Analysis of Spatial Point Pattern Shows No Desertion of Breeding Mute Swan Areas by the Other Waterbirds Within Fishpond

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Abstract. Mute Swan *Cygnus olor* numbers have recently increased in a dramatic fashion in Western Europe and in North America, suggesting there could be potential consequences for the rest of the waterbird community. Breeding Mute Swan pairs may behave territorially towards other waterbirds, taking advantage of their larger size, and hence cause concern regarding their potential effects on waterbird communities. We studied how the within-site distributions of breeding Mute Swans and other waterbirds were related to each other, in order to assess if there is support to the assertion that breeding Mute Swans may affect the distribution of the other waterfowl within waterbodies. We mapped waterbird and swan distribution within fishponds during the Mute Swan breeding period. Relying on spatial point pattern analysis, our first finding is that breeding Mute Swans were located in the vicinity of the other waterbirds, using the same area within fishpond. Waterbirds do not completely desert the area used by breeding swan pairs within a waterbody, hence not supporting the claim that Mute Swans dislodge the other species. If an exclusion process by Mute Swan breeding pairs towards waterbirds exists, it is not strong enough to generate deserted areas by waterbirds around breeding Mute Swans. Our second finding is that breeding Mute Swans were not located where the density probability function for waterbird presence was the greatest within a fishpond, i.e. breeding Mute Swans were not located in the centre of groups formed by other waterbirds within each fishponds. This may indicate slightly different micro-habitat preferences or use within fishponds, or could indicate the potential occurrence of interactions. In conclusion, these results question whether the increasing Mute Swan populations actually directly threaten the other waterbird communities in such habitats, and require population control as is often claimed.

Key words: community, spatial pattern of points, Ripley's K, waterbirds

Received — May 2016, accepted — Nov. 2016

INTRODUCTION

Processes which affect species assemblage in communities are of key interest for decision makers involved in bird conservation strategy development, especially where expanding species may affect communities. To identify circumstances in which expanding species are expected to affect communities, case studies about species interactions are required in a variety of contexts, as a preliminary to meta-analyses. Generally, a variety of processes affect species assemblage. Species coexistence is influenced by 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) and species interactions (Case & Gilpin 1974, Calsbeek & Sinervo 2002). Habitat selection

processes bring species together in ecosystems and may cause muti-species aggregations (Elmberg et al. 1993, Nummi & Pöysä 1993), but inter and intra-specific territoriality can limit theoretical densities within habitats, through the need for animals to adjust their shared boundaries (Gordon 1997). In such cases, one dominant species will occupy the optimal habitat from where subordinate species potentially may get excluded, being forced to use the suboptimal zones (Murray 1971). Such interspecific territorial spacing has already been suggested or reported in bird communities (e.g. Savard 1982, Temeles 1990, Martínez et al. 2008).

Mute Swan *Cygnus olor* numbers have recently increased in a dramatic fashion in Western Europe and in North America (see BirdLife International 2004, Gayet et al. 2013), causing concern regarding the potential consequences of such an increase for the rest of the waterbird community. Mute Swans may affect waterbirds indirectly through the depletion of shared vegetation food resources (e.g. Gyimesi et al. 2011), especially on sites where high densities of Mute Swans occur (Tatu et al. 2007, Gayet et al. 2011, Wood et al. 2012). Mute Swan breeding pairs may also behave territorially and aggressively towards the other waterbirds, their size and presumed territorial behaviour may confer a great competitive advantage to swans over smaller species under such circumstances. However, very little is actually demonstrated concerning the potential consequences of such swan territoriality for the distribution of the other waterbirds (see Gayet et al. 2013 for a review). Aggressive behaviours of swans towards other waterbirds have indeed been documented in Connecticut ponds (Conover & Kania 1994), where the Mute Swan is considered an invasive non-native species. However, in a different ecological context, the number of waterbirds was actually greater on these French fishponds where breeding swans were present, which may be the result of shared habitat (i.e. pond) preferences (Broyer 2009, Gayet et al. 2011). However, such agonistic behaviours may simply be too infrequent to be easily observed, but still affect the spatial distribution of birds within their commonly preferred waterbodies.

The strength of interspecific interactions between Mute Swan and other waterbird species has been documented to range from commensalism (e.g. Källander 2005) to territorial exclusion (Conover & Kania 1994). Harmful and beneficial interspecific relationships among waterfowl have already been documented for dabbling ducks (*Anas* spp.), having consequences on foraging niche shifts (Pöysä 1986). The consequent distribution pattern of waterbirds (ducks *Anas* spp. and *Aythya* spp. plus Coots *Fulica atra*) and swans could hence range from a general cluster of all birds (swans + other species) within the same part of a given fishpond, to the complete segregation of the two categories of birds within a waterbody. In this study, waterbirds and breeding Mute Swans were studied in a man-made fishpond eco-complex colonized several decades ago by the Mute Swan. To determine how the distributions of breeding Mute Swans and the other waterbirds are related to each other in each fishpond, and assess the likelihood that breeding Mute Swans affect the distribution of the other waterfowl within each fishpond, we tested the two following, mutually exclusive predictions: (1) If the shared habitat preference observed between fishponds (see Gayet et al. 2011) also exists within these waterbodies, with weak interspecific territoriality at best, inter-bird distances between swans and the other waterbirds should be shorter than under a random distribution of the individuals, leading to breeding Mute Swans and other waterbirds to be observed within the same areas of the waterbodies; (2) Conversely, if swans and waterbirds have distinct within-pond habitat preferences, or if swan territorial behaviour occurs infrequently but with strong effects, inter-bird distances should be similar or greater than under a random distribution of the individuals, leading to a clustering of the swans and of the other waterbirds in different parts of fishponds. Depending on the strength of swan territorial behaviour, the other waterbirds may or may not be able to use the area of the waterbody that they prefer.

Three major options were available to measure the likelihood that breeding Mute Swans affect waterbird distribution within fishpond. The first option was to compare waterbird abundance, community structure and distribution (i.e. mapping of each waterbird individuals with X and Y coordinates) in each fishpond before and after the Mute Swan colonized these ecosystems. However, since major shifts in macrophyte communities occur in fishponds at a very short time scale (see Arthaud et al. 2013), any observed change in waterbird numbers and distribution could equally be due to swans or to changes in other biotic factors driving waterbird communities. The second option was to compare waterbird abundance, community structure and distribution within

fishponds with a synchronic approach, comparing ponds with and without breeding swans. However, previous analyses showed that waterbird abundance and community structure differ strongly between fishponds with and without breeding Mute Swans (see Broyer 2009, Gayet et al. 2011), presumably reflecting different habitat conditions and shared habitat preferences between swans and other waterbirds. It was hence not relevant to compare waterbird distribution between these fishponds for measuring the likelihood that breeding Mute Swan affect the distribution of waterbirds within each of these. The third option, which was the one we retained, was to study waterbird distribution at time t within fishponds where swans were present, and to study how the distribution of the waterbirds was related with the position of swans.

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 mean area (± 0.2 SE), ranging from 0.5 ha to 109.5 ha. Fishpond depth is generally less than 1 m. In France, this region plays an important role for breeding dabbling ducks (especially Mallard *Anas platyrhynchos* and Gadwall *Anas strepera*) and diving ducks (especially Common *Aythya ferina* 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).

Large fishponds are uncommon in the Dombes region. Furthermore, breeding swan pair territoriality may affect the other waterbirds differently in large fishponds. We assumed that the negative effect of Mute Swan pairs could not always be measured on such large fishponds. Therefore, large fishponds were not included in the sample. 83 fishponds were randomly selected among those which could be covered by a unique observer in a minimum of time. These had a mean area of 9.9 ha (SE = 0.6), ranging from 1.2 ha to 23.5 ha, hence corresponding to the mean average fishpond size in the Dombes region. Fishponds representative of the Dombes region in terms of area and habitat composition were selected. The Dombes fishponds are depressions where water flow has been interrupted by the building of a

dam. The fishponds are fished annually, generally during three consecutive years, then drained and potentially cultivated on the fourth year. This particular management cycle prevents these shallow wetlands to gradually evolve towards a marsh habitat. Because the fishponds of the region are managed in a consistent way they follow the same short-term ecological cycle. We were hence confident that our sample of sites was representative of the Dombes fishponds in general. From the 83 fishponds where swans and waterbirds were sought, only those where swans were actively breeding were kept for the spatial analyses (see Introduction). A fishpond was considered as hosting breeding swans when either two adults (one male and one female) or one adult with brood were observed. Note that in the Dombes, there is usually only one breeding pair per fishpond, except on very large fishponds (> 50 ha) which were not included in the sample for this study.

Field surveys
Fishponds were visited every third week between mid-April and late June 2008, i.e. 3 times each except when practical reasons (see below) or draining of some fishponds occasionally made the monitoring impossible. Temporal limits of field surveys were arbitrarily determined (survey 1 from 15 April to 15 May, survey 2 from 13 May to 3 June and survey 3 from 3 June to 20 June). The surveys covered several successive phases of the waterbirds and Mute Swan biological cycles (survey 1: Swan incubation, laying and incubating of diving ducks, hatching of dabbling ducks; survey 2: Swan hatching, hatching of diving ducks, brood rearing and beginning of adult moult in dabbling ducks; survey 3: Swan brood rearing, hatching of the last diving ducks and moult of adults from this group). The different phases of the Coot breeding cycle are not clearly separated over surveys. Broadly speaking Coot moult occurs between late May and August (Cramp et al. 1986). Repeated surveys of the same fishponds were used because the spatial distribution of birds may differ between successive parts of their breeding period (see Gayet et al. 2011 for more details).

The distribution of individual birds was mapped by a unique observer (VV) from an observation site on the bank of each fishpond. The observation point was close to the fishpond emptier, which corresponds to the deepest part of the pond. It is generally scarcely used by waterbirds. 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 7×42 BDA). Bird distance could in some cases not be measured with the rangemaster (for instance due to unfavourable light conditions or excessive distance). A map of the fishpond and physical elements of its environment (e.g. hedges, islands, trees, reedbeds) from recent aerial photographs (BD ORTHO® of the Institut Géographique National taken in 2005) was then used to determine bird distance from the observation point with a ca. 50 m accuracy. The data considered in the present study are therefore very similar to those in Baddeley (2008), where an ungulate herd was photographed from the air daily 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 during the breeding period, the mapping being accomplished in ca. 20 minutes. Finally, birds were in some cases so close from each other (e.g. pair, brood with the female), that distinct distances and azimuths (i.e. coordinates X and Y) could not be measured for each individual separately, so that one single measurement was applied to all individuals of that group. 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. Although Coot and the different duck species may not represent exactly similar competitors to swans, owing to the characteristics of their species-specific ecological niches, the waterbird species encountered here all largely rely on macrophyte beds (plus potentially invertebrates living in those plant stands), and are broadly similar in size, especially compared to a Mute Swan. We thus expected a high niche overlap between swans and all other species, especially because fishponds were < 1 m deep (i.e. niche overlap was likely even between swans and diving ducks). It is thus likely that any territorial behaviour by swans would be generally similar towards the different other waterbird species, so all non-swan species were lumped together in the analyses. Conversely, since territorial behaviour may fluctuate across the various parts of the breeding period, potential changes in the distribution of breeding Mute Swan pairs and other waterbirds over time were considered in the analyses.

Habitat features within fishponds (e.g. reedbeds, aquatic macrophytes, depth, islets) were not considered here. Observers would have had to enter the fishponds to map such habitat features during each survey, which would presumably have affected the distribution of breeding Mute Swans and waterbirds.

Spatial point pattern analyses

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) being located by their geographical coordinates. This technique offers interesting perspectives to understand the way individuals spread over space (e.g. regularity, randomly or as clusters) and the biological processes underlying such patterns (e.g. intraspecific territoriality). It has largely been used to study plants (e.g. Goreaud et al. 2002, Couteron et al. 2003, Perry et al. 2006, Wiegand et al. 2007), but such analyses have long been ignored for wildlife studies, which rather more commonly use marked animals (i.e. identified individuals being (re)located over space and time). This has however changed over the last few years (e.g. Cornulier & Bretagnolle 2006, Fisher et al. 2007, Melles et al. 2009, Munroe & Noda 2009, Hibert et al. 2010), reflecting the increasing will to understand ecological processes in populations and communities through the study of individual distribution patterns.

For each fishpond, a polygon represented the observational window within which points could be located. This polygon comprised the open water area plus a 15 m buffer around it, so as to include most birds even when these were on nearby terrestrial land or sitting onto the banks. For every dot map, each individual bird (waterbirds or swans) was hence represented by a dot. Broods and the female are so strongly dependent that these were simplified to the single species presence, i.e. only one dot 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.

Theoretical background

The simplest parameter of the model representing a 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 identification of 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 corresponded to a 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 Swan distribution within fishponds
Because we selected only fishponds with breeding swans (pairs and families, see Introduction), aggregation of swan events (i.e. points) within fishponds was expected. L was computed for both observed points and randomisations to measure spatial dependence between Mute Swan observations. On every fishpond, 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 (except Mute Swan) were considered together (see above).

Since breeding swan points were few and *a priori* clustered within fishponds, it was easier to randomize their location than those of other, more numerous, waterbirds. Thus, waterbird 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 events respective to each other). From each simulated distribution map obtained, the distance between swans and the other waterbirds was computed.

Null model 2: Mute Swan locations according to waterbird presence probability. Since we expected a potential use of the same areas within fishponds by swans and waterbirds (because they likely share some habitat preferences), we pushed the analysis further by measuring if Mute Swans were in the area where the density probability function (dpf) for waterbird likelihood of presence was greater within each fishpond. We thus considered a second null model, which assumed no convergence between breeding Mute Swan presence and dpf, despite closer proximity of swans and other waterbirds than under a random

distribution. Under this scenario swans and other waterbirds could all be within the same corner of a waterbody, but swans would be slightly outside the flock of other birds.

We estimated a dpf, 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 clusters of waterbird points. In such cases, we therefore relied on a visual appreciation of the smoothing parameter following Wand & Jones (1995) recommendation. 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 barycenters 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 (Calenge 2006) and splancs packages (Barry & Peter 2010).

RESULTS

Complete mapping of breeding swans and all other 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. two adults, 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 numbers of points mapped per fishpond with breeding swans were 26.4, 33.0

and 26.9 during the three successive surveys, respectively (Table 1, see examples of surveys in Fig. 1, see also Gayet et al. 2011 for the mean abundance of waterbirds on fishponds with breeding Mute Swans).

Structure of swan point patterns within fishponds
Actual swan points were highly clustered within fishponds, as can be observed on Fig. 2. This is analytically corroborated by their L values clearly being above that of the randomisation envelope (i.e. their distribution deviated from randomness) for distances between 0 and 250 m, during all three surveys. The strongest increase in L occurred at very short distance (0 to 20 m) during all surveys, again highlighting the existence of clusters.

Distribution of swans according to waterbird presence within fishponds
Analyses of the L_{12} revealed swan aggregation around waterbirds during all three surveys (Fig. 3), i.e. swans were more numerous in the vicinity of waterbirds than expected if all waterbirds spread randomly within fishponds. Aggregation of swans around waterbirds occurred within a maximum radius of 175 m, with only few exceptions (see Fig. 3). However, the magnitude of the difference between observed and randomized patterns depended on surveys: aggregation was the clearest during survey 2 (i.e. greater departure of observed pattern to randomizations).

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 avoided excessive smoothing (Fig. 4). The above analyses revealed that swan clustering was particularly strong within a 20 metres radius. We identified swan clusters on fishponds for every

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

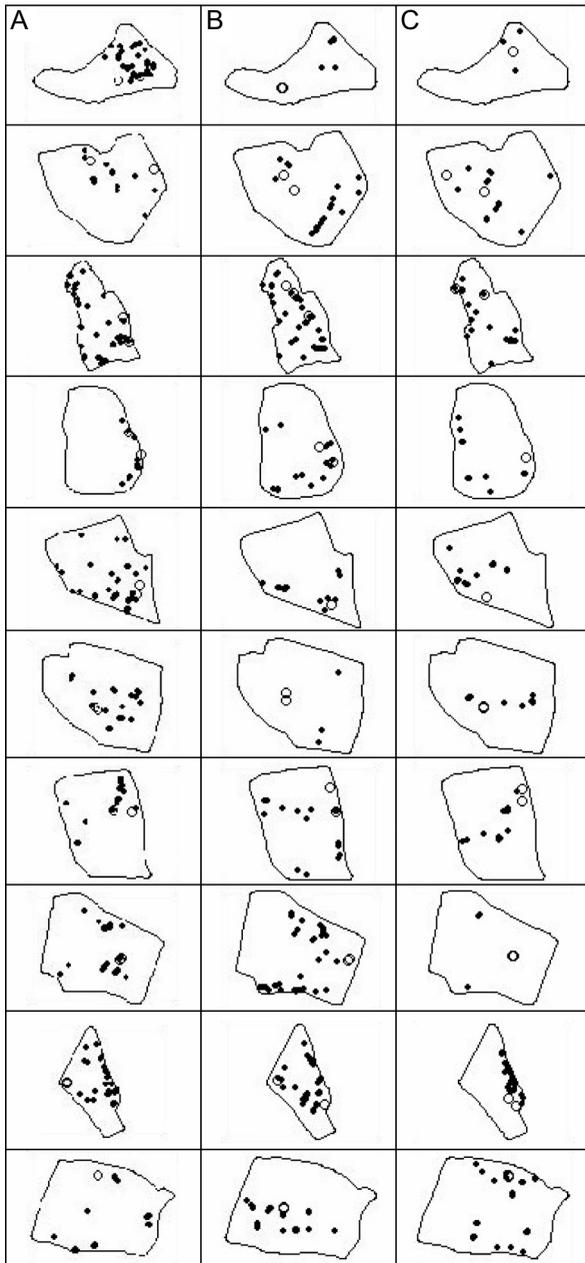| | Survey | | |
	1 — Mid-April to mid-May	2 — Mid-May to early June	3 — Early to late June
Coot	389	309	205
Diving ducks	254	198	189
Dabbling ducks	115	138	51
Mute Swan	60	47	40
Total number of points	818	692	485
Mean number of points per fishpond ± SE	26.4 ± 2	33.0 ± 4	26.9 ± 3.3

Fig. 1. Dot maps of the 10 fishponds where breeding swans have been observed during survey 1 (A), survey 2 (B) and survey 3 (C). Dot maps of other fishponds where breeding swans have not been observed during all three surveys are not shown. Circles represent swans and black points represent waterbirds (ducks and Coots). Dot maps are not to scales.

survey within a 20 m distance with an ascendant hierarchical classification, i.e. the minimum distance between observations within a cluster was < 20 m. We ensured swan clusters where located randomly with L (not shown). For all three surveys, the dpf values around actual breeding swan cluster barycentres were much lower than those
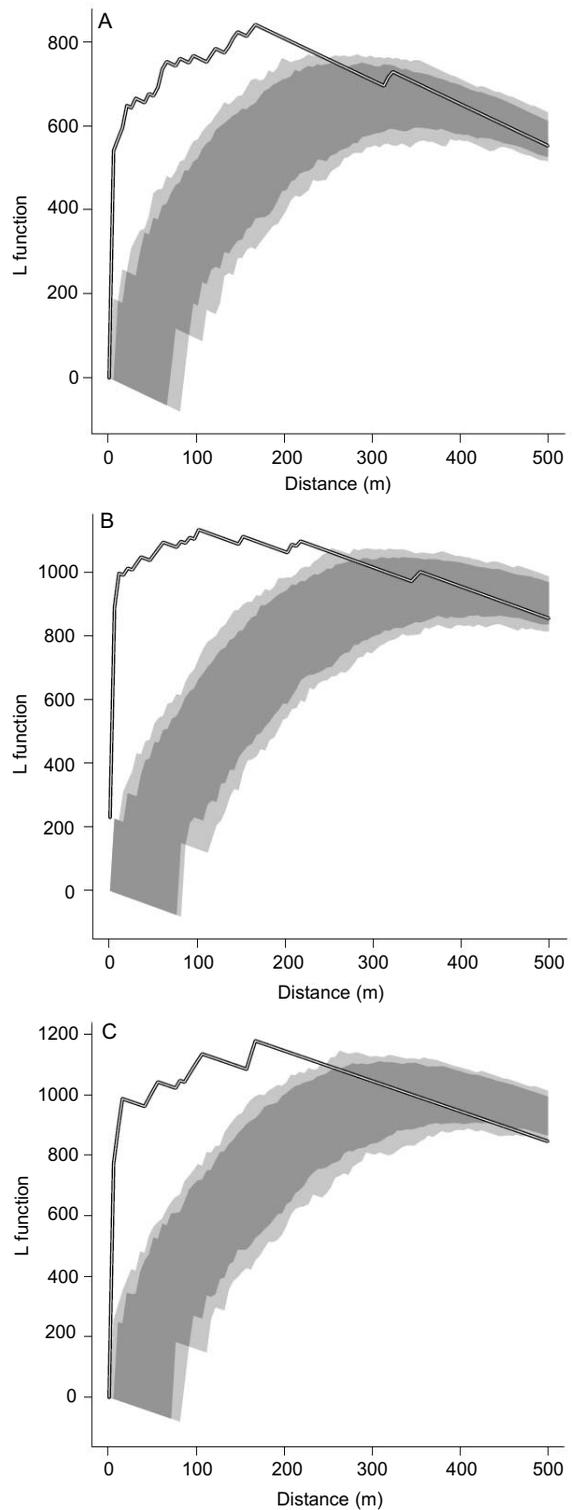

Fig. 2. L function of swan points on fishponds for survey 1 (A), survey 2 (B) and survey 3 (C). The black line indicates the observed pattern. Dark and light grey envelopes encompass 95% and 99% of the 500 randomizations, respectively. For all surveys, the observed patterns deviated from randomness (i.e. are above the 95% randomization envelope) between 0 and 250 metres.
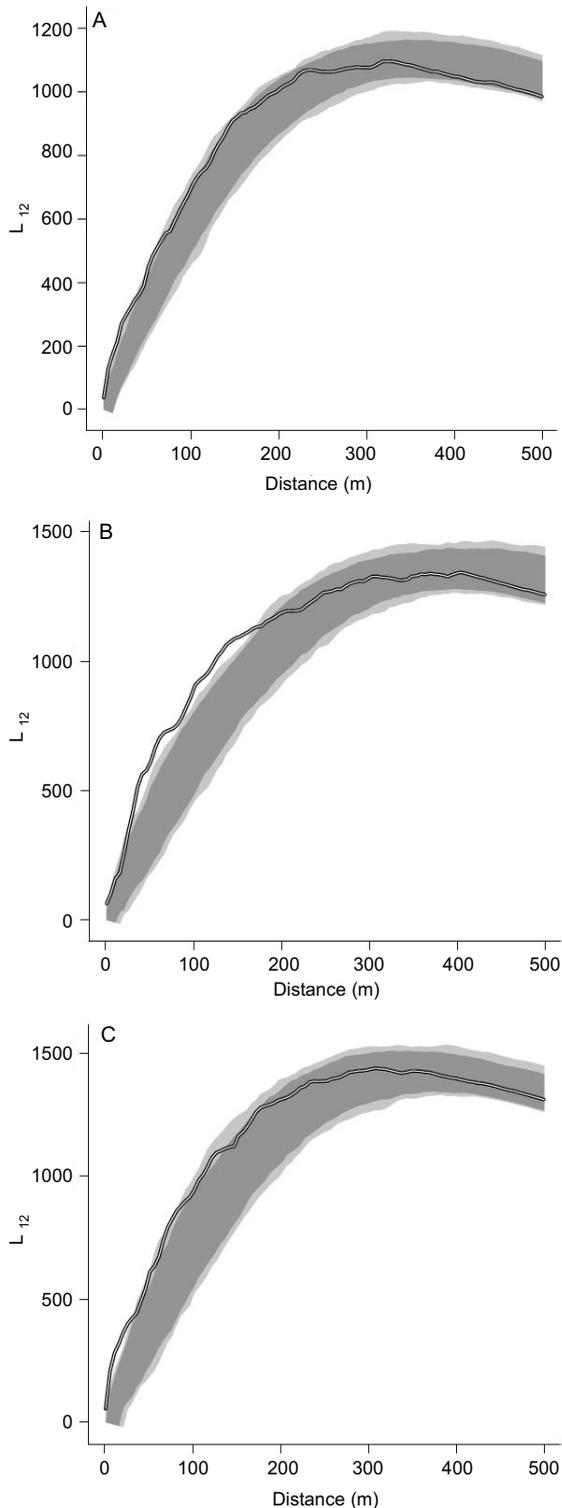
Fig. 3. L_{12} function of the interaction between breeding swans and waterbirds on fishponds for survey 1 (A), survey 2 (B) and survey 3 (C). The black line indicates the observed pattern. Dark and light grey envelopes encompass 95% and 99% of the 500 randomizations, respectively. Observed patterns deviated 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.
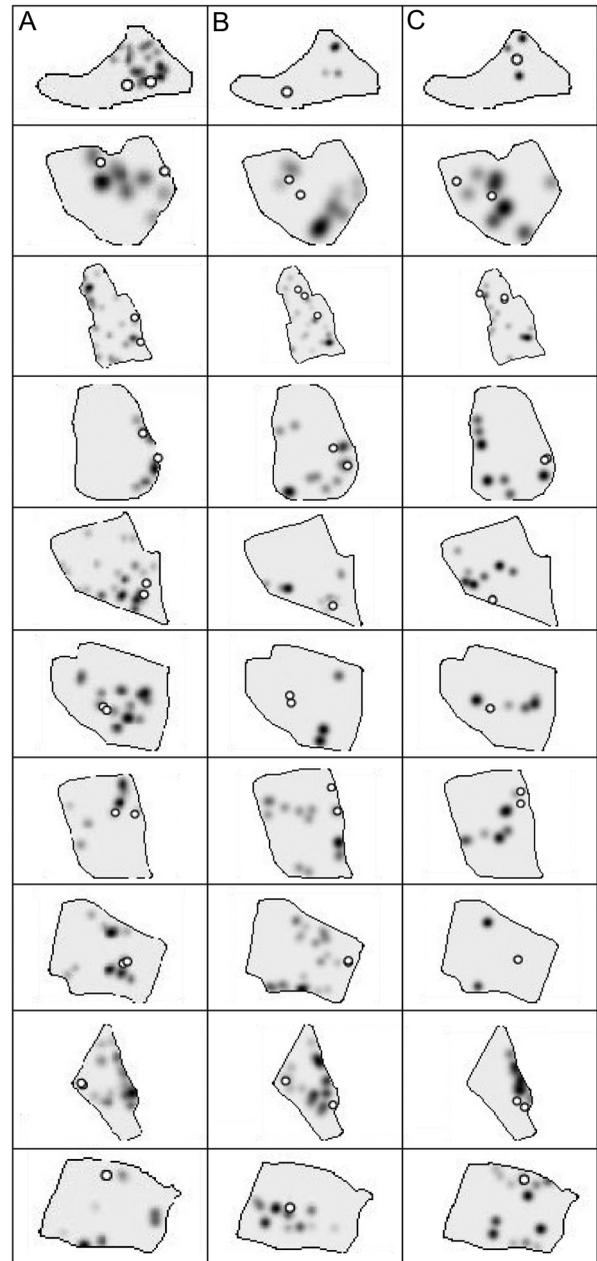

Fig. 4. Smoothing of waterbirds with the kernel method during survey 1 (A), survey 2 (B) and survey 3 (C) to measure the density probability function on the 10 fishponds where breeding swans have been observed during survey 1 (A), survey 2 (B) and survey 3 (C). Smoothing of waterbirds with the kernel method on other fishponds where breeding swans have not been observed during all three surveys are not shown. Smoothing parameter was fixed visually to 15 m (see text). An increasing dark grey level indicates higher waterbird density probability function. Circles represent swans.

recorded when swan clusters were randomized over waterbird cores of presence (Fig. 5). The results were similar with 50 m and 100 m smoothing parameters (not shown), suggesting the value
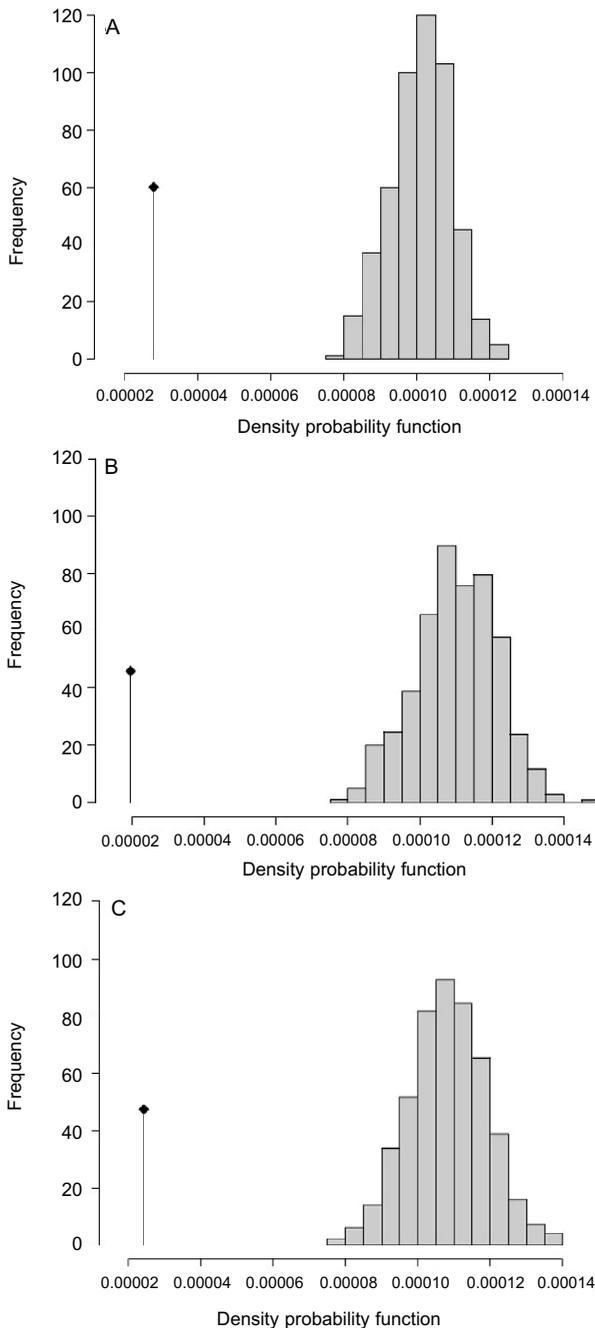
Fig. 5. Density probability function of waterbirds where swan clusters were randomly positioned (bar plots), and actual density probability function where swan clusters were observed in the field (black point) for survey 1 (A), survey 2 (B) and survey 3 (C).

of the smoothing parameter did not affect this result. Although swans were generally in the same parts of the fishponds than the other waterbirds, waterbird density was thus lower in the immediate vicinity of swans.

DISCUSSION

Our results highlight that waterbirds and breeding Mute Swans do simultaneously use the same large-scale areas within waterbodies, since the L function analysis suggests that the two types of birds were close to each other within fishponds. The patterns of distribution observed were hence consistent with prediction 1 of the Introduction.

The first key finding of this study is therefore that swans and the other waterbirds had preferences for the same parts of fishponds. The close proximity between breeding Mute Swans and waterbirds does not rule out the occurrence of interactions, but supports the hypothesis that, within fishponds, breeding Mute Swans do not lead to complete desertion of the areas they use by the other waterbirds. Conversely, breeding Mute Swans and the other waterbirds co-occurred in the same parts of fishponds. In ungulate communities, some forms of intra-specific, interspecific or intra-guild attractivity, e.g. for commensalism or vigilance reasons, have already been documented, with varying effects depending on species ecological requirements and habitat properties (e.g. Hibert et al. 2011, Darmon et al. 2012). Although the Mute Swans can be territorial and aggressive (Cramp et al. 1986), this study like a previous one conducted in the same region with a different approach (comparison of spatial distribution between fishponds, as opposed to distribution within fishponds here) does not give support to the claim that the establishment of breeding swans is fundamentally detrimental to the mere presence of the other waterbirds. Indeed, this previous study showed that waterbirds were generally more abundant in fishpond where swans were also present, suggesting shared fishpond selection processes (Gayet et al. 2011). The present study suggests a similar process occurs within waterbodies.

Varying breeding Mute Swan behaviours may explain why the aggregation magnitude with waterbirds varies across the breeding season. Mute Swans were indeed closer to waterbirds during survey 2. During this survey swans were mostly families of adults with cygnets, and adults were spending a considerable amount of time collecting vegetation and bringing it back to the water surface for the cygnets to feed on (Cramp et al. 1986). In addition to spending more time in hydrophyte bed areas also attractive to some waterbird species, this also increased commensalism opportunities for foraging by ducks and Coots

as adult swans were bringing some underwater vegetation to the surface, where it could be taken by other birds with lower diving or underwater vegetation collection abilities (see Oksanen et al. 1979, Källander 2005). For instance, Gyimesi et al. (2012) demonstrated that commensal foraging with Bewick's Swans *Cygnus bewickii* can double the instantaneous food intake rate of Common Pochard. Incubation of females on dry land during survey 1 and greater size as well as independence of the cygnets during survey 3 may explain the lower aggregation of breeding Mute Swans with waterbirds during these study periods.

The second finding of this study is that Mute Swans were not where the density probability function of waterbird presence likelihood was greater within each fishpond. There could be several non-mutually exclusive reasons for this. First, predation risk may not constrain the distribution of Mute Swans and the distribution of other waterbirds to the same extent, while it may be beneficial to small species like ducks and Coot to have central positions within flocks (see Hamilton 1971, Parrish & Edelstein-Keshet 1999) and to avoid tall vegetation close to the shores where predators may hide (see Lazarus & Symonds 1992), this may not be so much the case for Mute Swans which have much fewer predators in the study area. Secondly, Mute Swans and other waterbirds may have different food requirements: for instance, some duck species are omnivorous while Mute Swan is a strict herbivore, so the latter may be more restricted in their distribution by the position of the hydrophyte beds. Swans and the other waterbirds may also differ in their foraging methods. Pöysä (1983) indeed identified two main habitat use strategies on Finnish eutrophic lakes: dabbling ducks and Coots used the edges and shallow parts to a greater extent, while diving ducks generally occupied the centre of waterbodies. The situation may be even more extreme with swans given their large size compared to other waterbirds, allowing them to reach food virtually everywhere within these < 1 m deep waterbodies (Owen & Cadbury 1975). Pöysä & Sorjonen (2000) considered that expanding Whooper Swan *Cygnus cygnus* populations used a vacant niche (deep water areas) when they started to recover in Nordic lakes. Such a differential micro-habitat use may indeed allow coexistence of species within bounded environment like fishponds (see Guillemain et al. 2002 for such a process among dabbling ducks), and this seems to be the case of our fishponds.

The relatively minor effects on aquatic vegetation of paired Mute Swans (at least compared to flocks) (see Tatu et al. 2007, Gayet et al. 2011, Wood et al. 2012) may be one reason why no deserted area by waterbirds was found around breeding Mute Swans (i.e. because paired Mute Swans do not deplete the shared vegetation food resource to a significant enough extent).

Expanding or newly colonizing species may profoundly alter the existing wildlife communities, dislodging some species from their former distribution. Such a claim is often made for Mute Swans, whose populations have rapidly increased both in Europe and in North America. We have shown that breeding Mute Swans and other waterbird species were observed in close proximity in the fishpond ecosystem we studied. This suggests that breeding Mute Swans do not strongly alter the distribution of the other waterbirds within our studied ecosystems and does not support the common claim that Mute Swan dislodge the other bird species within these fishponds. The situation may be different in other wetland systems, e.g. waterbodies of different size or other bird communities. This opens interesting avenues for research on the distribution of waterbirds in the coming years, in order to provide the necessary scientific basis for policy making and land management in a context of rapidly changing waterbird communities.

ACKNOWLEDGEMENTS

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STRESZCZENIE

[Analiza rozmieszczenia danych punktowych w przestrzeni wskazuje na brak unikania przez ptaki wodne stref z miejscami przebywania łabędzi niemych]

Liczebność łabędzia niemego w ostatnich latach drastycznie wzrosła w Europie Zachodniej i Ameryce Północnej, co może wpływać na resztę zespołu ptaków wodnych. Łabędzie nieme mogą wywierać wpływ na inne ptaki wodne pośrednio poprzez zmniejszenie ilości dostępnego pokarmu, a także bezpośrednio poprzez agresywne zachowania terytorialne. Zachowania terytorialne zaobserwowano np. na zbiornikach wodnych na terenach, na których łabędź niemy uważany jest za gatunek inwazyjny. Jednocześnie w innym badaniu stwierdzono większą liczebność ptaków wodnych na zbiornikach, na których występowały lęgowe łabędzie nieme. Ogólnie jednak niewiele jest wiadomo na temat potencjalnego wpływu zachowań terytorialnych łabędzi na rozmieszczenie pozostałych ptaków wodnych.

W pracy badano czy istnieje zależność pomiędzy rozmieszczeniem lęgowych łabędzi niemych i innych ptaków wodnych (rozpatrywano kaczki pływające i nurkujące oraz łyski) w obrębie tego samego zbiornika wodnego. Badania prowadzono na stawach rybnych (o średniej powierzchni 9,9 ha) we wschodniej Francji, prowadząc trzykrotne mapowanie wszystkich ptaków wodnych na danym zbiorniku. Terminy kontroli dopasowano do cyklu lęgowego łabędzi: pierwsza kontrola została przeprowadzona w okresie wysiadywania, druga w okresie wykluwania się piskląt, a trzecia, gdy łabędzie wodzą pisklęta (Tab. 1). Analizy przeprowadzono za pomocą analizy rozmieszczenia danych punktowych w przestrzeni, w której jako punkty oznaczono lokalizację pojedynczych ptaków lub w niektórych przypadkach grupę ptaków (np. para ptaków, samica z pisklętami) (Fig. 1).

Stwierdzono, że na terenie badanych zbiorników wodnych łabędzie przebywały blisko siebie (Fig. 2). Łabędzie stwierdzano w sąsiedztwie innych ptaków wodnych, wykorzystywały one ten sam obszar w obrębie danego zbiornika. Takie rozmieszczenie skupiskowe obserwowano do 175 m (Fig. 3). Inne ptaki wodne nie unikają stref wykorzystywanych przez lęgowe łabędzie, co nie potwierdza sugestii, że łabędzie mogą wypierać inne gatunki. Nawet, jeśli istnieje pewne unikanie lęgowych łabędzi przez inne ptaki wodne, nie jest ono na tyle silne, aby generować obszary, na których nie obserwuje się innych ptaków wodnych. Analizy wskazują także, że łabędzie nie były zlokalizowane w centrum grup utworzonych przez inne ptaki wodne w obrębie każdego stawu (Fig. 4, 5). Może to wskazywać na nieco inne preferencje mikrosiedliskowe lub sposoby użytkowania przestrzeni stawów oraz występowanie potencjalnych interakcji.

Podsumowując, autorzy wskazują, że łabędzie prawdopodobnie bezpośrednio nie wpływają na inne ptaki wodne, a więc populacje łabędzi nie wymagają działań mających na celu kontrolę ich liczebności, jak często się twierdzi.