

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.

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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 allochthonous 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

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 km². 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 platyrhynchos* 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 \pm 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 to 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 behaviour 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 \times 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 land-owners 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 | |
|---------------------|--------------|----------------|---------------|-------------------|----------|
| | | | | <i>U</i> | <i>P</i> |
| 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 \pm SE | <i>df</i> | <i>F</i> | <i>P</i> |
|-------------------|---|---------------------|-----------|----------|----------|
| Count period 1 | | | | | |
| All waterbirds | Final model: $F_{2,69} = 14.18$; $r^2 = 0.27$; $P < 0.0001$ | | | | |
| | Swan pair present | 0.47 \pm 0.16 | 1 | 19.13 | <0.0001 |
| | Fishpond area | 5.89e-06 \pm 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 \pm 0.24 | 1 | 8.90 | <0.01 |
| | Fishpond area | 6.52e-06 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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 \pm 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. gregariness 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

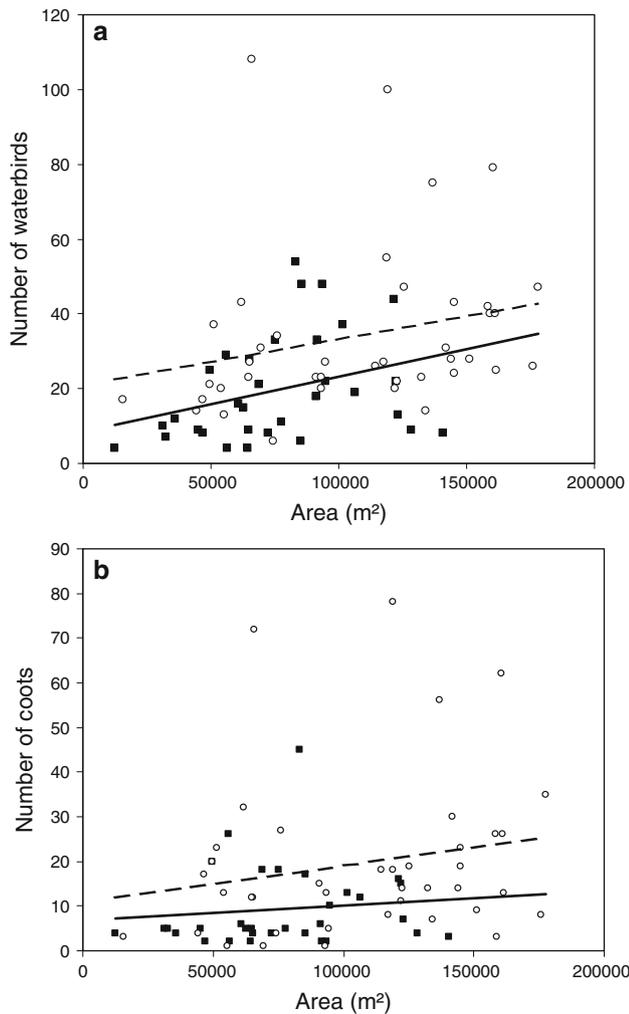


Fig. 1 Total number of waterbirds (a) and Coot (*Fulica atra*) (b) on fishponds with a Mute Swan (*Cygnus olor*) pair (circles, dotted regression lines) and without swans (black squares, plain regression lines) during the first count period according to fishpond size. See Table 3 for statistics

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. other 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. Leyequien 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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