aquaculture, mute swans should destroy support macrophyte beds, and then support for spawning. For hunting, mute swans should compete with other waterfowl species, and have a detrimental effect on their stay on waterbody.

Potential competition and damages due to swans are especially important to assess because swans are long-lived birds with a strong potential for demographic increase (Petrie & Francis 2003), with no real natural predator in Western Europe. This implies that processes potentially generated by swans are likely to become chronical disturbances of such ecosystems. In addition, their strong ecological plasticity (Wieloch 1991) suggests a variety of ecosystems are likely to get used by swans, with contrasted potential consequences on existing communities.

2. Colonization of freshwater ponds.

Fishpond regions are very singular wetlands. Fishponds are aquatic ecosystems entirely created by human activity. Superficial water flowing is being stopped by dykes in low areas with waterproof soil so as to create a standing water ecosystem of low depth (inferior than 1 meter on almost the open water area). Fishpond creation comes from the double objective to improve wetlands (previously considered as dangerous for human health) and to use some land for agriculture. Indeed, most fishponds are used for fish breeding. Although all fishponds are distinct aquatic units, within a landscape they are connected to each other by canals. This generates a complex network over space. Thanks to this network of canals, landowners can manage water flowing within fishponds.

Fishponds are flooded all the year, and are drained annually during autumn for fish harvest. Socioeconomic activities (mainly hunting and fish breeding) and ecologic stakes are now strongly dependant from each other on these wetlands, since the former depends on natural resources and provides the necessary funds to manage fishponds.

In France, ten main fishpond continental regions exist. The most famous are the Dombes, the Brenne, the Lorraine, the Sologne, the Forez and the Bresse. The ecologic value of these wetlands for biodiversity (avifauna and plants) is undisputed. For example, fishpond regions are important staging and breeding areas for duck populations. The ecologic value of such fishpond regions is recognized by international treaties or policy like the Ramsar Convention or the Natura 2000 network.

The Dombes is one of the widest fishpond regions from France. It is located in the East of the country, North-East to the city of Lyon. The management of Dombes fishponds is rather original compared to other fishpond regions. Fishponds are drained annually for fishing, but every third year they are not reflooded after fishing. They are then dried during one year before reflooding the following autumn. The temporary drying of fishponds during one year has several advantages like allowing mineralization of organic matter and culling of those fish species considered as pests. In most cases, fishponds are cultivated during the year when they are dried.

Continental freshwater ponds are among the wetlands that have been entirely created by man. Despite the fact that they have an important ecological role (patrimonial habitats and species) and are directly linked to human activity (e.g. aquaculture), **ecological functioning of ponds remains relatively unexplored** compared to other aquatic habitats such as lakes, rivers, marshes or gravel pits. One of the reasons for this may be their strong dependence on human activities, which induce highly complex and variable functioning. Research on such systems is consequently relatively new (e.g.: 4th European Pond Conservation Network in 2010), and has developed because this may provide new insights on wetland ecology and may have important conservation implications. Freshwater ponds are indeed important breeding sites for Anatidae and play a major role for wetland plant conservation.

Like most wetland types, ponds in Western Europe have been massively colonized by new species over the last decades (great cormorant, *Ludwigia spp*. or coypu *Myocastor coypus*). Mute swan is among such species (Musil & Fuchs 1994 ; Fouque *et al.* 2007). Mute swan arrival in aquatic habitats should be studied in a broad perspective, while simultaneously considering when and the scale at which such process occur. It is therefore of paramount importance to take into account the habitat selection modes of the species. This indeed provides some insights about the possible outcome of the species insertion in existing communities over space and time. This is necessary if one wants both to identify the habitats likely to get affected and to assess how the species will interact with the whole communities over time.

3. Mute swan and the waterbird community.

“Waterbirds” is here used for wildfowl (ducks, geese and swans) plus Rallidae (coot *Fulica atra* in the present case). **Waterbirds are among the bird populations whose life cycle depends the most on water resources**. The role of waterbirds has long been underestimated compared to that of other taxa like plants, fish or invertebrates, although they play a important role in aquatic ecosystems (see Elmberg 2009). They act on nutrient input (Kitchell *et al.* 1999, Post *et al.* 1998), help organism dispersal (Brochet *et al.* 2009a ; Brochet *et al.* 2009b ; Brochet *et al.* 2010), germination (Agami & Waisel 1986) or vegetationn growth (Hidding 2009). Waterbird populations are therefore a major conservation issue both in economical (e.g. hunting, tourism) and ecological terms for wetlands. Compared to other taxa, these species have a variety of needs and provide easy access information on aquatic habitat conservation status (productivity, functioning and biological stability), hence their frequent use as indicators (Frochot & Roché 2000). At the global scale, waterbirds are mostly threatened by habitat loss, hunting and exotic species (Green 1996).

Mute swan may use a vacant niche in the habitats it colonizes (see Oksanen *et al.* 1979 ; Pöysä & Sorjonen 2000), or may conversely exclude native species through its territorial behavior (e.g. Conover & Kania 1994). Interactions between mute swan and other waterbird species are seldom documented, although mute swan is considered to be territorial and aggressive during the breeding season. Given their specific characters, swans may likely establish in two different ways: (1) owing to their morphology and relative ecological plasticity they may have a competitive advantage over other species. This may especially be the case where resources are limiting, which would promote competition or exclusion principles; (2) differences with the other species may be so large that swans may establish in communities without affecting their structure, especially if resources are not limiting.

4. Swans and aquatic macrophytes.

Aquatic macrophyte beds are the **keystone of aquatic habitat bio-geochemical functioning**. They recycle and store nutrients (Conley 2000), hence limit phytoplankton, which likely reduces water turbidity (Van Donk & Van de Bund 2002). Many animal populations rely on these plant communities. Aquatic macrophytes are a direct or indirect food source for many invertebrates (Gregg & Rose 1985 ; Jeppesen *et al.* 1998 ; Mitchell & Perrow 1998), waterbirds (Staicer *et al.* 1994 ; Perrow *et al.* 1997) or fish (Crivelli 1983 ; Rozas & Odum 1988). These beds are also a favorable habitat for many invertebrates, which are prey to birds or fish. These birds or fish may themselves use macrophyte beds to lay their clutch or stick their eggs.

In terms of conservation, **some aquatic macrophyte beds** like Magnopotamion (e.g. *Potamogeton sp., Najas sp., Lemna sp., …*), Hydrocharition (e.g. *Hydrocharis morsus ranae*) or Characaes **are recognized of European importance** (DOCOB 2004). Other species like European waterclover *Marsilea quadrifolia*, naiads *Najas sp.*, Sharp-leaved Pondweed *Potamogeton acutifolius* or water caltrop *Trapa natans* are protected to some extent or are listed by the Bern Convention.

Swans are the largest wild aquatic herbivores in Western Europe. They forage on aquatic macrophytes (Bailey *et al.* 2007), of which they ingest 3 to 4 kg fresh biomass per day (Cramp *et al.* 1986). Mute swans may therefore likely deplete large amounts of aquatic vegetation through ingestion or disturbance. Most studies on the relationships between mute swans and aquatic macrophytes have been carried out in coastal areas and large lakes, and provide a range of conclusions: Badzinski *et al.* (2006) did not demonstrate any negative effect of Bewick's swan and Canada goose presence on *Chara spp.*, *Vallisneria americana* and *Potamogeton pectinatus* beds during migration over Lake Erie (Ontario). Similarly, despite their use of macrophyte reserve organs during migration in Alberta, trumpeter swans *Cygnus buccinator* apparently do not affect summer productivity of these plants (LaMontagne *et al.* 2003a). Sandsten & Klaassen (2008) even consider there could be mutualism relationships between swans and Fennel-leaved Pondweed. Hidding (2009) hypothesizes that some late growing species like naiads *Najas spp.* could benefit from swans grazing earlier plant species. Conversely, Tatu *et al.* (2007) have demonstrated a negative impact of mute swans in Chesapeake Bay (Maryland), just like O'Hare *et al.* (2007) in river ecosystems.

IV. Aims of the thesis.

As explained above, many aspects of mute swan ecology and that of other pond animals and plants remain unstudied. In this context, research on mute swan ecology provides the opportunity to both assess how a sedentary waterbird population uses such aquatic habitats, and to determine how it interacts with other animals and plants of the community. Studying such interactions may provide valuable information to stakeholders concerned by the consequences of swan presence on ponds.

Beyond the ecological adjustments their presence may require, swans are a good model species to try understanding bird communities in aquatic habitats. For these reasons, the different swan species are getting increasingly studied, especially at NIOO KNAW – Netherlands (Klaassen 2006 ; Hidding 2009). More applied studies are also being carried out in USA (University of Carbondale, under supervision of M. Eichholz) and in the UK (Bournemouth University, under supervision of R. Stillmann) to better understand swan-waterbirds and swan-macrophytes relationships.

The Dombes was here selected as a study area because of the wide variety of issues associated with swan presence, causing concern to local stakeholders. The aim of our study was to provide new knowledge about how an herbivorous waterbird like mute swan selects habitat within such a heterogeneous landscape, and to study the way such a species establishes within existing plant and animal communities (Figure 2).

Aquatic habitats in pond landscapes show both great spatial and temporal heterogeneity. At the same time, mute swan ecological requirements vary over seasons. These birds may therefore respond to habitat configuration in a variety of ways. Understanding habitat selection processes of such a species is important to assess its ecological needs and the sites where interactions occur between swans and the rest of the community. Chapter 1 therefore deals with mute swan habitat selection within a pond landscape. We first studied how mute swans disperse over ponds in winter and summer depending on pond spatial configuration (area and isolation) and resource availability (**Article 1**). On sites that are favorable to swans, we then tried to understand how swan stay varied over the annual cycle, so as provide pond use scenarios and assess the impact of the birds on their environment (**Article 2**). We eventually studied nesting site selection by the mute swan and measured when accounting for detectability (**Article 3**).

Chapter 2 aims at studying the relationships between mute swans and the other populations. We determined if the other waterbirds were apparently affected by the presence of swan pairs. We first assessed if waterbirds were less abundant where mute swan pairs were present, through a comparison of waterbird numbers on swan and swan-free ponds (**Article 4**). Where swans were present, we then used spatial point pattern analyses to determine if the presence of a swan pair lead to spatial segregation of the other waterbird species within a given pond (**Article 5**). We explored the potential consequences of aquatic macrophyte bed depletion by mute swans. This study was carried out experimentally during the period of macrophyte growth (**Article 6**).

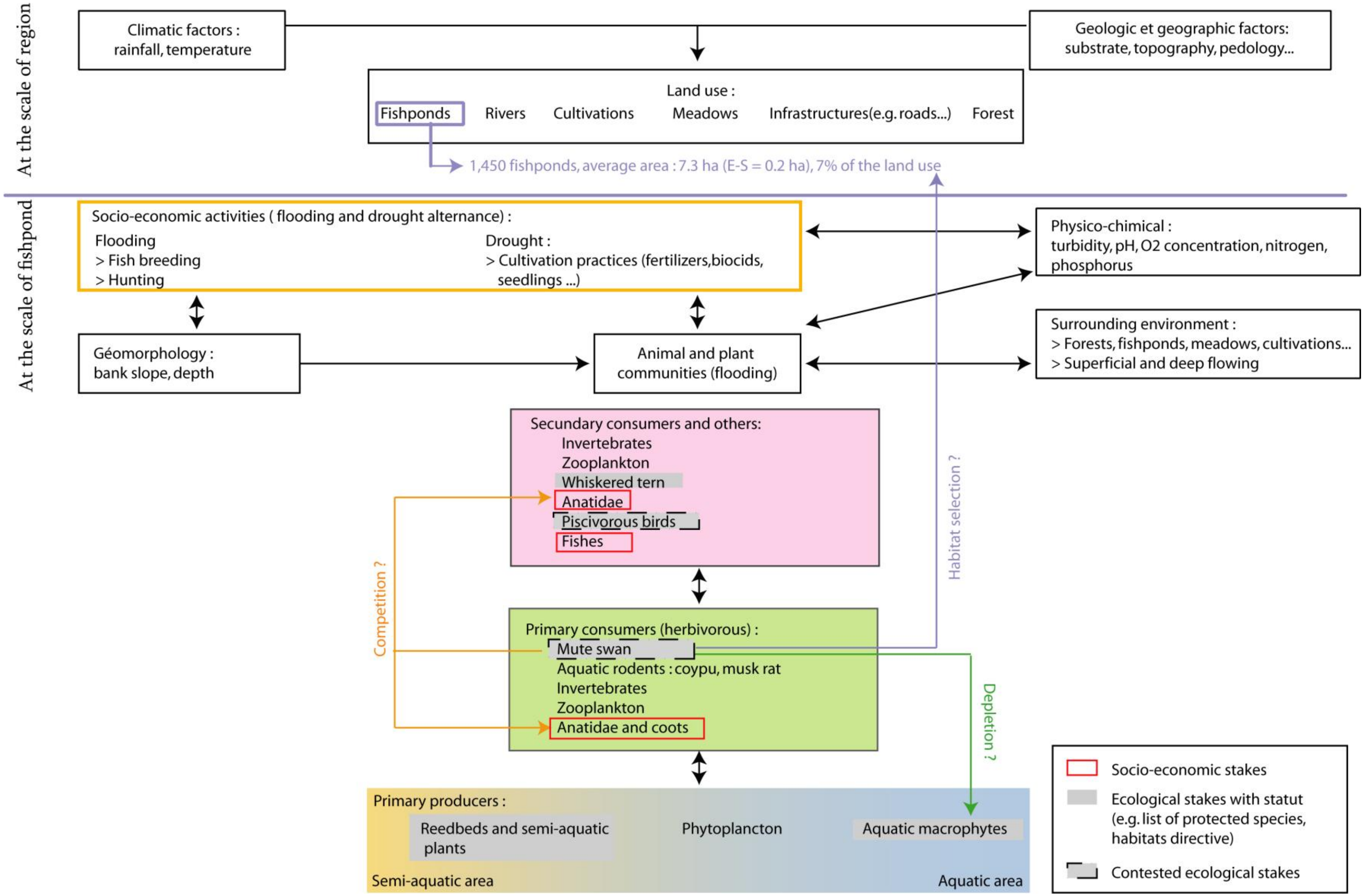

Figure 2 : Simplified model of pond functioning (Dombes, France) and main ecological questions associated with swan presence (Gayet, 2010).

A discussion then aims at assessing the role of mute swans within the whole pond ecosystem network. After summarizing our results, we put this study in a broader perspective so as to determine further research needs for the future.

CHAPTER 1 : MUTE SWAN HABITAT SELECTION WITHIN A FISHPOND LANDSCAPE.

The Dombes fishponds form a vast aquatic habitat landscape whose functioning strongly depends upon human activities. Colonization of these fishponds by mute swan occurred relatively recently, but individuals today form a proper population. We were interested in this chapter in the way such colonization now results in swan distribution over space, through the study of habitat selection processes. We first studied swan distribution (in terms if bird presence) within the fishpond landscape **(Article 1)**. We then assessed how swan stay (expressed in swan-days) varied over the year **(Article 2)**, and eventually considered nesting site selection processes **(Article 3)**.

In the first part **(Article 1)**, we tried to understand habitat selection mechanisms by swans during summer and winter, i.e. when inter-seasonal changes in bird behaviour (gregarious in winter, gregarious and territorial in summer) and fishpond characteristics (winter re-flooding of summer-drained fishponds) are the most pronounced. We monitored more than 750 fishponds over 6 years (2003 to 2008). Dried fishponds were not studied in summer, because swans never use these before re-flooding in Dombes. Drained fishponds are never re-flooded before the end of the following autumn. Each year, a bird count was organized during the period of moult and cygnet rearing (June). This monitoring therefore provides a snapshot of swan distribution over fishponds when they are the most permanently established on fishponds. Using Mixed General Linear Models, we measured the effect of fishpond area and surrounding aquatic environment parameters (number of fishponds and relative proximity over two scales : 2 km and 0,25 km) on swan distribution. We first carried out the analysis for all swans, then for breeders (swan families – breeding sites) and for non-breeders (swan flocks - moulting sites). We also assessed spatial independence of the observations with correlograms (Moran’s index). We show that swans do not distribute randomly over fishponds and that depending on what is considered (whole swan population, families or flocks), different factors explain such distribution. Swans preferentially use medium to large fishponds (>10 ha) and those with many surrounding fishponds or in a dense aquatic environment within 2 km. Swan families select fishponds after their size (> 10 ha) or their poor isolation at large distance (number of fishponds within 2 km), while flock presence mostly depends on fishpond size (> 30 ha). Even if fishpond sizes are not randomly distributed within the landscape (i.e. fishponds of similar size tend to be clustered) and if swan presence is positively correlated to this variable, we could not demonstrate a spatial aggregation of swan observations.

In winter we monitored a sample of 165 fishponds, selected after their size and depending on whether they were flooded or dried the previous summer (and, in the later case, then depending on whether they were cultivated in maize, in other cereals or non-cultivated). Such a sampling method allowed considering these factors both simultaneously and in isolation from each other to measure their effect on swan fishpond selection. Each fishpond was visited every second week from December 2006 to March 2007. During such visits, swans were counted and the proportion of fishpond area that was flooded got estimated. To take into account the increasing proportion of fishponds that were used as winter progressed we used proportional hazard models with Cox regressions. We show that swans likelihood of presence generally increases with increasing flooded area or is higher after summer drainage, while swan flocks are more frequent on large previously summer-drained fishponds once flooded. We did not observe an effect of the practice exerted on fishponds while they were dried in summer on their use by swans during winter.

This first part of the study allowed relating swan presence on fishponds to particular habitat features over two seasons. Beyond simple presence, we then considered swan stay (number of bird-days) over the whole year **(Article 2)**. The aim was then to assess when in the year swan stay is the highest, and what enhances such stay. Such a knowledge may eventually be helpful when considering the interactions between swans and animal and plant communities across the year. From the results above, hundred fishponds *a priori* favourable to swans were selected : fishponds over 10 ha, some drained and some flooded the previous summer. Swans were counted on these fishponds every second week from early December 2008 to late November 2009. We calculated swan use (swan-days/ha) on each fishpond and assessed the relationship between swan stay (swan-days) and habitat variables during each season. We first show that relative swan use (swan-days/ha) among fishponds does not vary over the year, i.e. the same proportion of fishponds is hardly, moderately and intensively used during each season.

In winter, large fishponds previously flooded or previously dried fishponds were those with the stronger swan stay. Swan stay did not differ between practices among previously dried fishponds. In spring, swan stay was positively correlated with fishpond area. In summer, such stay increases on fishponds whose aquatic environment comprises many other fishponds, or on fishponds with a high relative proximity within 2 km. Furthermore, higher plant cover on large fishponds also enhances swan stay. Summer is the period of the year when the selected model explained swan stay variation the most. In autumn, swan stay was positively correlated to fishpond area and poor fishpond isolation at short range (proximity within 0,25 km).

Mute swan has shown rapid demographic and geographic increases in Western Europe. Its relative ecological plasticity, i.e. ability to meet its biological requirements in habitats where food availability may strongly vary, is often put forward to explain such increases. To better assess the factors that may affect swan increases and the settling of new populations, we studied a key stage of the annual cycle for any bird species: nest site selection **(Article 3)**. On the same sample as above we recorded the presence of breeding swans (pairs or individuals on nest) from April to May (settling and nesting periods). Single-season occupancy models over one season were used to measure the relationship between swan pairs and their habitat. Habitat variables were human disturbance, fishpond management history (flooding or drainage), fishpond size and its surrounding aquatic environment (number of fishponds and isolation at 0,25 and 2 km scales). Among the studied fishponds, none of the tested factors had a significant effect on swan settlement. Despite swan being the largest wildfowl species and being non cryptic (i.e. white), we demonstrate swan breeding events are imperfectly detected, i.e. probability to detect a swan pair on a fishpond during a visit is lower than 1. The estimation of the number of fishponds with breeding swans thus increases in precision when repeated visits are carried out.

Article 1 : Effects of seasonality, isolation and patch quality for habitat selection processes by Mute swans (*Cygnus olor*) in a fishpond landscape.

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Effects of seasonality, isolation and patch quality for habitat selection processes by mute swans *Cygnus olor* in a fishpond landscape

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Foragers in patchy environments do not only select sites for single patch characteristics, but also have to consider the local environment of such patches. We studied habitat selection by mute swans *Cygnus olor* in a wide and heterogeneous fishpond region (the Dombes, eastern France). In this study, we considered fishpond isolation, resource quality within fishponds and breeding status of mute swans during both summer and winter. Mute swans did not select aquatic habitat randomly within the landscape. During summer, the population spread preferentially on medium to large fishponds, in subregions with numerous or closely related waterbodies, without generating a clumped distribution of birds. In addition to a positive effect of local fishpond number (2 km radius), breeding birds also responded positively to fishpond size. Non-breeders selected fishponds mainly according to their size. Intraspecific territoriality did not appear to limit the presence of non-breeders (i.e. moulting flocks), since both breeders and non-breeders could coexist on the larger fishponds. During winter, mute swans used medium to large reflooded fishponds after summer drainage. The surrounding aquatic environment of fishponds played a minor role in determining flocking, compared to actual patch quality. Flocking occurred on large fishponds that had reflooded after having dried the summer before, whatever the agricultural cultivation practiced in the summer following drainage. The results suggest that geographical aspects should be taken into account when considering the potential impact of this expanding species within such ecosystems, and also in more general management policies dealing with aquatic habitats for waterbird populations.

Spatially complex systems with a patchy resource occur frequently in the environment, and consumers therefore often forage in habitat patches which have a wide variety of shapes over space (Ritchie 1998). The way patches are distributed over space may play a key role in determining bird populations, including waterbirds, by affecting both demographic parameters of populations and community structure (Brown and Dinsmore 1986, Kurki et al. 2000, Boulinier et al. 2001, Paracuellos and Telleria 2004, Wilson et al. 2009). Studies of such systems may strongly benefit from multidisciplinary approaches combining optimal foraging and metapopulation theories (Senft et al. 1987): the former may help understand how patches are selected given their food depletion rates and potential profit for consumers (Charnov 1976), while the latter may help explain how patch isolation affects habitat occupancy and changes in occupancy over time (i.e. colonization and extinction; Moilanen and Hanski 1998).

To date, studies of wildlife resource selection processes which considered degree of fragmentation, quality of patches and population requirements during contrasting seasons simultaneously are lacking for wetland ecosystems. This is unfortunate, given that understanding waterbird habitat selection processes is a major current concern due to the loss of wetland habitats and the associated consequences for wildlife communities. Within the waterfowl community, the mute swan *Cygnus olor* is an appropriate model species to study how a waterfowl population may react to these combined factors. Indeed, mute swans may form sedentary herbivorous populations, whose spatial distribution among a given geographic area may nonetheless differ between seasons. Breeding and non-breeding swans can easily be distinguished during summer, providing a valuable opportunity to describe differential use of a wetland area by waterfowl according to breeding status. Such a study may be an opportunity to advance our knowledge about the distribution of a waterbird population in a patchy habitat from a theoretical point of view. In a more applied perspective, and because the mute swan is the largest herbivorous waterbird in Europe, such a study could be a means to locate potential damage caused by swans (e.g. through their consumption of macrophytes and interspecific territoriality) on natural habitats.

The aim of this study was to understand how Mute swan distribution may be influenced by the distribution and quality of patches over space and time in a large and dynamic wetland landscape, i.e. a fishpond region. In Europe, these fishpond regions are wetlands complexes whose waterbodies have been created artificially by man. Specifically, we tested whether variation in swan presence varied depending on individual fishpond characteristics (size and habitat management), properties of the surrounding aquatic environment (isolation, number of fishponds within 0.25 km (small scale) and 2 km (large scale)), and bird requirements. These included breeding status and attraction due to presence of conspecifics. Below we describe our predictions about how spatial properties of the waterbodies and mute swans' biological and social characteristics could affect their distribution.

We expected the population (all swans) to primarily select medium to large fishponds due to their larger carrying capacity than smaller sites (hypothesis 1). The presence of mute swans may also depend upon the surrounding aquatic environment, with a preference for sites encompassed within numerous waterbodies and/or large open water areas (hypothesis 2). In some regions, like the Dombes, fishponds are regularly drained for cultivation of cereals. Following reflooding of the fishponds the next winter, the availability, quality and quantity of resources (waste grains) may be so high compared to fishponds that remained flooded the summer before (containing only macrophyte organs), that cultivation the previous summer may matter more than the fishpond itself and its environment (hypothesis 3).

Within the population, birds may behave differently according to their breeding status and their own requirements. Pairs are expected to develop intraspecific territoriality due to their presumed exclusive occupation of the fishpond where they breed. In summer, non-breeders form gregarious bands and may be negatively affected by the presence of swan breeding territories, except when these are established on large fishponds where breeding and non-breeding birds may coexist (hypothesis 4).

Spatial autocorrelation of biological processes depends upon the physical properties of the environment (e.g. patch area), but may also be affected by the biological properties of the species considered (Dormann 2007). Thus, in addition to the dependence of the species to spatial properties of its habitat, philopatry of the mute swan (Spray et al. 2002 in Rowell and Spray 2004), and intraspecific attraction over space (Stamps 1988, Mönkkönen and Forsman 2002), may generate cores of presence in the landscape. Consequently, there would be non-independence in swans' presence according to fishpond properties, i.e. significant spatial autocorrelation in the models (i.e. the property of variables to take a given value, more or less similar to those associated randomly, according to their distance from their place of measurement to the neighboring measurement areas (Legendre 1993)) (hypothesis 5).

Methods

Study area

The Dombes is a complex of 1450 fishponds (average area = 7.3 ha ± 0.2 ha SE) spread over 1600 km^2 in eastern France (45°57'N, 05°02'E). Fishponds are mainly used for fishing, hunting and temporarily as arable lands. The 14 largest sites have an area between 40 and 110 ha. Fishpond depth is generally less than 1 m, and because of an almost total accessibility of the water column to swans, water depth is not expected to influence swan presence. Within the Dombes, different subregions were distinguished according to fishpond size and distance between fishponds (Fig. 1). Total area of open water represents ca 7% of the landscape. Fishponds are dried regularly, on average every third year, for summer cultivation. Boundaries of the study area were determined by the administrative limits of villages of the Dombes plateau. In Dombes, the summer mute swan population is estimated to be ca 1000 individuals (Benmergui et al. 2005).

Summer data

A first set of fishponds were sampled once per year, during the last 10 days of June, from 2003 to 2008, and all swans and cygnets were counted on each fishpond. The maximum number of flooded fishponds then surveyed varied between 753 and 1000 annually, depending on the number of available observers (Table 1). These surveyed fishponds were spread over the Dombes, and randomly selected after ensuring that the distribution of surveyed fishponds per class of area was similar to the distribution of all fishponds over these classes within all the Dombes (hypothesis 1).

Winter data

A second sample consisted in 165 fishponds counted every two weeks during winter, from December 2006 to March 2007. Fishponds were selected according to their area (0.5–5, 5–10, 10–15, 15–20, >20 ha) and cultivation status during summer 2006 (flooded (F), dried and not cultivated (Dn), cultivated with maize (Dm), cultivated with other cereals (Do)) (Table 2). We obtained a hierarchical sample which allowed us to identify the combined effects of fishpond size, drainage and cultivation, on swan presence (hypotheses 1 and 3). The number of swans, the percentage of area that was flooded, and the percentage of frozen flooded area were recorded during each visit.

Spatial configuration of fishponds

The spatial configuration of fishponds was described using two measurements: patch size (A in ha) and patch isolation (hypothesis 2). We measured patch isolation at two spatial scales as the number of patches within a 0.25 km radius (NB025) and a 2 km radius (NB2) from the border of a given fishpond. We considered 2 km as the maximal distance to measure relative isolation of fishponds, according to the scale at which philopatry has been described in mute swans (Spray et al. 2002 in Rowell and Spray 2004). The second measurement of isolation was

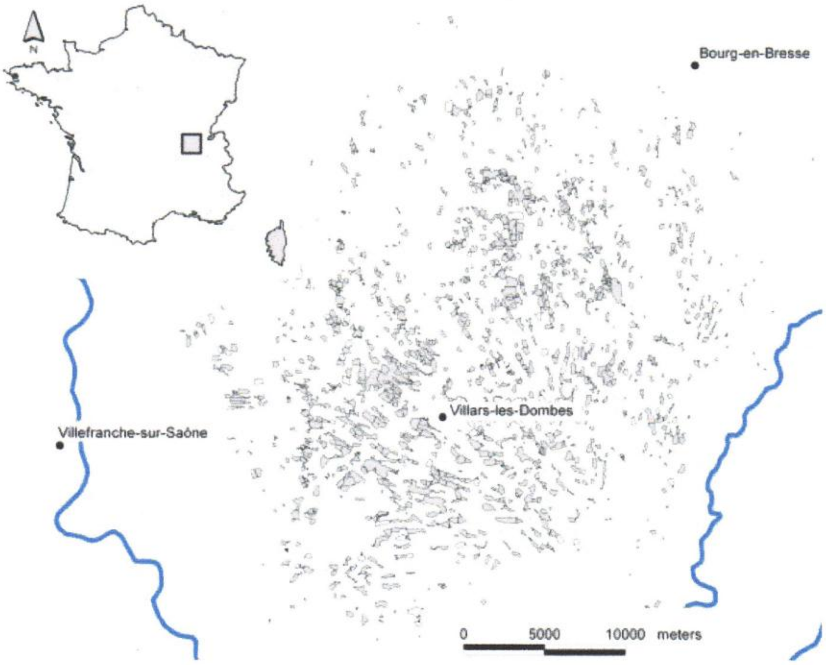


Figure 1. The fishponds of the Dombes plateau, and the position of the area in France.

considered at the scale of 0.25 km to describe the immediate environment of fishponds and to reduce multicolinearity with measures taken at a distance of 2 km. Distances between fishponds were calculated using Arcview 3.2 Nearest Feature extension (ver. 3.6). We also measured relative isolation of fishponds at these two distances using Gustafson and Parker's (1994) proximity index PI, calculated as the sum of the ratios of patch sizes and distances of fishponds within the considered radius. We termed these indices PI025 and PI2 for the 0.25 km and the 2 km radiuses, respectively. Both flooded and dry surrounding fishponds were included in the analysis of a given fishpond aquatic environment.

Statistical analyses

This study is an example of design I following Thomas and Taylor (2006) where available and used resources (fishponds) are known for the population, but individual birds are not identified. Johnson et al. (2006) advocate this design for monitoring mobile species at different times or when it is too complicated to survey all used units, as is the case here.

Table 1. Number of fishponds monitored each summer from 2003 to 2008 per class of area.

Area (ha)	2003	2004	2005	2006	2007	2008
0.5–5	350	380	416	393	252	245
5–10	296	308	311	291	266	259
10–15	138	139	147	140	131	133
15–20	56	61	66	58	58	57
>20	60	67	60	54	63	59
Total number	900	955	1000	936	770	753

Summer data

In the summer sample, flooded fishponds with at least one swan were scored 1, while other flooded fishponds surveyed without swans detected were scored 0. We distinguished those used by flocks of at least 10 adults (moulting sites, termed 'flock'), by swan families containing at least one cygnet (breeding sites, termed 'family') and by any type of swans (flocks, families or individuals of unknown breeding status, termed 'all swans'). The analyses were therefore conducted separately for these three indices of swan presence. We used general linear mixed models (GLMM) to identify the factors affecting swan presence on fishponds. Within the GLMMs, fishponds (replicated over years) were included as a random parameter, and fixed effects were the variables describing the aquatic fishpond environment (A, NB025, NB2, PI025 and PI2). Moreover, we added presence of swan family as a fixed effect for 'flock', given their potential dissuasive character through breeding birds territoriality (hypothesis 4). We formulated a set of models by focusing on hypotheses presented above. Hypothesis 4 expects 'flock' presence to be negatively affected by breeding birds depending on fishpond size during summer. Among others, we tested the following models: 'a × family', 'A + family' or 'family'. Hypothesis 3 expects that swan presence should be positively associated to dried fishponds once reflooded. We formulated the following models among others : 'Af × Dry', 'Af + Dry', 'Dry' or 'Af' for 'all swans' (Af representing the area flooded). By not considering all models possible with covariates (e.g. a model with all covariates retained for analyses), we limited the number of parameters within GLMMs, as advocated by Bolker et al. (2008). We compiled annual observations and obtained a final sample of 5314 fishpond-years (i.e. number of fishponds time the number of years these were monitored). This procedure increased

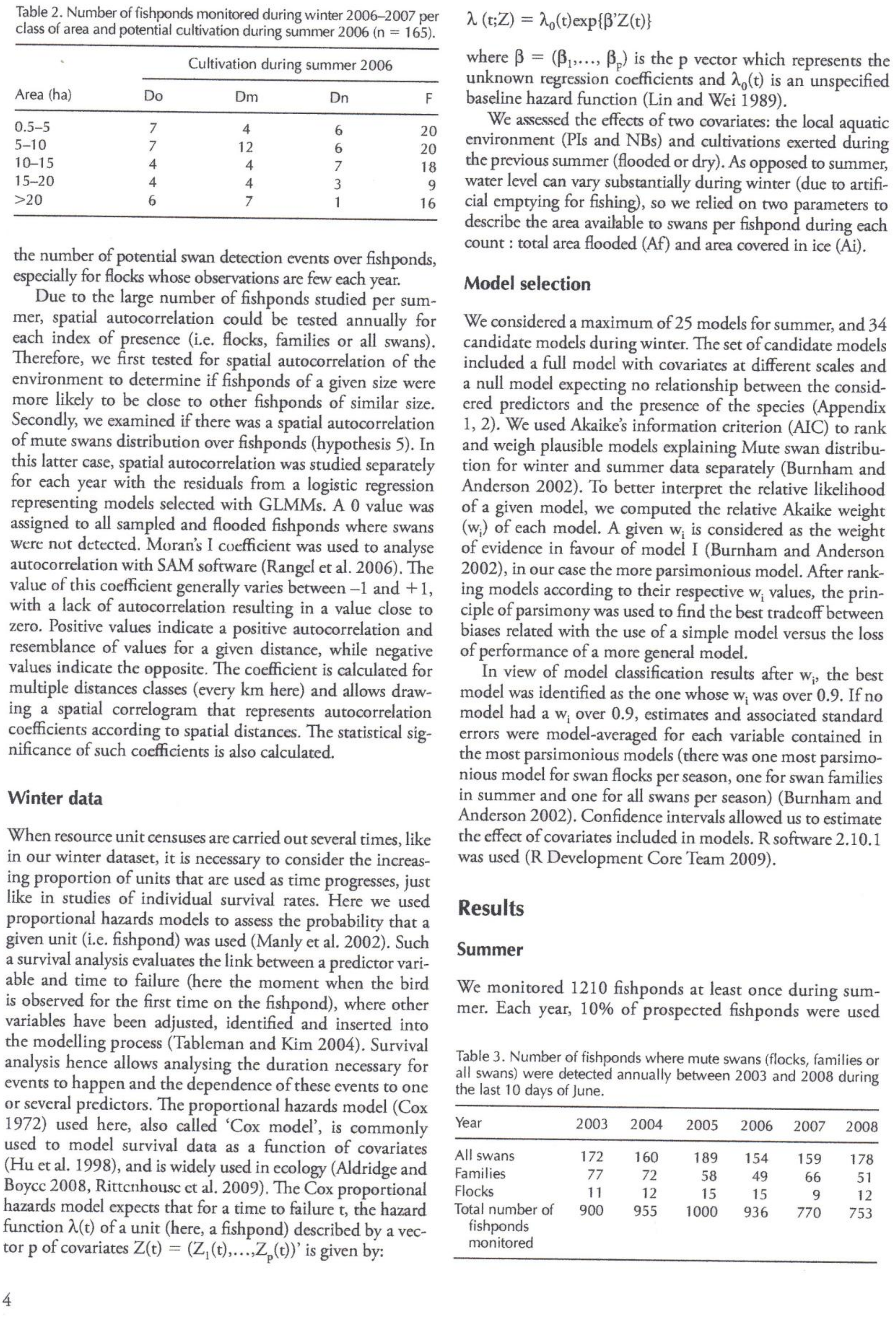


Table 2. Number of fishponds monitored during winter 2006–2007 per class of area and potential cultivation during summer 2006 (n = 165).

Area (ha)	Cultivation during summer 2006 Do	Dm	Dn	F
0.5–5	7	4	6	20
5–10	7	12	6	20
10–15	4	4	7	18
15–20	4	4	3	9
>20	6	7	1	16

the number of potential swan detection events over fishponds, especially for flocks whose observations are few each year.

Due to the large number of fishponds studied per summer, spatial autocorrelation could be tested annually for each index of presence (i.e. flocks, families or all swans). Therefore, we first tested for spatial autocorrelation of the environment to determine if fishponds of a given size were more likely to be close to other fishponds of similar size. Secondly, we examined if there was a spatial autocorrelation of mute swans distribution over fishponds (hypothesis 5). In this latter case, spatial autocorrelation was studied separately for each year with the residuals from a logistic regression representing models selected with GLMMs. A 0 value was assigned to all sampled and flooded fishponds where swans were not detected. Moran's I coefficient was used to analyse autocorrelation with SAM software (Rangel et al. 2006). The value of this coefficient generally varies between –1 and +1, with a lack of autocorrelation resulting in a value close to zero. Positive values indicate a positive autocorrelation and resemblance of values for a given distance, while negative values indicate the opposite. The coefficient is calculated for multiple distances classes (every km here) and allows drawing a spatial correlogram that represents autocorrelation coefficients according to spatial distances. The statistical significance of such coefficients is also calculated.

Winter data

When resource unit censuses are carried out several times, like in our winter dataset, it is necessary to consider the increasing proportion of units that are used as time progresses, just like in studies of individual survival rates. Here we used proportional hazards models to assess the probability that a given unit (i.e. fishpond) was used (Manly et al. 2002). Such a survival analysis evaluates the link between a predictor variable and time to failure (here the moment when the bird is observed for the first time on the fishpond), where other variables have been adjusted, identified and inserted into the modelling process (Tableman and Kim 2004). Survival analysis hence allows analysing the duration necessary for events to happen and the dependence of these events to one or several predictors. The proportional hazards model (Cox 1972) used here, also called 'Cox model', is commonly used to model survival data as a function of covariates (Hu et al. 1998), and is widely used in ecology (Aldridge and Boyce 2008, Rittenhouse et al. 2009). The Cox proportional hazards model expects that for a time to failure t, the hazard function $\lambda(t)$ of a unit (here, a fishpond) described by a vector p of covariates $Z(t) = (Z_1(t),\ldots,Z_p(t))'$ is given by:

$$\lambda\,(t;Z) = \lambda_0(t)\exp\{\beta' Z(t)\}$$

where $\beta = (\beta_1,\ldots,\beta_p)$ is the p vector which represents the unknown regression coefficients and $\lambda_0(t)$ is an unspecified baseline hazard function (Lin and Wei 1989).

We assessed the effects of two covariates: the local aquatic environment (PIs and NBs) and cultivations exerted during the previous summer (flooded or dry). As opposed to summer, water level can vary substantially during winter (due to artificial emptying for fishing), so we relied on two parameters to describe the area available to swans per fishpond during each count : total area flooded (Af) and area covered in ice (Ai).

Model selection

We considered a maximum of 25 models for summer, and 34 candidate models during winter. The set of candidate models included a full model with covariates at different scales and a null model expecting no relationship between the considered predictors and the presence of the species (Appendix 1, 2). We used Akaike's information criterion (AIC) to rank and weigh plausible models explaining Mute swan distribution for winter and summer data separately (Burnham and Anderson 2002). To better interpret the relative likelihood of a given model, we computed the relative Akaike weight (w_i) of each model. A given w_i is considered as the weight of evidence in favour of model I (Burnham and Anderson 2002), in our case the more parsimonious model. After ranking models according to their respective w_i values, the principle of parsimony was used to find the best tradeoff between biases related with the use of a simple model versus the loss of performance of a more general model.

In view of model classification results after w_i, the best model was identified as the one whose w_i was over 0.9. If no model had a w_i over 0.9, estimates and associated standard errors were model-averaged for each variable contained in the most parsimonious models (there was one most parsimonious model for swan flocks per season, one for swan families in summer and one for all swans per season) (Burnham and Anderson 2002). Confidence intervals allowed us to estimate the effect of covariates included in models. R software 2.10.1 was used (R Development Core Team 2009).

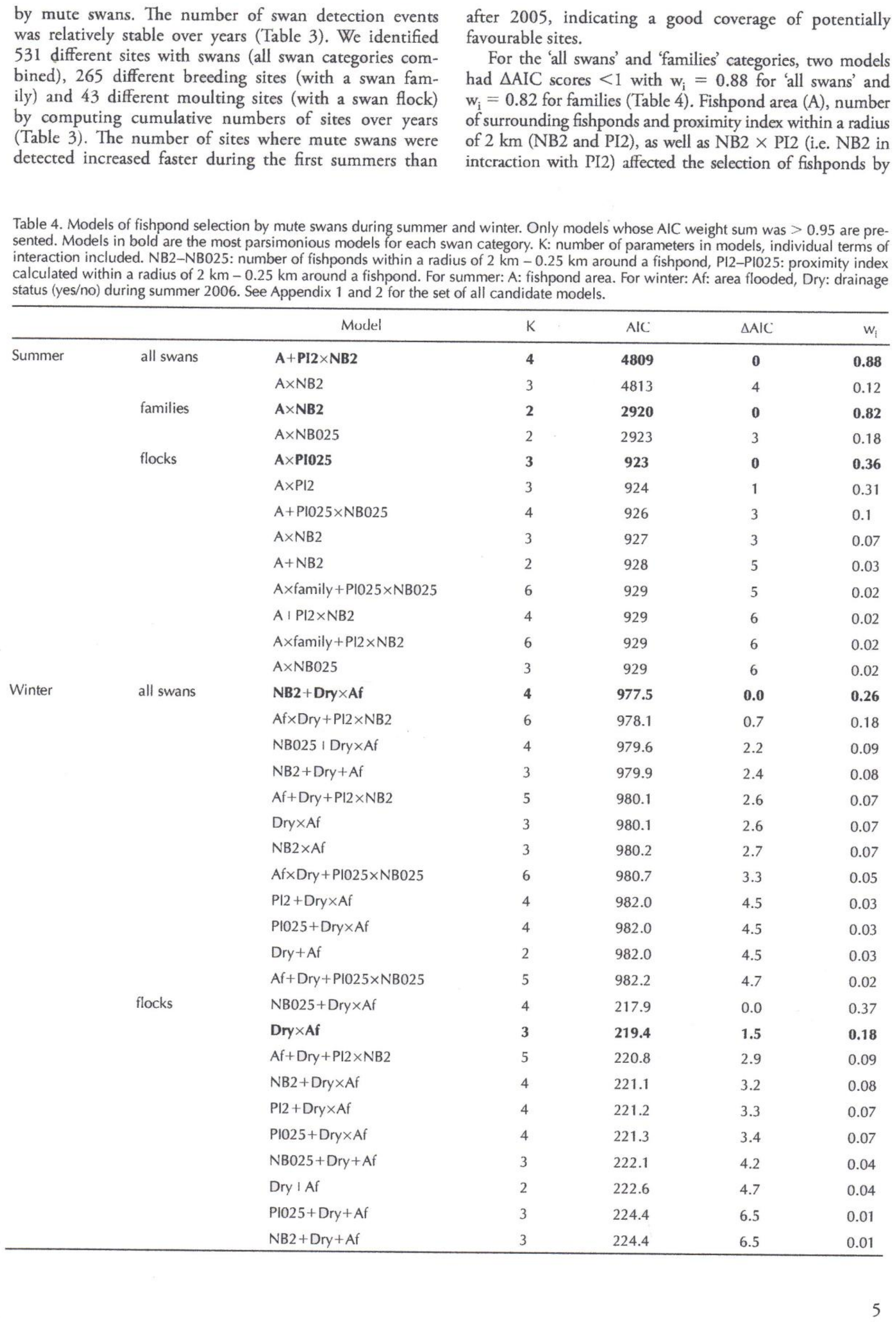
Results

Summer

We monitored 1210 fishponds at least once during summer. Each year, 10% of prospected fishponds were used

Table 3. Number of fishponds where mute swans (flocks, families or all swans) were detected annually between 2003 and 2008 during the last 10 days of June.

Year	2003	2004	2005	2006	2007	2008
All swans	172	160	189	154	159	178
Families	77	72	58	49	66	51
Flocks	11	12	15	15	9	12
Total number of fishponds monitored	900	955	1000	936	770	753



by mute swans. The number of swan detection events was relatively stable over years (Table 3). We identified 531 different sites with swans (all swan categories combined), 265 different breeding sites (with a swan family) and 43 different moulting sites (with a swan flock) by computing cumulative numbers of sites over years (Table 3). The number of sites where mute swans were detected increased faster during the first summers than after 2005, indicating a good coverage of potentially favourable sites.

For the 'all swans' and 'families' categories, two models had ΔAIC scores <1 with $w_i = 0.88$ for 'all swans' and $w_i = 0.82$ for families (Table 4). Fishpond area (A), number of surrounding fishponds and proximity index within a radius of 2 km (NB2 and PI2), as well as NB2 × PI2 (i.e. NB2 in interaction with PI2) affected the selection of fishponds by

Table 4. Models of fishpond selection by mute swans during summer and winter. Only models whose AIC weight sum was > 0.95 are presented. Models in bold are the most parsimonious models for each swan category. K: number of parameters in models, individual terms of interaction included. NB2–NB025: number of fishponds within a radius of 2 km – 0.25 km around a fishpond, PI2–PI025: proximity index calculated within a radius of 2 km – 0.25 km around a fishpond. For summer: A: fishpond area. For winter: Af: area flooded, Dry: drainage status (yes/no) during summer 2006. See Appendix 1 and 2 for the set of all candidate models.

		Model	K	AIC	ΔAIC	w_i
Summer	all swans	**A+PI2×NB2**	**4**	**4809**	**0**	**0.88**
		A×NB2	3	4813	4	0.12
	families	**A×NB2**	**2**	**2920**	**0**	**0.82**
		A×NB025	2	2923	3	0.18
	flocks	**A×PI025**	**3**	**923**	**0**	**0.36**
		A×PI2	3	924	1	0.31
		A+PI025×NB025	4	926	3	0.1
		A×NB2	3	927	3	0.07
		A+NB2	2	928	5	0.03
		A×family+PI025×NB025	6	929	5	0.02
		A+PI2×NB2	4	929	6	0.02
		A×family+PI2×NB2	6	929	6	0.02
		A×NB025	3	929	6	0.02
Winter	all swans	**NB2+Dry×Af**	**4**	**977.5**	**0.0**	**0.26**
		Af×Dry+PI2×NB2	6	978.1	0.7	0.18
		NB025+Dry×Af	4	979.6	2.2	0.09
		NB2+Dry+Af	3	979.9	2.4	0.08
		Af+Dry+PI2×NB2	5	980.1	2.6	0.07
		Dry×Af	3	980.1	2.6	0.07
		NB2×Af	3	980.2	2.7	0.07
		Af×Dry+PI025×NB025	6	980.7	3.3	0.05
		PI2+Dry×Af	4	982.0	4.5	0.03
		PI025+Dry×Af	4	982.0	4.5	0.03
		Dry+Af	2	982.0	4.5	0.03
		Af+Dry+PI025×NB025	5	982.2	4.7	0.02
	flocks	NB025+Dry×Af	4	217.9	0.0	0.37
		Dry×Af	**3**	**219.4**	**1.5**	**0.18**
		Af+Dry+PI2×NB2	5	220.8	2.9	0.09
		NB2+Dry×Af	4	221.1	3.2	0.08
		PI2+Dry×Af	4	221.2	3.3	0.07
		PI025+Dry×Af	4	221.3	3.4	0.07
		NB025+Dry+Af	3	222.1	4.2	0.04
		Dry+Af	2	222.6	4.7	0.04
		PI025+Dry+Af	3	224.4	6.5	0.01
		NB2+Dry+Af	3	224.4	6.5	0.01

the 'all swans' category (Table 5). Independently, all retained environmental factors positively influenced swan presence, but NB2 × PI2 had the opposite effect, meaning that PI2 negatively affected the relationship (i.e. decreased the value of the positive slope) between swan presence and NB2, and vice versa. Concerning families, the best model contained A in interaction with NB2. Occurrence of swan families on fishpond increased with A and NB2, but their interaction had a negative effect, implying that A negatively affected the relationship between family presence and NB2, and vice versa. For both the 'all swans' and the 'families' categories, the magnitude of the Area effect was larger than that of any other parameter included in the more parsimonious model.

The interaction of PI025 with A was included in the model selected to describe moulting sites (i.e. swan flocks, $w_i = 0.36$), the second best model included PI2 and its interaction with Area, and had similar weight of evidence ($w_i = 0.31$) (Table 4). Area had a large and positive effect, in contrast to other terms, especially interactions whose effect was negative and weak. The presence of swan families did not affect fishpond selection by moulting individuals in flocks, and therefore did not appear in the selected model.

Fishpond area was the only parameter included in all models, with a strong effect identified throughout model averaging, and its effect was therefore analysed in more detail with logistic regressions. The modelled function for the relationship between mute swan presence and fishpond area provided a good fit to the data for 'all swans' and 'flocks' on fishponds between 0.5 and 30 ha in area. The quality of the fit then weakened on larger fishponds (Fig. 2). Fishponds smaller than 10 and 30 ha had little chance of being selected by all swans or swans in flocks, respectively. The likelihood of occupancy increased with fishpond area for both categories. The quality of the fit was satisfactory between 0.5 and 20 ha for swan families, but was increasingly poor for increasingly large fishponds. The curve had a more linear shape for swan families than for the other two swan categories.

Spatial autocorrelation

There was some evidence of a non-random distribution of fishpond sizes over the landscape. Fishponds of similar size were more likely to be clumped, as shown by the positive (though relatively weak: < 0.1) and statistically significant value of the Moran's I coefficient within a 5 km radius. The value of that coefficient decreased gradually with distance (Fig. 3). We failed to demonstrate spatial autocorrelation within a larger radius (5 to 15 km), but significant negative spatial autocorrelations were found for distances superior to 15 km, although Moran's I coefficient was small. No strong evidence of spatial autocorrelation could be demonstrated on the residuals from models selected to describe the repartition of the 'all swans', 'flock' and 'families' categories according to fishpond characteristics every year (Fig. 4).

Table 5. Model-averaged parameter estimates, standard-errors and 95% confidence intervals of the variables present in models with ΔAIC ≤ 2 (Table 4), to explain fishpond selection by swans during summer and winter.

					95% CI	
			Estimate	SE	Upper	Lower
Summer	all swans	A	0.138	0.008	0.152	0.123
		PI2	0.046	0.012	0.070	0.022
		NB2	0.040	0.007	0.054	0.027
		PI2×NB2	–0.001	2.560×10^{-4}	-5.692×10^{-4}	–0.002
	families	A	0.206	0.028	0.261	0.151
		NB2	0.049	0.009	0.067	0.031
		A×NB2	–0.003	0.001	–0.002	–0.004
	flocks	A	0.252	0.067	0.383	0.121
		PI025	0.093	0.053	0.197	–0.011
		PI2	0.029	0.020	0.069	–0.011
		A×PI025	–0.003	0.002	0.001	–0.007
		A×PI2	–0.001	0.001	4.393×10^{-4}	–0.003
Winter	all swans	Af	0.044	0.009	0.062	0.026
		Dry	0.577	0.261	1.089	0.065
		NB2	0.024	0.013	0.049	–0.001
		PI2	0.007	0.009	0.024	–0.011
		Dry×Af	0.027	0.013	0.052	0.002
		PI2×NB2	-1.999×10^{-4}	1.984×10^{-4}	1.890×10^{-4}	–0.001
	flocks	Af	0.040	0.021	0.080	–0.001
		Dry	0.447	0.687	1.794	–0.899
		NB025	0.104	0.062	0.226	–0.019
		Dry×Af	0.057	0.025	0.106	0.008

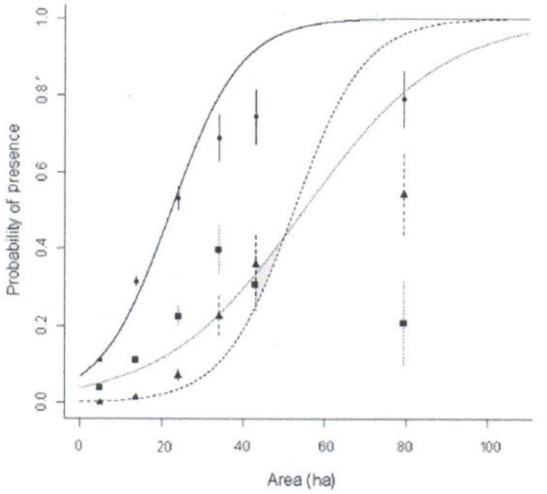


Figure 2. Logistic regression of mute swan presence ('all swans': circles and plain curve; 'families': squares and dotted curve; 'flocks': triangles and dashed curve) with their standard error on fishpond area for all summer observations. The model has been applied only to fishpond area without considering other spatial parameters.

Winter

A minimum of 133 fishponds were flooded during winter visits, hence were available to swans, but this number varied over counts (Table 6). Fishponds were frozen during two counts (Dec 2: 23.1% ± 37.7 of flooded area was frozen; Feb 1: 29.9% ± 38). At the end of the study period, the 'all swans' category had been detected on 112 different fishponds, and flocks on 26 different fishponds. Swans were not always detected on the same fishponds.

For the 'all swans' category, the more parsimonious model included NB2, plus Dry and its interaction with Af (Table 4). Af had the larger effect, which was positive, in addition to the effect of Dry and their interaction (Table 5). For the 'flocks' category, Af and its interaction with Dry appeared in the most parsimonious model (Table 4). The interaction term was the only parameter with a statistically significant (and positive) effect on swan flocking (Table 5).

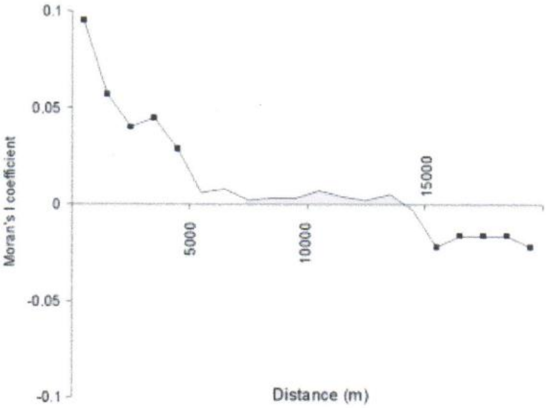


Figure 3. Correlogram of Moran's I coefficient for fishpond area, i.e. changes of this coefficient over classes of distances. A square indicates significant coefficients where appropriate.

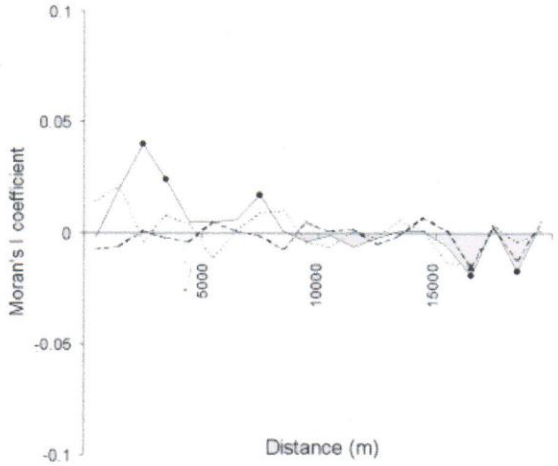


Figure 4. Correlograms of Moran's I coefficient calculated on residuals from the best-selected model to explain the presence of the 'all swans' (circles and plain curve), 'families' (squares and dotted curve) and 'flocks' (triangles and dashed curve) for 2003. Circles (for 'all swans') and triangles (for 'flocks') indicates when coefficient are significant. Correlograms for other years are similar (not shown).

As for the summer data, the logistic regressions for the presence of 'all swans' and 'flocks' relative to fishpond area are presented in Fig. 5. The presence of the 'all swans' category was correctly predicted by the regression between 0.5 and 30 ha, while fit quality weakened on larger fishponds. Occurrence likelihood by 'all swans' increased quickly with fishpond size, with sites over 10 ha being highly likely to be used during winter. The probability of swan flock presence was also adequately predicted (and was predicted to be low) from 0.5 to 20 ha, while the prediction was not as good for fishponds over 20 ha, although the likelihood of such fishponds to be visited by swan flocks was higher.

Fishpond drainage the previous summer increased attractiveness for swan flocks compared to fishponds that had been flooded throughout the year. In general, mute swans use of fishponds also differed between cultivations practiced on dried fishponds (Fig. 6). Mute swans preferentially used fishponds that got dried the summer before than those that remained flooded. Among dried fishponds, no statistically significant differences in preference could be detected between non-cultivated, cultivated in maize and cultivated other than in maize fishponds (all swans: $\chi^2 = 0.64$, DF = 2, p-value > 0.05; swan flocks: $\chi^2 = 2.59$, DF = 2, p-value > 0.05).

Discussion

Mute swan distribution over a fishpond mosaic landscape was influenced by individual fishpond characteristics (i.e. area), the environment surrounding fishponds (i.e. number of fishponds within varying distances and relative isolation), individual bird requirements (breeding versus non-breeding) and the effect of habitat management on available food resources (drainage and cultivation versus permanent flooding), all combining to affect the likelihood of bird presence, with varying effects over seasons.

Table 6. Number of fishponds monitored every two weeks from December 2006 to the beginning of March 2007 where we detected mute swans ('all swans' and 'flocks' categories). The same 165 fishponds were monitored throughout the study period.

	Dec-1	Dec-2	Jan-1	Jan-2	Feb-1	Feb-2	Feb-3	Mar-1
Flooded fishponds (>10% of total area flooded)	133	144	148	150	151	156	151	145
All swans	29	42	53	52	54	50	56	56
Flocks	15	12	12	11	7	12	7	7

At the scale of the region, the summer population was concentrated in sub-areas with numerous or poorly isolated fishponds (hypothesis 2). Within such subregions birds selected medium (10–30 ha) to large waterbodies (> 30 ha), as expected (hypothesis 1). During winter, fishpond drainage and cultivation during the previous summer as well as fishpond area explained most of the population distribution process. Fishpond drainage status was important because food availability, and therefore fishpond quality, differed drastically between fishponds that were flooded during the previous season (where only macrophyte dormancy organs were available the next winter) and those that got dried and subsequently cultivated (where swans could also rely on abundant crop remains). Consequently, the physical structure of fishponds and their surrounding landscape (i.e. number, and isolation) played a minor role in determining swan distribution on winter months (hypothesis 3). This may also explain why the effect of fishpond area on flock presence was weaker in winter compared to summer. This result suggests a strong dependence of winter flocks on patch quality.

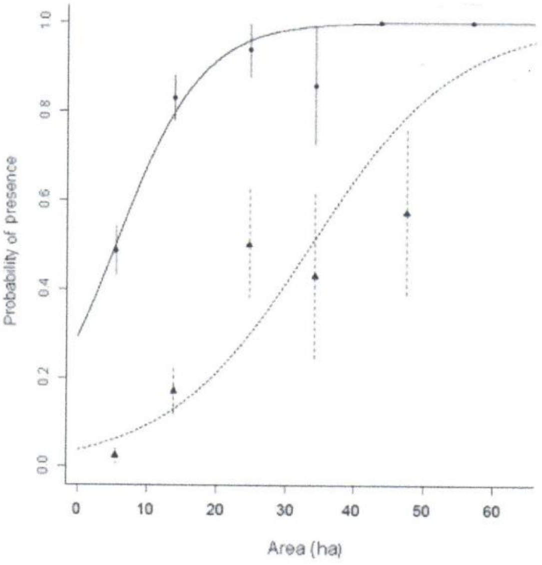


Figure 5. Logistic regression of swan presence ('all swans': circles and plain curve; 'flocks': triangles and dashed curve) with their standard error on fishpond area for all winter observations. Note that the relationship is here illustrated through fishpond area (A), not fishpond flooded area (Af) as in the models, because the latter is a more dynamic variable which may change over the course of the winter for a given fishpond. The model has been applied only to fishpond area without considering other spatial parameters.

Breeding status of birds also affected the fishpond selection process. Subadults and adults (i.e. flocks) which failed to breed have a preference for the larger waterbodies (> 30 ha) within subregions where fishponds are poorly isolated. This may allow birds to be faithful to the same subregion over successive summers, since they are likely to find an adjacent alternative moulting site if the waterbody they used the previous year is drained. Such moulting site fidelity has already been demonstrated for Brant *Branta bernicla* (O'Briain et al. 1998) and Steller's eider *Polysticta stelleri* (Flint et al. 2000).

Breeding birds considered the environment at a broader scale when selecting patches, and breeding occurred preferentially in subregions with either a great number of sites, or on medium to large fishponds. This explains the more linear trend of the logistic function between likelihood of occurrence and fishpond area for breeding as opposed to non-breeding birds, the latter showing a more sigmoid function. Non-breeders may completely avoid fishponds under a threshold area, therefore leading to a logistic curve that approximates a step function. Conversely, breeders may accept using a fishpond of smaller size, if this is within a favourable subregion (i.e. surrounded by numerous waterbodies). Such a pattern may be explained by swans being both philopatric (Spray et al. 2002 in Rowell and Spray 2004) and territorial (Conover and Kania 1994). They are therefore likely to come back to the same breeding area year after year, but may have to switch to local alternative fishponds within the subregion if their natal site is already occupied by a breeding pair, or unavailable because of drainage. The weaker dependence of breeding birds on patch size is likely due to more limited food requirements of a swan family than a swan flock.

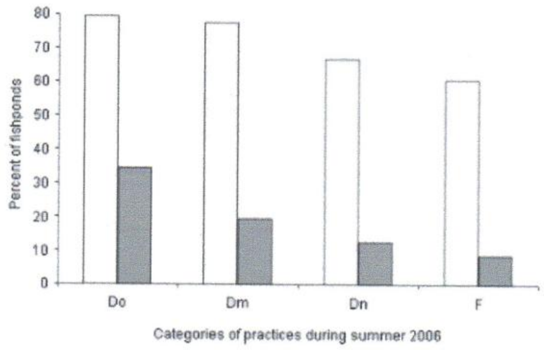


Figure 6. Percentage of fishponds where the 'all swans' category (white columns) and swan flocks (grey columns) were detected at least once during winter 2006–2007, depending on cultivation practices the summer before (Do: dry and cultivated with other cereals, Dm: dry and cultivated with maize, Dn: dry and not cultivated, F: flooded).

The presence of a family did not negatively affect the presence of bird flocks, because such moulting flocks are usually on larger sites, where resources are likely large enough to accommodate some swan families as well (hypothesis 4).

In complex habitats, species population dynamics depend upon the distribution of individuals on habitats as well as habitat-specific demographic rates, so that when habitat availability is reduced, mobile animals should use the remaining areas (Pulliam and Danielson 1991). The mute swan population in the Dombes is certainly not large enough to force breeding and non-breeding birds to coexist on the smaller fishponds, where territorial behaviour of the breeders could be a limiting factor in the presence of moulting birds, generating strong despotic distribution. The selection process described here is therefore liable to change depending on future population demography. If swan numbers were to increase in the coming years, the sites currently used may no longer be sufficient for all birds, so some birds may spread over other fishponds (smaller and more isolated). In the present case, it was not possible to detect inter-annual differences in the best models to explain swan presence. A more precise examination of temporal patterns in habitat selection by swans may require a specific study in the future over a longer time frame, through extinction/colonization processes in the landscape, as proposed by MacKenzie et al. (2003).

Wintering flocks occurred on fishponds (> 20 ha), preferentially those that got re-flooded after summer drainage. Cultivation type did not affect swan selection, which may indicate that crop type would be more likely to influence swan length of stay (number of swan-days) than swan single presence. Because waste grains represent a high energetic source both in terms of quality and quantity, it is expected than mute swans will maximize their net intake rate by preferentially staying on previously cultivated fishponds, until density-dependent processes lead to intake rate being similar to that in other patches, following the marginal value theorem (Charnov 1976). Nevertheless, swans already use in winter fishponds that remained flooded (and hence not cultivated) the previous summer. This may be due to swans also relying on macrophyte abundance (e.g. rhizomes or seeds), though this is difficult to quantify. The fact that some fishponds were underused given their size (see the gap between observed and predicted use in Fig. 2 and 5 for the largest fishponds) may be partly due to disturbance (hunting during winter), as well as food and nesting sites availability in these waterbodies. Rhizome availability in fishponds during spring migration has indeed been demonstrated to affect trumpeter swan *Cygnus buccinator* presence in Alberta (La Montagne et al. 2003).

In view of bird requirements for subregions with particular spatial characteristics, a greater spatial autocorrelation than the one observed would have been expected (hypothesis 5). Just like intraspecific segregation and selection processes by mute swans described above, the autocorrelation rate of swan distribution may also change in the future depending on population demography. The current swan population may not be large enough to create proper cores of presence. It would therefore be appropriate to study how spatial autocorrelation varies over time over longer periods, as suggested by Koenig and Knops (1998).

Results of this study provide insight into how herbivorous waterbird populations select resources within a fishpond complex, which may also be applied to ducks and particularly coot *Fulica atra.* Indeed, during the breeding period, preferential use of the same fishponds by mute swan pairs and by coots *Fulica atra* has already been demonstrated (Gayet in press). However, it should be kept in mind that not all species react in the same way to habitat configuration, as demonstrated for some forest birds by Villard et al. (1999). As opposed to the more traditional single site-oriented management and conservation procedures, the present study suggests that the scale of the patch itself may not be appropriate to understand the way waterbird populations behave and spread in such wetlands. As suggested by Haig et al. (1998), studies and conservation efforts should hence also consider connections between subunits to improve our understanding of the use and the importance of wetlands for waterbird communities.

In the Dombes region, the Mute swan is generally considered to have a negative impact on other waterfowl (through territorial behaviour) and on macrophytes (through grazing). However, any general impact demonstrated over a broad scale in such wetlands (e.g. decline of duck brood numbers, rarefaction of some macrophyte communities, euthrophication) should be considered with caution. Indeed, the way mute swans spread within specific subregions and use a limited number of fishponds implies that their potential impact should be limited in space if anything, so that broad ecological problems should not entirely be attributable to the swans. On the contrary, if mute swans cause any damage, this should be concentrated within some subregion, on few sites, over the long term. This may imply that the local plant or bird communities may hardly be able to compensate local swan macrophyte depletion or swan territoriality if they occur.

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Appendix 1. Models describing fishpond selection by mute swans during summer. Models are ranked according to their AIC weight. K: number of parameters in models, individual terms of interaction included. NB2 – NB025: number of fishponds within a radius of 2 km – 0.25 km around fishpond, PI2 – PI025: proximity index calculated within a radius of 2 km – 0.25 km around fishpond, A: fishpond area. For flocks: Family: presence of breeding birds (i.e. cygnets).

	Model	K	AIC	ΔAIC	w_i
All swans	A+PI2×NB2	4	4809	0	0.88
	A×NB2	3	4813	4	0.12
	A+NB2	2	4824	15	0
	A×NB025	3	4832	23	0
	A+PI025×NB025	4	4833	24	0
	A×PI2	3	4835	26	0
	A×PI025	3	4843	34	0
	A+PI2	2	4845	36	0
	A+NB025	2	4848	39	0
	A+PI025	2	4851	42	0
	A	1	4853	44	0
	NB2	1	5165	356	0
	PI025	1	5187	378	0
	PI2	1	5193	384	0
	NB025	1	5200	391	0
	Null	1	5259	450	0
Families	A×NB2	2	2920	0	0.82
	A×NB025	2	2923	3	0.18
	A×PI2	3	2935	15	0
	A×PI025	2	2939	19	0
	A+PI2×NB2	1	2941	21	0
	A+NB2	1	2946	26	0
	A+PI025×NB025	1	2952	32	0
	A	3	2955	35	0
	A+PI2	1	2956	36	0
	A+PI025	1	2957	37	0
	A+NB025	1	2957	37	0
	NB2	3	3040	120	0
	PI025	4	3059	139	0
	PI2	2	3060	140	0
	NB025	3	3063	143	0
	Null	4	3077	157	0
Flocks	A×PI025	3	923	0	0.36
	A×PI2	3	924	1	0.31
	A+PI025*NB025	4	926	3	0.1
	A×NB2	3	927	3	0.07
	A+NB2	2	928	5	0.03
	A×Family+PI025×NB025	6	929	5	0.02
	A+PI2×NB2	4	929	6	0.02
	A×Family+PI2×NB2	6	929	6	0.02
	A×NB025	3	929	6	0.02
	A+PI025	2	930	7	0.01
	A+PI2	2	930	7	0.01
	A×Family+NB2	4	931	8	0.01
	A+NB025	2	932	8	0.01
	A	1	932	9	0
	A×Family+PI025	4	932	9	0
	A×Family+PI2	4	933	10	0
	A+Family	2	934	11	0
	A×Family+NB025	4	934	11	0
	A×Family	3	935	12	0
	NB2	1	980	57	0
	PI025	1	981	58	0
	NB025	1	984	60	0
	PI2	1	985	62	0
	Null	1	993	70	0
	Family	1	995	71	0

Appendix 2. Models of fishpond selection by mute swans during winter. Models are ranked according to their AIC weight. K: number of parameters in models, individual terms of interaction included. Parameters as in appendix I except Af: area flooded, Ai: area taken in iced, Dry: drainage status (yes/no) during summer 2006.

	Model	K	AIC	ΔAIC	w_i
All swans	NB2+Dry×Af	4	977.5	0	0.26
	Af×Dry+PI2×NB2	6	978.1	0.7	0.18
	NB025+Dry×Af	4	979.6	2.2	0.09
	NB2+Dry+Af	3	979.9	2.4	0.08
	Af+Dry+PI2×NB2	5	980.1	2.6	0.07
	Dry×Af	3	980.1	2.6	0.07
	NB2×Af	3	980.2	2.7	0.07
	Af×Dry+PI025×NB025	6	980.7	3.3	0.05
	PI2+Dry×Af	4	982.0	4.5	0.03
	PI025+Dry×Af	4	982.0	4.5	0.03
	Dry+Af	2	982.0	4.5	0.03
	Af+Dry+PI025×NB025	5	982.2	4.7	0.02
	NB025+Dry+Af	3	982.2	4.8	0.02
	PI025+Dry+Af	3	983.6	6.1	0.01
	PI2+Dry+Af	3	984.0	6.5	0.01
	PI025×Af	3	993.3	15.8	0
	NB2+Af	2	997.8	20.3	0
	NB025×Af	3	998.4	20.9	0
	Af	1	998.7	21.2	0
	PI2×Af	3	999.1	21.6	0
	Af+PI2×NB2	4	999.2	21.7	0
	NB025+Af	2	999.6	22.2	0
	Ai+Af	2	999.7	22.3	0
	PI025+Af	2	1000.0	22.5	0
	Af+PI025×NB025	4	1000.2	22.7	0
	PI2+Af	2	1000.3	22.8	0
	Ai×Af	3	1000.3	22.9	0
	NB2	1	1029.6	52.2	0
	PI025	1	1030.9	53.4	0
	NB025	1	1031.9	54.4	0
	Dry	1	1034.6	57.2	0
	PI2	1	1038.5	61.1	0
	Null	1	1041.2	63.8	0
	Ai	1	1043.0	65.5	0
Flocks	NB025+Dry×Af	4	217.9	0	0.37
	Dry×Af	3	219.4	1.5	0.18
	Af+Dry+PI2×NB2	5	220.8	2.9	0.09
	NB2+Dry×Af	4	221.1	3.2	0.08
	PI2+Dry×Af	4	221.2	3.3	0.07
	PI025+Dry×Af	4	221.3	3.4	0.07
	NB025+Dry+Af	3	222.1	4.2	0.04
	Dry+Af	2	222.6	4.7	0.04
	PI025+Dry+Af	3	224.4	6.5	0.01
	NB2+Dry+Af	3	224.4	6.5	0.01
	PI2+Dry+Af	3	224.5	6.6	0.01
	Af×Dry+PI025×NB025	6	225.0	7.1	0.01
	Af×Dry+PI2×NB2	6	225.4	7.5	0.01
	NB025×Af	3	225.8	7.9	0.01
	NB2×Af	3	227.3	9.3	0
	Af+Dry+PI025×NB025	5	227.9	10.0	0
	PI025×Af	3	231.4	13.5	0
	PI2×Af	3	234.3	16.4	0
	Af	1	235.7	17.8	0
	NB025+Af	2	236.2	18.3	0
	PI025+Af	2	237.3	19.4	0
	Af+PI025×NB025	4	237.4	19.5	0
	Ai×Af	3	237.5	19.6	0
	PI2+Af	2	237.5	19.6	0

(Continued)

Appendix 2. *(Continued)*.

	Model	K	AIC	ΔAIC	w_i
Flocks	NB2+Af	2	237.7	19.7	0
	Af + Pl2×NB2	4	240.2	22.3	0
	NB025	1	254.1	36.2	0
	Pl025	1	254.3	36.3	0
	Dry	1	256.4	38.5	0
	NB2	1	257.2	39.3	0
	Pl2	1	258.1	40.1	0
	Null	1	261.3	43.4	0
	Ai	1	261.6	43.7	0

Article 2 : Mute swans (*Cygnus olor*) seasonal stay on fishponds over the annual cycle.

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In prep.

ABSTRACT

Capsule: Patterns of fishpond use intensity by Mute Swan *Cygnus olor* did not differ markedly between seasons, though individual fishponds were not repeatedly used by swans to the same extent over seasons.

Aims: To assess how swan stay patterns on fishponds vary over the year, if swan stay over a given fishpond differed between seasons, and to determine the factors responsible for potential differences.

Methods: Fishpond use (swan stay) was measured over 114 fishponds in the Dombes region, Eastern France. The effect of winter and summer resource availability as well as fishpond spatial configuration were considered as covariates.

Results: Birds responded both to fluctuating habitat properties and to their own requirements over the year. Fishpond area played a major role on swan stay. Food resources, i.e. crop remains and macrophytes, affected swan stay during winter and summer, respectively.

Conclusions: Different scenarios of food depletion by this expanding species may be formulated to predict their future distribution. Implications of these results for other wildfowl species (both migratory or semi-sedentary) are discussed, given the important role played by fishpond regions like the Dombes as a breeding or staging area for these birds.

INTRODUCTION

Species-specific requirements and environmental conditions both affect wildlife habitat selection processes throughout the year. In birds, many studies have dealt with waterfowl habitat selection during non-breeding period. Current knowledge underlines the combined roles of habitat patch size, resource availability and human disturbance on waterfowl habitat selection processes (see Tuite *et al.* 1984, Bell *et al.* 1997, Evans & Day 2001, Rees *et al.* 2005, Brochet *et al*. 2009, Fouque *et al*. 2009). During the non-breeding period, the gregarious behaviour of most waterfowl species (Owen & Black 1990), combined with heterogeneous resource availability, imply that individuals should be concentrated over space, generating flocks on the best quality sites, and concerns about which areas should better be preserved to provide optimum conditions to these species. The factors driving waterfowl stay during the breeding period have also been studied, though to a lesser extent, while the factors driving waterfowl stay in spring and autumn remain largely unexplored (see Arzel *et al*. 2006).

In any case, waterfowl habitat selection studies would benefit from approaches over several seasons, as pointed out by (MacKenzie *et al.* 2006). For waterfowl, such multiple season studies are often prevented by the migratory behaviour of most species. Among them, more sedentary populations are particular cases, but the way they select and use habitat patches over the year still has been poorly documented. Studying habitat use by sedentary waterfowl species may provide valuable information for themselves, but could also be relevant for either wintering or breeding populations of more migratory species (e.g. for wetland management). This should be of increasing importance over the coming years since some waterbirds may gradually loose their migratory behaviour due to human activities (e.g. winter foraging on cereal crops), climate change (global warming) or natural developments in ecosystems (e.g. natural successions, disease outbreaks) (Fiedler 2003). Furthermore, understanding how waterfowl stay on habitats over time is of prime interest given the impact large bird concentrations and repeated waterfowl use may have on the natural habitats. Indeed, several mechanisms are known to result from extended waterfowl stay: food resource depletion (Esselink *et al.* 1997, Tatu *et al.* 2006), nutrient loading (Post *et al.* 1998), transmission of avian influenza viruses (Olsen *et al*. 2006) or damages to crops (Loonen & De Vries 1995).

Fishpond regions of Western Europe and their mute swan (*Cygnus olor*) populations provide adequate environmental contexts to explore habitat use processes by waterfowl over the annual cycle. Indeed, habitat patches vary a lot over time and differ markedly over space in fishpond regions. They are also clearly spatially-delimited, allowing to easily assess waterfowl stay on individual ponds. Moreover, mute swans have *a priori* a sedentary behaviour, allowing to study their seasonal use of fishponds independently from massive arrival or departure of conspecifics. Solving the controversy over Mute swan in France (where it is both protected and suspected of damaging macrophyte beds), requires more detailed knowledge on their habitat use over time. Finally, inland freshwater fishponds play a key role for many breeding and migratory waterfowl populations. Mute swans stay may potentially be used as a proxy for other waterfowl, especially other herbivores like Coot (*Fulica atra*) and some ducks (e.g. Red-crested Pochard *Netta rufina*), given their shared preferences for the same sites during the breeding period (see Gayet *et al*. in press).

We already demonstrated in a previous study that swan presence depends on the birds' breeding status, fishpond size and aquatic environment (fishponds number and isolation) at different scales during summer and winter (Gayet et *al*. in press). Under 10 ha, fishponds were unlikely to be used by swans. A supplementary effect of resource availability was identified during winter. According to these preliminary results, we here expand the study to the whole annual cycle and aim at determining (1) if swan stay (rather than single presence) differs between seasons on a sample of fishponds, i.e. if the proportions of the fishpond sample that are used intensively, moderately or extensively are similar over seasons. Mute swans are gregarious throughout the year, except during the breeding period when breeders get territorial (Cramp *et al.* 1986). In addition, there are presumably strong differences in fishpond carrying capacity owing to agricultural practices when these are drained in summer (see below). We therefore expected a clear contrast in the pattern of swan use intensity between seasons, with a few sites heavily used and many sites lightly used during the swan's most gregarious periods (summer to winter), as opposed to a more heaven distribution of fishponds over use intensity classes during the rest of the year (spring).

We also assessed (2) if swan stay varies for a given fishpond over the year (or, conversely, if the level of use remains relatively stable for a given fishpond throughout the year). Fishpond use is expected to vary over time, according to the fluctuating nature of such environments and of swan behaviour over time.

Finally, we aimed at determining (3) the factors that drive swan stay on fishponds. It was especially expected that swan stay may increase with fishpond size and be affected by the aquatic environment just as swan presence does, swans being attracted to sites with more abundant food (i.e. flooded sites with macrophyte beds for summer, and previously dried and cultivated sites for winter).

METHODS

Study area

This study took place in the Dombes, in the Département of the Ain (Eastern France - 45°57'N, 05°02'E). The Dombes is one of the largest fishpond regions in France (1,450 fishponds spread over 1,600 km², average area = 7.3 ha ± 0.2 ha (SE)). One quarter of the fishponds have an area over 10 ha. The particularity of this region lies in the regular use of fishponds as arable lands (either cultivated or not). From September to March, fishpond status varies a lot due to temporary emptying of flooded fishponds for fishing, and due to re-flooding of previously dried fishponds. During spring and summer, fishpond status remains constant (i.e. either flooded or dried).

Fishpond sample

The sample consisted in 106 fishponds selected after their area and agricultural cultivations. We selected sites whose area was over 10 ha (average area = 18.1 ha ± 0.8 ha (SE)), as swans preferentially use fishponds above this size threshold. Note that we avoided larger sites (>50 ha), as they are rare in the Dombes, and thus represent rare cases (n=15 out of 1,450). Concerning agricultural cultivation types, 64 fishponds were flooded and 42 fishponds were dried during summer 2007 (of which 11 were non-cultivated, 20 were cultivated with maize and 11 were cultivated with other cereals).

Starting in early December 2007, fishponds were monitored over one year, i.e. until late November 2008. 17 of the 106 fishponds got dried during summer 2008. The sample was therefore unbalanced in favour of 2008-flooded fishponds during autumn 2008. We hence added eight 2008-dried fishponds to our sample for the autumn 2008 sample.

Swan stay

A unique observer (GG) visited fishponds every second week. During each visit, he estimated the flooded area with a 10% interval and counted swans (adults and cygnets) on each fishpond. To measure swan stay, we computed swan.days, using (Desnouhes *et al.* 2003) formula for geese:

$$\Sigma^{n}_{i=1} \mathrm{swans}_{i} + (((\mathrm{swans}_{i}+\mathrm{swans}_{i+1})/2)/*(\mathrm{date}_{i+1}-\mathrm{date}_{i}-1))$$

where n is the number of monitoring sessions, swans is the number of birds and i is for date. Swan.days were calculated per season, which divided the annual cycle into four three-months periods. Seasons were here related both to fishpond management and swan biological cycle rather than the traditional season dates. From March to May ("spring"), swan pairs establish breeding territories whereas subadults spread over fishponds. From June to August ("summer"), non-breeding subadults and adults which failed breeding flock on moulting sites while breeding swans with cygnets still remain on the breeding sites. From September to November ("autumn") swan families leave their breeding territories to flock with conspecifics. In the autumn swans are hence gregarious as they are during "winter" (December to February), when larger flocks are expected to occur. To compare seasonal patterns of fishpond use intensity (question 1), we standardized swan.days on sites by fishpond size, obtaining swan.days/ha. For the rest of the analyses (question 2 and 3) we assessed how stay vary over seasons according to covariates, and we used swan.days. Note that we ensured that swan.days and swan.days/ha were highly correlated for each season (not shown).

Fishpond environmental covariates

The first set of environmental covariates described fishpond spatial configuration. We measured fishpond area ("AREA", in ha) in addition to the number of fishponds within short (250m, termed "NB250") and longer (2km, termed "NB2000") distance. Such distances describe the proximate and the remote aquatic environment of fishponds, and distances were selected so as to avoid strong multicolinearity between measured values. We also measured fishponds isolation using a proximity index (Gustafson & Parker 1994) at the same distances than NB (termed "PI250" and "PI2000"). The proximity index was calculated as the sum of the ratios of fishpond sizes and distances within the considered radius.

The second set of environmental covariates considered food resources available to mute swans. During autumn and winter, there is a strong contrast of resource availability depending on recent fishpond management history. Indeed, previously dried fishponds provide waste grains or natural seeds easy available to swans compared to natural macrophyte dormancy organs (seeds, tubers, rhizomes) in the sediment of previously flooded fishponds. The quantity of grains available after harvest is non negligible and can represent several tens of kilograms per hectare (see e.g. with rice (Stafford *et al.* 2006)). Every season, we therefore differentiated fishponds that got dried or flooded the preceding summer (termed "HISTORY", i.e. flooded or dried; *nota bene*: all studied fishponds were obviously flooded while being monitored, so "HISTORY" stands for the flooding history of a given fishpond; fishponds were considered for analyses within a given season only when they were actually flooded for a sufficient part of that season, see below). During summer, aquatic macrophytes are the only resource available to swans (because even if the fishpond got dried and cultivated the previous year, potential waste grain get depleted during autumn and winter). We then estimated open water area that was covered with aquatic macrophytes during summer. This information comes from aerial photographs taken from an aircraft at the beginning of July 2008 (at the onset development of most macrophytes species and in the middle of summer). Open water area occupied by macrophytes was expressed per class of 10% (termed "MACROPHYTES").

Statistical analyses

Every season, we considered only fishponds that had water during at least one month and an half (i.e. a minimum of three visits) for estimating swan.days. As a first step in the analyses, we determined if the distribution of fishponds among use intensity classes (swan.days/ha) differed between seasons with χ^2 tests. We next measured if swan stay (swan.days) per fishpond varied seasonally by using Friedman tests.

As a second step, we assessed the relative potential influence of fishpond covariates on swan stay (swan.days) with General Linear Models (GLM). Analyses were performed separately for each season. All parameters were included in the departure model. AREA was in interaction with HISTORY for all seasons. In addition, AREA was in interaction with MACROPHYTES for summer. PIx and NBx were included in the departure model in interaction with each other at their respective distance of 250 and 2000m (i.e. NB250*PI250 and NB2000*PI2000). This model was then simplified during a backwards-stepwise model selection procedure. Parameters whose value was not significant at p=0.05 were gradually removed. Swan stay derived from normality, so that values were log-transformed to meet normality criteria. We used R 2.10.1 software for all statistical analyses (R Development Core Team 2009).

RESULTS

Number of swans counted over the year

The number of fishponds with water fluctuated over seasons due to emptying or their use as arable lands. 105 fishponds had water during winter, 94 during spring, 93 during summer and 107 during autumn, and were hence available to swans each season. The maximum number of swans counted was during the last week of December (n=835 swans in total over all surveyed fishponds) (Figure 1). It was the unique visit when fishponds were taken in ice, though icing covered only a part of most fishpond area. The number of swans counted then tended to decrease until the end of May where numbers peaked again (ca. 400 individuals), though to a more limited extent than in winter. The number of swans then re-decreased until reaching a minimum during the last week of September (n= 153 swans in total).

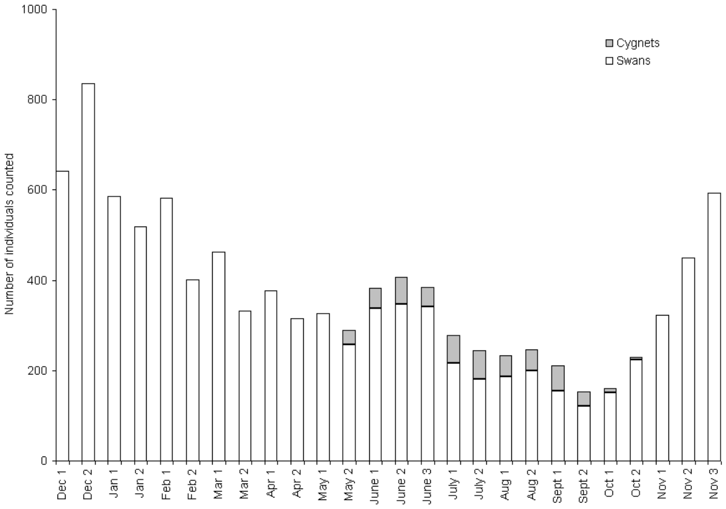

Figure 1 : Number of swans and cygnets counted every two weeks over the fishpond sample.

Flocking (defined as a group of at least 10 adult individuals observed during a minimum of two successive visits) occurred on 25 fishponds. Flocking was minimum during spring and summer (and then occurred on moulting sites), as it was recorded on only 6 sites. Flocking then occurred on 9 sites in autumn and reached its maximum during winter (14 sites). 8 fishponds were used during two seasons as flocking sites, and 2 fishponds were used as such during three seasons. Twenty-eight fishponds were used as nesting sites (i.e. swan clutches observed) and on 23 fishponds were swan families with cygnets observed during at least two successive visits. At the end of the monitoring period, fishpond use by swans remained undetected on 8 sites only.

Pattern of use intensity over seasons

Result of the χ^2 test failed to detect any difference in the distribution of fishponds over use intensity classes between seasons (χ^2= 6.82, df = 6, P = 0.34) (Table 1): there was a similar share of heavily (>20 swan.days/ha), moderately (>5 swan.days/ha) and lightly (<5 swan.days/ha) used fishponds in the sample in all seasons.

Table 1 : Number of fishponds in each swan stay category (expressed in swan.days/ha) per season.

	Winter 07/08	Spring	Summer	Autumn
<5 swan.days/ha	46	39	44	59
<20 swan.days/ha	38	38	28	34
>20 swan.days/ha	21	17	21	14

Swan stay over seasons

Mean swan stay on fishponds was highest during winter (> 500 swan.days per fishpond), but inter-fishpond variations were large (Figure 2). The longest stays (> 5,000 swan.days) occurred on 3 fishponds in winter, all of which having been dried the previous summer. Without these extreme values, mean winter swan stay was close from that of the other seasons (332.4 ± 67.8 (SE)). During spring, summer and autumn, mean use and variations between fishponds were lower (average : 300 to 400 swan.days). Friedman test however indicated that swan stay per individual fishpond varied over the year (Friedman χ^2 = 19.02, df = 3, p-value < 0.001), even when removing the three extreme winter values (Friedman χ^2 = 16.49, df = 3, p-value < 0.001): fishponds heavily used by swans in a season were not necessarily also used heavily in another season.

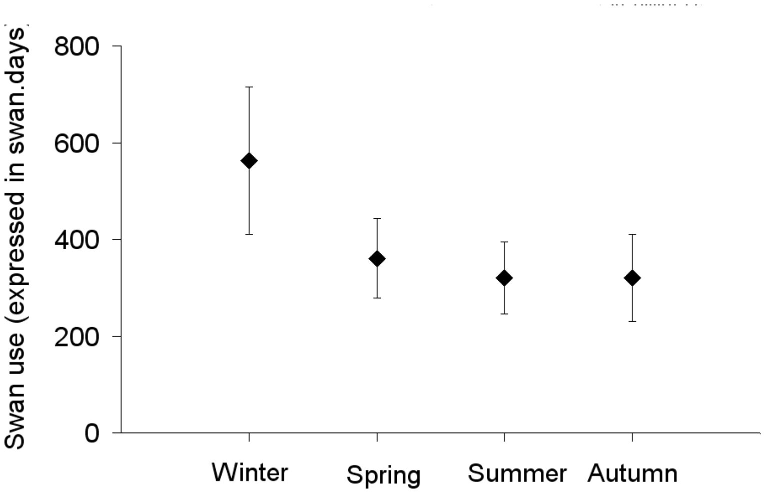

Figure 2 : Swan stay on fishponds from winter 2007/2008 to autumn 2008. Dots represent means and bars are standard-errors.

Factors affecting swan stay over seasons

For winter, the final model only included AREA and HISTORY. 13% of swan.days variations were explained by the model (Table 2). HISTORY (i.e. flooding versus non-flooding) had a negative effect, indicating that swan stay was higher on fishponds dried the previous summer. AREA had a positive effect, indicating high swan.days values on larger fishponds. By considering only dried fishpond in a supplementary analysis testing for the kind of cultivations as a unique parameter in the GLM, we did not detect any difference in winter swan.days between fishponds that got non-cultivated, cultivated with maize or cultivated with other cereals when dried the previous summer ($F_{2,39}$: 0.13; r^2: -0.04; p-value > 0.05).

During spring, 10% of the variance in swan stay variance was explained by the final model, which contained only AREA. Fishpond area had a positive effect on swan stay.

It was in summer that the maximum share of the variance got explained by the model (r^2=0.39). The final summer GLM included AREA and its interaction with MACROPHYTES, plus PI2000 and its interaction with NB2000. AREA and its interaction with MACROPHYTES had a statistically significant positive effect. Swan stay thus increased with fishpond size, especially when a large proportion of open water area was covered by aquatic macrophytes, or vice versa. PI2000 and NB2000 terms were positive and statistically significant. Their interaction had the opposite effect, meaning that swan stay increased on sites with numerous, or dense aquatic environment at a 2000m distance.

Finally, for autumn, 11% of swan stay variance was explained by the final model, which included AREA, PI250 and its interaction with NB250. AREA and PI250 had a statistically significant positive effect, but the interaction term (PI250*NB250) unbalanced the effect of PI250. Swan stay therefore increased with fishpond size or on sites which form dense and large aquatic environments, except when these were surrounded by numerous waterbodies.

Table 2 : Results of General Linear Models after a backwards stepwise selection procedure of parameters at P=0.05 to explain swan stay on fishponds each season. “AREA” is for fishpond size (square meters). “PIx” and “NBx” are indices of isolation and number of fishponds within a radius of 250 m and 2000 m. “HISTORY” represents the practice exerted on fishpond the previous summer (flooded versus dried). “MACROPHYTES” is the percentage of fishponds area occupied by submerged aquatic vegetation during summer.

		Estimate ± SE	t value	P
Winter	Final model : $F_{2,102} = 8.78$; $r^2 = 0.13$; $P < 0.001$			
	Intercept	3.83 ± 0.50	7.65	***
	AREA	0.08 ± 0.02	3.29	**
	HISTORY	-1.14 ± 0.40	-2.85	**
Spring	Final model : $F_{1,92} = 11.64$; $r^2 = 0.10$; $P < 0.001$			
	Intercept	2.68 ± 0.49	5.45	***
	AREA	0.08 ± 0.03	3.41	***
Summer	Final model : $F_{6,86} = 10.59$; $r^2 = 0.39$; $P < 0.0001$			
	Intercept	-2.33 ± 1.37	-1.70	.
	AREA	0.07 ± 0.04	1.56	
	MACROPHYTES	-0.03 ± 0.02	-1.47	
	PI2000	$1.22^{e-05} \pm 4.14^{e-06}$	2.95	**
	NB2000	0.12 ± 0.03	4.32	***
	AREA*MACROPHYTES	$2.14^{e-03} \pm 9.39^{e-04}$	2.28	*
	PI2000*NB2000	$-2.91^{e-07} \pm 8.69^{e-08}$	-3.34	**
Autumn	Final model : $F_{4,102} = 4.18$; $r^2 = 0.11$; $P < 0.01$			
	Intercept	1.43 ± 0.69	2.07	*
	AREA	0.07 ± 0.03	2.28	*
	PI250	$2.13^{e-05} \pm 8.59^{e-06}$	2.48	*
	NB250	0.09 ± 0.14	0.63	
	PI250*NB250	$-2.58^{e-06} \pm 1.16^{e-06}$	-2.22	*

“***”: $p < 0.001$; “**”: $p < 0.01$; “*”: $p < 0.05$; “.”: $p < 0.1$

DISCUSSION

Swan use intensity over the annual cycle

The patterns of site use intensity by a sedentary wildfowl such as mute swan did not differ between seasons in a fishpond region: a similar share of the fishponds were heavily, moderately and lightly used, despite extreme values on a few wintering sites. Given our sampling design limited to relatively large fishponds (i.e. over 10 ha), we expected more numerous flocking sites. Such heavy use may sometimes, however, only be temporary if birds regularly switch from a fishpond to another when resources get depleted. The largest number of flocking sites was observed during winter. Temporary stay of the same individuals over the season may explain why only 3 sites with high densities were identified. Large numbers of swans were recorded both during winter and late autumn, but variations in swan stay over seasons were of lower magnitude than expected.

Such stability in the distribution of fishponds over swan use classes may however hide relatively large intra-seasonal differences in use at the fishpond level. Indeed, small numbers of birds for long periods may result in the same use than larger numbers of birds during shorter periods. It is known in swans that some pairs remain on their breeding site throughout the year (see Scott 1984), while at the same time there could be flocks of non-breeders even in spring. These opposite and simultaneous strategies may buffer any pattern of aggregation over the year, hence making it difficult to detect any change in the distribution of fishponds over use intensity classes.

Swan stay on fishponds over seasons

Despite the above result, individual fishponds were not repeatedly used by swans to the same extent over seasons, because swans were responding to fishpond specific properties as well as being guided by their own fluctuating requirements. There were, however, some cases where flocks occurred repeatedly on the same sites over successive seasons. As a consequence, swans may exert a high grazing pressure on the food resources of such fishponds. In addition to grazing, indirect consequences associated with high waterfowl stay (e.g. nutrient loading or transmission of diseases) would be likely to accumulate over the year over such repeatedly used fishponds. Further studies on the effects of long waterfowl stay and associated biological mechanisms would be necessary.

Factors affecting seasonal swan stay

This approach based on swan stay provides new insights into habitat selection processes by swans, and corroborates their winter dependence for previously dried or large fishponds (Gayet *et al.* in press). On the one hand, swan dependence to large sites demonstrates that stay does not depend only on drought, but that swans can also select sites that remained flooded if these are large enough. In this case, swans likely rely on macrophytes dormancy organs. On the other hand, their dependence on drought is particularly illustrated here by the occurrence of higher winter swan stay on such sites. This result underlines the role of such temporarily dried wetlands for wildlife. Rice fields after harvest have a similar role for wintering wildfowl in the Mississippi Alluvial Valley (see Stafford *et al.* 2006) or in the

Central Valley of California. In this latter case, waterfowl are considered to accelerate straw decomposition, which benefits both waterfowl and rice growers (Bird *et al.* 2000). That the effect of fishpond history was not significant in autumn may be explained by the process of re-flooding, which started in November, and the late persistence of macrophytes on sites which remained flooded. Given the later harvest of maize as well as the presumed higher detectability and nutritional value of maize seeds (McNab & Shannon 1974) compared to other cereals, we expected that cultivation types would further explain differences in winter swan stay among dried and cultivated fishponds. The lack of such an effect may be due to a quick depletion of such waste grains.

The preferential use of previously dried fishponds by wintering swans has a range of potential consequences. Firstly, the consumption of waste grains by swans may limit access to a large quantity of easily accessible food to other animals like Carp (*Cyprinus carpio*) or wildfowl, and hence potentially be detrimental to these species through a competition process. On the other hand, the fact that swans preferentially stay on previously dried fishponds may limit the negative impact of their grazing on fishpond ecosystems over the region. Indeed, Dombes fishponds are regularly dried (one year) and reflooded (three years on average). Despite wintering site fidelity over the long term, swans should therefore regularly switch between fishponds over years, preventing extended stay from always occurring on the same, preferred, sites. Finally, the preference of swans for previously dried fishponds may limit more intensive winter use of natural plants on previously flooded sites: this would be especially beneficial to such macrophytes which are in dormancy stage in winter, when plants are known to be less resistant to consumption by herbivores (Boege & Marquis 2005). Summer-dried fishponds should therefore play a similar role in the Dombes fishpond ecosystem than sacrificed cultures in some areas (e.g. Montrose Basin in England), that are used to avoid swan from damaging other fields. In the same way, Gauthier *et al.* (2005) suggested that such use of arable lands by Snow geese (*Chen caerulescens*) in Canada may prevent overgrazing of natural marshes.

During summer, fishpond spatial configuration and macrophyte cover play an important role on swan stay. Mitchell & Perrow (1998) reviewed the literature on such relationships between wildfowl abundance and macrophytes. Even if not systematic, this review highlighted that wildfowl abundance was indeed generally associated with high development of macrophytes beds in lakes. The lack of a relationship between swan stay and macrophyte cover alone may result from early macrophyte depletion by swans on the smaller fishponds we sampled. On such sites, swans may have already established and depleted macrophyte beds before vegetation measures (aerial photographs in July). The relationship with macrophyte beds may therefore be observable on larger fishponds owing to their higher carrying capacity and the greater attractiveness of large sites with dense vegetation. The role of fishpond spatial configuration may be detected during summer only (although affecting breeding swans even in spring, see Gayet *et al.* in press) because high swan.days values could be associated with lower isolation only when the simultaneous presence of adults and cygnets increases swan stay measurement. The sole presence of adults in spring may result in too low swan.days values for this association to be detected.

During autumn, swan stay increased with both fishpond area and fishpond aggregation at short distance. Such patterns may result from a combination of habitat changes (e.g. gradually re-flooding of fishponds that got cultivated the previous summer) and changes in the birds' behaviour (e.g. families leaving their territories). On top of this, the composition of macrophyte beds in terms of early-growing (spring) and late-decaying (autumn) plants may also affect fishpond attractiveness to swans. Such processes would require further studies.

Implications for wildfowl populations

The present study is based on a sedentary bird population, but its conclusions may also apply to the wintering and breeding populations of migratory waterfowl (especially herbivores). Our results confirm the role of fishpond area for waterfowl in such an environment. Depending on the biological stage of both wildfowl and freshwater habitats, some covariates such as habitat management, fishpond spatial configuration and food resource play an additional role on wildfowl stay. In such disturbed and artificial environments, appropriate summer habitat management, sometimes including some sort of agricultural use, should be regarded as an opportunity to promote carrying capacity for wintering wildfowl through increased food availability. Because it leads to the aggregation of foragers in some specific waterbodies, this may also be beneficial to the general fishpond environment by decreasing average wildfowl pressure over their natural food resources.

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Article 3 : Breeding Mute Swan habitat selection when accounting for detectability : a plastic behaviour consistent with rapidly expanding populations.

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ABSTRACT

A number of native and exotic animal species show dramatic population increases in terms of both numbers and geographic range. Understanding the habitat selection processes behind such increases is crucial to implement adequate management measures. Mute swan *(Cygnus olor)* populations have experienced a tremendous demographic and geographic expansion in Western Europe during the twentieth century, colonizing a wide variety of aquatic habitats. We aimed at assessing how swans select nesting sites during the pre-laying and laying periods on medium to large fishponds (from 10 to 50 hectares) in Eastern France, while accounting for detectability biases and testing for the effects of fishpond spatial configuration, vegetation resources, human disturbance and habitat management. Our results demonstrate that the Mute Swan is a non-selective species regarding its nesting habitat among such fishponds, using these independently from the parameters considered. Although Mute Swan is one of the least cryptic Anatidae, owing to its white colour and large size, detection of breeding pairs remains imperfect for each over several sampling occasion. However, because we repeated the sampling sessions, detection of swan pairs by the end of the monitoring period was as high as 0.94. These results are consistent with previous assertions that the Mute swan is a species of high ecological plasticity, which may partly explain its recent colonization rates. Given that even swan breeding events were imperfectly detected on each occasion, we highlight the fact that most studies of breeding ducks (which are more cryptic) would be considerably improved by better considering detection biases.

INTRODUCTION

Habitat selection processes are crucial to consider before implementing management procedures, since habitat selection affects the spatial distribution of individuals, and hence demographic parameters of populations, especially during the breeding season. Wildfowl breeding habitats have been intensively studied, because the dynamics of these populations have important economic consequences (most of these are hunted) while they are at the same time threatened by wetlands destruction. During the breeding period, wildfowl habitat selection is affected by a range of factors including vegetation shelter, predation risk, waterbody size, food supply and the presence of congeners (Merendhino & Anknew 1994; Pöysä *et al*. 1998; Rodway 1998; Clark & Shutler 1999).

Mute swans (*Cygnus olor*) are now present in a wide variety of habitats (see Kirby *et al.* 1994; Fouque *et al.* 2007), including e.g. fishponds, lakes, urban ponds or fluvial canals during the breeding season. Such plasticity may partly explain the wide geographic expansion of the species in Western Europe over the last decades. Swan families are nonetheless showing preferences during their site selection process within a given habitat type: in the context of a fishpond region, we already demonstrated that they are especially using medium to large fishponds, as well as fishponds that are poorly isolated from other, neighbouring ones (Gayet *et al*., in press). Breeding sites (i.e. sites where a swan family with cygnets was observed) may however not adequately represent nesting sites (i.e. where nests were actually located), as swans may emigrate after hatching as several other waterfowl do (e.g. Pöysä & Paasivaara 2006). Just like other wildfowl, swans may also likely select nesting sites after other parameters than their sole spatial configuration. In this paper, we examined how environmental (surrounding fishpond number, isolation, relative fishpond size, disturbance), and resource parameters (fishpond management, emergent and submerged aquatic vegetation) may both affect Mute swan pair occupancy of fishponds during the pre-laying and laying periods (from March to May), independently from the size of these fishponds. Such habitat selection studies may be severely affected by biases associated with imperfect detection (Manly *et al.* 2002), possibly generating inappropriate inferences (MacKenzie *et al*. 2005). In order to overcome such limitations, all the analyses were carried out after assessing detection probability of swan pairs.

METHODS

Study area and species

The study took place in the Dombes (Eastern France), a wide fishpond region of approximately 1,450 waterbodies (average area = 7.3 ha ± 0.2 ha SE) spread over 1,600 km² in Eastern France (45°57’N, 05°02’E). One of the Dombes particularity is the artificial drought conducted on fishponds by landowners during summer every third year on average. Most fishponds are bordered or covered to some extent by reedbeds. Some of the fishponds hence have blind splots due to emergent vegetation or to the shape of the fishpond itself.

The Mute swan (*Cygnus olor*) nested for the first time in Dombes during the 1970s, and extended since then until reaching a summer population estimated to be of ca. 1,000 individuals (Benmergui *et al.* 2005). This species is well known for its territorial behaviour during the breeding period, though swans can also sometimes remain on their territory throughout the year (Scott 1984). Mute swans establish on nesting sites during the pre-laying period. After building the nest (often in reedbeds), the female lays eggs from April onwards, incubation then lasting for 36 days. If the first clutch fails, a replacement clutch may be laid after 2-4 weeks (Cramp *et al*. 1986). Once cygnets hatch (May), swans either stay on the same waterbody or switch to another site to rear the cygnets. If reproduction fails, swans most often join non-breeders in moulting flocks.

Bird surveys

The presence of breeding Mute Swans was monitored over 94 selected fishponds, during the pre-laying and laying periods (i.e. from the end of March until early May) of year 2008. Though waterbodies under 10 ha represent 75% of the Dombes fishponds they are hardly used by Swan families (i.e. adults and cygnets), which preferentially use sites over this size threshold (Gayet *et al.* in press). Furthermore, we expected the closure assumption required for analyses (see below) to be violated on fishponds under 10 ha, because of swan culling operations leading either to complete failure of the breeding event or to subsequent movement of the adults to alternative fishponds to lay a replacement clutch (personal observation). Indeed, landowners mostly consider swans like a pest in the Dombes, and are both more likely to be able to detect a swan pair and to easily access the nest for egg destruction on smaller fishponds. For these reasons, fishponds under 10 ha were discarded from the analyses, bounding our conclusions to fishponds over this area.

Diurnal surveys were performed using a 20 x 60 telescope from the best sighting site on the bank of each fishpond. A survey consisted in a 1 to 2 minutes scan performed by one single observer (GG). Each fishpond was monitored on 4 occasions at two weeks interval. During each of such scans, presence/absence records were encoded as a binary variable to generate detection histories consisting in a series of four ‘0’ (in the case of the species not being detected) and ‘1’ values (in the case of the species being detected). As we were interested in examining only occupancy by breeding Mute Swans, the species was considered as being present when we detected the presence of a pair of adults or a single adult with a nesting behaviour. As non-breeders are gregarious throughout the year, we are confident that the presence of only two individuals represents a swan pair.

Fishpond and landscape characteristics

Based on previous knowledge of the species ecology, we gathered data on several environmental characteristics of the surveyed fishponds. A first set of variables aimed at describing the main characteristics of each fishpond: using ArcGIS software (ESRI Inc. 2009) and aerial photographs, we calculated open water area (AREA), perimeter length (PERIMETER), shape complexity (SHAPE, calculated as perimeter length divided by pond area) and the fraction of the fishpond covered by reedbeds (REEDBED) and by submerged aquatic vegetation (MACROPHYTES), defined as the proportion of fishpond area occupied by submerged aquatic vegetation in early July (at the onset of most aquatic macrophyte growth). REEDBED and MACROPHYTES represented potential nesting habitats and food resources for swans, respectively. We also recorded the management practice exerted on each pond during the previous summer (PRACTICE, categorized as either flooded, $n = 53$ or dried, $n = 41$). As human disturbance may affect swans (Rees *et al*. 2005), we also recorded the presence of adjacent main roads (if less than 30 m from fishpond bank) as a potential disturbance factor (ROAD, categorized as a binary variable). A second set of variables aimed at describing the proximate (i.e. within a radius of 0.25 km) and more distant (i.e. within a radius of 2 km) surrounding aquatic environment of surveyed fishponds. We determined the relative isolation of fishponds at each spatial scale by calculating the number of adjacent fishponds (N_{proxi}, $N_{distant}$) and by computing a proximity index (P_{proxi}, $P_{distant}$, see Gustafson and Parker 1994). To investigate whether fishponds were more likely to be occupied if they were among the largest sites within a bounded environment, we also computed the z-standardized difference between fishpond size and average size of all fishponds within 0.25 and 2 km radii ($MEAN_{proxi}$ and $MEAN_{distant}$, respectively).

Analytical procedure

We modelled site occupancy as a function of site-specific covariates using the likelihood-based method designed by (MacKenzie *et al*. 2002). This modelling approach, based on the framework of closed-population mark–recapture analysis, allows the probability that a site is occupied to be estimated, while accounting for imperfect detectability. One important assumption of the closed-population mark-recapture theory is the within-season closure assumption (i.e. site are "closed" to changes in occupancy during the monitoring period, MacKenzie *et al*. 2002). By limiting our 4 sampling occasions within a temporal window that encompassed the pre-laying and laying periods of the species, we could be confident that the closure assumption was met.

Analyses were conducted using the single-season occupancy model implemented in Program MARK (White & Burnham, 1999). The basic parametrization (Ψ, p) of this class of models allows estimation of the following parameters: Ψ_i, the probability that a breeding Mute Swan is present at fishpond i during the sampling period and p_{it}, the probability (given presence) that a breeding event is detected at fishpond i on occasion t. In a first step, we used the information-theoretic approach to build a reference model that provided adequate description of the pattern of spatio-temporal variation in the probability of detection. Practically, we held occupancy constant while building models with variables most likely to explain detectability. Variables related to spatial variation included fishpond size (AREA), the fraction of the fishpond covered by potential refuge for the species where it could remain undetected (i.e. REEDBED) and the presence of a blind spot from the sighting site on the bank (BLIND, categorized by the observer as a binary variable). Regarding temporal variation in p, hypotheses included constant (.) occasion-specific (t) and temporal autocorrelation (AutoCorr). This later source of variation was modelled by adding a survey-specific covariate specifying the detection/non detection of the species (a binary variable) in t-1 occasion (Betts *et al*. 2008). In a second step and using the selected parametrization for detection probability, we then investigated whether site occupancy varied as a function of our *a priori* set of site-specific covariates. To limit the total number of models considered, we followed a step up procedure (Grosbois & Thompson 2005). Practically, we first assessed the fit of single-covariate models, testing for all the covariates considered as potentially influencing occupancy. We then proceeded by adding other single covariates to the favoured single-covariate model, i.e. the most parsimonious until obtaining a final model that included all covariates whose addition improved model fit. Throughout the analytical procedure we used a logit link function, and site-specific covariates were not standardized as this did not hamper numerical optimization of the likelihood.

Model selection was based on the Akaike information criterion (AICc, Anderson & Burnham 1999). Similar fit quality between two competitive models was assumed when the difference in AICc scores between models was lower than two points (ΔAICc < 2). In this case, we selected the model with the lowest number of parameters (Lebreton *et al*. 1992). The strength of support for a given model relative to other models was assessed using normalized AICc weights (w_i; White & Burnham 1999).

RESULTS

Swan pairs were observed on 46 fishponds, and nesting was detected on 28 fishponds. Swan pairs were observed less than three times on twelve of the nesting sites.

Sources of variation in detection probability

According to the ranking of the candidate model set that considered sources of variation in detection probability (*p*, Table 1), we found little support that detectability varied spatially as a function of fishpond size, the amount of potential un-detection areas or the presence of a blind spot for the observer. Regarding temporal variation, we also found no evidence that detectability differed among sampling occasions. However, we found evidence for including a form of temporal autocorrelation in detectability over the monitoring period. The best parametrization for *p* was *p*(AutoCorr) (Table 1), indicating that variation in detection probability was related to the presence of the species during the previous weekly survey. Examination of the slope parameter shows that this relationship was positive ($\beta_{\mathrm{AutoCorr}} = 0.78 \pm 0.35$): for a given sampling occasion, the detection probability was higher if the species was already observed the previous week ($p = 0.65 \pm 0.05$) compared to the situation where the species was not ($p = 0.46 \pm 0.07$). Overall, the probability to have detected breeding Mute Swans (given presence) by the end of the 4 sampling occasions was 0.94 (95% IC: 0.87-0.98), indicating that detectability was close to –but different from - perfection.

Table 1: AIC-ranked models used to test various sources of variation in detection probability of breeding Mute Swan (p). Notation for occupancy (Ψ) is omitted since occupancy was held constant while fitting models with a priori variables most likely to explain detectability. The selected parametrization for p is shown in bold.

Model	AICc	Δ AICc	*wi*	K
***p*(AutoCorr)**	**388.15**	**0.00**	**0.44**	**3**
p(AutoCorr + AREA)	389.84	1.69	0.19	4
p(AutoCorr + REEDBED)	390.07	1.92	0.17	4
p(.)	391.45	3.29	0.09	2
p(AREA)	392.93	4.78	0.04	3
p(REEDBED)	393.00	4.85	0.04	3
p(BLIND)	393.53	5.38	0.03	3
p(*t*)	397.44	9.29	0.00	5

Models are ranked by ascending AICc and ΔAICc. See text for model notation.

K number of parameters, wi normalized AICc weight (the larger the number, the more evidence for that model)

Sources of variation in occupancy rate

When assessing the fit of single-covariate occupancy models, the ranking of models suggested that several models fitted the data equally well (i.e. ΔAICc < 2, Table 2). However, we found no real support that fishpond occupancy by breeding Mute Swans varied as a function of our candidate variables describing fishpond and landscape features. Indeed, the model Ψ(.) was among the top-ranked models and confidence intervals for all covariates bounded zero (Table 2). Hence, considering that a constant occupancy rate was the most parsimonious parametrization, we did not proceed to try building more complex models.

On the basis of the Ψ(.) model, we calculated that breeding Mute Swans occupied 56% (± 3%) of our 94 selected fishponds.

Table 2: AIC-ranked single-covariate models used to test sources of variation in occupancy rate (Ψ) by breeding Mute Swans. Slope estimates (β) for covariate/factor and 95% confidence intervals (CI) are shown. Notation for detection probability is omitted since it was the same for all models (i.e. p(AutoCorr) see Table 1). The selected model is shown in bold.

Model	AICc	Δ AICc	*wi*	K	*β* covariate	*LCI*	*UCI*
Ψ (N_{proxi})	387.84	0.00	0.15	4	-0.17	-0.40	0.05
Ψ (.)	**388.15**	**0.31**	**0.13**	**3**	**.**	**.**	**.**
Ψ (PRACTICE)	388.70	0.86	0.10	4	0.59	-0.33	1.52
Ψ (SHAPE)	389.10	1.26	0.08	4	101.08	-83.80	285.97
Ψ (REEDBED)	389.28	1.44	0.07	4	0.10	-0.10	0.31
Ψ ($MEAN_{proxi}$)	389.42	1.58	0.07	4	-0.22	-0.67	0.23
Ψ ($N_{distant}$)	389.44	1.60	0.07	4	0.02	-0.02	0.06
Ψ (MACROPHYTES)	389.48	1.63	0.06	4	0.74	-0.84	2.33
Ψ (PERIMETER)	389.69	1.84	0.06	4	0.27	-0.40	0.94
Ψ (P_{proxi})	390.04	2.19	0.05	4	-0.14	-0.65	0.37
Ψ (AREA)	390.20	2.35	0.05	4	-0.01	-0.06	0.04
Ψ ($MEAN_{distant}$)	390.23	2.39	0.04	4	-0.07	-0.51	0.37
Ψ ($P_{distant}$)	390.24	2.39	0.04	4	-0.03	-0.23	0.16
Ψ (ROAD)	390.25	2.41	0.04	4	0.14	-0.81	1.09

Models are ranked by ascending AICc and ΔAICc. See text for model notation.

K number of parameters, wi normalized AICc weight (the larger the number, the more evidence for that model), LCI lower 95% confidence interval, UCI upper 95% confidence interval.

DISCUSSION

In this study, we investigated habitat selection by breeding mute swan on medium to large waterbodies (>10 hectares) in a wide and heterogeneous fishpond region. One of our findings has shown that detection of pairs was imperfect for each sampling occasion, but was close to perfection by the end of the monitoring period (i.e. 4 sampling occasions). The temporal autocorrelation of detection events may depend on swan pair behaviour on fishponds, i.e. breeding behaviour would be more likely to be observed on some sites over all the monitoring period (e.g. if the nest is in the open water area or if it is close from the observer point).

Being large and white, swans (*Cygnus spp.*) are the least cryptic Anatidae species. It thus seems rather natural to get such a high detection rate. The probability of detection would be lower in wetlands with more complex shapes, or where obstacles to detection vary a lot over time (e.g. depending on bird behaviour or emergent vegetation). As an example, in the Camargue (South of France), approximately half of the breeding Red-crested pochards (*Netta* *rufina*) remained undetected during field surveys, leading to a massive underestimation of breeding population size, and hence potentially inappropriate conservation status (Defos du Rau *et al*. 2003). As shown for other species (e.g. Jakob *et al*. 2010) taking into account detection biases should not be neglected for wildfowl surveys, in particular during the breeding season, because it is likely to improve the results from such studies (e.g. Pagano & Arnold 2009) as well as making management policies more appropriate.

The main result of our study suggests that breeding pairs appeared to be non-selective towards their nesting habitat. Several factors may explain the non-dependence of swan pairs to fishpond characteristics. The lack of a preference for fishponds with denser reedbeds as breeding sites may result from the quasi-absence of natural predators in such regions. Swans do not have to use reedbeds as a refuge for nesting and hiding from predators here. That breeding swans did not respond to macrophyte abundance may be related to the period when the study was conducted: swans may be more selective towards macrophyte beds later in the year, when macrophyte beds are fully developed and the birds’ food requirements increase. This may explain fishpond switch by swan families after cygnets hatching (personal observation). Human disturbance did not play a significant additional role on fishpond selection. Disturbance should be more likely to affect the location of nesting sites (i.e. remote from roads within fishponds) than the single presence of breeding pairs on fishponds. The frequency of use of such roads may possibly affect birds more than the sole presence of the road, but measuring disturbance in this way seems particularly difficult on such large areas. No effect of the surrounding aquatic environment could be detected. Such fishponds are certainly so large, with sufficient carrying capacity for swan pairs, that they may satisfy swan requirements for breeding, independently from surrounding fishponds properties. It is presently very rare that more than one swan pair uses the same fishpond for breeding in the Dombes. Swans may hence not be currently limited by the carrying capacity of fishponds, but this may change in the future if the population was to keep on increasing. As for many studies, we expected the swan population to be in pseudo-equilibrium in such environment. It is therefore possible that selectivity was here underestimated simply because there are at present too few breeding birds for the most favourable fishponds to all be used (see Guisan & Thuiller 2005). As species which invaded space are often not at equilibrium stage, it should be more convenient to study them in their native range (Peterson 2003), or once equilibrium reached in colonized environment. However it seems rather difficult to identify this equilibrium stage.

The results of the present study are consistent with the dramatic geographical expansion of the European Mute swan populations. Swans colonized a vast array of habitats over the last decades, suggesting it is a species of highly plastic ecology (Wieloch 1991; Fouque *et al*. 2007). This is further supported by the present results, which demonstrates that their presence is not restricted to the richer sites during the pre-laying and laying periods. Prolonging this study to the cygnet growth period would allow comparing successful and unsuccessful nesting sites, representing proper fitness of the parents. This may reveal differential breeding success depending on covariates that actually do not affect nesting site selection: though it may be very difficult to discriminate the role of biological factors from the consequences of illegal culling, considering the whole breeding season (i.e. until fledging) has indeed been advocated to properly evaluate waterbird nesting habitat selection (Clark & Shutler 1999).

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CHAPTER 2 : INTERACTIONS BETWEEN MUTE SWAN AND FISHPOND COMMUNITIES.

The second chapter of this study deals with swan – waterbirds and swan – aquatic macrophytes interactions in fishponds. In the first case, mute swan may be competing with the other waterbirds for available resources. This may be highlighted by interspecific agonistic behaviours from paired swans. Such behaviour may be the consequence of interspecific territoriality, leading to exclusion of the other waterbirds. In the second case, mute swans may damage macrophyte beds while foraging. Through descriptive as well as experimental approaches, we aimed in this chapter at assessing the consequences of mute swan presence on these two fishpond communities.

Article 4 aims at measuring the relationship between swan pair presence and fishpond use by the other waterbirds during the breeding season. A sample of over 80 fishponds was monitored from April to July 2008. Since the effect of territoriality may weaken with fishpond size, we discarded from the sample those fishponds whose area was over 20 ha. Waterbird counts (swans, coot and ducks) were carried out every third week (4 visits). Twenty minutes focal behavioural samples were recorded from males on fishponds with a swan breeding pair. We could not detect agonistic behaviour from swan pairs towards other waterbirds. Furthermore, we show that waterbird abundance was actually higher on fishponds with than without swan pairs. This was mostly due to the correlation between coot, and to a lesser extent common and red-crested pochards, and swan pair presence. Such association was particularly strong when birds were the most gregarious (moult).

Fishponds are relatively large aquatic ecosystems. It is thus possible that some exclusion processes that remained undetected between fishponds occur within fishponds. Swan pairs may hence exclude the other waterbirds from the areas they preferentially use within a fishpond without the frequency of agonistic behaviours being large enough to get detected. On the same fishpond sample we thus mapped the distribution of all waterbirds during the first three visits (**Article 5**). Such dot maps show where waterbird individuals are within each fishpond. Using spatial point pattern analyses developed by Ripley and further developments of these, we measured the relationship between swan and other waterbird point patterns. Our results show that swan dots are strongly aggregated (within a 20 m radius) in fishponds. Although these swan clusters are not in the areas that are the most densely used by waterbirds, proximity between swans and other waterbirds within a fishpond is higher than if the two distributions were independent from each other. In other words, instead of demonstrating an avoidance process between waterbirds and swans, we conversely showed that some sort of spatial convergence occurs.

In the second part of this chapter (**Article 6**), we assessed if grazing by swans affected aquatic macrophyte development during the vegetative period. We thus relied on an experimental approach based on exclosures (control) and open plots. The control was a fenced area that was inaccessible to swans but accessible to other fishpond herbivores. Open plots were marked with a stick within a 10 m distance from the exclosures. This allowed measuring plant development with and without the considered biological effect. The difference in development between the two states hence represents the effect of grazing independently from any other variable. 116 of such experimental set-ups were deployed on 29 fishponds (i.e. 4 per fishpond) from early April to late July 2008 and 2009. Before installing the set-ups (March), physico-chemical analyses of sediment interstitial water were carried out to measure how much nutrients were available to plants during the vegetative period. This allowed ranking the fishponds after their trophic level. After the experimental set-ups were installed, weekly bird counts were carried out to measure swan grazing pressure (swan-days/ha). Botanical measurements (specific plant cover) were carried out at the end of May, June and July. Beyond the demonstration of a simple effect of grazing, we also studied how such effect varied depending on swan grazing pressure, fishpond trophic level and macrophyte growth stage.

We demonstrate that swan grazing can profoundly affect macrophyte beds during the study period. Macrophyte beds were more frequent inside than outside exclosures. At the beginning of macrophyte growth period (May), the effect of grazing could only be detected where high swan densities were recorded. In addition to affecting macrophyte bed presence, we also show that grazing affects macrophyte cover during the last two vegetation samples (June and July). Such an effect is partially buffered by fishpond trophic level at the end of the study period (July). On average, plant biomass also tends to be lower in open plots than in exclosures, although the difference was not statistically significant. In addition to grazing affecting macrophyte bed presence and cover, we show that plant diversity was lower in open plots, especially during early stages (May and June). Swan stay hence affects presence, cover and structure of fishpond aquatic macrophyte communities.

Article 4 : Are Mute Swans (*Cygnus olor*) really limiting fishpond use by waterbirds in the Dombes, Eastern France.

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ORIGINAL ARTICLE

Are Mute Swans (*Cygnus olor*) really limiting fishpond use by waterbirds in the Dombes, Eastern France

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Abstract The Mute Swan (*Cygnus olor*) is a protected species whose population has shown a dramatic demographic expansion over the last decades in France. Today, Mute Swans are suspected of causing damages to wetlands, partly through their territorial behaviour towards other waterbirds. The behaviour of Mute Swan pairs and the distribution of other waterbirds was monitored over 84 fishponds in the Dombes, Eastern France, from April to July 2008. Interspecific aggressive behaviours by Mute Swan pairs were not detected during behavioural observations, and no negative impact of swan pair presence was demonstrated on waterbird distribution. Waterbirds were more abundant on fishponds where Mute Swan pairs were present, maybe due to the flocking of waterbirds where Mute Swans were established owing to shared habitat preferences. Indeed, the waterbirds whose presence was the most closely correlated to that of Mute Swan pairs were Coot (*Fulica atra*), Common Pochard (*Aythya ferina*) and Red-Crested Pochard (*Netta rufina*), all foraging on deep macrophyte beds as do the swans. All these species, including swans, may therefore be attracted to the same fishponds without massive interspecific competition occurring, due to abundant submerged aquatic vegetation resources.

Keywords Mute Swan (*Cygnus olor*) · Coot (*Fulica atra*) · Ducks · Territoriality · Fishpond

Introduction

Land use, industrial activities and the transport of animal and plant species through natural barriers are among the factors that can damage biodiversity (Chapin et al. 2000). In some cases, introduced exotic species can proliferate until they exclude native species and become dominant within ecosystems (Mooney and Cleland 2001; Didham et al. 2005). They can then be considered as "invasive" sensu Valéry et al. (2008): "a species acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population". The territorial behaviour of allochtonous species can be the mechanism by which they exclude native species from a given area. Indeed, some species forbid their territories not only to their congeners but also to other species (Mikami

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and Kawata 2004). Many birds behave in this way, defending their territory against usually closely related species (Orians and Willson 1964). Many wildfowl species are indeed territorial during the breeding period (Owen and Black 1990). The result can cover a wide range of consequences, with the dominant species eventually occupying the optimal habitat from which subordinate species get excluded, these being forced to suboptimal areas (Murray and Bertram 1971).

Considering a species as invasive implies that it may eventually become dominant in the receiving ecosystem. In Western Europe, the demographic expansion of the Mute Swan (*Cygnus olor*) (BirdLife International 2004; Rowell and Spray 2004; Fouque et al. 2007) and its protected status in numerous countries, associated with its reputation as a territorial species, have all led to a growing concern regarding the preservation of waterbird communities. However, nothing to date allows the assertion that Mute Swan is indeed an invasive species in this area, as the limits of its demographic expansion are unknown and even the origin of populations is doubtful (recolonisation, feral and/or natural arrival). Nevertheless, the position of this species within aquatic ecosystem food webs (few natural predators and easy access to most food resources owing to its long neck) suggests it could have a competitive advantage over some other waterbirds.

Intra and interspecific aggressiveness of Mute Swan has already been demonstrated in North America (Conover and Kania 1994), where it is a non-native species negatively affecting both waterbirds and macrophyte beds (Petrie and Francis 2003). In other ecological contexts, Pöysä and Sorjonen (2000) suggest that the Whooper Swan (*Cygnus cygnus*), a closely related species, has not taken the place of dabbling ducks, and occupies a previously vacant ecological niche while recovering in Finnish lakes. Similarly, Broyer (2009) did not detect any negative impact of Mute Swan presence on duck reproduction in fishpond areas. Agonistic behaviour is not the only possible relationship between swans and other waterbirds. Conversely, imitation, delocalisation, commensalism or kleptoparasitism may all develop within such communities (Amat and Soriguer 1984; Amat 1990; Källander 2005). To our knowledge, however, no study has so far investigated simultaneously the direct interactions of swan pairs with the rest of the waterbird community and the resulting effects on the spatial distribution of other waterbirds during the breeding period.

The Mute Swan is a gregarious herbivore in autumn and winter. The rest of the year, non-breeding individuals form mobile groups while breeding pairs are confined to their territories (Scott 1984). Broyer (2009) studied the consequences of the presence of Mute Swan pairs on duck pair establishment and brood success in the same study area as ours. However, our approach here is singular in that the potential effect of swans was tested on all waterbird populations (including Coot *Fulica atra* that may share the largest part of the Mute Swan ecological niche), and during several distinct parts of the breeding period. The aim of the present study was thus to test the following hypotheses:

1. If swans are indeed territorial towards other waterbirds,
   - (a) the number of these waterbirds should be lower (for a given fishpond size) in fishponds with compared without a breeding swan pair, and
   - (b) the negative effect of swan presence should also increase with decreasing fishpond size and in periods when the other species concentrate on fishponds (e.g. for moult).
2. Alternatively, if swans are indifferent to the presence of other waterbirds, there should be no such effect, and the number of other waterbirds for a given fishpond size should not differ between fishponds with or without swans, or may even be higher in species that share habitat preferences with swans.
3. Lastly, there may be a combination of the above two mechanisms, with least herbivorous species being fewer at swan fishponds because of territoriality, especially on smaller fishponds, but such a negative effect being at least partly compensated for by shared habitat preferences for plant-rich fishponds by other more herbivorous waterbirds, which should not be negatively affected to the same extent by the presence of swans.

Methods

Study area

The Dombes region (Eastern France: 45°57′N, 05°02′E) is composed of 1,450 fishponds of 7.3 ha on average (±0.2 SE), spread over 1,600 km^2. Most of these fishponds are emptied out in autumn and during winter for fish harvesting. In France, the Dombes is a key area for breeding dabbling ducks (especially Mallard *Anas plathyrynchos* and Gadwall *Anas strepera*) and diving ducks (especially Common Pochard *Aythya ferina* and Red-crested Pochard *Netta rufina*). Mute Swans nested in the Dombes for the first time in 1974 (Miquet 2003). In 2005, a summer population of about 1,000 individuals was recorded (Benmergui et al. 2005).

Fishponds sample

Wildfowl (including Mute Swan) numbers and distribution were monitored on a sample of 84 fishponds of 1–18 ha (mean = 9.4 ha ±0.4 SE), all located within the same 20-km radius. Because territoriality of a breeding swan pair may not affect other waterbirds to the same extent in larger waterbodies, fishponds larger than 20 ha were not considered (i.e. it was assumed that the negative effect of the presence of one Mute Swan pair could not always be measured beyond 20 ha). Fishponds under 20 ha were randomly selected and the random process was repeated until the set of selected fishponds could be covered by a coherent circuit in a minimum of time.

Study periods

The set of all selected sites had do be visited in a maximum of 3 weeks to avoid monitoring different fishponds during different biological phases of the waterbird breeding cycle outside the hunting season. Four counts were performed per fishpond between mid-April and mid-July 2008. The different count periods (whose limits were arbitrarily determined) hence corresponded to different phases of the waterbird biological cycle:

- Mid-April to mid-May: incubating of swans, laying and incubating of diving ducks, hatching of dabbling ducks.
- Mid-May to early June: hatching of swans, brood rearing of dabbling ducks, hatching of diving ducks and beginning of adult dabbling duck moult.
- Two counts from early June to mid-July: hatching of the last diving ducks and moult of adults from this group.

The different phases of the Coot breeding cycle are more difficult to determine, but broadly speaking their moult occurs between late May and August depending on the reproductive status of individuals. Studying birds over several biological periods allowed us to identify potential intraspecific processes (e.g. territoriality) that could affect the distribution of a given species independently from the presence of swans. The structure of the waterbird communities was compared during each period between fishponds with a swan pair (2 adults: 1 male and 1 female) and fishponds without swans (control fishpond). Fishponds with only 1 swan or with flocks of more than 2 swans were discarded, because in the first case it was not possible to assess if a pair was actually breeding there (i.e. if the second member of the pair remained undetected in the vegetation), while in the latter case it is possible that the other waterbirds respond differently to the presence of other swans than to a breeding pair (e.g. commensalism; see Källander 2005). Conversely, the presence of 2 adults on a fishpond could be considered by other waterbirds as indicating a potential swan territory. A given fishpond may have changed category between count periods depending on the presence of swans, e.g. have a breeding pair for some count periods and be without swans for some other count periods. Unfortunately, not enough swan broods were observed during each period to compare fishponds with and without actual swan families. Since counts were performed with a minimum interval of 3 weeks on each fishpond, they were considered as being independent of each other.

Waterbird counts

Swans, Coot and other Anatidae (the most common being Mallard, Gadwall, Common Pochard and Red-crested Pochard) were counted while distinguishing males, females and pairs for each species. Waterbird broods were not considered, as young individuals may not respond to swan presence independently from their mother or from the rest of the brood. A female with broods was thus considered as a unique individual during the analyses. Counts were performed at each fishpond from a pre-determined and constant observation point on the bank, by a unique observer. The distribution of birds was also mapped for further analyses not presented here. Given the time spent on each fishpond per visit by the observer, it is therefore expected that swans were very unlikely to remain undetected if they were present.

Behaviour recordings

Each time a swan pair was detected on a fishpond, focal observations were performed on males (distinguished from females by their larger knob; Horrocks et al. 2009). Males are indeed more likely to establish conflicting relationships than the females (Lind 1984). Focal observations consisted in following an individual during a given length of time and recording each behavioural activity (Martin and Bateson 1993). The information collected thus corresponded to "states", i.e. successions of behaviours whose duration was known (Altmann 1974). Focal observations were limited to 20 min, to prevent tiredness of the observer altering the quality of the measures (Altmann 1974). For the purpose of the study, only aggressive behaviours generated by the observed bird were recorded, i.e. the Mute Swan threatened other waterbirds directly or swam with its wings raised in display. For each such agonistic behaviourm the species towards which it was directed was recorded. From the focal samples, the frequency of aggressive interactions (i.e. number of events per unit of time) was later computed and analysed.

Statistical analyses

Differences in the abundance of waterbirds with respect to the presence of swans were tested by pooling data from all species and by considering separately the main species encountered, i.e. Coot, Common Pochard, Red-crested Pochard, Mallard and Gadwall. To test for differences in total waterbird abundance on fishponds with and without a swan pair, an analysis of covariance (ANCOVA) simultaneously taking into account both the presence/absence of a swan pair and fishpond size effects was performed for each count period. The total numbers of individuals and numbers of Coot were log-transformed before the analyses to approach normality criteria. Non-significant terms (at $P > 0.05$) in the models associated to count period were gradually removed in a backwards stepwise procedure, starting by the interaction term (fishpond size × swan presence). The distribution of individual duck species was analysed with non-parametric Mann–Whitney tests, because of the large number of null values and the consequent strong deviation from normality even after log-transformation. R software 2.9.2 was used for all analyses (R Development Core Team 2009).

Results

Waterbird counts

The total number of fishponds monitored during each count period varied because of draining of some fishponds (Table 1). The small number of swan broods during each count period does not represent the real number of fishponds where breeding pairs were established, because swan nests naturally failed or were often destroyed by landowners on some fishponds. The total number of fishponds where a breeding behaviour was recorded (i.e. brooding, building of the nest or brood presence) was 36. The largest number of swan pairs was observed in April, and then decreased rapidly, probably because of pairs leaving the least attractive fishponds after breeding failures. Mute Swan pairs were more likely to be on larger fishponds during each count period (logistic regressions, all P values >0.001 and <0.05), even if some pairs were also recorded on the smallest fishponds of the sample.

The interaction term between swan presence and fishpond size never had a significant effect in any of the ANCOVAs (see below): the presence of a swan pair on a fishpond did not affect the potential relationship between fishpond size and waterbird numbers. The interaction term was therefore removed from all models during the backwards stepwise model selection procedure, as was fishpond size in some cases. Conversely, swan pair presence always had a statistically significant effect (Tables 2 and 3). For all waterbirds combined (i.e. wildfowl + Coot), the average number of birds was higher, often twice as high, on swan fishponds than on non-swan fishponds during the 4 count periods (Table 2), and increased with increasing fishpond size during the first count period (Table 3, Fig. 1), while fishpond size did not have a significant effect in the models from count periods 2–4. The same pattern of differences was observed for Coot at the beginning of the study period. The difference in numbers of waterbirds and Coot was smaller during the first count period, and more marked during the last one. From 9 to 27% of the variance in the total number of birds present was explained by fishpond size and swan presence (Table 3) depending on count period, with such r^2 values decreasing from count period 1 to count period 4. A similar pattern of decreasing r^2 value for count period 4 was observed when considering only Coot, with 6–28% of the variance in Coot numbers being explained by swan presence (plus fishpond size in count period 1), but the maximum determination coefficients being recorded during count periods 2 and 3.

Mean numbers of Common Pochard and Red-Crested Pochard were always larger, often more than twice as large, on swan fishponds. Significant differences were observed at the beginning of the monitoring period for Common Pochard alone (count period 1), and in the middle of the study period for Red-crested Pochard alone (count periods 2 and 3). In most of cases, mean numbers of Mallard and Gadwall were larger on fishponds with swan pairs (Table 2). No statistically differences were detected in the mean numbers of Mallard and Gadwall between swan and swan-free fishponds. Overall, the observed trends were similar for numbers and densities of birds in each waterbird species (results not shown).

The two duck species on which a swan effect was observed are Common Pochard and Red-crested Pochard. Both are diving ducks with similar phenology, which may depend on macrophyte beds to feed during the breeding

Table 1 Numbers of fishponds where waterbird counts were carried out during each time period in the Dombes area in 2008

	Count period 1: mid-April to mid-May	Count period 2: mid-May to early June	Count period 3: early to late June	Count period 4: late June to mid-July
At least one swan observed	52	36	34	22
Presence of swan pair (two adults)	40	23	26	17
Presence of swan brood	3	10	9	7
Any swan observed	32	46	47	59
Total number of fishponds counted	84	82	81	81

Table 2 Average number (±SE) of waterbirds on fishponds with and without a Mute Swan (*Cygnus olor*) pair in the Dombes area from April to July 2008

	Count period	With swan pair	Without swans	Mann–Whitney test	
				U	*P*
Waterbirds	1	34.2 ± 3.5	19.8 ± 2.5	–	
	2	40.9 ± 5.9	16.0 ± 1.9	–	
	3	33.0 ± 5.7	12.7 ± 2.0	–	
	4	40.4 ± 14.9	12.6 ± 2.4	–	
Coot	1	19.7 ± 2.9	9.3 ± 1.6	–	
	2	21.7 ± 4.0	5.9 ± 0.8	–	
	3	20.0 ± 4.2	6.3 ± 1.5	–	
	4	27.2 ± 10.8	8.6 ± 1.7	–	
Common Pochard	1	7.0 ± 1.1	3.5 ± 1.1	382	<0.01
	2	9.3 ± 2.4	4.7 ± 0.9	430	>0.05
	3	7.1 ± 2.1	2.8 ± 0.9	475	>0.05
	4	3.8 ± 2.3	1.5 ± 0.5	413	>0.05
Red-crested Pochard	1	2.2 ± 0.6	1.9 ± 0.5	660	>0.05
	2	3.8 ± 1.3	0.7 ± 0.3	376	<0.05
	3	2.8 ± 1.0	0.7 ± 0.3	423	<0.01
	4	4.1 ± 2.8	0.4 ± 0.2	397	>0.05
Mallard	1	3.3 ± 0.4	2.9 ± 0.5	565	>0.05
	2	3.9 ± 1.6	3.3 ± 1.0	510	>0.05
	3	1.1 ± 0.3	1.7 ± 0.5	610	>0.05
	4	0.9 ± 0.5	0.4 ± 0.1	462	>0.05
Gadwall	1	1.3 ± 0.2	1.5 ± 0.3	644	>0.05
	2	1.4 ± 0.4	0.8 ± 0.2	392	>0.05
	3	1.3 ± 0.5	1.1 ± 0.3	602	>0.05
	4	0.9 ± 0.8	0.1 ± 0.0	459	>0.05

P values obtained with Mann–Whitney test. See Table 3 for statistics concerning waterbirds and Coot

period (see Cramp et al. 1986). Consequently, to understand more precisely the phenomenon and verify any swan effect in interaction with fishpond size, we combined these two species under the name "herbivorous ducks" to meet normality assumptions and perform ANCOVA. Except during count period 4, where the final model did not provide a significant fit to the data, swan pair presence was always retained, and was the only parameter which was, to explain the variance in the abundance of "herbivorous ducks" over fishponds, which it affected positively though a small share of the variance was explained (5–9%).

Behaviour recordings

A total of 104 focal observations, i.e. 20-min survey periods, were recorded between April and July, for a total of 35 h. Only four agonistic behaviours by Mute Swans were observed (in June and July), among which one was aggressiveness towards a congener and three were patrols (patrol behaviour occurring when the male is displaying with its wings and neck raised and is swimming quickly but without threatening a given other individual). The frequency of agonistic behaviours was therefore as low as 0.11 events/h.

Discussion

During the Mute Swan breeding period, our results did not demonstrate any significant negative impact of swan pair presence on the distribution of other waterbirds on the fishponds. Following the predictions of our second possible scenario, the total number of waterbirds was even higher where swan pairs were present. These results tend to confirm the hypothesis of a lack of any strong interspecific territoriality by Mute Swan, since a higher abundance of birds was recorded on fishponds with swan pairs. This is likely to be due to shared requirements of Mute Swan on the one hand, and Coot and ducks like Common Pochard and Red-crested Pochard on the other hand, all being strongly dependent upon the presence of macrophyte beds. During the first count period, the total number of waterbirds, Coots and herbivorous ducks were all positively correlated with the presence of Mute Swan pairs and with fishpond size.

During the first count period, the association between swan pairs and waterbirds was the strongest, which may be due to the formation of waterbird pairs on the same fishponds as those occupied by swans. Later on, the association

Table 3 Results of the ANCOVAs testing for the effects of swan pair presence, fishpond size and their interaction on the number of waterbirds recorded per count period

		Estimate ± SE	*df*	*F*	*P*
Count period 1					
All waterbirds	Final model: $F_{2,69} = 14.18$; $r^2 = 0.27$; $P < 0.0001$				
	Swan pair present	0.47 ± 0.16	1	19.13	<0.0001
	Fishpond area	5.89e−06 ± 0.00	1	9.24	<0.01
Coot	Final model: $F_{2,69} = 6.90$; $r^2 = 0.14$; $P < 0.01$				
	Swan pair present	0.47 ± 0.24	1	8.90	<0.01
	Fishpond area	6.52e−06 ± 0.00	1	4.90	<0.05
Herbivorous ducks	Final model: $F_{1,70} = 7.88$; $r^2 = 0.09$; $P < 0.01$				
	Swan pair present	0.67 ± 0.24	1	7.88	<0.01
Count period 2					
All waterbirds	Final model: $F_{1,67} = 18.17$; $r^2 = 0.20$; $P < 0.0001$				
	Swan pair present	0.97 ± 0.23	1	18.17	<0.0001
Coot	Final model: $F_{1,67} = 26.90$; $r^2 = 0.28$; $P < 0.0001$				
	Swan pair present	1.16 ± 0.22	1	26.90	<0.0001
Herbivorous ducks	Final model: $F_{1,67} = 4.49$; $r^2 = 0.05$; $P < 0.05$				
	Swan pair present	0.62 ± 0.29	1	4.49	<0.05
Count period 3					
All waterbirds	Final model: $F_{1,71} = 15.27$; $r^2 = 0.17$; $P < 0.001$				
	Swan pair present	0.92 ± 0.24	1	15.27	<0.001
Coot	Final model: $F_{1,71} = 20.91$; $r^2 = 0.22$; $P < 0.0001$				
	Swan pair present	1.12 ± 0.25	1	20.92	<0.0001
Herbivorous ducks	Final model: $F_{1,71} = 7.37$; $r^2 = 0.08$; $P < 0.01$				
	Swan pair present	0.71 ± 0.26	1	7.37	<0.05
Count period 4					
All waterbirds	Final model: $F_{1,74} = 8.02$; $r^2 = 0.09$; $P < 0.01$				
	Swan pair present	1.00 ± 0.35	1	8.02	<0.01
Coot	Final model: $F_{1,74} = 5.79$; $r^2 = 0.06$; $P < 0.05$				
	Swan pair present	0.83 ± 0.35	1	5.79	<0.05

Only the final model of the backwards stepwise model selection procedure is presented in each case

somewhat weakened between swans and ducks, though it remained strong between swans and Coots in May and June. This could be due to the presence of moulting Coots on fishponds occupied by swans because of their abundant vegetation resources. Intraspecific processes within waterbird species (e.g. gregarity during moult) may thus also influence the strength of the relationship between their own distribution and Mute Swan presence during the breeding period. Although the presence of herbivorous ducks was also correlated with swan pair presence, the precise period when this relationship was the strongest differed between Common and Red-crested Pochard, probably because of species-specific changes in ecological requirements during the breeding period. The number of swan pairs on the monitored fishponds decreased over the count periods, possibly because pairs could have left fishponds whose resources were insufficient and/or where they failed to breed. Failed breeders are indeed known to move to join moulting flocks (Coleman et al. 2002). This may also have partly contributed to the weakening of the relationship between swan pairs and waterbirds at the end of the study period. Conversely, swan pairs that did not fail to reproduce were still established on their territory (cygnets are only able to fly after approximately 120–150 days; Cramp et al. 1986), while Coots and herbivorous ducks could have been able to spread over other fishponds after moult. Whatever caused the relative weakening of the relationship between swans and other herbivores over the count periods, it is clear from the results of this study that Mute Swans do not prevent other waterbirds (mainly Coots and ducks) to use fishponds where they breed, but conversely the present results suggest that the latter may use the same fishponds as swans as a result of shared preferences for fishponds with more abundant aquatic plant food. This statement is

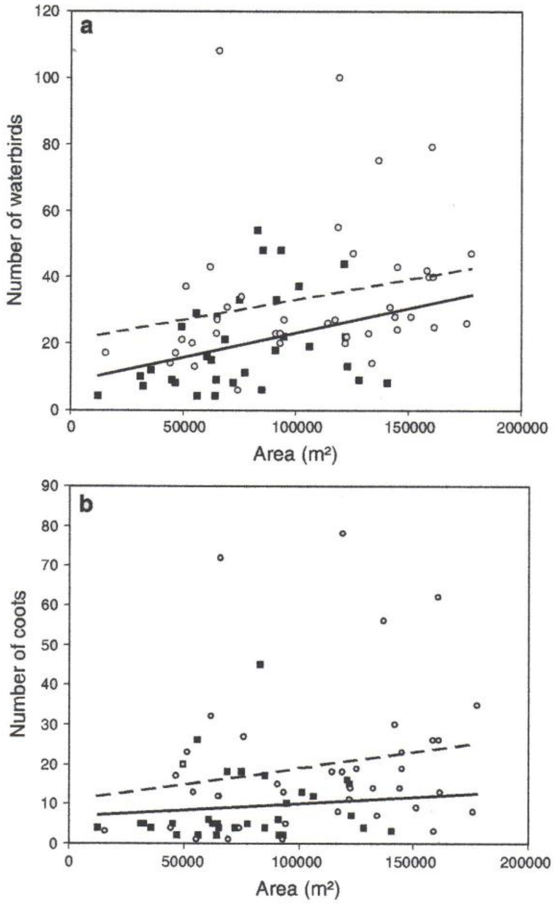
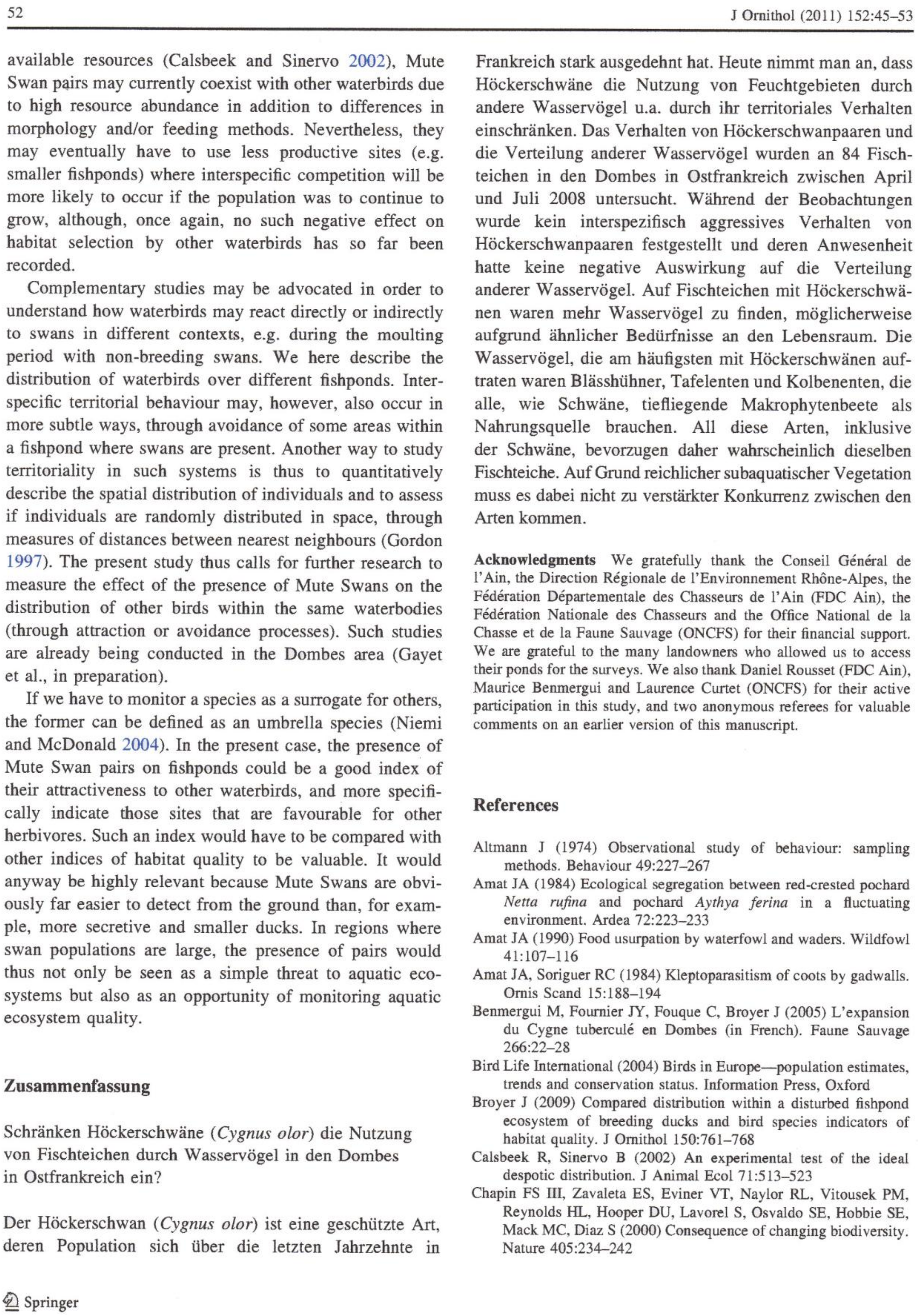


Fig. 1 Total number of waterbirds (**a**) and Coot (*Fulica atra*) (**b**) on fishponds with a Mute Swan (*Cygnus olor*) pair (*circles, dotted regression lines*) and without swans (*black squares, plain regression lines*) during the first count period according to fishpond size. See Table 3 for statistics

confirmed by the fact that the distribution of Mallard and Gadwall was more independent of swans, and hence potential swan food resources. These ducks may indeed have limited access (as dabbling ducks) to the macrophytes on which Mute Swans and diving ducks forage, and thus have a distribution that depended on other factors than the abundance of submerged beds.

That Mute Swans did not prevent other waterbirds from using the fishponds where they established to breed is also supported by the very low frequency of aggressive interactions between swans and other waterbirds. It should be kept in mind, however, that Conover and Kania (1994) detected a much higher frequency of agonistic interactions (more than 1/h, versus 0.11 interactions/h in the Dombes). Interspecific territoriality may therefore be exhibited by Mute Swans under some circumstances. Swan pairs here often occupied fishponds without congeners (Gayet, personal observation). Though this may indicate intraspecific territoriality, it may also simply be due to the large number of available fishpond breeding sites relative to the size of the current Mute Swan population, which may allow swans to distribute within the habitat without strong intraspecific competition occurring. This latter hypothesis is again supported by the very low frequency of intraspecific agonistic behaviours recorded by the focal samples. All of the above suggest that the increasing Mute Swan population of the Dombes simply relies on an available niche within the existing herbivore bird community of this food-rich ecosystem. This of course does not imply that swans do not affect the other waterbirds: to confirm that waterbird density would not be higher in the absence of swan, an experimental approach (by removing swan pairs) may be useful though ethically difficult to undertake.

Haapanen (1991) demonstrated that, during its re-colonization, the Whooper Swan occupied the most productive boreal lakes. If a similar scenario happens in the Dombes, it is possible that Mute Swan pairs are also using the richer fishponds (with abundant submerged aquatic vegetation), so that defending a territory towards other potentially competing waterbirds was not beneficial to the swans here. Territorial behaviour by an expanding Mute Swan population may be more intense in other ecological contexts with saturated ecosystems where the carrying capacity has already been reached, such as less productive oligotrophic lakes or newly created gravel pits. The same may also occur where food webs are more complex and direct potential competitors to swans (e.g. others swan species, geese) are more abundant or where Mute Swan density is already higher. The fact that Mute Swans are morphologically very different from the other waterbirds (owing to their body size and neck length, in particular) of the Dombes community may also explain why competitive relationships were weak (e.g. Leyequièn et al. 2007). In addition to differences in morphology, differences in foraging methods can also contribute to species coexistence (see, e.g., Amat 1984 for Red-crested Pochard and Common Pochard). In the present case, it is very likely that Mute Swans and the other waterbirds can forage in such different ways (specifically, different foraging depths) for the former to consider it worth displaying territoriality towards the latter. In this sense, our results support those of Pöysä and Sorjonen (2000) on the Whooper Swan, who suggested that upon its return on Finnish lakes Whooper Swans occupied an ecological niche that was left vacant by ducks, without interfering with them. If the process is similar for the Mute Swan in the Dombes, then the species may continue to increase in numbers relatively rapidly, which may eventually become detrimental to the ecosystem. Territory size is generally influenced by the quality of



available resources (Calsbeek and Sinervo 2002), Mute Swan pairs may currently coexist with other waterbirds due to high resource abundance in addition to differences in morphology and/or feeding methods. Nevertheless, they may eventually have to use less productive sites (e.g. smaller fishponds) where interspecific competition will be more likely to occur if the population was to continue to grow, although, once again, no such negative effect on habitat selection by other waterbirds has so far been recorded.

Complementary studies may be advocated in order to understand how waterbirds may react directly or indirectly to swans in different contexts, e.g. during the moulting period with non-breeding swans. We here describe the distribution of waterbirds over different fishponds. Interspecific territorial behaviour may, however, also occur in more subtle ways, through avoidance of some areas within a fishpond where swans are present. Another way to study territoriality in such systems is thus to quantitatively describe the spatial distribution of individuals and to assess if individuals are randomly distributed in space, through measures of distances between nearest neighbours (Gordon 1997). The present study thus calls for further research to measure the effect of the presence of Mute Swans on the distribution of other birds within the same waterbodies (through attraction or avoidance processes). Such studies are already being conducted in the Dombes area (Gayet et al., in preparation).

If we have to monitor a species as a surrogate for others, the former can be defined as an umbrella species (Niemi and McDonald 2004). In the present case, the presence of Mute Swan pairs on fishponds could be a good index of their attractiveness to other waterbirds, and more specifically indicate those sites that are favourable for other herbivores. Such an index would have to be compared with other indices of habitat quality to be valuable. It would anyway be highly relevant because Mute Swans are obviously far easier to detect from the ground than, for example, more secretive and smaller ducks. In regions where swan populations are large, the presence of pairs would thus not only be seen as a simple threat to aquatic ecosystems but also as an opportunity of monitoring aquatic ecosystem quality.

Zusammenfassung

Schränken Höckerschwäne (*Cygnus olor*) die Nutzung von Fischteichen durch Wasservögel in den Dombes in Ostfrankreich ein?

Der Höckerschwan (*Cygnus olor*) ist eine geschützte Art, deren Population sich über die letzten Jahrzehnte in Frankreich stark ausgedehnt hat. Heute nimmt man an, dass Höckerschwäne die Nutzung von Feuchtgebieten durch andere Wasservögel u.a. durch ihr territoriales Verhalten einschränken. Das Verhalten von Höckerschwanpaaren und die Verteilung anderer Wasservögel wurden an 84 Fischteichen in den Dombes in Ostfrankreich zwischen April und Juli 2008 untersucht. Während der Beobachtungen wurde kein interspezifisch aggressives Verhalten von Höckerschwanpaaren festgestellt und deren Anwesenheit hatte keine negative Auswirkung auf die Verteilung anderer Wasservögel. Auf Fischteichen mit Höckerschwänen waren mehr Wasservögel zu finden, möglicherweise aufgrund ähnlicher Bedürfnisse an den Lebensraum. Die Wasservögel, die am häufigsten mit Höckerschwänen auftraten waren Blässhühner, Tafelenten und Kolbenenten, die alle, wie Schwäne, tiefliegende Makrophytenbeete als Nahrungsquelle brauchen. All diese Arten, inklusive der Schwäne, bevorzugen daher wahrscheinlich dieselben Fischteiche. Auf Grund reichlicher subaquatischer Vegetation muss es dabei nicht zu verstärkter Konkurrenz zwischen den Arten kommen.

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Article 5 : Do breeding Mute swans (*Cygnus olor*) exclude the other waterbirds from some fishpond areas ? An analysis based on spatial point patterns.

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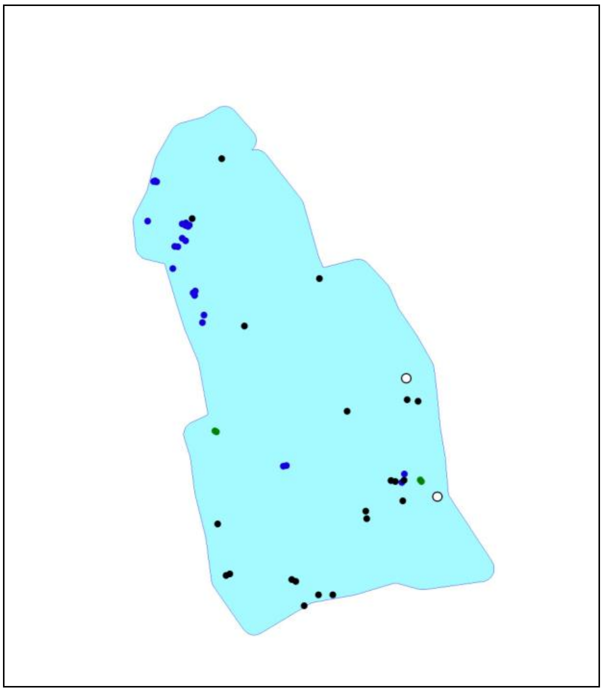
In prep.



ABSTRACT

Considering the spatial distribution of individuals is crucial to better understand intra- and interspecific competition processes. Spatial point pattern analyses are increasingly used in the field of wildlife ecology to assess such distributions. In this paper, we aimed at determining if the presence of a presumed territorial species, the Mute swan (*Cygnus olor*), affects the distribution of the other waterbirds within fishponds, relying on spatial point pattern analyses. Swans, ducks and coots (*Fulica atra)* were mapped (X and Y coordinates) on fishponds during the breeding period, from April to June 2008 (3 visits). The analyses revealed the same patterns for all visits: swan individual distribution was highly clustered within fishponds, reflecting swan pairs and families. Such clusters were located in areas where the density of other waterbirds was the lowest, but swans were nonetheless less distant from other waterbirds than expected if swan and waterbird distributions were independent and if breeding swans had a repulsive effect on waterbirds. On fishponds, this pattern may be explained by the structuring role of the depth gradient on waterbird distribution (i.e. swans have a quasi unlimited access to all submerged aquatic habitats compared to dabbling ducks and to a lesser extent diving ducks and coot), and/or relationships between waterbirds and swans (e.g. potentially commensalism). We conclude that breeding swans within in such an ecological context do not exclude the other waterbirds from the areas of the fishponds they are using. As opposed to common assertions, interspecific territoriality by swans therefore appears to be weak in such ecosystems.

INTRODUCTION

Species-specific requirements and habitat heterogeneity are the two main factors generating spatial distribution of individuals within communities, leading to species assembly and coexistence within a given habitat. Coexistence requires that individuals of different species differ in the way they use the habitat. More precisely, species-specific ability to forage in a structured habitat (Orians 2000), habitat heterogeneity (e.g. Tilman 1982), species average size (Oksanen *et al.* 1979 ; Leyequièn *et al.* 2007) or particular species interactions (Case & Gilpin 1974 ; Calsbeek & Sinervo 2002) all influence coexistence, this set of biotic and abiotic interactions eventually defining the ecological niche of each species. Among such interactions, territoriality is known to potentially limit the distribution of individuals, since the need for animals to permanently adjust their shared boundaries will affect settlement rates and duration of stay within the habitat (Gordon 1997). In such cases, one dominant species is likely to eventually occupy the optimal habitat, from where subordinate species potentially get excluded and forced to suboptimal habitats (Murray JR & Bertram 1971). Arrival of a new species is therefore very likely to affect the community as a whole when the newcomer is territorial and has the potential (given its morphology or behaviour) to become dominant.

Mute Swan (*Cygnus olor*) numbers have recently increased in a dramatic fashion in Western Europe (BirdLife International 2004), implying colonization of new areas. Their size and presumed territorial behaviour may confer a great competitive advantage to swans over smaller waterbird species within colonized habitats. In the Dombes region, Eastern France, we demonstrated that the abundance of other waterbirds was, however, actually higher on fishponds with than without breeding swans, and we did not detect any aggressive behaviour from swans towards other waterbird species (Gayet *et al.* in press). This process was considered to result from aggregation of both swans and waterbirds on fishponds where aquatic macrophytes are expected to be more abundant (i.e. shared habitat preferences). However, fishponds are relatively large waterbodies, so that waterfowl exclusion by swans may have remained undetected in this earlier study because it rather occurs at shorter spatial and temporal scales. For instance, exclusion may occur within a waterbody rather than among waterbodies, i.e. swans may use some areas within fishponds from which they exclude subordinated species.

Spatial point pattern analyses were first introduced by Ripley (1977), and rely on the exhaustive inventory of all individuals from a population within a study area at time t, with individuals (represented by points) located by their geographical coordinates. This technique offers interesting perspectives to understand the way individuals spread over space (e.g.

regularity, randomness or clustering) and biological processes underlying such patterns (e.g. intraspecific territoriality). In the past, it has been largely used for plant studies (e.g. Goreaud *et al.* 2002 ; Couteron *et al.* 2003 ; Perry *et al.* 2006 ; Wiegand *et al.* 2007). Spatial point pattern analyses have conversely long been ignored for wildlife studies, which rather commonly used marked animals (i.e. identified individuals being located over space and time), until the last few years (e.g. Cornulier & Bretagnolle 2006 ; Fisher *et al.* 2007 ; Melles *et al.* 2009 ; Munroe & Noda 2009 ; Hibert *et al.* 2010). Such recent use reflects the increasing will to understand ecological processes in populations and communities, but also major improvements of the analytical methods.

Relying on the analysis of spatial point patterns, we here further explored the processes involved in the spatial distribution of breeding mute swans and waterbirds (ducks and coot *Fulica atra*) within fishponds, with the aim of assessing if breeding swans do exclude other waterbirds from the areas they use within fishponds, testing the following predictions :

(1) If breeding swans develop strong interspecific territoriality and/or if waterbirds and swans use the aquatic environment differently, then distance between breeding swans and other waterbirds should be larger than that derived from a random distribution of points.

(2) If breeding swans do not exhibit any interspecific territoriality, distance between swans and other waterbirds should be lower than that derived from a random distribution of points. Indeed, there should be shared habitat preferences (e.g. attraction to areas that are more beneficial to both swans and other species) within fishponds as there are between fishponds (Gayet *et al.* in press), and/or beneficial relationships between swans and other waterbirds (e.g. commensalism between swans and Wigeon (*Anas Penelope*), Common pochard (*Aythya ferina),* Mallard (*Anas plathyrynchos*) or Coot (Källander 2005)).

(3) Lastly, distance between swans and other waterbirds should not differ from that derived from a random distribution of points within the fishpond if no such convergence or divergence occurs and if all species use the aquatic habitat equally.

METHODS

Study sites

The study took place in the Dombes region (Eastern France 45°57'N, 05°02’E), which is composed of 1,450 fishponds of 7.3 ha on average (± 0.2 SE). In France, this region plays an important role for breeding dabbling ducks (Mallard and Gadwall *Anas strepera*) and diving ducks (Common and Red-crested Pochards (*Netta ruffina*)). The first Mute swan nesting event was recorded in 1974 (Miquet 2003), and the swan population then increased until currently reaching approximately 1,000 individuals (Benmergui *et al.* 2005).

Study period

Waterbirds were monitored on a sample of 83 fishponds (mean = 9.9 ha ± 0.6 SE). Sites larger than 20 ha were avoided, since waterbird distribution cannot be described with the same precision over such large fishponds, and because waterbirds may react differently to swan breeding pairs within such large waterbordies (where swan-free areas are more likely to exist). Fishponds were visited every third week between mid-April and late June 2008, i.e. 3 times each except when practical reasons or emptying of some fishponds prevented these to be monitored on some occasions.

Field surveys

Distribution of individual birds was mapped from an observation site on the bank of each visited fishpond, by a unique observer (VV). In most cases, the observer was located near the emptier due to easy access and good visibility from there over the fishpond. The observer scanned the fishpond with a telescope and each time a bird was encountered, its azimuth and distance were determined using a rangemaster (Leica geovid 7x42 BDA). Bird distance could in some cases not be measured with the rangemaster (because of e.g. unfavourable light conditions or excessive distance). A map of the fishpond and physical elements of its environment (e.g. hedges, islands, trees, reedbeds) from aerial photographs were then used to measure the bird distance within the fishpond map with a ca.50 m accuracy. The data considered in the present study are therefore very similar to Baddeley (2008) example, where an ungulate herd was photographed from the air each day for 10 days, and where each photograph represented a spatial point pattern. In our case, each map obtained during a given visit represented a distinct spatial point pattern. Finally, birds were in some cases so close from each other (e.g. pair, brood with the female), that distinct distance and azimuth (i.e. coordinates X and Y) could not be measured for each bird separately, so that one single measurement was applied to all individuals. Swans, coots and all Anatidae were mapped. On a few occasions (4 fishponds during the first and second surveys, 5 fishponds during the third survey), coots were so numerous (more than 50 individuals) that it was impracticable to map them accurately, so that these samples were discarded for the analyses.

Observational windows and dot maps

For each fishpond, a polygon represented the observational window within which points could be located. This polygon comprised the open water area and a 15 m buffer around it, so as to include most birds even when these were on nearby terrestrial land or onto the banks. For each dot map, each individual (waterbirds or swans) was hence represented by a point. Broods and the female are so strongly dependent that these were simplified to the single species presence, i.e. only one point attributed to a given species when a female with brood was observed. The simplicity assumption does not admit 2 points being at exactly the same place (Ripley 1977). Birds assigned to the same location (e.g. the two members of a Mallard pair) were hence represented by distinct points located at random within 5 metres of the actual measured location.

Statistical analyses

For each survey, only fishponds where breeding swans were detected and mapped were considered for the analyses, since waterbirds may behave differently in the presence of non-breeding swans (i.e. potentially non-territorial) than in the presence of potentially territorial breeding birds. A fishpond was considered as hosting breeding swans when either two adults (one male and one female) or one adult with brood were observed and mapped.

Theoretical background

The simplest parameter of the model representing spatial point pattern is termed intensity (λ), the expected number of points per unit area (Ripley 1977). With respect to stationarity (i.e. statistical features of the process are the same at any location) and isotropy (i.e. properties of the process are invariant to rotation) assumptions, Ripley’s K(r) function (Ripley 1977) corresponds to $\lambda K(r)$: the number of points expected in a circle of radius r, whose centre is fixed on an arbitrary point divided by λ of the pattern under study (Wiegand & Moloney 2004). Thus, for different r distances similarity is compared between the observed pattern and the expected number of neighbours under a simulated random pattern, allowing to identify potential aggregation or regularity (Goreaud *et al.* 2002). Ripley’s K function describes the characteristics of the point pattern over a range of distance scales, and can therefore detect mixed patterns (e.g clustering within a given distance interval and randomness within another) (Wiegand & Moloney 2004).

K function has been extended by Lotwick & Silverman (1982) to provide K_{12}-function, which describes interactions between two point patterns, i.e. bivariate patterns (e.g. two species) which generate their own spatial distributions in the observational window (under assumption of isotropy and stationarity). In a circle of radius r, whose centre is on an arbitrary point of type 1, $\lambda_2 K_{12}(r)$ is the expected number of points of type 2 in r, with its symmetric correspondence (i.e. $\lambda_1 K_{21}(r)$) providing the expected number of type 1 points within r of an arbitrary point of type 2 (Goreaud & Pélissier 2003).

Whatever the function considered, K or K_{12}, we used their linearized forms, L and L_{12} respectively, to stabilize the variance of estimated value and ease interpretation. These linearized forms are estimated with the square-root of the ratio of the function on pi, subtracted by radius at every interval distance, e.g. :

$$L_{12}(r) = \sqrt{(K_{12}(r)/\pi)}-r.$$

L and L_{12} have been computed on the observed spatial point pattern and on a set of random simulations (i.e. after a randomization process). In this paper, simulated patterns were obtained after 500 randomizations carried out on all fishponds together. This number of computerizations was indeed a good compromise between the number of replicates to compute functions and computation time. Following Hibert *et al.* (2010), we represented the envelopes containing the results of 95% and 99% of the randomizations. Departure of the observed patterns from randomness was considered when their values were outside the 95% randomization envelope. When L and L_{12} values of observed data were upper than the envelope containing 95% of the randomisations, the observed point pattern was considered as being clustered. When these values for observed data were conversely lower than the 95% envelope, the observed point pattern was considered as being regular for L, or as reflecting inhibition for L_{12}.

Mute swans distribution within fishponds

Because only fishpond with breeding swans (pairs and families) were selected, aggregation of swan events within fishponds was expected. L was computed for both observed points and randomisations to measure spatial dependence between mute swan observations. On every fishponds we randomized swan locations with the constraint of sampling the same number of points than the number of swan points actually observed on that fishpond.

Null model 1 : Mute swan and waterbird spatial distribution within fishponds

In Null model 1, we measured the relationships between swan and waterbird distributions over fishponds under a hypothesis of independence. All waterbird species had to be considered together, because there were too many fishponds with few observations per guild to separate these, which otherwise would have generated inconstancy in results.

Since breeding swan points were few and *a priori* clustered within fishponds, it was easier to randomize swan points than the location of other, more numerous waterbirds. Thus, waterbirds points on each fishpond remained unchanged during the process, which actually randomized the position of swans (translated and rotated within its fishpond) while preserving their structure (i.e. locations of the different swan event respective to each other).

Null model 2 : Mute swans locations according to waterbird presence probability

Due to potentially shared preferences of swans and waterbirds for some aquatic habitat features, both could conglomerate within specific areas at the scale of the fishpond. We thus pushed the analysis further by measuring if swans use the same fishpond areas than do the other waterbirds, rather than just measuring if swan and waterbird points are more or less distant from each other as done above. We here considered a second null model, which assumed there are no interactions between mute swans and other waterbirds.

We estimated a density probability function (dpf) for waterbird likelihood of presence within fishponds, smoothing waterbird points with the kernel method (Wand & Jones 1995). The least square cross validation method failed to converge while trying to estimate the smoothing parameter, owing to numerous waterbird points at short distance. We therefore relied on a visual appreciation of the smoothing parameter following Wand & Jones (1995) recommendation in such cases. We then identified swan clusters with an ascendant hierarchical classification based on distance between swan points. We first assessed waterbird dpf value where swan clusters were actually located then, like in precedent steps (rotation, translation – see Null Model 1), we randomized swan cluster barycentres within the areas used by the other waterbirds (i.e. on waterbird points), and recorded for each randomisation the dpf value where swan clusters were randomly positioned.

We used R software version 2.10.1 (R Development Core Team 2009) with adehabitat package (Calenge 2006) and splancs (Barry & Peter 2010).

RESULTS

Waterbirds were mapped on 77 to 80 fishponds per survey. Breeding swans with complete mapping of all waterbirds were obtained on 31 fishponds during survey 1, 21 fishponds during survey 2 and 22 fishponds during survey 3. Over the three surveys, swans were considered as breeding (i.e. brooding, observed with cygnets or observed while building the nest) on a total of 36 different fishponds. All surveys pooled, a total of 1,995 points (waterbirds) were mapped, which corresponded in decreasing order of abundance to Coot, diving ducks, dabbing ducks and mute swans. The average number of points mapped per fishpond with breeding swans was maximum during survey 2 and minimum during survey 3 (Table 1).

Table 1 : Number of points mapped on breeding swan fishponds during each survey.

	Survey 1 Mid-April to mid-May	Survey 2 Mid-May to early June	Survey 3 Early to late June
Mute swan	60	47	40
Coot	389	309	205
Diving ducks	254	198	189
Dabbling ducks	115	138	51
Total number of points	818	692	485
Mean number of points ± standard-error	26.4 ± 2	33 ± 4	26.9 ± 3.3

Visual examination of dot maps (see e.g. Figure 1 for survey 1), suggested waterbird distribution had a particular structure on fishponds (i.e. was not at random). Some factors like e.g. bank proximity apparently drove the distribution of waterbirds over fishponds. Mute swan locations were few per fishpond, 1 to 3 points in most cases. These swan points were indeed clustered and seemed to be located close to the other waterbirds.

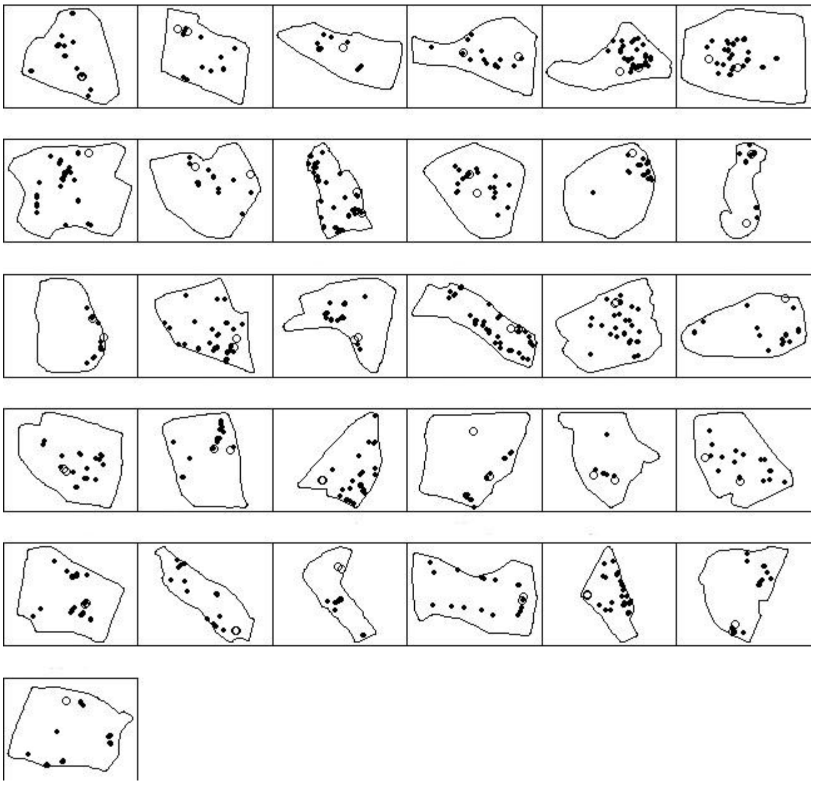


Figure 1 : Dot maps of the 31 fishponds with breeding swans during survey 1. Circles represent swans and black points represent waterbirds (ducks and coots). Dot maps are not to scales.

Structure of swan point pattern within fishponds

Actual swan points were highly clustered over fishponds (Figure 2), as their L value was clearly above that of the randomisation enveloppe (i.e. their distribution derived from randomness) for distances between 0 and 250 m, during all three surveys. The strongest increase of L occurred at very short distance (0 to 20 m) during all surveys. These results confirm the first observation from dot maps: breeding swan points generate clusters within fishponds. These clusters of swan events have been taken into account during the following analyses.

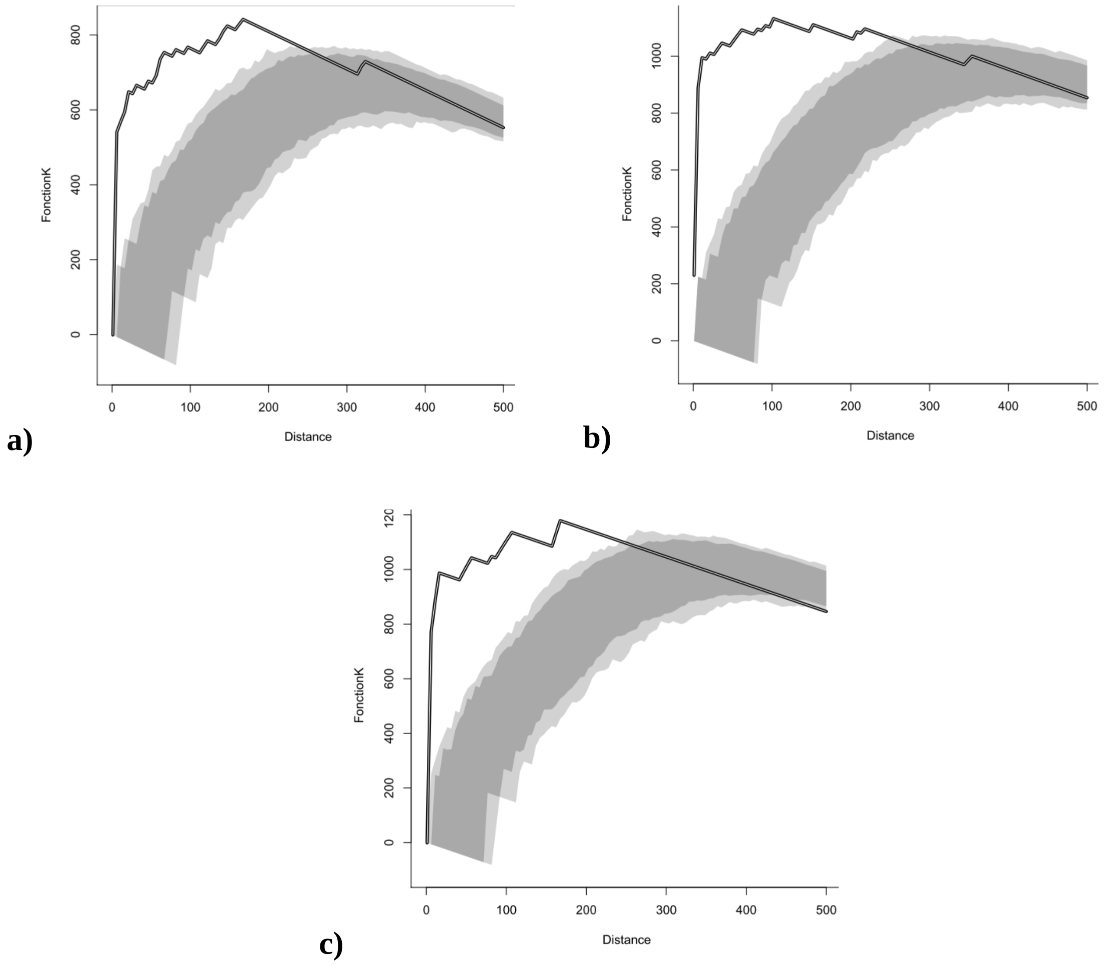


Figure 2 : L function of swan events on fishponds for survey 1 (a), survey 2 (b) and survey 3 (c). The black line indicates the observed pattern. Dark and light grey envelopes encompass 95% and 99% of the 500 randomizations, respectively. For all surveys, the observed patterns derive from randomness (i.e. are above the 95% randomizations envelope) between 0 and 250 metres.

Distribution of swans according to waterbird presence within fishponds

Analyses of the L_{12} revealed swan aggregation around waterbirds during all three surveys (Figure 3), i.e. swans were more numerous in the vicinity of waterbirds than expected if the former spread randomly within fishponds. Aggregation of swans around waterbirds occurred within a maximum radius of 135 m, with few exceptions (see Figure 3). However, the magnitude of the difference between observed and randomized patterns depended on surveys. The weakest aggregation was observed during survey 1, while aggregation was the clearest during survey 2.

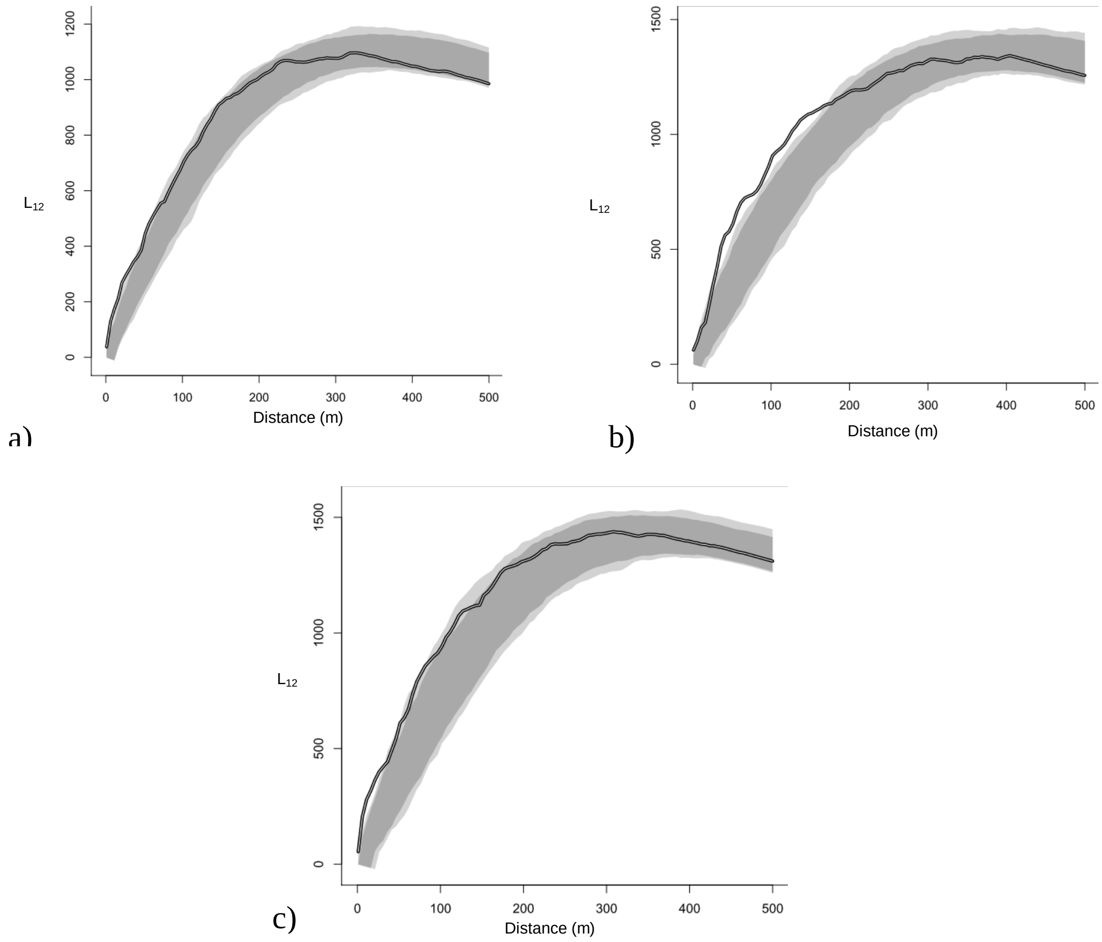


Figure 3 : L_{12} function of the interaction between breeding swans and waterbirds on fishponds for survey 1 (a), survey 2 (b) and survey 3 (c). The black line indicates the observed pattern. Dark and light grey envelopes encompass 95% and 99% of the 500 randomizations, respectively. Observed patterns derived from randomness between 0-45 m, 55-75 m and 145-160 m for survey 1 - between 0-5 m and 30-175 m for survey 2 and between 0-135 m for survey 3.

Swan distribution compared to other waterbird main presence areas

A 15 m smoothing parameter on waterbird points was selected to calculate dpf. This distance was adequate to identify waterbird cores of presence and avoid excessive smoothing (Figure 4). The above analyses revealed that swan clustering was particularly strong within a 20 metres radius. We identified swan clusters on fishpond for every survey within a 20 m distance with an ascendant hierarchical classification, i.e. the minimum distance between observations within cluster is smaller than 20 m. We ensured swan clusters where located randomly with L (not shown). For all three surveys, dpf value around actual breeding swan cluster barycentres was much lower than that recorded when swan clusters were randomized over waterbird cores of presence (Figure 5). The null model of shared preferred areas with no interactions between swans and the other waterbirds can therefore be rejected: breeding swans were not located within waterbird cores of presence, but rather in areas of lower waterbird density. The results were similar with 50 m and 100 m smoothing parameters (not shown), suggesting the value of the smoothing parameter did not affect this result.

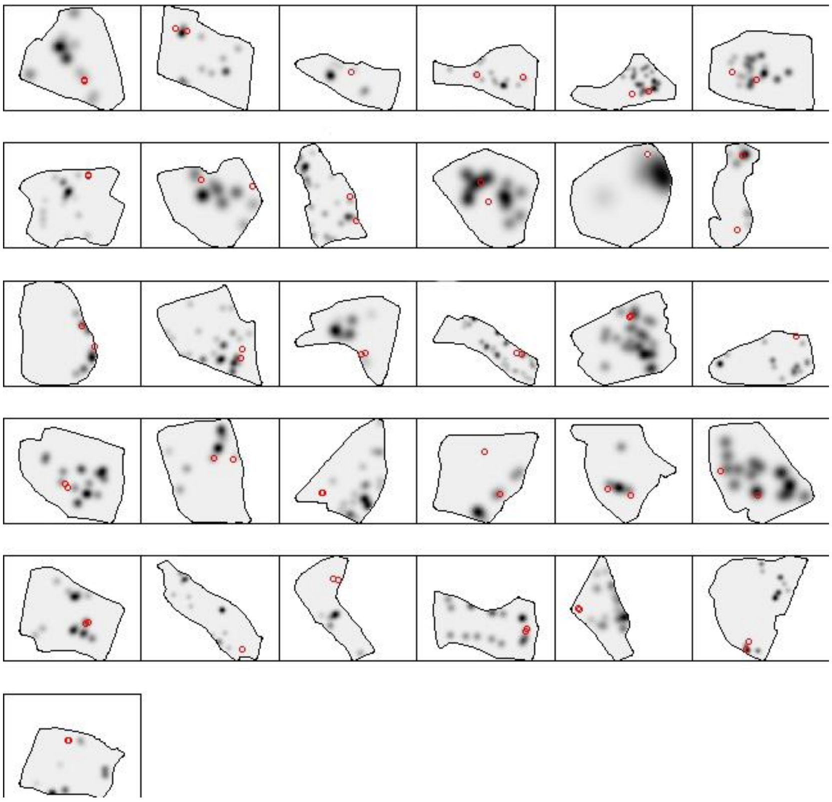
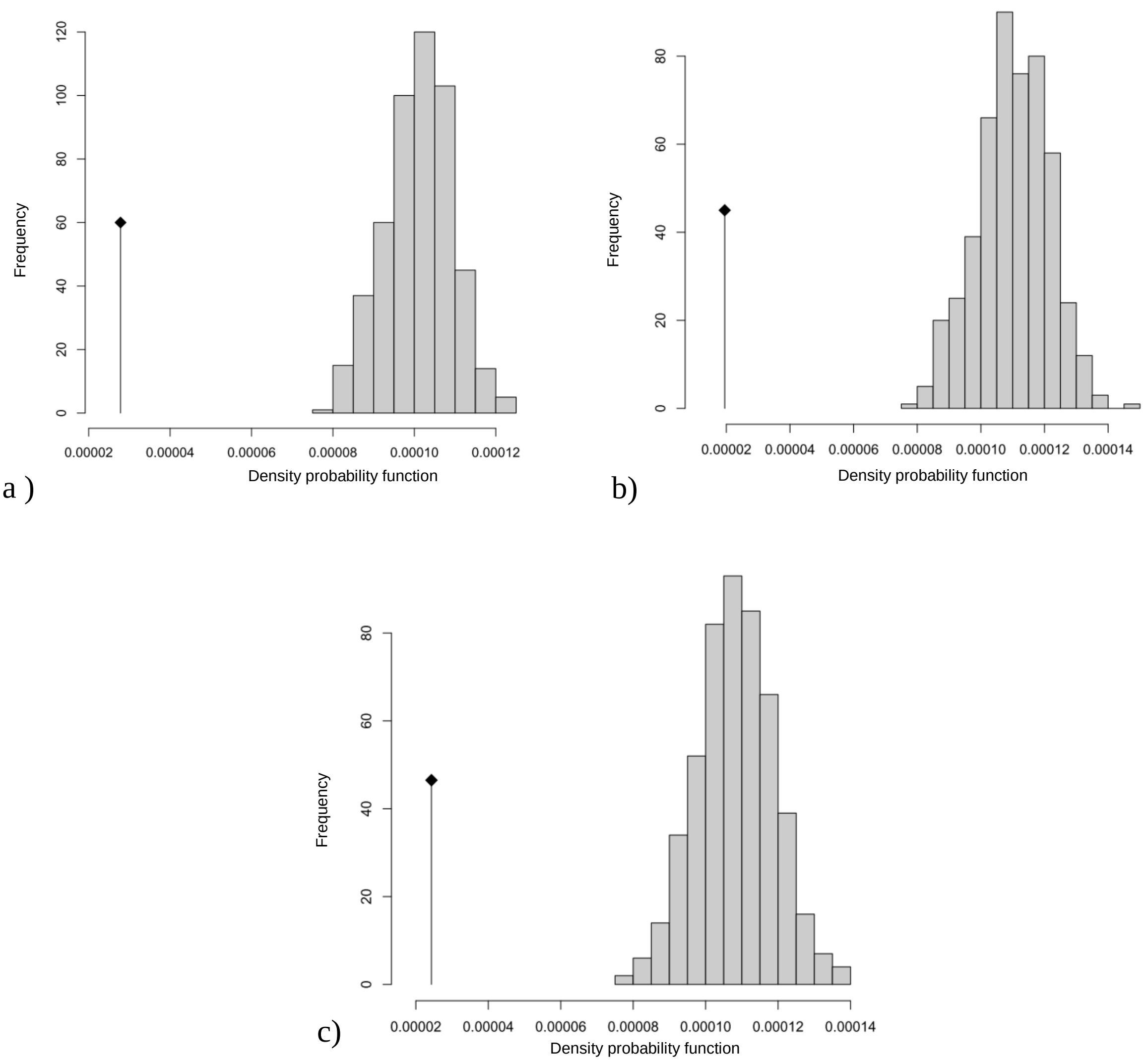


Figure 4 : Smoothing of waterbirds with the kernel method during survey 1 to measure the density probability function. Smoothing parameter was fixed visually to 15 m (see text). An increasing dark grey level indicates higher waterbird density probability function. Circles represent swans.



a)

b)

c)

Figure 5 : Density probability function of waterbirds where swan clusters were randomly positioned (bar plots), and actual density probability function where swan clusters were observed in the field (black point) for survey 1 (a), survey 2 (b) and survey 3 (c).

DISCUSSION

Our results highlight that waterbirds and breeding mute swans can simultaneously use the same areas within fishponds, breeding mute swans even being closer to the other waterbirds than expected if the two distributions were independent. Such aggregation process occurs at a relative large distance on fishponds (up to ca. 130 m). However, mute swans are located within areas of lower waterbird density. These results suggest breeding swans do not exclude other waterbirds either from fishponds altogether (see Gayet *et al.* in press), nor from some areas within fishponds, even if they are known to behave in a territorial way towards other waterbird species in specific ecological contexts (e.g. Conover & Kania 1994).

The decreasing number of breeding swans observed especially between period 1 and 2 is likely to reflect fishpond desertion after brood failure (be this failure due either to natural causes or to illegal destruction), swans then leaving their territory to join non-breeders in moulting flocks (Coleman *et al.* 2002). The limited number of mute swan points observed per fishpond and their clustering at short distance are simply reflecting the way we selected study sites, i.e. only fishponds with breeding swans. Here, swan events corresponded to pairs or families with cygnets, which are always close from each other, hence the clusters observed. Despite this local clustering of swan events, we detected that swans were closer from the other waterbirds than expected by chance in a radius over 100 m. In other words, mute swan proximity with waterbirds is higher than that of random points spread on the entire fishpond, though swans were generally not in the core areas of other waterbird presence (Hypothesis 2 confirmed).

That swans and other waterbirds did not have exactly matching cores of higher presence may indicate they do not share exactly the same habitat preferences, owing for example to different biological requirements and abilities to reach food. Pöysä (1983) indeed identified two main habitat use strategies on Finnish eutrophic lakes : diving ducks generally occupying the centre of the waterbody, whereas dabbling ducks and coot relying on the edges and shallow parts to a greater extent. The situation may be even more extreme with swans given their very large size compared to other waterbirds. Pöysä & Sorjonen (2000) considered that expanding whooper swan (*Cygnus cygnus*) populations found a vacant niche when they started to recover in Nordic lakes. Such a differential habitat use may allow coexistence of species within a bounded environment like most aquatic ecosystems are (see Guillemain *et al.* 2002). Further analyses taking into account habitat properties (e.g. depth, reedbeds) as covariates in the modelling process (e.g. the function K_{inhom} see Baddeley & Turner 2005) would be necessary to test this and hence to assess the potential role of habitat heterogeneity (e.g. depth) on the pattern of points observed. It was not possible with the present dataset to assess if individuals from some guilds (i.e. herbivores) were closer to swans than other waterbird guilds, because the number of points per guild was too low. Only a massive increase in fishpond sample size may allow testing such patterns in the future, which will provide some insight into whether different habitat preferences between swans and some or all other waterbirds was responsible for their differential distribution.

Nevertheless, swans and the other waterbirds were more closely distributed that what a random process would have produced. This may be related to mute swans having an attractive effect on the other waterbirds, stretching them from their core areas of presence. Swans indeed potentially rely on food that is inaccessible to other species, owing to their large size (Oksanen *et al.* 1979). This may for instance provide some waterbirds with an easier access to deeper macrophyte beds in the fishpond: swans often bring plants back to the water surface before ingesting them. By doing so, they make some resource available to other waterbirds unable to reach the macrophyte beds themselves. Such a relationship may hence take the form of commensalism (e.g. Källander 2005), which may explain why some waterbirds are closer to swans than expected by chance. Coots for instance were observed feeding behind foraging mute swan families during the present surveys (personal observations). Simultaneous behavioural recordings of swans and associated waterbirds may help assessing if such commensalism occurs frequently enough to explain the distribution of waterbirds relative to swans. That the other waterbirds were closer to swans during survey 2 may actually be due to the fact that this period corresponds to when cygnets are the youngest: this is when adult swans often collect vegetation and bring for the cygnets to feed on it (Cramp *et al.* 1986), thus increasing commensalism opportunities for the other species.

Despite spatial point patterns have poorly been used for waterbird studies so far, the present study shows they are an efficient tool to understand ecological processes in addition to patterns within such communities. They may in particular be a very powerful tool to test presumed detrimental effects of new species arrival in environments where they are assumed to have a despotic behaviour. Such methods may hence help deriving appropriate management and conservation policies from distribution patterns of wildlife species.

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Article 6: Combined effects of Mute swan (*Cygnus olor*) grazing intensity, plant growth stage and fishponds trophic status on macrophyte abundance and diversity.

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ABSTRACT

The mute swan (*Cygnus olor*) is one of the largest herbivorous waterbirds in the world. Its population increased dramatically over the last decades in Western Europe, leading to concerns about its potential impact on aquatic ecosystems. Indeed, the consequences of waterfowl grazing for fishpond macrophytes remain poorly investigated, although fishponds' animal communities and economic value both largely depend on them. We carried out an experiment in the Dombes region (Eastern France) with 116 exclosures on 29 fishponds. Our aim was to assess the impact of swan grazing on aquatic macrophyte presence, abundance and structure during the growth season (April to July). We also considered the potential effect of plant growth stage, swan density (i.e. number of swan.days/ha) and fishpond trophic status on macrophyte communities. Swan grazing negatively affected the presence and abundance (cover) of macrophyte communities. Depletion was more pronounced later in the season, presumably because plants could not compensate for herbivory to the same extent after having reached their mature stage. Such effects were exacerbated by longer swan residence per hectare during earlier stages of the growth season. During the later stages of the growth season, the impact of swans was buffered by the trophic status of fishponds. Furthermore, swan grazing negatively affected macrophyte community structure (diversity and equitability), suggesting that mute swan may promote the dominance of a few macrophytes species. The impact of the expanding population of mute swans should be monitored in the future, since both the repeated use of the same fishponds by birds and their expansion within the landscape may lead to more acute and broader consequences for macrophyte beds over the long term.

INTRODUCTION

Macrophytes play a key role in aquatic ecosystems. These plants regulate biogeochemical cycles (Conley, 2000) and provide habitats and food for a wide variety of animals: macroinvertebrates (Gregg & Rose, 1985 ; Jeppesen *et al*., 1998 ; Mitchell & Perrow, 1998), waterfowl adults and broods (Staicer *et al*., 1994 ; Perrow *et al*., 1997), as well as fish (Crivelli 1983; Rozas & Odum, 1988). Many factors may affect macrophyte growth (listed in Lacoul & Freedman, 2006). Though it has long been considered to play a minor role among these factors (Lodge, 1991), hydrophyte depletion by grazing herbivores has received a growing interest over the last decades. Indeed, grazing has a wide range of possible effects on aquatic plant communities, by modifying dominance relationships (Santamaria 2002; Rodriguer-Villafane *et al*., 2007), limiting abundance (Idestam-Almquist 1998; Rodriguez-Perez & Green 2006) or indirectly stimulating the development of the consumed resource (Sandsten & Klaassen 2008).

The growing interest in herbivore/macrophyte relationships also partly results from the expanding populations of some grazers, such as large waterbirds. Numerous studies on geese and swans have shown a wide range of vegetation responses to herbivory by these animals (Esselink *et al*., 1997; Badzinski *et al*., 2006; Gauthier *et al*., 2006; Tatu *et al*., 2006; O'Hare *et al*., 2007; Hidding *et al*., 2009). Most of these studies conclude that swans have a negative effect on macrophyte abundance, but most work has been carried out on large lakes, rivers, estuaries and coastal areas. Conversely, few studies have considered the potential impact of swans on inland ecosystems such as fishponds (non-flowing shallow freshwater ecosystems), despite the particularly high population growth rate of swans in such habitats, where macrophyte communities also face specific constraints. Mute swan is an expanding species in Europe since the 1970s (BirdLife International, 2004), and fishponds also represent a large proportion of available wetlands in the continent. Potential depletion of macrophytes by swans is therefore a major concern in such ecosystems: a mute swan is considered to consume 3 to 4 kg of aquatic vegetation daily (Cramp *et al*., 1986). Moreover, it has been suggested that losses generated by grazers may also result from non-consumptive destruction in aquatic ecosystems, e.g. disturbance generated by herbivores during their foraging activities (Lodge 1991). Eventually, grazing may also have longer-term consequences in addition to the effect on vegetation biomass, through changes in species richness and abundance (Lodge & Lorman 1987). Being one of the largest waterbird species, mute swans may disturb macrophyte beds over large areas in fishpond ecosystems, thereby affecting macrophyte communities and other components of the aquatic ecosystem both quantitatively and qualitatively.

It is likely, however, that the potential impact of swans on macrophytes may vary over the year, depending on the period and intensity of grazing, as well as nutrient availability. Indeed, the compensatory response of plants to grazing decreases over the growth season (Maschinski & Whitham 1989). The relatively short stay of numerous birds in moulting flocks and the repeated use of the same waterbody by a territorial nesting pair over the breeding season should thus entail very different consequences (Tatu *et al*. 2006). Theoretically, macrophytes should also be affected differently by swans depending on the trophic status of the waterbody, as has been suggested in other ecological contexts (e.g. Maschinski & Whitham 1989 ; Hawkes & Sullivan 2001). Most earlier studies on grazing processes in aquatic ecosystems have considered the potential effects of the grazing period, residence and waterbody trophic status separately, although it is likely that these factors have combined effects. We thus considered here how these factors simultaneously interact with grazing in affecting the dynamics of macrophyte communities. Our aim was to assess how mute swan may affect the presence and structure of macrophyte beds, by investigating the following questions : (1) Does mute swan grazing affect the presence, abundance and structure of macrophyte communities during the plant growth season ? and (2) If depletion of macrophytes by swans is significant, does it vary with time, bird stay and the trophic status of fishponds ?

METHODS

Study area

The study took place in the Dombes region (Eastern France 45°57'N, 05°02'E), which contains 1,450 freshwater fishponds of 7.3 ha (± 0.2 SE) on average. In Dombes, macrophyte beds play an important role for duck broods, fish spawning (mainly carp *Cyprinus carpio*) and many other animal taxa. The main macrophytes in the area are Eurasian water-milfoil (*Myriophyllum spicatum*), various-leaved pondweed (*Potamogeton gramineus*), curled pondweed (*Potamogeton crispus*), holly-leaved naiad (*Najas marina*), brittle naiad (*Najas minor*) and pond water-crowfoot (*Ranunculus peltatus*) (Curtet, unpublished data), but macrophyte communities differ greatly between fishponds. Mute swans nested in the area for the first time during the 1970s. The population then gradually increased and reached ca. 1,000 individuals (Benmergui *et al*. 2005).

Study sites, period and experimental design

The experiment to assess the impact of mute swan on aquatic macrophytes was carried out on 29 fishponds (mean area: 16.4 ha ± 1.9 SE) in 2008 and 2009, from April until the end of July. Fishponds known to be regularly used by nesting and moulting swans were selected.

The experimental design comprised an exclosure (i.e. an area that was inaccessible to mute swans but accessible to the other herbivores, such as coot *Fulica atra*, carp and coypu *Myocastor coypus*, which were all observed inside the exclosures), and four open plots (accessible to all species including swans) (Figure 1). The exclosure was made of 1.2m high wire netting (mesh size 0.15 m) delimiting an area of 5 x 5 m². Two threads between the opposite corners of the exclosure prevented swans from entering the area from above. Due to potential consumption by swans from the outside, the outer 1 m of the exclosure was not considered in the analyses (so that the effective exclosure area was 9m²). Each open plot was 10 m from the exclosure, and positioned in areas of similar depth to that of the exclosure. A pole was placed in the centre of each 4m² open plot. We identified quadrats of 1m² by numbering them in open plots and exclosures. Four such experimental sets (one exclosure and four associated 4m² open plots) were used per fishpond, hence a total of 116 experimental sets.

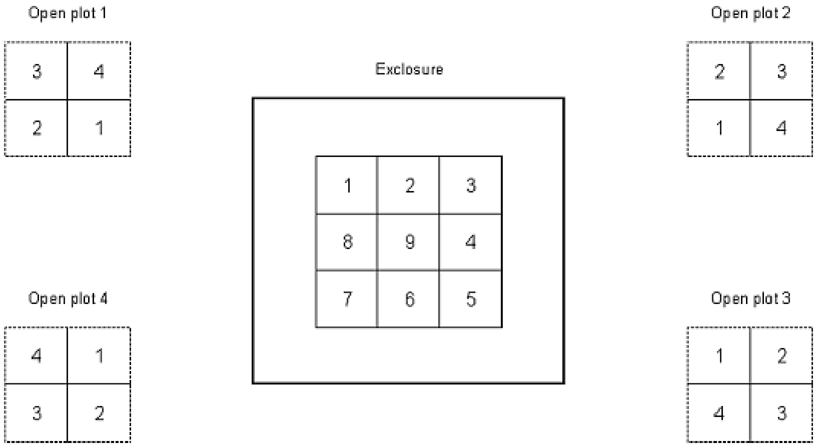

Figure 1: Experimental design with the exclosure area inaccessible to swans (n = 9 quadrats of 1 m²) and its four associated open plots available to swans (n = a total of 16 quadrats of 1 m² each).

Fishpond trophic status

Fishponds are heterogeneous meso-eutrophic ecosystems. Since one of the aims of the study was to unravel the relative effect of nutrient availability compared to the potential effect of swans, we measured the fraction of nutritive elements contained in interstitial water, following Enell & Löfgren (1988). Sediment samples were taken with an Ekman grab on each site in March, so as to assess the amount of nutritive resources available to macrophytes during spring and summer. Sediment was sampled at three random points per fishpond, and interstitial water was obtained by aqueous extraction after mixing of the three samples. Physico-chemical parameters measured were total phosphorus, Kjeldhal nitrogen, pH, Ca^{2+} and orthophosphates. A Principal Component Analysis (PCA) was used to rank fishponds on a trophic gradient after their coordinate on the first axis (not shown). The major structuring parameters in the PCA were total phosphorus, Kjeldhal nitrogen and orthophosphates, which all highly contributed to the definition of the first axis (63%), the second axis explaining 22% of the total inertia.

Swan.days and non-destructive vegetation measurements

Swans were counted weekly from April until the end of July. The total number of swan.days (number of birds time their length of stay) from the beginning of the experiment was then calculated monthly so as to get an estimate of swan grazing intensity on macrophytes. In order to control for the influence of fishpond size in assessing the effect of swan stay, the total number of swan.days was calculated per area unit, i.e. swan.days/ha. Swan.days/ha thus represents the grazing intensity exerted on macrophytes for a given site.

Plant cover was estimated in each 1 m² quadrat within exclosures (n= 9 quadrats each) and associated open plots (n = 16 quadrats each), the last week of May, June and July. In each quadrat, total plant cover and species composition (10% percentage classes) were visually estimated. Monthly measures represent stages in the growth season, and allowed testing for the effect of grazing depending on when this occurred.

Vegetation biomass

Destructive measurements of vegetation biomass through plant harvest were taken at the end of the monitoring period, before the exclosures were taken out from fishponds in July. This provided an exhaustive measurement of the absolute response of the macrophyte community to swan depletion (i.e. all plant species in the water column were recorded) at the end of the experiment. Vegetation biomass varied greatly between fishponds, and was so high in some cases (i.e. > 3 kg fresh mass/m²) that it was impractical to sample all quadrats. Vegetation was thus sampled on 109 experimental sets (7 experimental sets were removed due to minor problems during July). 8 quadrats systematically selected per set were sampled (4 in the exclosure plus 4 in associated open plots), except for 18 experimental sets where vegetation was so abundant that only one or two quadrats were sampled. Biomass samples were collected within each 1m² quadrat after it was delimited by a 1m high and 1mm mesh size net, fixed with 4 poles in the corners. Collected vegetation was then dried for 72hours at 55°C before being weighed (to the nearest 0.1 g) separately for each species in each quadrat being sampled.

Dry biomass and plant cover measured in July were significantly correlated within quadrats (rho $_{\text{spearman}}$: 0.85 ; p-value < 0.001), which confirmed that the non-destructive plant cover measurements in May, June and July were appropriate indicators of vegetation biomass in the water column.

Statistical analyses

The number of experimental sets considered during each step of the analyses was constrained by two parameters : the fast dynamics of macrophyte communities between and within fishponds over months (i.e. overall plant presence and plant species varied significantly), and the nature of the questions being considered.

Firstly, we aimed at testing whether swan grazing caused macrophytes to gradually disappear, with a potentially combined effect of trophic status and swan stay. To identify such a process, we used a binary response variable (hereafter termed variable PRESENCE): quadrats with aquatic macrophytes were scored 1, as opposed to 0 where plants were absent.

Secondly, we analyzed the effect of swan grazing on macrophyte abundance. Only experimental sets that contained macrophytes during at least one month were retained for this analysis. We estimated mean cover (in %) and mean biomass (in g dry weight) differences between exclosure and open plots for all these fishponds in April, May and June. Differences in mean values were tested using Wilcoxon tests. Even when only experimental sets that contained macrophytes for at least one month were considered, there was still a large number of quadrats with no vegetation, leading to a non-Normal distribution of the data. To overcome this problem, we therefore computed mean plant cover on a monthly basis on comparable areas for each experimental set, by systematically selecting and pooling data from the eight quadrats from open plot 1 and 3 on the one hand, and the nine exclosure quadrats (see figure 1) on the other hand. For dry biomass, the mean value was also computed monthly outside and inside the exclosure of each experimental set. The difference between mean cover (termed COVER) and mean dry biomass (termed BIOMASS) in exclosure and open plots was calculated for all experimental sets, and we analyzed how trophic status or swan stay may buffer or, conversely, increase potential differences between areas that were accessible to swans (open plots) or not (exclosures).

Thirdly, we tested whether swan grazing affects the structure of macrophyte communities. Each month, experimental sets that contained several species in at least one quadrat were selected to measure the consequences of grazing activity. The number of such experimental sets varied over months, which prevented us from testing for combined effects of swan stay and trophic status with grazing activity over the growth season. We thus limited the analyses to the grazing effect (i.e. without covariates) on macrophyte community composition for April, May and June. We used Shannon's index of diversity (H') (Shannon & Weaver 1949) in addition to equitability (E) to assess community composition independently from species richness. Indices were derived from the plant cover value for each species estimated monthly in the quadrats. As H' and E on quadrats deviated from Normality (due to a large number of quadrats with zero values), we computed these indices on two sets of pooled quadrats in each exclosure (first vegetation set : quadrat 1, 2, 7, 8; second vegetation set : quadrat 3, 4, 5, 6), and in two open plots of 4 quadrats each (first vegetation set : open plot 1; second vegetation set : open plot 3). This featuring of quadrats within experimental sets decreased the distance between open plots and exclosure areas, and thus increased the chance of meeting similar macrophytes beds (see Figure 1).

We used a General Linear Mixed Model (GLMM) to analyse data separately for each month, as explained above. GLMMs allow specifying a random effect, which corresponded here to the nested structure of the experiment, as well as fixed effects. For PRESENCE, fixed effects were swan grazing ("GRAZING", i.e. exclosures versus open plots), swan stay ("STAY" in swan.days/ha) and fishpond trophic status ("TSTATUS", i.e. the coordinate of a fishpond on the first PCA axis). Single terms were included simultaneously in the complete model as well as key interactions only (i.e. GRAZING*STAY and GRAZING*TSTATUS for COVER), as advocated by Bolker *et al*. (2008). COVER, STAY and TSTATUS were considered in the same initial model. GRAZING was the only fixed parameter considered for H' and E. Non-significant terms (at $P = 0.05$) were gradually removed from the models in a backwards-stepwise procedure. R 2.10.1 software was used for all statistical tests (R Development Core Team, 2009).

RESULTS

Swans used all 29 fishponds during the study period. One fishpond was only temporarily occupied, 2 fishponds were used as flocking sites and 26 as nesting sites. Among the nesting sites, 15 were genuine breeding sites, i.e. adults with cygnets occupied the fishpond during at least one month, as opposed to the other 11 fishponds where no family was ever observed though adult swans may have used the site, including after clutch failure. Swan stay thus differed markedly between fishponds, depending on the duration of swan presence, the number of swans and fishpond size (Appendix A). Swan stay (swan.days/ha) was negatively, but not strongly, correlated with fishpond size (May: $\text{rho}_{\text{spearman}}$: -0.40, p-value = 0.03 ; June: $\text{rho}_{\text{spearman}}$: -0.33, p-value = 0.08 ; July: $\text{rho}_{\text{spearman}}$: -0.26, p-value = 0.17).

Each month, 19 to 24 fishponds contained macrophytes. Macrophyte communities varied significantly between months, and differed between fishponds (Appendix A). 4 fishponds never contained aquatic macrophytes, and were hence only considered for analyses of GRAZING effect on PRESENCE with TSTATUS and STAY below.

Presence of macrophyte beds within experimental sets

Owing to drought or other minor problems, a few experimental sets could not be monitored every month. The true presence of aquatic vegetation was recorded in 70 experimental sets in May and 82 experimental sets in June among the 114 monitored, and 52 in July among the 105 monitored. In May, the final model to explain the presence of macrophytes only included the interaction between swan stay and swan grazing (Table 1): indeed, grazing at a high swan density had a measurable and significantly negative effect on the presence of aquatic macrophytes (see example Figure 2a). In June and July, the final models only included the effect of swan grazing, which was negative and statistically significant to describe the presence of macrophyte beds: macrophytes were less likely to be present where swans could graze (i.e. in open plots as opposed to exclosures) (see example Figure 2a and 2b). The magnitude of the effect of grazing increased in June and July compared to May.

Table 1: General linear mixed models selected after a backwards stepwise model selection process to measure the potential effect of swan grazing (GRAZING), swan stay (STAY) and fishpond trophic status (TSTATUS) on the presence of a plant cover (PRESENCE).

		Estimate ± SE	z	*P*
PRESENCE	*May (n: 29 fishponds and 114 experimental sets)*			
	Intercept	-2.24 ± 1.64	-1.37	
	GRAZING	0.04 ± 0.37	0.12	
	STAY	0.04 ± 0.07	0.63	
	GRAZING*STAY	-0.08 ± 0.02	-4.69	***
	June (n: 29 fishponds and 114 experimental sets)			
	Intercept	1.13 ± 1.35	0.84	
	GRAZING	-2.05 ± 0.18	-11.39	***
	July (n: 29 fishponds and 105 experimental sets)			
	Intercept	-2.89 ± 2.41	-1.20	
	GRAZING	-1.78 ± 0.24	-7.29	***

"***": p < 0.001 ; "**": p < 0.01 ; "*": p < 0.05 ; ".": p < 0.1

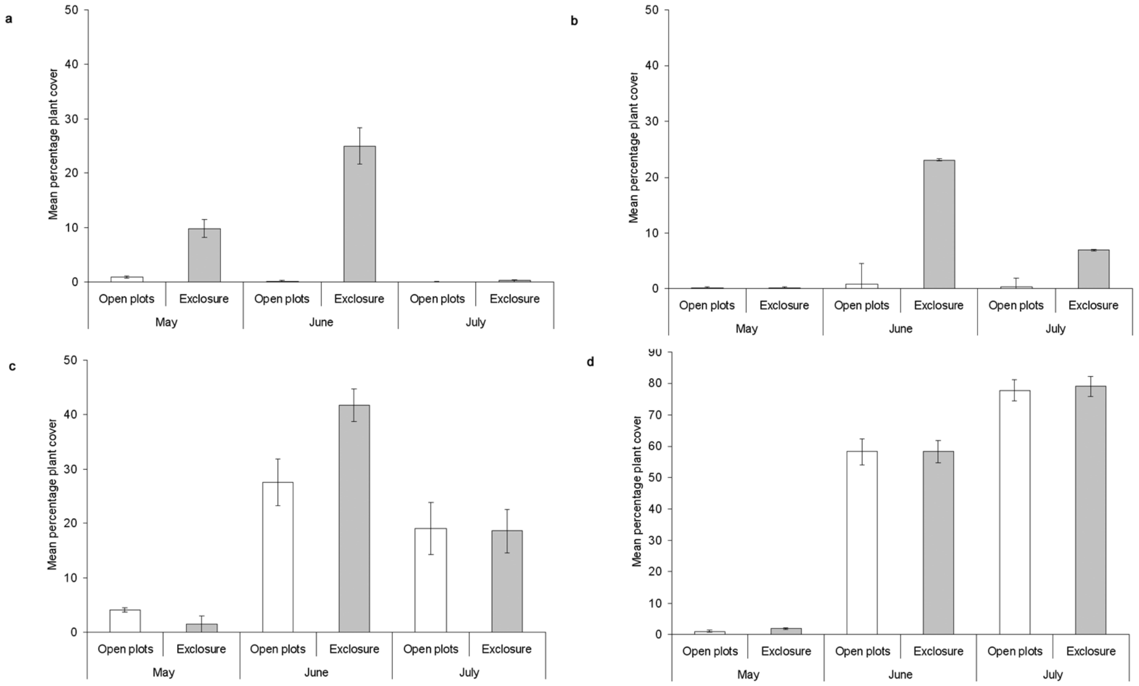

Figure 2 : Mean macrophyte cover in experimental sets in May, June and July on a sample of four fishponds (a : fishpond number 10 with high swan density, b: fishpond number 18 with strong swan effect, c : fishpond number 4, a highly eutrophic waterbody and d : fishpond number 3 without strong differences observed). See appendix A for more details on these fishponds.

Abundance of macrophyte beds

Twenty-five fishponds contained macrophytes beds at least once within experimental sets, providing 90, 89 and 80 experimental sets available for analyses in May, June and July, respectively. Plant cover was 2.1%±1.3 (SE) lower (Wilcoxon test: V=74 - p=0.05) in open plots than in exclosures in May. The corresponding value was 5.8%±1.7 (SE) and was also significant (Wilcoxon test: V=34 – p=0.001) in June. The difference was over 10% on 8 fishponds during May and 11 fishponds during June (Figure 3). In May and June, the final models were the null models, indicating that neither the inclusion of swan stay nor that of trophic status had a significant effect on vegetation depletion rate by swan grazing (Table 2). The mean cover difference was –3.3%±1.3 (SE) between exclosures and associated open plots in July on the 25 fishponds (Wilcoxon test: V=40 – p=0.03). The difference was over 10% on 6 fishponds during July (Figure 3). The final model in July retained trophic status as a single factor, with a negative effect , meaning that the negative effect of Grazing was buffered by higher trophic status (i.e. differences between open plots and exclosures were smaller in more eutrophic fishponds; see Figure 2c, one of the most eutrophic fishponds). In some fishponds only minor differences were observed anyway throughout the monitoring period (see example Figure 2d).

Eighty-four experimental sets on 24 fishponds contained at least one quadrat with dry biomass over 0g. In such experimental sets, mean plant dry biomass was 7.8g±4.1 (SE) (Wilcoxon test: V=186 – p=0.06) lower in open plots than in exclosures. The difference was over 25g on 5 fishponds during July (Figure 3). However, neither TSTATUS nor STAY had a significant effect on the magnitude of the difference in average biomass between open plots and exclosures (Table 2).

Table 2: General linear mixed models selected after a backwards stepwise model selection process to measure the potential effect of swan stay (STAY) and fishpond trophic status (TSTATUS) on mean cover (COVER) and mean dry biomass (BIOMASS) differences observed between exclosure and open plots per experimental sets.

		Estimate ± SE	t	*P*
COVER	*May (n: 25 fishponds and 90 experimental sets)*			
	Not significant			
	June (n: 25 fishponds and 89 experimental sets)			
	Not significant			
	July (n: 25 fishponds and 80 experimental sets)			
	Intercept	-1.55 ± 2.06	-0.75	
	TSTATUS	-3.59 ± 1.33	-0.71	*
BIOMASS	*July (n: 24 fishponds and 84 experimental sets)*			
	Not significant			

"***": p < 0.001 ; "**": p < 0.01 ; "*": p < 0.05 ; ".": p < 0.1

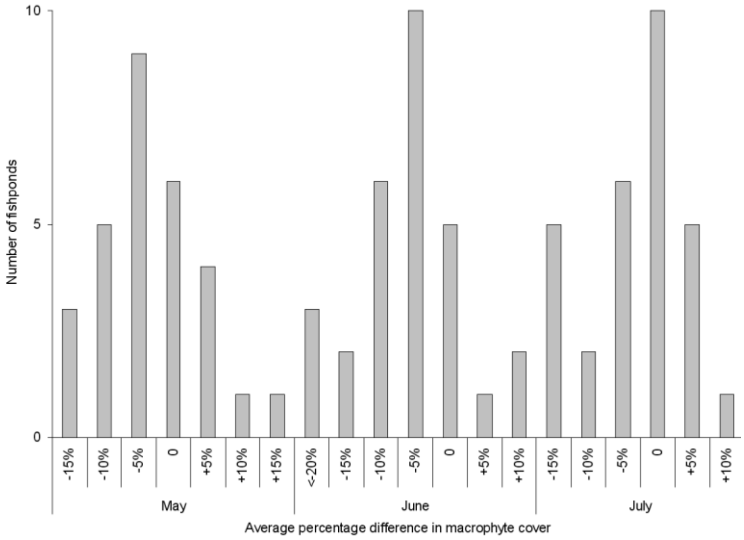

Figure 3: Number of fishponds with a given average % difference in macrophyte cover between exclosures and open plots in May, June and July.

Community structure

Multispecific macrophyte communities were observed in 49 experimental sets on 18 fishponds in May, in 54 experimental sets on 20 fishponds in June and in 31 experimental sets on 15 fishponds in July. Grazing had a significant effect on H' and E in May and June, indicating that the dominance of a few species was enhanced by mute swan grazing, which reduced the diversity of communities (Table 3). Unfortunately, with such heterogeneous macrophyte communities it was not possible to assess which plant species' growth was promoted by swan grazing. In July, the effect of grazing on H’ was weaker, while the effect on E was statistically non-significant.

Table 3: General linear mixed models selected after a backwards stepwise model selection process to measure the potential effect of swan grazing (GRAZING), on the Shannon index of diversity (H’) and equitability (E) of macrophyte communities.

		Estimate ± SE	t	*P*
May (n: 18 fishponds and 49 experimental sets)				
H’	Intercept	0.28 ± 0.03	8.56	***
	GRAZING	-0.08 ± 0.02	-4.85	***
E	Intercept	0.63 ± 0.04	14.84	***
	GRAZING	-0.18 ± 0.05	-4.05	***
June (n: 20 fishponds and 54 experimental sets)				
H’	Intercept	0.28 ± 0.03	8.31	***
	GRAZING	-0.09 ± 0.02	-4.96	***
E	Intercept	0.58 ± 0.04	14.44	***
	GRAZING	-0.18 ± 0.04	-4.12	***
July (n: 15 fishponds and 31 experimental sets)				
H’	Intercept	0.22 ± 0.03	6.50	***
	GRAZING	-0.04 ± 0.02	-2.21	*
E	Intercept	0.23 ± 0.06	3.56	***
	GRAZING	-0.02 ± 0.03	-0.74	.

“***”: $p < 0.001$; “**”: $p < 0.01$; “*”: $p < 0.05$; “.”: $p < 0.1$

DISCUSSION

Our results clearly demonstrate that grazing by swans induces significant depletion of macrophyte beds within fishponds. As a consequence of mute swan foraging activity, plant presence and abundance as well as macrophyte community structure were all affected. The magnitude of the effect of grazing varied depending on when and to which extent swans stayed during the plant growth season. Similarly, the effect of grazing was also sometimes reduced by higher trophic status. Our results are therefore consistent with those of earlier studies in other ecological contexts, though the interaction between grazing and some covariates was here explicitly documented.

Sondergaard *et al*. (1996) suggested that depletion of macrophytes by waterbirds “*will be greatest in relatively small lakes, in which the total lake surface area is small in relation to the littoral zone*”. Conversely, in fishpond ecosystems, virtually all the open water area is available to swans due to the generally low depth of such waterbodies. This may explain why we could record high densities of swan.days independently from fishpond area (since the negative relationship between swan stay and fishpond area, although genuine, was of limited magnitude): the adverse effects of grazing may therefore occur for macrophyte beds independently from waterbody size.

It should be kept in mind, however, that many other factors in addition to grazing by swans may affect the development of macrophyte beds (e.g. Toivonen & Huttunen 1995; Perrow *et al*. 1997; Lake 2003; Mäkela *et al*. 2004). Many of the fishponds without vegetation, or where vegetation was scarce, were among the most eutrophic sites we studied, which could have limited macrophyte development. Some of them also hosted large numbers of Coots during the study period, which could have masked the swan effect through their consumption of vegetation in the exclosures.

The effect of swan grazing was weak at the beginning of the monitoring period (pre-reproductive phase of most aquatic macrophytes), presumably because the growth season was only beginning and aquatic macrophytes could quickly compensate for herbivory. In addition, this weak effect may be combined with the low grazing pressure exerted by swans during this period of the year, when most birds incubate, i.e. juveniles are not yet massively present and swans do not form large moulting flocks either (Cramp *et al*., 1986). This is supported by the fact that the effect was mostly evident on fishponds where swan stay per hectare was higher. Aquatic macrophytes were absent from fishponds with longer stay in May (Appendix A). The effect of swan grazing then became more pronounced in June and July, when macrophyte beds were fully developed but the plants probably lost most of their ability to compensate for grazing. The intensity of depletion observed over our study period is therefore consistent with the known ontogeny of plants and their resistance strategies, which generally involve an increased tolerance and defence to herbivory during the sapling and pre-reproductive period, whereas this resistance effort decreases after the mature stage (Boege & Marquis 2005).

As previously mentioned by Strauss & Agrawal (1999) , opposite paradigms explained how nutrient availability increased or buffered the effect of herbivory. During our experiment, we demonstrated that an increasing availability of nutrients (under a threshold, some of the more eutrophic sites never contained macrophytes), tended to buffer the effect of grazing during the later stage of the growth season. This may result from the larger development of macrophyte beds in richer fishponds, which enables a greater absolute impact of grazing swans, and hence also a more detectable one. We also hypothesize that nutrient availability did not affect the relationships between macrophyte beds and swan grazing during the earlier stage of the growth season because the growth rate was simply higher than the consumption rate during this stage on most sites (except for sites where high swan pressure was exerted early enough to prevent any growth, leading to the absence of any macrophyte bed).

We demonstrated an effect of swan grazing on the structure of macrophyte communities. The effect of grazing on Shannon's index of diversity and equitability was demonstrated during the early stages of vegetation growth, suggesting that the dominance of some plants was enhanced by swan foraging activity. Conversely, some early species (like *Zannichelia palustris*) and subdominant species (like *Potamogeton crispus*) may particularly suffer from the effect of swans. During July, the grazing effect on the community structure was lower, certainly due to the disappearance of most earlier subdominant species which may be more sensitive to grazing. A similar process of herbivorous wildfowl affecting dominance relationships within plant communities has been documented by Sandsten & Klaassen (2008), who showed that swans (*Cygnus* spp.*)* mostly consumed *Potamogeton pectinatus*, but that this indirectly affected *P. perfoliatus*, which became dislodged. Consequently, the consumed species was actually promoted by grazing through the indirect limitation of a competing species.

It is important to discriminate the direct consequences of swan foraging, which we identified through the exclosure experiment, from its more indirect effects. Rip *et al*. (2006) suggested that herbivores may enhance nutrient concentration, phytoplankton biomass and, indirectly, turbidity (e.g. by accelerating nutrient cycles through herbivory or promoting the transfer of nutrients from agricultural to natural communities), which all have a negative impact on some aquatic macrophytes, especially in already eutrophic lakes. Moreover, by consuming macrophytes, swans have an adverse effect not only on submerged aquatic vegetation, but also potentially on the densities of associated macroinvertebrates (Marklund & Sandsten 2002). General relationships between fish, macroinvertebrate food supply and aquatic vegetation are difficult to demonstrate in the short term (see Diehl & Kornijow 1998). Most fishponds we studied have fish, especially Carps, which need a vegetation substrate for spawning (Balon 1995). By impacting macrophytes, mute swan may prevent carps from spawning efficiently, and may thus generate indirect economic costs for fishpond landowners, though this will be difficult to establish. Within standing water ecosystems, mute swan may therefore potentially be responsible for trophic cascades (see Pace *et al*. 1999) through its grazing effect on macrophytes, but further research is necessary to properly test this hypothesis.

Grazing may drive community shifts in aquatic ecosystems over a long period (e.g. Van Donk & Adrie 1996). Such processes may obviously occur in fishponds, if different plant species are not all equally affected by mute swan. Significant macrophyte depletion was demonstrated here even within a limited time window centred on the plant growth season. However, it is generally considered that the main impact of grazing birds occurs between summer and winter, after the plant growth season and bird reproduction (Perrow *et al*. 1997). Mute swans may indeed deplete macrophytes throughout the year, generating the emergence of a more dramatic effect which may only be measured after several plant growth seasons. Such an effect may be favoured by the non-random distribution of swans over fishponds throughout the year (Gayet *et al.* in press), and massive flocking on some fishponds during the non-breeding period. Tatu *et al*. (2006) suggested that the effect of grazing could be additive over years, especially where birds flock in large numbers. We demonstrated a negative effect of the mute swan on macrophytes within a single season, but this impact may increase over years, if the demographic expansion of the mute swan over the previous decades (BirdLife International 2004) continues in the future. In addition to an increased effect on already occupied sites, mute swans may also gradually spread over more fishponds within the Dombes area, and hence affect an increasing number of sites. Any further study of the effect of this waterbird on inland aquatic ecosystems would therefore benefit from combining a variety of explanatory variables and from being conducted over successive seasons.

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Appendix A: Sample of fishponds with their corresponding swan stay (cumulative number of swan.days/ha). Nesting sites (N), nesting sites with families (B), flocking sites (F) and other sites (O) are indicated. The development of macrophyte communities (mean cover % ± SE) inside and outside the exclosures is indicated, together with the dominant plant species, which represented at least 20% of total cover (in bold italics), and other species accounting for at least 10% of total cover (in italics).

		May (swan stay includes April + May)					June					July				
	Area (ha)	Stay	Exclosures		Open plots		Stay	Exclosures		Open plots		Stay	Exclosures		Open plots	
			Cover	Species	Cover	Species		Cover	Species	Cover	Species		Cover	Species	Cover	Species
1 B	31.1	11.6	17.9 ± 3.4	***Potamogeton pectinatus***	35.5 ± 3.8	***Potamogeton pectinatus***	22.2	4.4 ± 1.1		1.5 ± 0.3		27.3	0.6 ± 0.3		0.1 ± 0.1	
2 N	6.5	29.1	25.8 ± 4.4	*Filamentous algae, Myriophyllum spicatum*	10.6 ± 2.2		29.1	36.3 ± 4.7	***Myriophyllum spicatum***	19.1 ± 2.6	*Myriophyllum spicatum*	29.1	84.2 ± 1.8	***Myriophyllum spicatum,*** *Ceratophyllum demersum*	66.0 ± 2.9	***Myriophyllum spicatum***
3 B	24.7	5.7	0.1 ± 0.1		0.1 ± 0.1		7.3	23.1 ± 3.7	*Potamogeton crispus*	0.9 ± 0.2		12.9	6.9 ± 1.6		0.2 ± 0.1	
4 N	12.2	8.7	1.9 ± 0.4		1.0 ± 0.3		13.9	58.3 ± 4.1	***Myriophyllum spicatum***	58.3 ± 3.5	***Myriophyllum spicatum***	18.9	79.0 ± 3.5	***Myriophyllum spicatum***	77.8 ± 3.3	***Myriophyllum spicatum***
5 B	15.9	23.1	38.1 ± 5.2	*Potamogeton gramineus, Potamogeton lucens*	24.9 ± 3		35.0	78.1 ± 4.9	***Potamogeton crispus***, *Potamogeton lucens, Potamogeton gramineus*	56.3 ± 3.7	*Potamogeton crispus, Potamogeton gramineus*	49.1	74.0 ± 4.2	***Potamogeton crispus***, *Potamogeton gramineus, Potamogeton lucens*	62.8 ± 4.2	*Potamogeton gramineus, Potamogeton crispus*
6 N	12.3	9.0	0 ± 0		0 ± 0		11.8	0 ± 0		0 ± 0		12.1	0 ± 0		0 ± 0	
7 B	11.7	8.4	16 ± 3.8		17.9 ± 3		12.5	26.9 ± 6.0	*Potamogeton lucens, Oenanthe aquatica*	22.7 ± 4.0	*Potamogeton lucens*	26.1	81.1 ± 2.6	***Najas marina***	65.6 ± 5.5	***Najas marina***
8 B	10.6	6.7	32.6 ± 4	***Alopecurus aequalis***	25.1 ± 2	***Alopecurus aequalis***	6.8	38.8 ± 3.6	*Alopecurus aequalis, Filamentous algae*	31.0 ± 2.1	*Alopecurus aequalis*	21.4	81.1 ± 0.7	***Filamentous algae***	81.3 ± 0.6	***Filamentous algae, Nymphoides peltata***
9 B	19.1	3.6	0 ± 0		0.2 ± 0.2		3.6	0 ± 0		0 ± 0		3.6	0 ± 0		0 ± 0	
10 F	40.4	38.2	9.8 ± 1.7		0.9 ± 0.2		91.1	25 ± 3.3	*Potamogeton crispus, Potamogeton pectinatus*	0.2 ± 0.1		120.4	0.2 ± 0.2		0.1 ± 0.1	
11 O	43.2	1.6	0 ± 0		0 ± 0		1.6	0 ± 0		0 ± 0		1.8	0 ± 0		0 ± 0	

Appendix A (second part)

		May (swan stay includes April + May)					June					July				
	Area (ha)	Stay	Exclosures		Open plots		Stay	Exclosures		Open plots		Stay	Exclosures		Open plots	
			Cover	Species	Cover	Species		Cover	Species	Cover	Species		Cover	Species	Cover	Species
12 N	4.5	19.1	0 ± 0		0.2 ± 0.1		19.1	0.2 ± 2.2		0.0 ± 0.1		19.1	8.1 ± 2.8		6.3 ± 1.9	
13 B	16.1	16.8	0 ± 0		0 ± 0		26.1	0 ± 0		0.2 ± 0.2		32.4	0 ± 0		0 ± 0	
14 F	29.7	11.8	25.6 ± 4.7	***Filamentous algae***	15.4 ± 2.8		15.3	18.1 ± 3.9		12.5 ± 2.3		27.3	57 ± 6.1	***Nymphoides peltata***	57.5 ± 3.3	***Nymphoides peltata***
15 N	12.5	11.7	35.1 ± 3.6	*Myriophyllum spicatum*	27.7 ± 2.8	*Myriophyllum spicatum*	12.2	73.1 ± 3.8	***Myriophyllum spicatum,*** *Filamentous algae*	67.8 ± 3.9	***Myriophyllum spicatum,*** *Filamentous algae*	12.8	79.2 ± 3.6	***Myriophyllum spicatum***	82.0 ± 1.3	***Myriophyllum spicatum***
16 N	13.4	7.0	0.6 ± 0.3		0 ± 0		8.4	1.1 ± 0.4		0.3 ± 0.2		8.4	16.3 ± 4.1	*Ceratophyllum demersum*	2.7± 0.7	
17 B	16.2	12.4	24.1 ± 6.5	*Spirodela polyrhiza*	25.9 ± 5.7	***Trapa natans***	25.3	32.8 ± 8.3	*Trapa natans, Spirodela polyrhiza*	35.1 ± 7.1	***Trapa natans***	38.1	1.4 ± 0.5		0 ± 0	
18 B	7.3	32.3	1.5 ± 0.4		4.0 ± 1.5		67.4	41.7 ± 4.3	*Filamentous algae, Najas marina*	27.6 ± 3.0	*Filamentous algae*	98.0	18.6 ± 4.7	*Najas marina*	19.1± 4.0	*Najas marina*
19 B	3.0	88.1	0.6 ± 0.3		0 ± 0		177.2	8.8 ± 3.3		2.3 ± 0.6		259	35.8 ± 6.4	*Filamentous algae, Myriophyllum spicatum*	32.5 ± 4.9	*Filamentous algae*
20 N	12.7	3.9	0 ± 0		0 ± 0		3.9	0.8 ± 0.3		0.6 ± 0.2		3.9	0 ± 0		0 ± 0	
21 B	13.9	15.2	46.5 ± 7.4	*Characea*	45.2 ± 4.8	*Characea*	17.3	11 ± 3.4		7.1 ± 2.1		25.8	0 ± 0		0 ± 0	
22B	9.3	28.2	41.3 ± 6.9	***Alopecurus aequalis,*** *Ranunculus peltatus*	40.1 ± 5.4	*Alopecurus aequalis*	49.5	45.2 ± 5.3	***Alopecurus aequalis***	36.6 ± 4.5	***Alopecurus aequalis***	56.8	68.9 ± 6.2	***Alopecurus aequalis,*** *Utricularia australis, Trapa natans*	56.4± 6.4	***Alopecurus aequalis,*** *Utricularia australis*
23 N	21.8	4.9	46.4 ± 7	*Filamentous algae, Characea*	54.2 ± 4.6	*Filamentous algae, Characea*	6.6	47.1 ± 4.8	*Filamentous algae, Characea*	54.2 ± 4.7	*Filamentous algae, Characea*	7.9	22.2 ± 3.8	*Characea*	22.2± 3.2	
24 N	9.3	2.9	0 ± 0		0 ± 0		2.9	0 ± 0		0 ± 0		2.9	0 ± 0		0 ± 0	
25 B	11.9	21.9	0.3 ± 0.2		0.1 ± 0.1		33.6	0.1 ± 0.1		0 ± 0		37.1	0 ± 0		0 ± 0	
26 N	10.7	9.9	46.7 ± 3.6	*Filamentous algae, Glyceria fluitans*	39.4 ± 3.3		10.9	82.5 ± 2.3	***Filamentous algae,*** *Glyceria fluitans*	72.6 ± 2.7	***Filamentous algae,*** *Glyceria fluitans*	10.9	79.6 ± 1.7	***Nymphoides peltata,*** *Filamentous algae, Glyceria fluitans*	70.8 ± 2.8	***Nymphoides peltata,*** *Filamentous algae*
27 B	32.4	4.8	0.6 ± 0.3		0 ± 0		6.6	0.7 ± 0.3		0 ± 0		9.4	0 ± 0		0 ± 0	
28 N	8.0	23.2	0.1 ± 0.1		0 ± 0		47.2	1.3 ± 0.4		0.6 ± 0.2		51.7	0.3 ± 0.2		0.6 ± 0.2	
29 B	15.9	15.4	0 ± 0		0 ± 0		24.1	0 ± 0		0 ± 0		26.3	0 ± 0		0 ± 0	

GENERAL DISCUSSION

Within a wetland, habitat units have a very complex functioning, which mostly depends on their spatial distribution, connexions, climatic conditions, human activity (e.g. : disturbance, habitat fragmentation, water management, nutrient input) or even the animal and plant populations they host. At the scale of the landscape, the plant and animal communities present in a given habitat unit hence result from all these parameters. Although colonization by new species can sometimes profoundly affect such structure, the disturbance caused to the ecosystem can also sometimes be more limited. This all depends on how much the species has already colonised the habitat, the species own ecology as well as on the way the ecosystem receiving this species functions.

I. Mute swan habitat selection within fishponds.

In this study, we aimed at understanding mute swan habitat selection processes in a fishpond complex it colonized a few decades ago. Because Mute swan is a sedentary species, it was possible to study the relationships between this bird and its habitat throughout the year, which is often impossible in waterbirds due to their general migratory behaviour. Taking seasons into account was crucial to be able to consider the changes linked with the phenology of this species and the changing nature of such aquatic habitats simultaneously. The specificities of such ecological systems as well as that of the study methods provide new insights into habitat selection processes of waterbirds in general. **Across the year, swans select their habitat according to available resources, spatial configuration of habitat units (area – isolation) and individuals’ own requirements (e.g. breeders versus non-breeders).** To meet these requirements, swan presence and length of stay are eventually concentrated on a limited number of fishponds at the scale of the landscape. Such knowledge is crucial: considering natural differences between sites (e.g. contrasted size) indeed allows a better assessment of the consequences of the species’ presence (see Hewitt *et al.* 2001).

1. Mute swan population distribution within the fishpond landscape.

a. During the breeding season.

Fishpond area, proximity and number of surrounding fishponds (within a 2 km radius) all affect mute swan distribution within the landscape in summer (Article 1). Increased area or, to a lesser extent, lower isolation, both promote fishpond use by swans. This is consistent with the area-isolation paradigm, which states that the presence of a species (colonization) is favoured by a larger area and a lower isolation of habitat units, while the probability of absence (i.e. of extinction) is associated with the opposite properties (Hanski 1998). Given the relative aggregation of fishponds of similar size in Dombes **(Article 1)** and the relationship between swan presence and this parameter, some sort of spatial autocorrelation (Legendre 1993) could have been observed in the distribution of swans in the landscape: the distance between actual swan presence events could have been lower than that of randomly distributed events. **We could not detect swan aggregations at the scale of the landscape.** This may on the one hand result from the properties of the environment (e.g. the physical environment of Dombes fishponds may not be constraining enough), and on the other hand be linked with the species own ecology (e.g. : the population may not yet be large enough to create cores of presence) (Dormann 2007).

Within an animal population, the contrasting requirements of individuals, owing for example to their breeding status, may cause differential habitat selection processes. **We have shown that depending on their breeding status, swan individuals indeed do not use the same habitat types in summer (Article 1)** : at the scale of the region, non-breeders select large fishponds (generally over 30 ha), while breeders (i.e. swan families) use medium to large waterbodies (generally over 10 ha) surrounded by many other fishponds within 2 km. Absolute food requirements of a flock of non-breeders (when these are moulting) should theoretically be larger than those of a family, because the former consist of more individuals. This may explain why flocks select fishponds over 30 ha (as moulting sites) **(Article 1).** Furthermore, a low sensitivity to human disturbance on such large fishponds during the moult period, may explain the presence of non-breeding birds, and then occurrence of swan flocks on such fishponds. Among these, those with a higher aquatic macrophyte bed cover had high swan stay values **(Article 2).** Beyond the sole effect of fishpond size, the presence of many other fishponds within a 2km radius is favourable to the presence of swan families **(Article 1)**. This may explain why swan stay is higher on poorly isolated fishponds in summer **(Article 2).** Indeed, poorly isolated fishponds, even if they are small, provide a larger range of alternative habitats for swan families to raise the cygnets if the nesting site itself is not favourable for this purpose, before the young are able to fly (through terrestrial movements, pers. obs.). Similarly, Goldeneye *Bucephala clangula* broods are more likely to leave the nesting site for another site when the number of neighbouring sites is higher (Pöysä & Paasivaara 2006).

In a different matter, swan families do not exclude non-breeders from the fishponds they use. The fact that non-breeders preferentially select larger fishponds allows individuals with different statuses (non-breeders and families) to coexist on the same sites without any exclusion process to occur **(Article 1)**. In such a case, it is likely that swan families use a clearly defined territory within the fishpond, from which their non-breeding congeners would be excluded.

In western Europe, mute swan has recently colonized a wide variety of habitats (canals, rivers, city parks, marshes, etc…). Within a fishpond complex like the Dombes, the habitats are so diverse that swan pairs are likely to use specific sites where they can expect their breeding success to be optimal. We hence further analysed breeding habitat selection processes by swans during the pair settlement and nesting periods on the potentially most favourable fishponds (> 10 ha, see **Article 1**). We then considered other factors than just the spatial configuration (area – isolation) of fishponds: management practices (flooding or drainage the previous summer), available plant food resources (aquatic macrophytes and helophytes) or even human disturbance. **That breeding site selection was independent from all these parameters (Article 3) supports the idea that mute swan is a poorly selective species when it comes to breeding sites.** These birds hence use a variety of habitats to breed. Swans virtually have no predators in areas like the Dombes, and can therefore breed independently from helophyte shelter. The fact that swans were indifferent to food resource (aquatic macrophyte) availability when nesting is consistent with their capital breeding behaviour (De Haan 2009). Food availability should thus rather play a more important role before or after breeding itself, but weaker during the nesting period (see below).

b. Outside the breeding season.

In this study system, the non-breeding period is particular because food availability then differs a lot between fishponds, and because all birds can then respond to habitat fluctuations under limited constraints, since all of them are then fledged. **During winter, we have demonstrated that re-flooding of fishponds dried the summer before had a**

considerable effect on swan distribution in the landscape (Article 1) and their length of stay on the various fishponds (Article 2). Indeed, swans preferentially use re-flooded fishponds, and to a lesser extent larger fishponds whatever their previous drainage status **(Article 1).** Winter swan flocks preferentially form on large re-flooded fishponds **(Article 1).** Our results thus mitigate the expected major role of isolation and area on habitat selection. **Indeed, we here demonstrate a major -sometimes more important than habitat unit isolation- role of habitat quality (i.e. food availability) on swan habitat selection processes.** Other studies have also suggested habitat quality can differ enough between landscape units to play a greater role that habitat area or isolation on community structure or presence of some species (Summerville & Crist 2004, Yamanaka *et al.* 2009). Fleishmann *et al.* (2002) hence suggest that other factors than just habitat area or isolation can have a major effect where the environment is highly variable, whether this variation is genuine or due to human activity. Ecosystems profoundly impacted by man, such as fishponds, do meet such criteria, owing to the major contrast created by summer drought on subsequent resources available to swans in winter. Just like for the breeding period, fishpond area however still plays a major role, since small waterbodies (< 10 ha) are more hardly, though sometimes, used **(Article 1).**

Although swans select re-flooded fishponds preferentially, some of those that remained flooded during summer are also used anyway (Articles 1 and 2). This suggests that the energy benefit may sometimes be similar between fishponds that remained flooded and those that got dried. The amount and type of aquatic macrophyte reserve organs may increase carrying capacity and attractivity of fishponds that remained flooded during summer (see LaMontagne *et al.* 2003b), while on those fishponds that got drained, remains from summer drought (i.e. natural seeds or crop remains) may play a greater role. Beyond the effect of available resources on habitat selection, food depletion may induce habitat switches if carrying capacity of different habitats become similar or if profitability to birds changes (e.g. *Branta bernicla bernicla ;* Vickery *et al.* 1995). The use of large fishponds that remained flooded in summer may thus result from quicker depletion of resources on fishponds that were dried, which could decrease the difference during the following winter between fishponds submitted to different summer management practices. Summer-flooded fishponds may therefore have a carrying capacity that is eventually quite similar to that of dried fishponds. **We could not detect a difference in fishpond use among summer-dried waterbodies submitted to different management practices (cultivated in maize, cultivated with other cereals or non-cultivated) (Articles 1 and 2).** This may be due to dried and non-cultivated fishponds growing a natural aquatic vegetation once re-flooded, which may produce non-negligible amounts of seeds. Elphick (2000) even demonstrated that some non-cultivated sites (semi-natural habitats) could produce more seeds than crop remains in rice fields.

c. Swan stay on fishponds.

Several mechanisms may result from a higher bird stay or repeated use of habitat units: low food depletion (Esselink *et al.* 1997, Tatu *et al.* 2006), nutrient input (Post *et al.* 1998), virus transmission (Olsen *et al.* 2006), crop damage (Loonen & De Vries 1995), etc… Such mechanisms may depend on habitat properties as well as on how the pressure exerted by individuals is distributed over time, in terms of intensity or in its nature. **We have demonstrated that on supposedly favourable fishponds (> 10 ha), fishpond use patterns (in terms of classes of swan-days/ha) did not differ between seasons.** Even if some fishponds (large re-flooded ones after summer drought) have particularly high winter swan concentrations, the same proportion of fishponds are hardly, moderately or intensively used each season **(Article 2).** Such a relatively constant distribution pattern over seasons may be due to the extended presence of breeding birds on their territory, even outside the breeding season, as well as the gregarious behaviour of subadults throughout the year. **However, fishpond as well as swan properties result in birds not always using the same individual fishponds (Article 2), even if some of these can be used over successive seasons (flocks of individuals or settling of breeding birds).** Even if fishpond use intensity does not vary much over seasons, the consequences of birds' presence may vary over the year. For example, considering a given swan stay, the consequence of aquatic macrophyte use in winter (vegetative dormancy, no compensatory mechanism) may be very different from those during the vegetative period. Plant use during the growth period (from spring onwards) may affect future macrophyte production, while the consequences would be more limited if the plant was used later in the season (e.g. in summer) (Mitchell & Perrow 1998).

2. Studying a dynamic system.

The study we have carried out is a snapshot of habitat use by a swan population. Even if study systems often have to be at pseudo-equilibrium for their functioning to be assessed, mute swan in our case may still be in a colonization process of fishpond habitat. Consequently, what we observed as the habitat used by swan may under-estimate what will be used in the future (Guisan & Thuiller 2005). **What determines habitat use by swans may thus change in the coming years, depending on the species own demographic parameters as well as changes in the properties of its habitat.** Peterson (2003) hence suggests it is better to study the distribution of any species in its native habitat, to avoid such biases. In the case of mute swan, however, the diversity of habitats it now uses (from Mediterranean marshes to vegetable fields in Northern France, for example) is such that the habitats it initially used in its former range (Eastern Europe) may be poorly informative on what swans actually prefer. Human disturbance to aquatic habitats is so widespread, even in areas where the species is considered to be native, that it is difficult to predict from these original areas the type of habitats that will be colonized by swans in the future. Individuals preferentially select habitat units where their gain is expected to be the highest (Optimal Foraging Theory; Krebs 2001). However, if exclusion processes from habitat units currently used develop in the future, individuals may have to switch to less attractive areas, where the consequences of their presence may be completely different.

3. Implications in terms of conservation.

Within ecosystems, the least isolated habitat units are commonly considered to be those showing the highest richness and diversity (see Fahrig 2003 ; for a review). They therefore represent major conservation issues. This has to be taken into account in any conservation strategy, in addition to other parameters like water regime, nutrient availability or disturbance patterns (listed in Zedler 2000). **That mute swan select the least fragmented fishponds within the landscape (Articles 1 and 2) make its integration to the local fauna and flora of Dombes a major concern. This is especially the case because such sites can be repeatedly used by swans over the long term (several years). On the other hand, any correlation between habitat degradation at the regional scale and the relatively recent presence of swans should be considered with caution**. The differential effect of habitat fragmentation on different species, as demonstrated by Villard *et al.* (1999) may mitigate the interactions between swans and local animal and plant communities.

More generally, the fact that we could demonstrate a major effect of habitat spatial configuration on swan selectivity corroborates earlier work with other waterbird populations on small reservoirs in Spain (Paracuellos & Telleria 2004, Paracuellos 2006, Sebastian-Gonzalez *et al.* 2010). To maintain bird diversity in wetlands it is thus of paramount importance to plan conservation policies at the landscape scale rather than at the scale of sites

(Whited *et al.* 2000). **Any waterbird habitat study or conservation strategy should thus consider the spatial functioning and habitat connexions at a broad scale (Haig *et al.* 1998), including in fishponds.** Nevertheless, other site-specific parameters like water depth, salinity, vegetation, etc. should also be considered during habitat restoration projects (see Ma *et al.* 2010 ; for a review).

Despite the consequences of summer drought are more poorly understood for lentic (e.g. fishponds) than for lotic habitats (Bond *et al.* 2008)**, such an agricultural practice may be seen as a management opportunity for fishponds in a conservation or hunting perspective.** Post-drainage crop remains likely provide an easily accessible and energy-rich food resource during waterbird post-nuptial migration on a stopover like the Dombes, compared to macrophytes in the sediment. That drainage occurs on different sites each year may also prevent repeated concentration of waterbirds on natural habitats, and potential consequent habitat degradation. This may also provide alternative temporary foraging habitats. Winter concentration of waterbirds may indeed be detrimental to the local plant communities, even if massive depletion of reserve organs in winter does not necessary affect macrophyte beds during the following vegetative period (LaMontagne *et al.* 2003a).

To assess the carrying capacity of previously dried fishponds for wintering waterbirds, **combining field habitat selection studies and a modelling of fishpond carrying capacity** (see Goss-Custard *et al.* 2003 ; Nolet *et al.* 2006) **would help suggesting management procedures for these habitats.** It would then be possible to predict the level of bird concentration in some habitat units managed for this purpose, and to measure the benefit in terms of protection (via non use) of surrounding areas managed for other purposes (protection of biodiversity, aquaculture, hunting, waterbird migration stopover). These sites would then be « sacrificed », as suggested by Chisholm & Spray (2002) for some rape *Brassica napus* fields in Scotland. Even if temporary summer drainage may benefit waterbirds over the short term it should be kept in mind, however, that intensification of agricultural practices in wetlands at a large scale can on the contrary be much detrimental to them (Duncan *et al.* 1999), requiring further work on the consequences of such practices for aquatic communities.

Although mute swan is a very visible species (large white waterfowl), we have shown that detection of its presence on nesting sites was only partial, only increasing after repeated surveys **(Article 3). We therefore suggest that most studies dealing with more cryptic waterbirds would benefit from better considering detection biases,** which would provide more precise results and hence allow more appropriate management decisions (Defos du Rau *et al.* 2003, Pagano & Arnold 2009). Such biases are indeed a common problem of wildlife monitoring schemes (Nichols *et al.* 1998), that are increasingly taken into account (e.g. O'Connell JR *et al.* 2006, Pollock *et al.* 2006). Considering the rate at which new species colonize ecosystems, it is important not to overlook detection biases. Taking such biases into account would indeed allow detecting the presence of new species as soon as only a few individuals have established, which is crucial to improve the efficiency of potential management procedures (e.g. ruddy duck culling).

4. Perspectives.

At a broader scale, other studies should be carried out to study aquatic habitat colonization process by mute swan in Europe. Because swans only colonized western Europe relatively recently, a study based on historical data (including introductions) would help understanding how swan colonization occurred over a large scale, but also to assess how different aquatic habitat were colonized depending on factors such as spatial configuration of the aquatic habitat (e.g. available open water area), presence of feral populations, weather conditions, presence of human activities, distance to the nearest population, etc…

At the regional scale, understanding swan colonization right from when the first individuals arrive, i.e. at time zero, would provide a practical case to understand the mechanisms behind the propagation of a waterbird population over the long term. Such knowledge indeed is necessary to elaborate adequate management options for these wildfowl populations. It is important to consider these aspects both at the regional and broad scales, so as to be able to predict the geographic expansion of such species (e.g. Greylag Goose *Anser anser* currently increase in western Europe), for threatened (e.g. White-headed duck *Oxyura leucocephala*) as well as non-native ones (e.g. Egyptian Goose *Alopochen aegyptiaca* or Canada Goose *Branta canadensis*), and thus be able to adopt the best possible management options.

At a finer scale than populations, some studies should now be carried out at the individual level to better understand habitat selection processes. Fitting radio-transmitters to swans would allow describing their movements, which is crucial if one wants to understand their decision rules over space (Patterson *et al.* 2008) and acquire more knowledge useful to waterbird management and conservation (Gauthier-Clerc & Le Maho 2001). Despite experiments on habitats are seldom used in studies of marked animals, relationships between two variables can only be demonstrated in this way, when a perturbation can be artificially applied onto the ecological system (White & Garott 1990). In the Dombes, temporary fishpond drainage may help understand how individuals react to the temporary loss of some habitat units (nesting or moulting sites). Such methods may also help studying philopatric processes, when these are combined with exclusion processes or habitat loss (temporary drought). This seems important to carry out given the current degradation, fragmentation or even destruction of natural habitats in general, and wetlands in particular.

Two main aspects have to be considered in habitat selection processes: why some habitats are preferentially used than others, and the fitness consequences of such choices (Jones 2001). To understand bird nest site selection processes, it is necessary to assess if breeding success indeed differs between breeding habitats (Clark & Shutler 1999). Nummi & Saari (2003) observed for example that swan breeding success could vary depending on how early habitats are used. To confirm that mute swans are indeed relatively plastic regarding their nesting habitat, it would therefore be necessary to continue the monitoring after hatching (for example through marked individuals), to determine if breeding success differs between nesting sites.

II. Mute swans in the waterbird community.

In waterbird communities, differences in morphology and food requirements may limit competition processes, allowing different species to coexist through the use of different niches (Kear 2005). Competition processes, whatever their type, are more frequent among more similar species, in terms of species size for example (Leyequièn *et al.* 2007). In our study, we relied on several complementary methods to assess if mute swan exhibited territorial behaviour towards the other waterbirds, or if some sort of passive exclusion may result from their presence, at the scale of the landscape **(Article 4)** as well as within fishponds themselves **(Article 5).**

1. Relationship between breeding swan presence and waterbird distribution over fishponds.

Although mute swan can show intra (Lind 1984) **or interspecific territorial behaviour under some circumstances** (Conover & Kania 1994)**, like other wildfowl do** (Owen & Black 1990)**, we could not detect such interspecific interactions on the Dombes fishponds, and no massive desertion from fishponds where swan pairs were established (Article 4 and Appendix 1).** Frequent accusations to mute swans, linked with their presumed aggressive behaviour towards other birds, were therefore not supported in the present ecological context. Swan pair settlement can therefore not be put forward as a major factor directly linked to fishpond avoidance by other waterbirds. **As opposed to such a scenario, we conversely recorded the abundance of other waterbirds to be higher where swans were present**. The abundance of herbivorous species (coot and red-crested pochard) or species whose foraging behaviour is linked with the presence of aquatic macrophyte beds (e.g. common pochard) (Cramp *et al.* 1986) was more closely correlated with swan pair presence **(Article 4).** Those diving ducks (common and red-crested pochards) have the ability to forage deeper in the water column than dabbling ducks can. The use of a similar habitat to those used by mute swans may explain why diving ducks are more abundant on fishponds with swan pairs **(Annexe 1)**.

No passive exclusion could be detected at the scale of the fishpond (Article 5). Although swans do not use the areas that are the most preferred by other waterbirds, we have demonstrated that swans are closer to these other waterbirds than they would be if

they were randomly distributed within fishponds. Such a spatial distribution pattern at the scale of the fishpond may result from indirect relationships between mute swans and the other waterbirds, as well as from spatial segregation due to habitat diversity and different foraging methods. Swans likely have access to most aquatic habitats, including relatively deep ones, given their body size compared to other waterbird species (Oksanen *et al.* 1979). Swan foraging activity in the areas that are the least accessible to other species may attract other waterbirds, as this may make some food accessible to other species (e.g. swans bring plant material back to the water surface and also disturb invertebrates). Such a commensalism has already been demonstrated between waterbirds and swans *Cygnus spp.* (Källander 2005). That swans are located in fishpond areas where waterbird density is the lowest may result from different requirements and behaviours of the different species (e.g. ducks may be more gregarious) as well as from potential resource depletion, which may cause differential habitat use. This may also reflect the fact that these different species simply have different ecological niches. Pöysä (1983) hence suggested dabbling ducks are mostly relying on shallow parts of lakes, while diving ducks and coots would preferentially use the deeper areas. Differential use of the aquatic habitat by waterbirds (Guillemain *et al.* 2002) may promote coexistence of mute swan and the other wildfowl and coot, and thus partially explain the observed distribution pattern within fishponds.

Since it colonized Dombes fishponds, mute swan may have become a proper part of the waterbird community, i.e. it may have entered this community without greatly affecting the other waterbird species. **The particular place of this species in Dombes fishponds may indicate it relies on a vacant niche,** as suggested by Pöysä & Sorjonen (2000) when Whooper swan *Cygnus cygnus* recovered in Finnish lakes. **In the case of Dombes fishponds, the structure of the waterbird communities (no direct competing species to swans), the relative ecological plasticity of swans (Article 3) and the relative fishpond richness, compared to other habitats (e.g. gravel pits, oligotrophic lakes), may not constrain swans to compete with other wildfowl or coot populations.** In the same way, one can question the consequences of mute swan presence in North America. Where it is not sympatric to Trumpeter swan and where Trumpeter swan has disappeared, maybe mute swan should rely on a niche that was left vacant until its arrival ?

2. Implications in terms of conservation.

The presence of breeding swans is relatively easy to detect on a fishpond **(Article 3),** and it may indicate favourable habitat conditions also to other species **(Article 4)**, which corresponds to the definition of an **umbrella species** (Niemi & McDonald 2004). **Instead of representing some sort of disturbance and richness loss, the presence of mute swan may thus rather be considered as a source of ecosystem enrichment, or as an indicator species for a given ecosystem conservation status** for other species also relying on fishpond aquatic macrophyte beds.

If some competition occurs between swans and the other waterbirds, this may more likely be through indirect competition (interference) than direct processes. Indeed, because they negatively affect aquatic macrophyte bed cover in fishponds **(Article 6),** swans may limit the role of such beds for macro-invertebrates (Bortolus *et al.* 1998, Marklund & Sandsten 2002), while availability of such macro-invertebrates is crucial both for the settlement of duck pairs and for foraging ducklings (Cox *et al.* 1998, Sjöberg *et al.* 2000, Broyer & Calenge 2010). Brood density, aquatic plant cover and invertebrate abundance indeed can be tightly correlated (Staicer *et al.* 1994).

Another form of indirect competition may also occur during winter. Temporarily flooded sites, like rice fields *Oryza sp.* flooded post-harvest in USA, can indeed represent a considerable food source to wintering birds (Elphick 2000). By using in winter those sites that were temporarily drained the previous summer **(Articles 1 et 2),** swans may reduce food availability to other birds in the most favourable sites, while such resources may have been crucial to other wildfowl species during prenuptial migration and for the breeding season (see Arzel *et al.* 2006). During migration, the other waterbirds may get constraint to sites of lower quality, hence decreasing their energy gain if predation or foraging conditions differ markedly on these alternative fishponds, for example. Similarly, biomass loss associated with the presence of greylag goose and wigeon *Anas penelope* on the richest wet grasslands may lead Bewick's swans *Cygnus columbianus* to use suboptimal habitat during winter (Rees 1990). The first individuals to arrive on the wintering grounds may thus get the most favourable wintering conditions: « first come-first served » (Nolet & Drent 1998), and the relative sedentary behaviour of swans in Dombes may provide this species with a greater advantage over migratory ones.

3. Perspectives.

The descriptive approach we relied on to measure the effect of swan pair presence on the other waterbirds **(Articles 4 et 5)** would benefit form an experimental validation. Even if waterbird abundance is higher where swans are present, the effect of swan pair settlement may have remained undetected: waterbird abundance may still have been higher to that observed if swan pairs had not been present. An experiment with fake (silhouettes or plastic swans) or live swans (wing-clipped birds) may help to compare the initial state with the situation after swan arrival.

In a broader context, experiments could be developed to best assess what determines the coexistence of the different species and the limits to such coexistence, through manipulation of community structure and food availability. A variable number of individuals from very different species may be introduced on experimental fishponds, i.e. species with contrasted requirements and accessibility to aquatic habitats (e.g. mute swan, greylag goose, mallard, coot, red-crested pochard), in habitats where carrying capacity varies a lot (through e.g. fishpond size, plant richness). It would then be possible to determine if commensalisms or other relationships develop between swan pairs and the other waterbirds.

III. Consequences of swan presence for aquatic macrophyte beds.

Herbivores play a major role on freshwater ecosystem functioning. Given the many roles played by macrophyte beds, it seems important to better understand the relationships between herbivores and these macrophytes (Lodge *et al.* 1998b), especially in fishpond habitats where this has seldom been examined. Beyond a simple effect of mute swan grazing activity, we also considered the circumstances under which such depletion occurs. We demonstrate that swans can have a major effect on macrophyte beds during the vegetative period. They affect presence, abundance (i.e. cover) as well as structure of the aquatic macrophyte communities. Such a depletion rate is affected by several covariables, such as intensity of use by birds (swans-days/ha), fishpond trophic level and macrophyte development stage **(Article 6).**

1. Relationship between swans and macrophytes.

Our exclosure experiment was conducted over a wide range of fishpond environmental conditions. Grazing pressure by swans (swan-day/ha), plant communities and trophic level of fishponds indeed all differed a lot.

At the beginning of the macrophyte growth period (May), swan grazing leads to macrophyte bed disappearance in fishponds where such grazing is both intense (in terms of swan-days/ha) and occurs early (Article 6). During the growth period, compensation mechanisms exist in plants to respond to the losses to herbivores, until the period of plant reproduction (Boege & Marquis 2005). This may explain why the effects of swan foraging were only important where grazing was intense enough to limit plant growth despite such compensation mechanisms. On the sample of sites we studied there was a high pressure (swan-days/ha) on fishponds of all sizes. As opposed to lake ecosystems where high bird density can be observed on small lakes, where total area is small compared to the size of the littoral zone (accessible to waterbirds ; Sondergaard *et al.* 1996), we show that high swan densities can also be recorded on the largest fishponds we studied. During this part of the year (May), this implies that the negative consequences of swan presence for macrophyte beds can occur on fishponds of any size, not only the smaller ones. This is explained by the fact that swan flocks on large fishponds may be equivalent to longer stay of swan pairs on smaller fishponds **(Articles 1 and 2)**.

Swan grazing has a more pronounced effect on aquatic macrophyte presence during the later parts of the plant growing period (June and July)**, independently from fishpond trophic level and swan pressure (Article 6).** Indeed, plant compensation ability decreases over the growth period (Maschinski & Whitham 1989) : plants show less resistance to grazers once their breeding cycle is accomplished. Despite the fact that swan grazing has no visible effect on vegetation any when during the season on some fishponds, in general swan grazing leads to lower aquatic macrophyte cover on fishponds. **The magnitude of the difference in cover between accessible areas and exclosures was partially limited by higher trophic level of fishponds** (July) **(Article 6).** Comparing this result with that from other studies is difficult: despite trophic levels generally can mitigate the consequences of herbivore grazing onto plant communities, different paradigms explain how nutrient load can either limit or increase depletion (Strauss & Agrawal 1999).

Mute swan grazing of macrophyte beds also lead to a simplification of fishpond plant communities. The plant communities under study got more homogeneous if grazing occurred earlier in the macrophyte growth period (May and June). Swans may particularly affect the earlier et sub-dominant species of the communities, which would be beneficial to other species whose contribution to the communities would be enhanced. Given the size of our sample and the diversity of fishpond plant communities, our results do not allow a deeper examination of macrophyte sensitivity to herbivore grazing.

In addition to swan grazing, other factors affect aquatic macrophyte development. During our experiment, some fishponds with extreme trophic levels or hosting many coots indeed lacked any macrophyte bed, in exclosures as well as in areas open to swans. Beyond a certain threshold, fishpond trophic level may limit macrophyte beds (through plankton bloom) even before swans may cause any depletion. Coots concentrated at high density on a limited number of fishponds, and may have hidden the effect of swans on vegetation (by grazing inside swan exclosures).

2. Implications in terms of conservation.

Over the long term, grazing can profoundly affect the composition of plant communities (e.g. Van Donk & Adrie 1996). Tatu *et al.* (2006) thus demonstrated in Chesapeake Bay (Maryland), that the longer (in terms of year) the exposure of Widgeon Grass *Ruppia maritima* beds to mute swans, the greater the difference between exclosures and open areas. **It is therefore likely that the effect we observed over the growing season (Article 6) was**

only a snapshot of what happens at a broader spatial scale and over the longer term. Macrophyte bed depletion by swans may affect a significant number of fishponds over the long term. These fishponds would have specific characteristics (e.g. : area and isolation) in the fishpond landscape, and swans may use these fishponds repeatedly over years **(Article 1)**. That their pattern of fishpond use did not vary over seasons (swan-days/ha, see **Article 2)** may lead to greater consequences of grazing, especially in winter (vegetative dormancy) when plants are more sensitive to grazing (Boege & Marquis 2005). **In Dombes, regular drainage of fishponds may however partially limit the effects of swan grazing for macrophytes**. Fishponds dried in summer are indeed preferentially used the following winter **(Article 1),** and this is also where winter swan use peaks **(Articles 1 and 2)**. Remains from temporary drought may thus provide alternative food to macrophytes, which would limit the pressure on these during winter, as suggested by Gauthier *et al.* (2005) in a different ecological context. For dried fishponds to be able to play this role, drainage should be less detrimental to macrophytes than swan activity.

Grazing does not only cause immediate plant destruction, but also negatively affects future production of these growing macrophyte beds (Mitchell & Perrow 1998). The consequences of grazing are therefore more limited if this occurs once the plant breeding cycle is accomplished. Even if the effect of early grazing could only be detected on fishponds where mute swan had an intensive pressure, animal communities of such fishponds may also be affected. Trophic cascades occur when a mechanism affecting the abundance or biomass of a trophic level has repercussions on the other elements of the trophic chain (Carpenter & Kitchell 1993). Given the major role played by aquatic macrophytes, changes due to swan grazing are likely to have cascade effects on fishpond animal communities. In Dombes, fish and waterbird communities may be affected by destruction or damage of fishpond macrophyte beds where swans have a significant effect, while these communities are socio-economical as well as ecological issues themselves. Even if the benefit to aquatic wildlife does not increase linearly with the volume of macrophyte beds (Diehl & Kornijow 1998), **loss of plant cover to swans leads to the loss of nesting or spawning support, as well as loss of foraging opportunities or shelter for a wide variety of aquatic animal communities that depend on macrophyte beds**. Dombes fish communities are mostly composed of carp *Cyprinus carpio*, roach *Rutilus rutilus*, tench *Tinca tinca* and pike *Esox lucius*, whose spawning may depend on aquatic vegetation (Bruslé & Quignard 2001). The Dombes is one of the few continental areas in France where whiskered tern *Chlidonias hybrida* breeds. Nesting by this species is also tightly related with plant resources, especially floating vegetation (Paillisson, *et* *al.* 2006), so that the population would suffer from plant cover loss on its nesting sites. Furthermore, some exploitative competition may occur between mute swan and the other waterbirds relying on food resources that are in the macrophyte beds (e.g. invertebrates, seeds) or the macrophyte beds themselves. **The impact of swans on plant community structure, especially through simplification of these, is particularly important to take into account because some companion species in these plant communities are of conservation importance in Dombes** (e.g. *Potamogeton acutifolius*).

Other processes than simple depletion may also occur in fishponds over time. The relationship between swans *Cygnus spp.* and fennel-leaved pondweed illustrates such mechanisms. Sandsten & Klaassen (2008) consider there is a mutualism relationship between fennel-leaved pondweed and swans, which is detrimental to clasping-leaf pondweed *Potamogeton perfoliatus*. Clasping-leaf pondweed (which reproduces through rhizomes or turions), may get dislodged from sediment by swans foraging on potamots pectinés (which reproduces through tubers). The later would then use aquatic habitats from where clasping-leaf pondweed got excluded. Fennel-leaved pondweed can also develop adaptation strategies (deeper tuber burial in sediment) to maintain in the habitat despite winter tuber use by Bewick's swans *Cygnus columbianus* (Hidding *et al.* 2009).

3. Perspectives.

We have shown that several covariates may further increase the consequences of swan depletion. In experimental studies of herbivore-plant relationships, we hence suggest to consider those variables likely to modulate the effect of herbivores on aquatic macrophytes (e.g. herbivore pressure, trophic level or herbivore as well as plant growth stage). This may indeed provide a finer understanding of the relationships between herbivores and plants, including in other aquatic habitats than fishponds.

Aquatic macrophyte communities are highly heterogeneous at the scale of fishponds in Dombes. A study of swan diet, through the analysis of plant epiderms in droppings, may help assessing the relative food preference of this species among macrophytes. Some of these plant communities have a particular conservation or functional importance (e.g. as bird food source), which is the case for example of *Potamogeton spp.* communities. Their particular sensitivity to herbivores (Lodge & Lorman 1987 ; Weisner *et al.* 1997 ; Rodriguer-Villafane *et al.* 2007) compared to more common communities like water milfoil *Myriophyllum spp.* also calls for further studies on the effect of swan grazing. Given the difficulties we had to predict *in situ* the future composition of macrophyte communities when we installed the exclosures in fishponds, *ex-situ* experiments may be easier to carry out to measure the impact of swans on the different plant species. An experiment relying on mesocosms may allow controlling a wide range of grazing consequences (changes in plant succession, mutualism) interacting with other variables (grazing date, trophic level, interspecific competition …). That such experiments are valuable and feasible has been demonstrated in the case of alkali bulrush *Scirpus maritimus* use by Greylag geese in Camargue (Durant *et al.* 2009). Similarly, an experiment in mesocosms may be the best option to measure the consequences of macrophyte grazing on carp growth and reproduction (e.g. in small pools while simulating swan grazing).

In a different ecological context than the Dombes, the direction régionale Alpes-Méditerranée-Corse of ONCFS has initiated in 2010 in Camargue a study aiming at measuring the impact of swan grazing on *Zostera spp*. and *Ruppia spp*. beds of conservation importance over several growth seasons (several years). This study partly relies on the same methods than those used in Dombes.

IV. Integration of a colonizing species within ecosystems.

As an external element to ecosystems, mute swan arrival in fishponds may have been a perturbation in itself. However, we did not detect any consequence on the waterbird community, while the impact of this herbivore on aquatic macrophytes is real. **Compared to all perturbations occurring on fishponds, such as temporary drainage, agricultural practices on fields surrounding fishponds, aquaculture or hunting, the effects of swan presence for the other communities are now relatively well understood.** The Dombes fishponds thus have a functioning that is constantly affected by major and repeated disturbances. It is therefore necessary to rank such disturbance causes so as to be able to consider the relative impact of more recent ones, such as mute swan arrival.

Disturbance caused by exotic species in any habitat, whatever these arrived by their own means or were introduced by man, does not necessary imply major changes in the structure of host ecosystems. The consequences of such disturbance thus depend on both the ecological properties of the species, the structure of the native communities and the constraints caused by abiotic factors. Integration of a colonizing species depends on the equilibrium between these factors. In different ecological contexts than fishponds, integration of new species to native communities may thus sometimes also occur without the functioning of the ecosystem to be affected, even if arrival of exotic species is often, rightly, considered as one of the main threats to biodiversity, causing a lot of concern relative to the management procedures that should be implemented (Sutherland *et al.* 2006).

Evaluating the consequences of a species presence in a colonized ecosystem is difficult. **Indeed, such consequences are likely to be under-estimated when the species is still in its integration phase, and its ultimate development stage is unknown.** The maximum disturbance can sometimes only occur at this stage, once the population has reached equilibrium. In an ideal situation, the impact of a species should be evaluated right from its establishment (time 0) in order not to considered already altered ecosystems as the initial state, and thus underestimate the consequences of a species colonization. In the longer term, processes such as changes in biological successions may be observed and get related to disturbance caused by the new species presence. The role of human activities helping integration of species to new environments should not be overlooked, though. In the case of sedentary populations like mute swan in Dombes, living in an aquatic environment that is regularly used as cropland, human activity may indeed help species integration through both easier settlement (e.g. : drought may supply easy food resource for swans, what should have ease the species establishment) and limitation of the consequences on the ecosystem structure. Broadly speaking, disturbance caused by human activity tend to increase aquatic ecosystem nutrient load, which can negatively affect biodiversity (Brinson & Malvarez 2002). In the case of waterbirds, however, the increase in primary production linked with such artificial eutrophication may be favourable to some species like mute swan, especially during winter . From this angle, colonization of aquatic habitats by mute swan may be regarded as an indicator of habitat changes.

In terms of conservation, it is important to understand how new species integrate ecosystems. This allows attributing these species appropriate legal statuses, relying on independent scientific facts, and thus concentrate monitoring and management efforts on species requiring these the most. However, such procedures are still most often based on political decisions and discussions with socio-economical representatives, rather than being proper conservation policies based on scientific knowledge.

CONCLUSION

In addition to pure ecological questions dealt with by the present work, it seems necessary to broaden the discussion more widely. In this case, the history of the Dombes may help considering the relatively recent presence of mute swan in the general perspective of large-scale changes occurring in the area.

The Dombes has been constantly changing over the past. As early as during the XIVth century, man changed those marshes into ponds for agricultural purposes. The Dombes was then massively drained, for health (malaria) as well as economical reasons (e.g. building of a train line) at the end of the XIXth century, before being flooded back at the beginning of the XXth century, thus corresponding to changing society requirement over time (Bernard 2008). Such changes, in addition to more global ones (global warming, for example), certainly lead to frequent changes in animal and plant community structure, but these were too old to be documented. However, a constant remains: the ecological functioning of ponds was always driven by agricultural needs (especially aquaculture and crop cultivation), which because of their diversity made the Dombes such an important area for animal as well as plant biodiversity at the international scale. The Dombes agriculture has changed a lot recently, switching from polyculture-cattle rearing to systems dominated by crops. Urbanisation has also increased in the area, while aquaculture would be declining and hunting activity is poorly documented. At the same time, local animals and plants have changed dramatically: decline of aquatic macrophyte beds and reedbeds, lower duck breeding success, decrease in coot numbers, lower aquaculture productivity and colonization by new animal species. If the changes in the Dombes agricultural landscape are self-evident, many of the changes in fauna and flora are subject to speculation, because they are virtually undocumented.

Recent arrival of new species like coypu *Myocastor coypus*, cormorant *Phalacrocorax carbo* or swan are often considered as being the cause of presumed fishpond functioning problems. Such colonization processes, at least for those species that were not introduced by man, are however a natural part of ecosystem evolution over the long term, which are affected by regular perturbations while they are relatively stable over the short term. Upon arrival, new species necessary imply adjustments in native communities. It is however difficult to determine when a species impacts the system or not. This is especially complicated since several approaches, not necessarily opposite to each other, may be combined to evaluate such impacts depending on whether it is the losses for mankind (economic issues) or for Nature intrinsic value (anthropocentrism versus ecocentrism, Kortenkamp & Moore 2001) that are considered. Furthermore, society issues have to be taken into account in addition to economic and ecologic ones. Mute swan is indeed a species that is globally « appreciated » by society, which has to be considered before formulating management options (Ellis & Elphick 2007). We could demonstrate an impact of mute swan on aquatic macrophyte communities, on fishponds with particular ecological conditions, without such impact being general in the Dombes. Conversely, no adverse negative effect could be detected for other waterbird species. The results of this study are consistent with earlier knowledge on other ecological contexts. Because they are under heavy human pressure, it is likely that fishponds are affected by other disturbance sources than only colonization by new species. It is indeed known that more polemical factors (because these are directly linked with human activity) may affect fishponds more than these new species, without a place to discuss the necessary conservation strategies being provided, even if knowledge to implement such strategies is available.

Without a good understanding of how the fishponds function without these species, the fact that colonization is already largely completed makes the evaluation of its consequences difficult. Acquiring long term data is necessary to detect any impact and minimize the risk to only detect effects that are part of longer term processes (Hewitt *et al.* 2001). Integration of mute swan in this ecosystem is indeed already almost accomplished, so that present day relationships may already result from their presence, without their contribution to the above-mentioned disequilibria being possible to assess. We thus recommend to monitor biodiversity over the long term in biodiversity hotspots like the Dombes, using precisely selected indicators to determine changes over time, disturbance events causing such changes and hence be able to assess the real contribution of species like mute swan to such phenomena. Such studies would strongly benefit from multidisciplinary approaches. The research effort hence has to be structured and should not solely focus on colonizing species, or there would be a risk of overlooking other factors of greater importance, the final goal being not to jeopardize conservation efforts.

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ANNEXES

Annexe 1 :

Impact du cantonnement des couples reproducteurs de cygne tuberculé (*Cygnus olor*) sur l'avifaune des étangs : le cas de la Dombes. Bourgogne nature 11.

GAYET, G., BROYER, J., VAUX, V. & GUILLEMAIN, M.

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Impact du cantonnement des couples reproducteurs de cygne tuberculé (*Cygnus olor*) sur l'avifaune des étangs : le cas de la Dombes

Guillaume GAYET [1 2], Joël BROYER [2], Vincent VAUX [1 2] & Matthieu GUILLEMAIN [3]

Résumé

Le cygne tuberculé (*Cygnus olor*) est une espèce protégée dont les populations ont connu un essor démographique important au cours des dernières décennies en France. Aujourd'hui, il est soupçonné de causer des dysfonctionnements sur les milieux naturels, notamment en raison de son comportement territorial à l'égard des autres oiseaux d'eau. Les conséquences de la présence de couples de cygnes sur la répartition des oiseaux d'eau ont été étudiées sur 84 étangs en Dombes (Ain) d'avril à juillet 2008. Aucun impact n'a pu être démontré sur la distribution des oiseaux d'eau au sein du complexe d'étangs. L'effectif moyen et la densité moyenne d'oiseaux d'eau sont le plus souvent plus importants sur les étangs où les couples de cygnes sont présents. L'importance de cette différence varie au cours de la saison, probablement en raison de phénomènes de concentration des oiseaux à certaines périodes de l'année (mue par exemple), sur des sites comportant des ressources attractives à la fois pour les cygnes et le reste de la communauté d'oiseaux d'eau.

Mots clefs : Cygne tuberculé (*Cygnus olor*), Foulque (*Fulica atra*), Anatidés, étang, territorialité.

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Introduction

Depuis quelques décennies, le rythme d'apparition de nouvelles espèces dans les milieux naturels s'est considérablement accentué. Les écosystèmes aquatiques et l'avifaune qui leur est inféodée sont directement concernés par ce phénomène. Si dans certains cas l'introduction, accidentelle ou non, de ces espèces ne fait aucun doute (Bernache du Canada - *Branta canadensis*, Ouette d'Egypte - *Alopochen aegyptiacus*, Ibis sacré - *Threskiornis aethiopicus*, Erismature rousse - *Oxyura jamaicensis*), il est d'autres espèces comme le cygne tuberculé (*Cygnus olor*) dont l'origine est peu documentée : férale, extension d'aire de répartition ou les deux simultanément ? Il n'en demeure pas moins que les interrogations quant aux impacts potentiels de ces espèces sont importantes.

Le cygne tuberculé est le plus grand herbivore aquatique sauvage d'Europe de l'ouest ; il se nourrit principalement d'herbiers aquatiques de pleine eau (Cramp *et al.* 1986; Bailey *et al.* 2007). Réputé territorial (Rowell and Spray 2004) et agressif envers les autres espèces oiseaux d'eau durant la reproduction (Cramp *et al.* 1986; Conover and Kania 1994), les conséquences de la présence des couples de cygne sur les communautés d'oiseaux d'eau ont été peu étudiées jusqu'alors.

Le cygne tuberculé a connu une forte expansion démographique en Europe de l'Ouest durant les dernières décennies (BirdLife International 2004). Occasionnelle en France avant les années 1970, l'espèce a été protégée par la loi de protection de la nature en 1976 et est devenue relativement commune depuis. En France, chaque hiver entre 1987/1988 et 2002/2003, le taux d'expansion annuel moyen de l'espèce a été supérieur à 7% sur 98 zones humides d'importance nationale pour les oiseaux d'eau (Fouque *et al.* 2007). Aujourd'hui, l'essor des populations est tel que celles implantées localement sont soupçonnées de causer des dégâts sur les milieux naturels et agricoles (Dombes, littoral vendéen, Camargue, Val de Saône, Lorraine, Audomarois...), au point de susciter des demandes de régulation (Dombes, Audomarois, Val de Saône par exemple). En l'état, les connaissances sur l'écologie du cygne tuberculé ne sont pas toujours suffisantes pour statuer objectivement sur de telles demandes.

Cet article présente en partie une étude de l'impact du cygne tuberculé sur l'écosystème d'étang. Du fait des questionnements et des a priori qui entourent le comportement territorial de cette espèce, ce sont les résultats relatifs aux relations entre le cygne tuberculé et le reste de l'avifaune qui sont développés ici. Si le cygne développe un comportement territorial interspécifique, on peut s'attendre à ce que l'abondance et la densité des oiseaux d'eau soient moindres sur les étangs occupés par un couple de cygne par rapport aux étangs sans cygnes. A l'inverse, si le cygne ne développe pas une territorialité interspécifique forte, les abondances et densités d'oiseaux d'eau ne devraient pas être inférieures où les cygnes sont présents. On pourrait même observer davantage d'oiseaux d'eau là où sont les couples de cygne. En effet, les foulques et les canards plongeurs peuvent exploiter directement ou indirectement les mêmes ressources que les cygnes (herbiers aquatiques submergés), et donc être attirés par les mêmes étangs que ces derniers. Les canards de surface, au contraire, exploitent un espace plus limité sur les étangs (non plongeurs) et leur abondance ne devrait pas, en cas d'absence de territorialité des cygnes, être corrélée à la présence des cygnes.

Méthodes

Le but de cette étude est de déterminer si les cygnes tuberculés développent une territorialité susceptible d'affecter l'utilisation des étangs par les autres oiseaux d'eau en période de reproduction. En raison de leur proximité écologique relative, les foulques (*Fulica atra*) et les Anatidés peuvent être en compétition avec les cygnes. Nous avons donc déterminé si la présence des cygnes affectait la répartition et la structure des communautés d'oiseaux aquatiques à l'échelle des étangs.

Aire d'étude

La Dombes est une vaste région de 1450 étangs dans l'Est de la France (Ain). Les étangs ont une surface moyenne de 7,3 ha (se : 0,2). Jusqu'en 1970, c'était la zone humide avec le plus grand nombre de canards reproducteurs en France (Broyer 2009). Dans cette région, les espèces d'Anatidés reproducteurs les plus courantes sont le canard colvert (*Anas plathyrynchos*) et le canard chipeau (*Anas strepera*) pour les canards de surface ; le fuligule milouin (*Aythya ferina*) et la nette rousse (*Netta rufina*) pour les canards plongeurs. En ce qui concerne le cygne, la première nidification date de 1974 (Miquet 2003), puis la population a augmenté jusqu'à atteindre environ 1000 individus lors de l'été 2005 (Benmergui *et al.* 2005). Cette région a été sélectionnée comme site d'étude en raison des enjeux écologiques présents, des interrogations des acteurs locaux et du peu de connaissances qu'il existe sur le cygne dans de tels contextes écologiques.

Echantillon d'étangs

Les canards et foulques ont été suivis sur un échantillon de 84 étangs, dont la taille varie entre 1 et 18 ha (moyenne : 9,4 – se : 0,4). Si la territorialité du cygne a un effet, son impact sur les oiseaux doit se dissiper avec la surface du site, c'est pourquoi nous avons évité les étangs de plus de 20 ha. Les étangs ont été tirés au hasard en veillant toutefois à ce qu'ils soient inscrits dans un circuit réalisable en un minimum de temps. Nous avons vérifié que les cygnes étaient bien répartis sur les différentes gammes de surface d'étangs suivis.

Comptages d'oiseaux d'eau

Les cygnes, les autres Anatidés et les foulques ont été comptés en distinguant par espèce les couples, les mâles et les femelles. Les comptages ont été réalisés toutes les 3 semaines depuis un point fixe sur la berge. Les nichées n'ont pas été intégrées dans le suivi car les juvéniles ne répondent pas à la présence des cygnes indépendamment de la femelle ou du reste de la nichée. L'observateur a réalisé d'autres mesures sur les étangs sans quitter le point de comptage (cartographie de la distribution des oiseaux d'eau). Vu la durée passée sur chaque site, on peut considérer qu'il y a peu de chances que la présence de cygnes n'ait pas été détectée par l'observateur. Le même observateur a réalisé tous les relevés.

Dans un premier temps, pour mesurer l'abondance d'individus nous avons fait la somme du nombre d'oiseaux comptés sur chaque site à l'exception des cygnes. L'analyse sommaire des effectifs permet de mesurer la taille des communautés d'oiseaux d'eau indépendamment de la surface des étangs. Les comptages sont analysés en comparant les effectifs moyens de foulque, de canards plongeurs et de canards de surface. L'appartenance taxonomique (foulque versus Anatidés) et les méthodes de recherche alimentaire des oiseaux (canards plongeurs versus canards de surface) ne les exposent pas de la même manière aux interactions avec les couples de cygnes. Les foulques et la plupart des canards plongeurs, qui dépendent plus des herbiers submergés pour leur alimentation, seraient potentiellement plus exposés que les canards de surface en général (Cramp *et al.* 1986). La très grande majorité des effectifs de canards plongeurs dénombrés correspondent au fuligule milouin (herbivore à omnivore) puis à la nette rousse (herbivore).

Dans un deuxième temps, une comparaison des densités d'oiseaux d'eau (nombre d'individus/ha) a été réalisée entre étangs avec et sans couples de cygnes cantonnés. Cet indice permet d'intégrer la surface des étangs dans le comparatif et de mesurer la concentration des individus sur les sites avec couples et sans cygne. C'est donc sur cette mesure que les différences ont été testées statistiquement. En raison de l'écart des données à la normalité, un test non paramétrique de Mann-Whitney a été utilisé. Un seuil de 5% ($p\text{-value} < 0{,}05$) a été choisi pour déterminer si les différences sont significatives ou non.

Période d'étude

4 comptages ont été réalisés sur les étangs entre mi-avril et mi-juillet 2008. La délimitation des périodes de comptages correspond aux différentes phases biologiques des oiseaux d'eau :

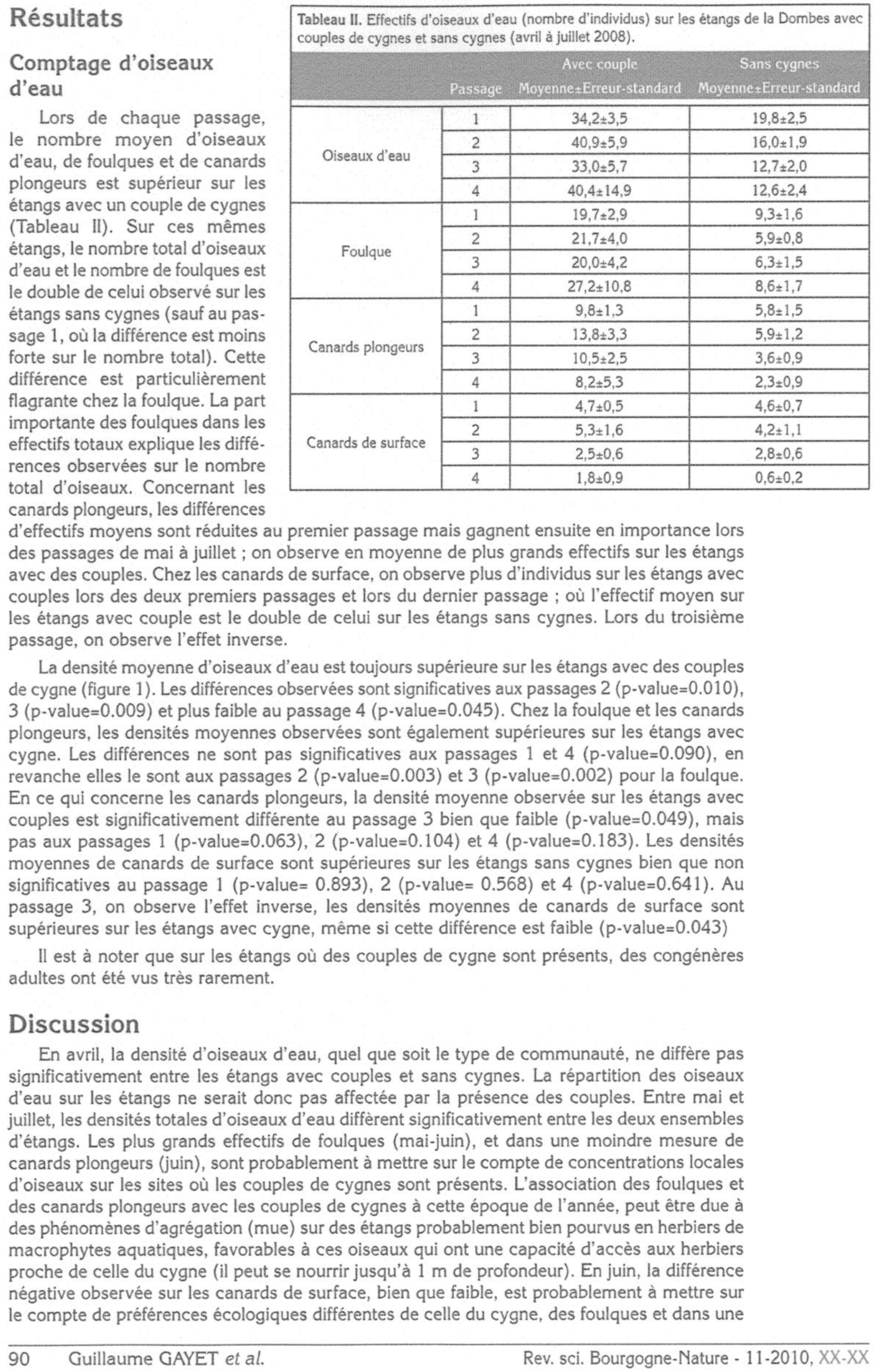
- Mi-avril à mi-mai : couvaison des cygnes, ponte et couvaison des canards plongeurs, éclosion des canards de surface.
- Mi-mai à début juin : éclosion des couvées de cygnes, élevage des nichées de canards de surface, éclosion des nichées de canards plongeurs et début de la mue des adultes.
- Début juin à fin juillet : éclosion des dernières nichées (canards plongeurs) et mue des adultes.

Le nombre d'étangs suivis lors de chaque comptage a pu varier en raison des vidanges de certains sites (tableau I). Le plus grand nombre de couples est observé en avril, puis il décroît rapidement. Il est fort probable que ce phénomène soit lié à des échecs de reproduction ; les couples de cygne auraient alors quitté l'étang. La comparaison de la structure des communautés d'oiseaux d'eau est réalisée lors de chaque comptage sur les étangs avec couples (présence de 2 adultes : 1 mâle et 1 femelle) et sans cygnes. Les étangs avec un seul cygne adulte ou un groupe de plus de 2 individus ont été écartés de l'analyse. Dans le premier cas, cela pourrait correspondre à un couple non détecté (le second membre du couple peut être dans la végétation). Dans le cas suivant, la réponse des oiseaux d'eau à la présence d'un groupe ou d'un couple pourrait être différente. Nous avons donc conservé la présence de 2 cygnes comme indice de territorialité, en raison de l'association que les autres espèces d'oiseaux peuvent faire entre la présence de 2 cygnes et celle d'un territoire défendu.

Tableau I. Répartition du nombre d'étangs où sont réalisées les observations de cygnes lors de chaque comptage en Dombes.

	Passage 1 : 15/4/8 au 9/5/8	Passage 2 : 13/5/8 au 2/6/8	Passage 3 : 3/6/8 au 20/6/8	Passage 4 : 26/6/8 au 17/7/8
Présence de cygne	52	36	34	22
Présence de couple de cygne	40	23	26	17
Nichée de cygne présente	3	10	9	7
Aucun cygne observé	32	46	47	59
Nombre total d'étangs suivis	84	82	81	81

Durant le suivi, le même étang peut se trouver d'un comptage sur l'autre dans la première partie de l'échantillon (avec couple) ou la seconde (sans cygne). Malheureusement, nous ne disposons pas de suffisamment de nichées de cygnes lors de chaque comptage pour réaliser la comparaison sur les étangs avec des familles et sans cygnes. Comme les relevés sont réalisés à un intervalle de 3 semaines sur des périodes différentes du cycle biologique des oiseaux, les comptages sont considérés comme indépendants.



Résultats

Comptage d'oiseaux d'eau

Tableau II. Effectifs d'oiseaux d'eau (nombre d'individus) sur les étangs de la Dombes avec couples de cygnes et sans cygnes (avril à juillet 2008).

		Avec couple	Sans cygnes
	Passage	Moyenne±Erreur-standard	Moyenne±Erreur-standard
Oiseaux d'eau	1	34,2±3,5	19,8±2,5
	2	40,9±5,9	16,0±1,9
	3	33,0±5,7	12,7±2,0
	4	40,4±14,9	12,6±2,4
Foulque	1	19,7±2,9	9,3±1,6
	2	21,7±4,0	5,9±0,8
	3	20,0±4,2	6,3±1,5
	4	27,2±10,8	8,6±1,7
Canards plongeurs	1	9,8±1,3	5,8±1,5
	2	13,8±3,3	5,9±1,2
	3	10,5±2,5	3,6±0,9
	4	8,2±5,3	2,3±0,9
Canards de surface	1	4,7±0,5	4,6±0,7
	2	5,3±1,6	4,2±1,1
	3	2,5±0,6	2,8±0,6
	4	1,8±0,9	0,6±0,2

Lors de chaque passage, le nombre moyen d'oiseaux d'eau, de foulques et de canards plongeurs est supérieur sur les étangs avec un couple de cygnes (Tableau II). Sur ces mêmes étangs, le nombre total d'oiseaux d'eau et le nombre de foulques est le double de celui observé sur les étangs sans cygnes (sauf au passage 1, où la différence est moins forte sur le nombre total). Cette différence est particulièrement flagrante chez la foulque. La part importante des foulques dans les effectifs totaux explique les différences observées sur le nombre total d'oiseaux. Concernant les canards plongeurs, les différences d'effectifs moyens sont réduites au premier passage mais gagnent ensuite en importance lors des passages de mai à juillet ; on observe en moyenne de plus grands effectifs sur les étangs avec des couples. Chez les canards de surface, on observe plus d'individus sur les étangs avec couples lors des deux premiers passages et lors du dernier passage ; où l'effectif moyen sur les étangs avec couple est le double de celui sur les étangs sans cygnes. Lors du troisième passage, on observe l'effet inverse.

La densité moyenne d'oiseaux d'eau est toujours supérieure sur les étangs avec des couples de cygne (figure 1). Les différences observées sont significatives aux passages 2 (p-value=0.010), 3 (p-value=0.009) et plus faible au passage 4 (p-value=0.045). Chez la foulque et les canards plongeurs, les densités moyennes observées sont également supérieures sur les étangs avec cygne. Les différences ne sont pas significatives aux passages 1 et 4 (p-value=0.090), en revanche elles le sont aux passages 2 (p-value=0.003) et 3 (p-value=0.002) pour la foulque. En ce qui concerne les canards plongeurs, la densité moyenne observée sur les étangs avec couples est significativement différente au passage 3 bien que faible (p-value=0.049), mais pas aux passages 1 (p-value=0.063), 2 (p-value=0.104) et 4 (p-value=0.183). Les densités moyennes de canards de surface sont supérieures sur les étangs sans cygnes bien que non significatives au passage 1 (p-value= 0.893), 2 (p-value= 0.568) et 4 (p-value=0.641). Au passage 3, on observe l'effet inverse, les densités moyennes de canards de surface sont supérieures sur les étangs avec cygne, même si cette différence est faible (p-value=0.043)

Il est à noter que sur les étangs où des couples de cygne sont présents, des congénères adultes ont été vus très rarement.

Discussion

En avril, la densité d'oiseaux d'eau, quel que soit le type de communauté, ne diffère pas significativement entre les étangs avec couples et sans cygnes. La répartition des oiseaux d'eau sur les étangs ne serait donc pas affectée par la présence des couples. Entre mai et juillet, les densités totales d'oiseaux d'eau diffèrent significativement entre les deux ensembles d'étangs. Les plus grands effectifs de foulques (mai-juin), et dans une moindre mesure de canards plongeurs (juin), sont probablement à mettre sur le compte de concentrations locales d'oiseaux sur les sites où les couples de cygnes sont présents. L'association des foulques et des canards plongeurs avec les couples de cygnes à cette époque de l'année, peut être due à des phénomènes d'agrégation (mue) sur des étangs probablement bien pourvus en herbiers de macrophytes aquatiques, favorables à ces oiseaux qui ont une capacité d'accès aux herbiers proche de celle du cygne (il peut se nourrir jusqu'à 1 m de profondeur). En juin, la différence négative observée sur les canards de surface, bien que faible, est probablement à mettre sur le compte de préférences écologiques différentes de celle du cygne, des foulques et dans une

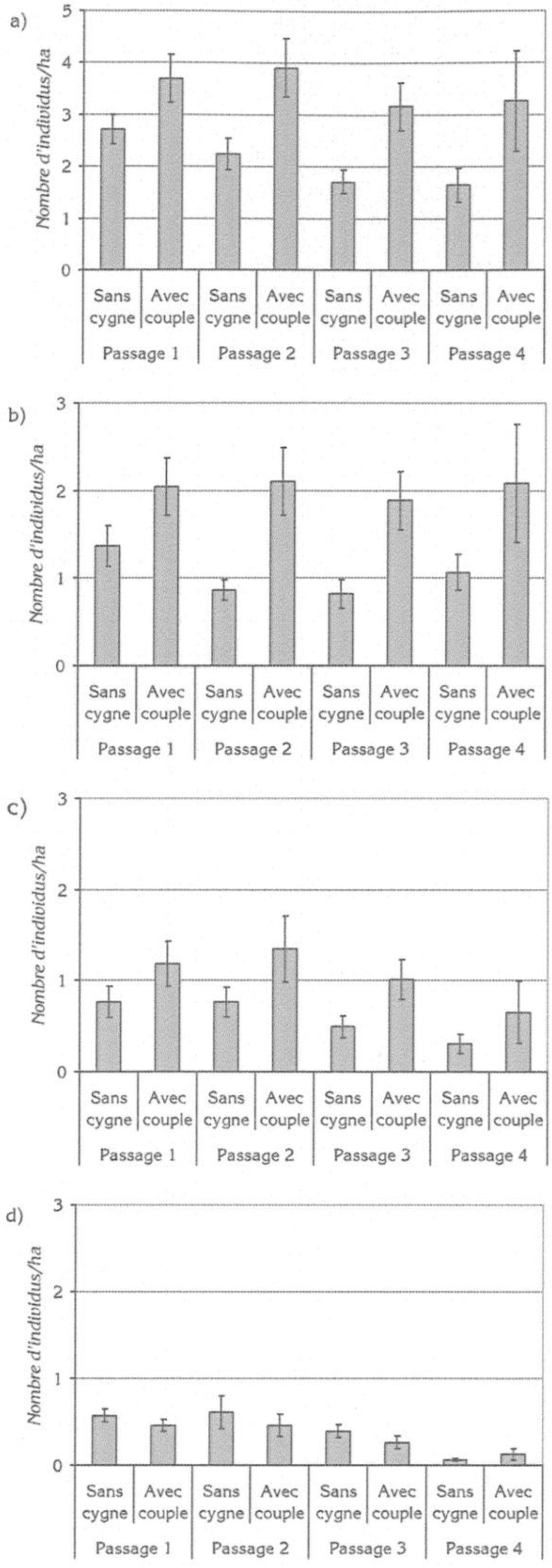


Figure 1. Densité d'oiseaux d'eau (a), de foulques (b), de canards plongeurs (c) et de canards de surface (d) sur les étangs de la Dombes selon la présence des cygnes (avril à juillet 2008).

moindre mesure des canards plongeurs. L'absence de différences prononcées le reste de l'année sur les densités de canards dans leur ensemble, suggère une répartition relativement homogène de cette communauté. Cette analyse (répartition des oiseaux par groupe taxonomique) sera suivie d'un second travail qui tiendra compte plus en détail des exigences écologiques des espèces d'oiseaux d'eau dans le détail (Gayet *et al.* in press).

Nos résultats n'ont pas démontré d'impact des couples de cygnes sur la répartition des autres espèces d'oiseaux d'eau à l'échelle des étangs. Contrairement à ce que l'on observerait en cas de territorialité interspécifique marquée de la part des cygnes, les effectifs et les densités d'oiseaux d'eau sont en général supérieurs sur les étangs où les couples sont présents. De la même manière, Broyer (2009) n'a pas démontré d'impact sur le cantonnement et la reproduction des canards. Les scénarios de désertion par les oiseaux d'eau due à une territorialité interspécifique des cygnes sont peu crédibles. D'autres résultats, non présentés ici (Gayet *et al.* in press), corroborent les présents résultats en montrant une très faible fréquence d'interactions aggressives entre les mâles en couple et les autres oiseaux d'eau. A l'inverse Conover and Kania (1994) ont détecté une fréquence de comportements territoriaux beaucoup plus importante que la notre. Cette différence entre les deux constats dressés peut être due à la variabilité et à la quantité de ressources présentes sur les étangs de la Dombes, qui ne génère pas un comportement exacerbé de territorialité interspécifique vu la quantité d'oiseaux présents sur les sites. D'autres contextes écologiques, dans des milieux saturés seraient certainement plus favorables à l'apparition de comportements territoriaux chez le cygne : lac oligotrophe, mare, gravière.... En effet, si les ressources alimentaires où les habitats sont en quantité réduite, un mécanisme de compétition peut apparaître alors que si elles sont plus abondantes de tels mécanismes n'apparaissent pas (Sale 1974). La présence de compétiteurs plus directs, de taille comparable au cygne (congénère, autres espèces de cygnes, bernaches, oies par exemple) que ceux observés en Dombes pourrait favoriser des comportements territoriaux interspécifiques. Leyequièn et al. (2007) soutient ce postulat selon lequel une grande variation dans les tailles d'espèces sympatriques favorise la coexistence des espèces au sein d'une communauté. Notre résultat tend donc vers celui obtenu par Pöysä and Jorna (2000) sur le Cygne sauvage (*Cygnus cygnus*) qui émet l'hypothèse que lors de sa recolonisation des lacs finlandais, cette espèce aurait pu occuper une niche écologique disponible sans entrer en compétition avec les autres espèces. Depuis sa colonisation de la Dombes, le cygne tuberculé peut avoir occupé une niche écologique disponible sans impliquer une compétition interspécifique forte avec l'avifaune « locale ».

Aucun impact n'a pu être démontré à partir d'une analyse comparée des étangs avec couples et sans cygnes. Ce travail en appelle cependant un autre qui permettra de mesurer, à l'échelle du site, l'effet de la présence des couples de cygnes tuberculés sur la distribution des oiseaux d'eau au sein même d'un étang (processus d'attraction, évitement). Cet aspect sera traité dans le futur. Dans tous les cas, le cantonnement des couples de cygnes pourrait être un bon indicateur de l'état de conservation relatif des étangs, plus spécifiquement des sites favorables à la présence du reste des foulques et canards plongeurs. Cet indicateur aurait alors d'autant plus d'intérêt qu'il peut être facilement récolté sur le terrain (les cygnes sont plus faciles à détecter et à compter que la plupart des autres espèces). Dans le cas de régions où la population de cygne connaît une forte expansion démographique, la présence des couples reproducteurs ne serait pas seulement perçue comme une simple menace pesant sur les écosystèmes (déplétion des herbiers et territorialité exclusive) mais aussi comme une opportunité de monitoring quant à l'état de conservation des milieux aquatiques.

Conclusion

Le cygne tuberculé véhicule le plus souvent l'image d'une espèce agressive qui exclut le reste de l'avifaune de ses sites de reproduction, alors que peu de connaissances existent en fait sur le sujet. Les résultats de cette étude illustrent la nécessité d'acquérir les éléments de connaissances sur l'écologie des espèces avant d'opérer trop hâtivement toute démarche de gestion des populations. L'intérêt d'une telle démarche réside dans le fait de pouvoir au final rejeter ou valider toute association entre des dégradations constatées sur les milieux naturels et les caractéristiques écologiques des espèces étudiées. Au final, de tels résultats valent pour un contexte écologique bien particulier et ne sont pas toujours applicables directement à d'autres situations. De plus, la question de l'impact du cygne tuberculé sur d'autres compartiments de l'écosystème (herbiers de macrophytes aquatiques) reste posée.

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Colonisation d'un écosystème d'eau douce hétérogène par un oiseau d'eau herbivore :

le cygne tuberculé (*Cygnus olor*) dans les étangs piscicoles de la Dombes.

Dans certains cas, la colonisation des zones humides par les espèces animales et végétales peut être une menace majeure pour la biodiversité. Il est donc primordial de mieux connaître l'écologie des espèces colonisatrices pour définir leurs relations avec le reste de l'écosystème. Nous avons étudié les conséquences de la colonisation relativement récente des étangs piscicoles français par le cygne tuberculé (*Cygnus olor*). Nous nous sommes intéressés à l'expression de cette colonisation dans l'espace par l'étude des processus de sélection de l'habitat. Nos résultats montrent que dans un paysage d'étangs, la répartition des cygnes tuberculés dépend à la fois de la configuration spatiale des étangs (aire – isolement), des ressources disponibles et du statut de reproduction des cygnes tuberculés. Nous avons ensuite étudié les interactions entre le cygne tuberculé et les communautés animales et végétales des étangs. Sur les sites de cantonnement des couples, nous n'avons pas montré d'effet de la présence des cygnes tuberculés sur l'abondance des oiseaux d'eau, et aucune forme d'exclusion spatiale à l'échelle de l'étang. En revanche, les cygnes tuberculés peuvent générer une déplétion significative des herbiers de macrophytes aquatiques, suggérant des effets en cascade sur les autres communautés des étangs piscicoles. Comme toute perturbation générée par une espèce colonisatrice, celle associée à l'arrivée des cygnes doit néanmoins être replacée dans le contexte plus large des régimes de perturbations à l'œuvre sur l'écosystème, ce qui importe particulièrement dans le cas d'écosystèmes aussi dépendants de l'activité humaine que les étangs piscicoles.

Mots clefs : cygne tuberculé, étangs piscicoles, canards, foulque, macrophytes aquatiques, Dombes, perturbation, sélection de l'habitat, herbivorie, compétition.

Colonization of an heterogeneous freshwater ecosystem by a waterbird herbivore :

Mute swan (*Cygnus olor*) in Dombes fishponds.

In some cases, wetland colonization by animals and plants may be a major threat to biodiversity. It is therefore crucial to better understand the ecology of colonizing species to assess their relationships with the other elements of ecosystems. We studied the consequences of the relatively recent colonization of French fishponds by mute swan (*Cygnus olor*). We especially considered how such colonization now translates into space, through the analysis of habitat selection processes. Our results show that swan distribution within a fishpond landscape depends on fishpond spatial configuration (area – isolation), available resources as well as mute swan breeding status. We then analysed the relationships between mute swan and fishpond animal and plant communities. Where swan pair settle, we do not demonstrate any effect of swan presence on the abundance of other waterbirds, nor any spatial exclusion within fishponds. Conversely, mute swans can significantly deplete aquatic macrophyte beds, suggesting cascade effects on other fishpond communities are possible. Like any perturbation caused by a colonizing species, that associated with swan arrival however has to be considered in the broader context of perturbation regimes onto the ecosystem. This is especially crucial in ecosystems like fishponds, that are so much dependent upon human activity.

Key words : mute swan, fishponds, ducks, coot, aquatic macrophytes, Dombes, perturbation, habitat selection, herbivory, competition.