



## 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  $\pm$  0.2 ha SE) spread over 1600 km<sup>2</sup> 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

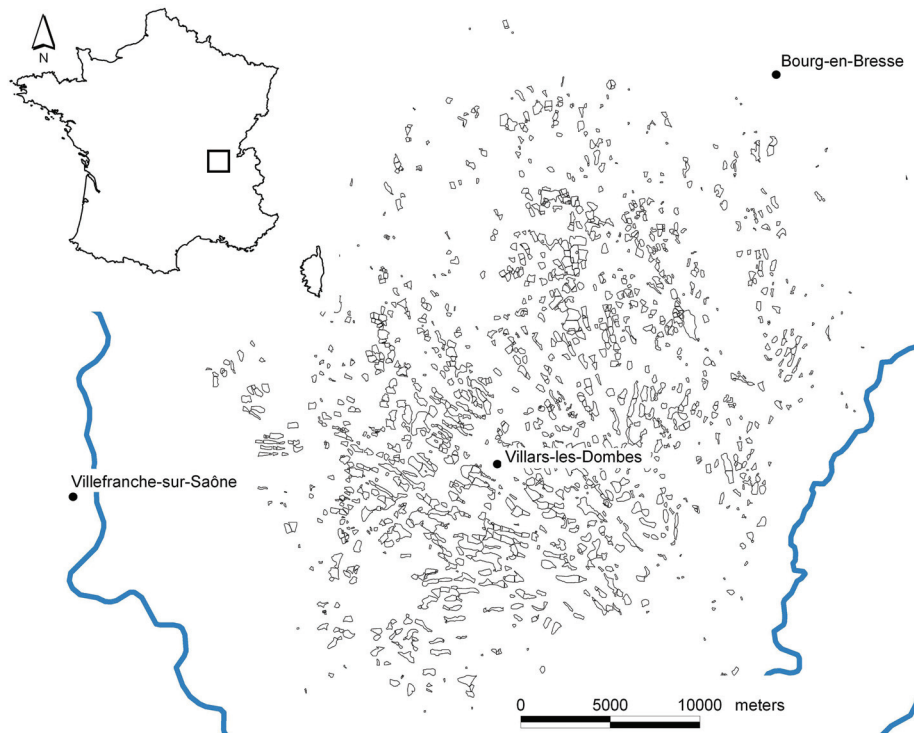


Figure 1. The fishponds of the Dombes plateau, and the position of the area in France.

considered at the scale of 0.25 km to describe the immediate environment of fishponds and to reduce multicollinearity 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			F
	Do	Dm	Dn	
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  $Z(t) = (Z_1(t), \dots, Z_p(t))'$  is given by:

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

where  $\beta = (\beta_1, \dots, \beta_p)$  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 ( $A_f$ ) and area covered in ice ( $A_i$ ).

## 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  $\Delta AIC$  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  $NB2 \times PI2$  (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	$\Delta AIC$	$w_i$	
Summer	all swans	<b>A+PI2×NB2</b>	<b>4</b>	<b>4809</b>	<b>0</b>	<b>0.88</b>	
		A×NB2	3	4813	4	0.12	
	families	<b>A×NB2</b>	<b>2</b>	<b>2920</b>	<b>0</b>	<b>0.82</b>	
		A×NB025	2	2923	3	0.18	
	flocks	<b>A×PI025</b>	<b>3</b>	<b>923</b>	<b>0</b>	<b>0.36</b>	
		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	<b>NB2+Dry×Af</b>	<b>4</b>	<b>977.5</b>	<b>0.0</b>
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
	<b>Dry×Af</b>			<b>3</b>	<b>219.4</b>	<b>1.5</b>	<b>0.18</b>
	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  $\Delta AIC \leq 2$  (Table 4), to explain fishpond selection by swans during summer and winter.

			Estimate	SE	95% CI	
					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	$2.560 \times 10^{-4}$	$-5.692 \times 10^{-4}$	-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	$4.393 \times 10^{-4}$	-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	$-1.999 \times 10^{-4}$	$1.984 \times 10^{-4}$	$1.890 \times 10^{-4}$	-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

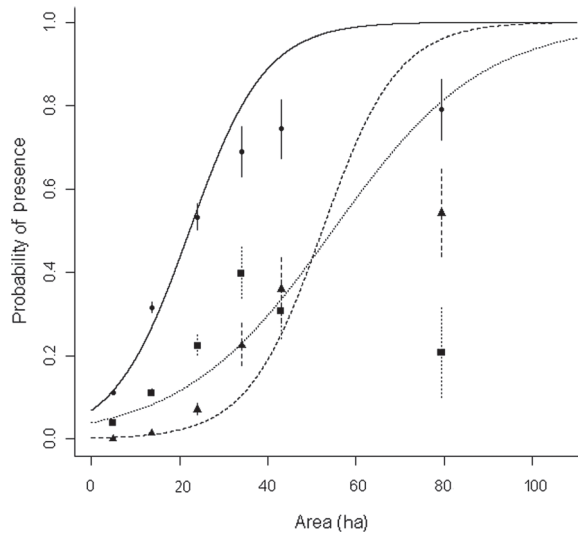


Figure 2. Logistic regression of mute swan presence ('all swans': circles and plain curve; 'families': squares and dotted curve; 'flocks': triangles and dashed curve) with their standard error on fishpond area for all summer observations. The model has been applied only to fishpond area without considering 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%  $\pm$  37.7 of flooded area was frozen; Feb 1: 29.9%  $\pm$  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).

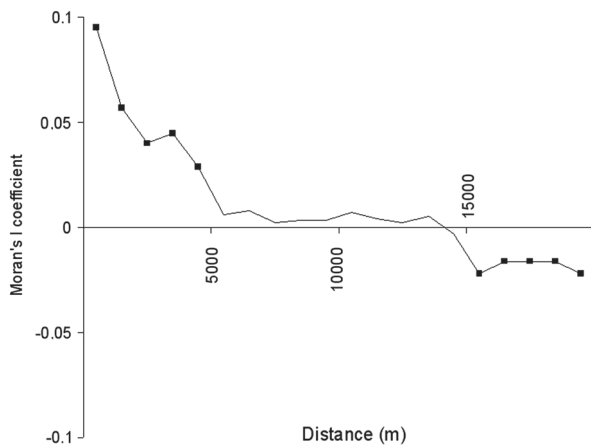


Figure 3. Correlogram of Moran's I coefficient for fishpond area, i.e. changes of this coefficient over classes of distances. A square indicates significant coefficients where appropriate.

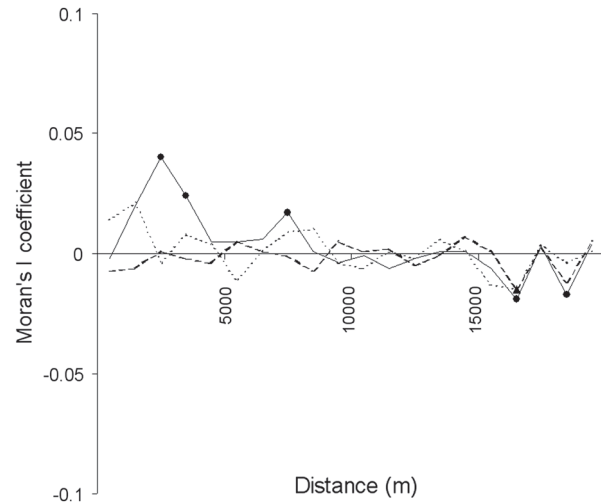


Figure 4. Correlograms of Moran's I coefficient calculated on residuals from the best-selected model to explain the presence of the 'all swans' (circles and plain curve), 'families' (squares and dotted curve) and 'flocks' (triangles and dashed curve) for 2003. Circles (for 'all swans') and triangles (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 ( $\geq 10\%$ 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.

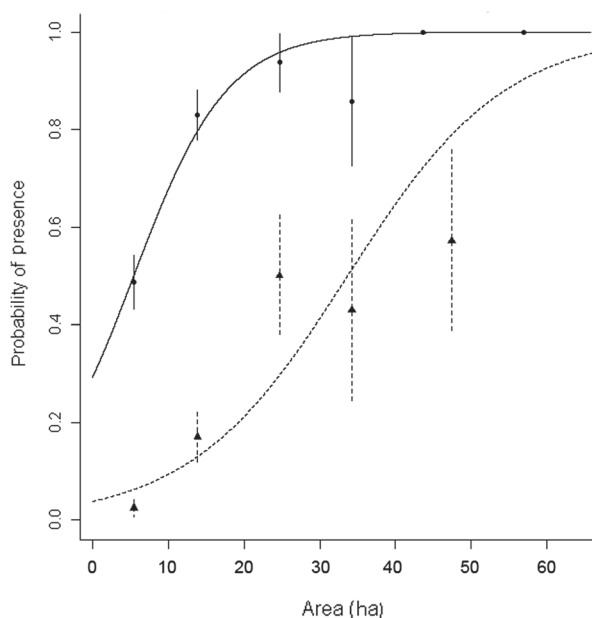


Figure 5. Logistic regression of swan presence ('all swans': circles and plain curve; 'flocks': triangles and dashed curve) with their standard error on fishpond area for all winter observations. Note that the relationship is here illustrated through fishpond area (A), not fishpond flooded area (Af) 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.

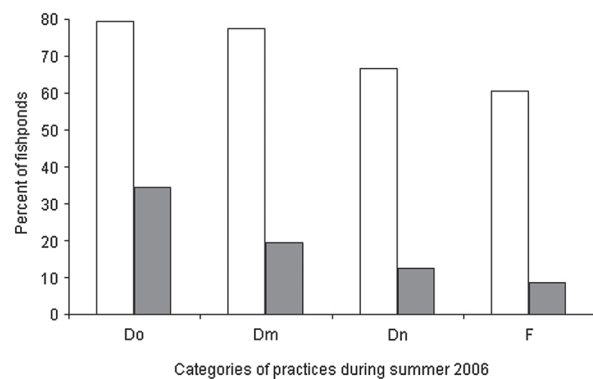


Figure 6. Percentage of fishponds where the 'all swans' category (white columns) and swan flocks (grey columns) were detected at least once during winter 2006–2007, depending on cultivation practices the summer before (Do: dry and cultivated with other cereals, Dm: dry and cultivated with maize, Dn: 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 that 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 et al. 2011). 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, eutrophication) 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.

*Acknowledgements* – We deeply thank the Conseil Général de l'Ain, the Direction Régionale de l'Environnement Rhône-Alpes, the Fédération Départementale des Chasseurs de l'Ain (FDC Ain), the Fédération Nationale des Chasseurs and the Office National de la Chasse et de la Faune Sauvage (ONCFS) for their financial support. We are grateful to the landowners and to observers that conducted field survey (Service départemental de l'Ain, Direction Régionale de l'ONCFS, Direction des Etudes et de la Recherche de l'ONCFS, Fondation Vérots, students and secretaries). We also thank Daniel Rousset (FDC Ain), Laurence Curtet, Dominique Bellette, Laurence Henry and Sandrine Ruetter (ONCFS) for their help with this study, Anne-Laure Brochet and Clément Calenge for their help with the statistical analyses as well as Steven Larcombe who helped us improving an earlier version of the manuscript.

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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	$\Delta$ AIC	$w_i$
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
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
	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 1 except Af: area flooded, Ai: area taken in iced, Dry: drainage status (yes/no) during summer 2006.

	Model	K	AIC	$\Delta$ AIC	$w_i$	
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	$\Delta$ AIC	$w_i$
Flocks	NB2+Af	2	237.7	19.7	0
	Af+PI2×NB2	4	240.2	22.3	0
	NB025	1	254.1	36.2	0
	PI025	1	254.3	36.3	0
	Dry	1	256.4	38.5	0
	NB2	1	257.2	39.3	0
	PI2	1	258.1	40.1	0
	Null	1	261.3	43.4	0
	Ai	1	261.6	43.7	0