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Annual use of man-made wetlands by the mute swan (*Cygnus olor*)

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A B S T R A C T

This is essential to understand habitat selection by wildlife to manage habitats and populations. Studying the annual use of aquatic habitats provides information on how to manage wetlands for waterfowl, and to predict possible detrimental effects associated with extended usage by these birds. This is particularly important for species like the mute swan (*Cygnus olor* Gmelin), given its recent dramatic demographic expansion, causing concern in both Europe and America. We studied the extent of usage (swan.days.ha^{-1}) of habitat patches by mute swans in a heterogeneous and fluctuating fishpond landscape. We assessed seasonal differences of swan usage of fishponds, annual variation for a given fishpond, and determined which habitat factors drive swan usage over the year. The seasonal use pattern was regular: a similar proportion of fishponds was used heavily, moderately or lightly in all seasons. Flocking throughout the year and breeding during summer were associated with heavy use of fishponds, i.e. large number of swan.days.ha^{-1}. Flocking on some fishponds during several successive seasons demonstrated that some waterbody provide valuable habitats over time for swans. However, swans did not use individual fishponds to the same extent each season, mostly depending on the fluctuating ecological requirements of swans and variation in habitat properties. Agricultural practices on fishponds drastically affected swan usage during autumn and winter: formerly dried fishponds were used preferentially once reflooded. The specific agricultural crops used during the drought period had no influence though. The large-sized fishponds and fishponds within a dense network of waterbody were the most heavily used by swans throughout the year. Our results may thus be helpful to predict and prevent possible habitat damage by swans. They also provide information on habitats that are valuable for waterfowl species in general, by using mute swans as a proxy for waterfowl requirements.

1. Introduction

Species-specific requirements and environmental conditions affect wildlife habitat selection processes across the year. Many studies have dealt with waterfowl habitat selection during the non-breeding period, and current knowledge underlines the combined roles of habitat patch size, resource availability and human disturbance (see Tuite et al., 1984; Bell et al., 1997; Evans and Day, 2001; Rees et al., 2005; Brochet et al., 2009; Fouque et al., 2009). During the non-breeding period, the gregarious behavior of most waterfowl species (Owen and Black, 1990) combined with a heterogeneous availability of resources leads to a concentration of individuals on sites with the best quality. The factors that promote waterfowl use of a site during the breeding season have been studied in a range of studies (e.g. Paquette and Ankney, 1996; Elmberg et al., 2005), though generally independently from winter studies, while the factors driving waterfowl use in spring and autumn remain largely unexplored (see Arzel et al., 2006). Our understanding of habitat selection processes would be much improved if standardized research protocols were applied throughout the annual cycle, as advocated by MacKenzie et al. (2006).

Such multiple-season studies of a waterfowl species, defined here as studies undertaken throughout the year at a site or region and thereby encompassing its annual life-cycle, are often limited by

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migratory behaviors. This is unfortunate, since such studies would help improving the management of the wetland habitats used by waterfowl. Indeed, such management must not only consider the large concentrations of birds that may be present during some periods (so as to provide safe roosts and–or suitable foraging areas), but should also take into account the potential carry-over effects of such use over successive seasons on the habitat itself. Several effects are indeed known to result from extended waterfowl stay: food resource depletion (Esselink et al., 1997; Tatu et al., 2006; Gayet et al., 2011a), nutrient loading (Post et al., 1998), transmission of avian influenza viruses (Olsen et al., 2006) or crop damage (Loonen and De Vries, 1995). Studying habitat use by waterfowl which remain throughout the year within the same region may therefore provide valuable information for other waterbirds, albeit migratory. Indeed such knowledge would help to assess the potential ecological requirements of migratory species which use wetlands at different seasons and with similar ecological requirements than species studied. This should lead to efficient habitat management knowledge in the perspective of creating valuable wetlands dedicated to waterfowl for instance.

In Europe, fishponds are colonized by mute swan (*Cygnus olor* Gmelin) (Musil and Fuchs, 1994; Fouque et al., 2007), thus providing an adequate context to explore habitat use processes by waterfowl over the annual cycle. Fishpond areas are networks of clearly defined habitat patches which differ markedly from each other despite their close geographical proximity. Mute swans are often present in such fishpond areas throughout the year, and hence may potentially be used as a proxy for other waterfowl species, especially for herbivores like Coot (*Fulica atra* L.) and some ducks (e.g., Red-crested Pochard *Netta rufina* Pallas), given their shared preferences for the same sites (Gayet et al., 2011b). In terms of species and habitat conservation it is necessary to better understand its habitat selection process. This will also help to evaluate the potential impact of the presence of Mute swan on ecosystems. The mute swan is indeed an exotic and potentially invasive species in some parts of the world (e.g. North America, see Perry, 2004). In Europe, the species is protected in many countries. It has shown a dramatic demographic expansion over the last decades, causing damage to macrophyte beds in some situations (O'Hare et al., 2007; Gayet et al., 2011a). Owing to their size, food intake rates, diet and energy requirements, swans obviously have a greater impact on standing crops than other waterfowl groups (Wood et al., 2012).

An earlier study demonstrated that mute swan presence on a fishpond depends on both the birds' breeding status and fishpond properties at that time: food availability, fishpond size and fishpond surrounding aquatic environment (e.g. number of fishponds, ratios of fishpond sizes and distances of other fishponds within a given radius). Swans were more likely to be observed on fishponds with surfaces >10 ha and close to other fishponds (Gayet et al., 2011c). However, what determines temporary presence in a habitat patch may be different from what allows its repeated use over the long term. For habitat managers it is often the latter that is more crucial to assess, since extended use at a site (e.g., flocking during several weeks) is more likely to subsequently affect habitat properties than the temporary presence of individuals.

We hence studied the extent of use (swan.days.ha^{-1}) of habitat patches by mute swans on fishponds throughout the year. We assessed whether or not swan usage over a sample of fishponds differs between seasons, i.e., if the proportions of the fishpond sample that are used heavily, moderately or lightly are similar over successive seasons (Question 1). We also assessed if swan usage varied for a given fishpond across the year (Question 2). Finally, we aimed at determining the factors that affect swan usage on fishponds over the year (Question 3). It was expected that swan usage at the annual scale would increase with fishpond size and be affected by food availability in the aquatic environment, since these have been demonstrated to be the main drivers of swan presence (Gayet et al., 2011c).

2. Methods

2.1. Study area

This study took place in the Dombes (45°57'N, 05°02'E) in Eastern France. The Dombes is one of the largest fishpond regions in France (1450 fishponds spread over 1600 km^2; average area = 7.3 ha ± 0.2 SE). One quarter of the Dombes fishponds are larger than 10 ha. The Dombes is also an important breeding and staging area for ducks. The ecological value of such regions is recognized by European international policy (Natura 2000 network), notably due to its remarkable aquatic plant communities (DOCOB, 2004).

Fishponds are entirely created by man. They are temporarily drained annually during autumn for fish harvest and, in the Dombes, every third year they are not reflooded after fishing but rather get dried for 1 year and in most cases are then cultivated until reflooding the following autumn. This is important to keep in mind for the present study, since such agricultural practices affect food availability and strongly drive swan presence during winter (Gayet et al., 2011c).

2.2. Fishpond sample

The initial sample consisted of 106 fishponds larger than 10 ha (average area = 18.1 ha ± 0.8 ha SE), since swans are most likely to be observed on such sites in the Dombes (Gayet et al., 2011c). Sixty-four fishponds were flooded and 42 were dried during summer 2007 (11 of 42 were non-cultivated, 20 were cultivated with corn and 11 with other cereals) (Table 1). Starting in early December 2007 the 106 fishponds were monitored for one year, until late November 2008. Of the 64 fishponds that were flooded during summer 2007, 11 and 12 were dried during spring and summer

Table 1
Number of fishponds sampled and their management per season (flooded versus dried or drained) from winter 2007/2008 to autumn 2008. Fishpond management the previous summer is indicated.

	Winter 2007/2008		Spring 2008	
	Flooded	Dried	Flooded	Dried
Fishpond management during summer 2007				
Flooded	63	1	53	11
Drained and non-cultivated	11	0	11	0
Drained and cultivated with corn	20	0	19	1
Drained and cultivated with other cereals	11	0	11	0
Total number of fishponds	105	1	94	12
	Summer 2008		**Autumn 2008**	
	Flooded	Dried	Flooded	Drained
Fishpond management during summer 2007				
Flooded	52	12		
Drained and non-cultivated	11	0		
Drained and cultivated with corn	19	1		
Drained and cultivated with other cereals	11	0		
Total number of fishponds	93	13		
Fishpond management during summer 2008				
Flooded			92	0
Drained and non-cultivated			3	3
Drained and cultivated with corn			8	2
Drained and cultivated with other cereals			4	2
Total number of fishponds			107	7

2008, respectively. Of the 42 fishponds that were drained during summer 2007, one was dried during both spring and summer 2008. These were removed from the sample (dry fishponds not being used by swans), hence leaving 94 spring sites (of which 41 were previously dried and 53 were previously flooded in 2007) and 93 summer sites (of which 41 were previously dried and 52 were previously flooded in 2007). Before reflooding, which started at the beginning of autumn 2008, the fishpond sample was strongly unbalanced, since it contained 93 flooded fishponds for only 13 that were previously dried during summer 2008. To overcome this, nine new fishponds dried in summer 2008 were added to our 2008 autumn sample (hence total size = 114 fishponds sampled) (Table 1).

2.3. Swan use of fishponds

A single observer (GG) visited fishponds every second week for the whole period, from winter 2007/2008 (start date: December 12th 2007) to autumn 2008 (end date: November 27th 2008). One day and a half were necessary to cover all fishponds in a census session. During each visit, the observer estimated for each fishpond the surface flooded using 10% classes, i.e. from 0% (emptied fishpond) to 100% (completely flooded fishpond). The observer counted the swans (adults and cygnets) on each fishpond. To measure swan usage, we computed 'swan.days', using the formula of Desnouhes et al. (2003) where n is the number of monitoring sessions, swans is the number of birds and i is date. Swan.days were calculated per season:

$$\sum_{i=1}^{n} \text{swans}_i + (((\text{swans}_i + \text{swans}_{i+1})/2)^*(\text{date}_{i+1} - \text{date}_{i-1}))$$

Based on four weekly counts, swan.days is thus an extrapolation of the theoretical number of swans on each fishpond each day over the period. The year was divided into four seasons which correspond to fishpond management stages and the main stages of the Swan's annual cycle: 'spring', covering the early breeding season between March and May; 'summer', or late-breeding between June and August; 'autumn', or post-breeding, between September and November; and 'winter', or non-breeding, between December and February. Non-breeding swans are more gregarious during summer and winter. To measure swan usage independently from habitat patch size, we standardized swan.days for fishpond size, obtaining swan.days.ha^{-1}. The relationship between swan.days and swan.days.ha^{-1} was positive and statistically significant for all seasons, i.e. numbers and densities of swans were correlated (not shown).

2.4. Fishpond environmental covariates

Since interactions between habitat variables are poorly studied in waterbirds (see Ma et al., 2010), we here considered a set of variables so as to understand how mute swans use the aquatic habitat in a heterogeneous wetland landscape. The first set of environmental covariates describes fishpond spatial configuration. For each fishpond, we measured area ('AREA', in ha) as well as the number of fishponds within short (250 m, termed 'NB250') and long distance (2 km, termed 'NB2000'). Distances were selected so as to avoid strong multicollinearity between measured values. We also measured fishpond isolation using a proximity index (Gustafson and Parker, 1994) at the same distances as NB (termed 'PI250' and 'PI2000'). The proximity index was calculated as the sum of the ratios of fishpond sizes and distances within the considered radius. High proximity index values therefore indicate less isolated fishponds independently from the number of surrounding fishponds.

The second set of environmental covariates considers the food resources available to swans. During autumn and winter, resource availability strongly contrasts depending on recent fishpond management history. Fishponds that were dried the previous summer provide waste grains or natural seeds that are easily available to swans once the water body is reflooded. The quantity of grains available after harvest can be considerable and represent several tens of kilograms per hectare (e.g. for rice see Stafford et al., 2006). Conversely, food available to swans in fishponds that remained flooded in summer mostly consists in dormant natural macrophyte organs (seeds, tubers, rhizomes) that obviously constitute a more difficult food source to use. Therefore every season we differentiated fishponds that had been flooded versus dried the preceding summer (termed 'HISTORY': stands for the flooding history of a given fishpond, i.e. flooded or dried).

2.5. Statistical analyses

Fishponds were considered for analysis within a given season only when they were actually flooded for a sufficient part of that season. Every season we considered only fishponds that had had water for at least six weeks (i.e., a minimum of three visits) for estimating swan usage (i.e. swan.days.ha^{-1}). We determined if the distribution of fishponds among swan usage classes differed between seasons by using χ^2 tests considering equal swan usage classes (Question 1), and if it varied seasonally per fishpond by using Friedman tests (Question 2). We assessed the relative potential influence of habitat variables on swan usage with General Linear Mixed Models (GLMM) (Question 3). Fishponds (replicated between seasons when flooded) were included as a random parameter whereas AREA, HISTORY and fishpond spatial configuration (PIs and NBs) were included in the initial model as fixed parameters. HISTORY represents fishpond practice (flooded versus dried) during the summer prior to the season considered. AREA and HISTORY were initially included in interaction in the initial model (AREA*HISTORY). PIs and NBs were included in the initial model in interaction with each other at their respective distance of 250 and 2000 m (i.e., NB250*PI250 and NB2000*PI2000). The initial model was then simplified during a backwards-stepwise model selection procedure. Parameters whose values were not significant at $P > 0.05$ were gradually removed, starting with interaction terms. Swan usage values were log-transformed to meet normality criteria. We used R 2.10.1 software for all statistical analyses (R Development Core Team, 2009).

3. Results

3.1. Number of swans counted throughout the year

The number of flooded fishponds fluctuated during the year due to emptying for fishing or drainage for cereal farming. Water was present in 105 fishponds in winter, 94 in spring, 93 in summer and 107 in autumn. The maximum number of swans was counted during the last week of December: 835 swans in total over all surveyed fishponds (Fig. 1). Conditions were special during this visit, because all fishponds were at least partially frozen. The number of swans on fishponds decreased over the months until reaching a minimum in September ($n = 153$) with the exception of June where they marginally re-increased (ca. 400 individuals).

3.2. Fishpond use patterns between seasons

Flocking (i.e. a group of at least 10 adults observed during a minimum of two successive visits) occurred on 25 fishponds. Flocking reached its maximum during winter (14 sites). It was less

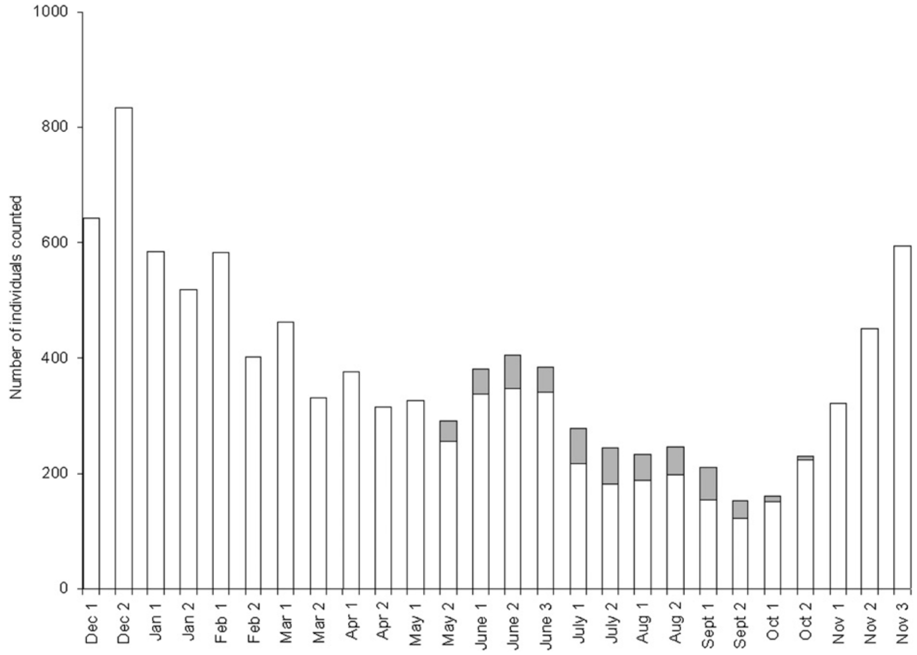

Fig. 1. Total number of adult swans (white) and cygnets (gray) counted every second week on the fishpond sample.

frequent during spring and summer (on molting sites), occurring on only 6 fishponds. Flocking occurred on nine sites in autumn. Eight fishponds were used in two seasons as flocking sites, and two fishponds were used as such in three seasons. Twenty-eight fishponds were used as nesting sites (i.e., swan clutches observed) and on 23 fishponds, swan families with cygnets were observed on at least two successive visits (Table 2). At the end of the monitoring period, no swans were ever recorded on eight fishponds of our sample.

We distinguished several swan usage classes of equal interval: <5 swan.days.ha^{-1} representing very little or occasional usage; 5–10 swan.days.ha^{-1} representing low-medium usage, 10–15 swan.days.ha^{-1} representing medium–high usage; >15 swan.days.ha^{-1} representing high swan usage (see Table 3). There was no difference in the distribution of swan usage over fishponds between seasons ($\chi^2 = 13.48$, df $= 9$, $P = 0.14$): the relative share of heavily (>15 swan.days.ha^{-1}), moderately (>10 swan.days.ha^{-1}; >5 swan.days.ha^{-1}) and lightly used fishponds (<5 swan.days.ha^{-1}) remained similar in the site sample in all seasons. Flocks were always present within fishponds classed as within the high swan usage category. Nesting sites were homogeneously distributed over swan usage classes during spring ($\chi^2 = 6$, df $= 3$, $P = 0.11$) whereas breeding sites during summer were mostly from the two highest classes ($\chi^2 = 23.09$, df $= 3$, $P < 0.0001$) (Table 3). During summer, flocking and breeding sites were all associated with the highest usage classes but mean swan usage was higher on flocking sites than on breeding sites (flocking sites $= 70.24 \pm 18.6$ swan.days.ha^{-1}; breeding sites $= 27.7 \pm 4.59$ swan.days.ha^{-1}).

3.3. *Mean swan usage between seasons*

Mean swan usage per fishpond was highest during winter (>27 swan.days.ha^{-1} per fishpond on average), but inter-fishpond variations were large (Fig. 2). Extreme swan usage values (>300 swan.days.ha^{-1}) occurred in winter on two fishponds, that were both dried the previous summer. During spring, summer and autumn, mean usage and differences between fishponds were lower (mean: 13 to 18 swan.days.ha^{-1}). Without the extreme values from the two fishponds described above, mean winter swan usage was close to that in the other seasons (20.7 ± 4.1 SE).

Swan usage per individual fishpond varied across the year (Friedman $\chi^2 = 19.02$, df $= 3$, $P = 0.0003$), even after removing the two extreme winter values (Friedman $\chi^2 = 17.83$, df $= 3$, $P = 0.0005$). Fishponds were used to different extent by swans between seasons.

Table 2
Number of fishponds in each swan usage category (expressed in swan.days.ha^{-1}) per season.

	Winter 2007/2008			Spring		
	Number of fishponds	Swan.days		Number of fishponds	Swan.days	
		Average	Standard error		Average	Standard error
<5 swan.days.ha^{-1}	46	39.6	6	39	20.6	4.1
<10 swan.days.ha^{-1}	21	153.2	19.7	25	136.6	11.4
<15 swan.days.ha^{-1}	10	169.5	10.2	10	206.6	22.8
>15 swan.days.ha^{-1}	28	1868.8	498.4	20	1382.5	290.1
	Summer			Autumn		
<5 swan.days.ha^{-1}	44	20.6	3.6	59	24.9	5
<10 swan.days.ha^{-1}	11	116.7	9.9	22	148.1	17
<15 swan.days.ha^{-1}	14	204.6	17	7	228.9	59.2
>15 swan.days.ha^{-1}	24	1029.3	234.4	19	1469.7	424.2

Table 3
Number of fishponds used as flocking, nesting (during spring) and breeding site (during summer) by swans in each swan usage category (expressed in swan.days.ha^{-1}) per season.

	Winter 2007/2008	Spring		Summer		Autumn
	Flocking site	Flocking site	Nesting site	Flocking site	Breeding site	Flocking site
<5 swan.days.ha^{-1}	0	0	3	0	0	0
<10 swan.days.ha^{-1}	0	0	12	0	2	0
<15 swan.days.ha^{-1}	0	0	6	0	6	0
>15 swan.days.ha^{-1}	14	6	7	6	15	9

3.4. Habitat factors affecting swan usage throughout the year

The final GLMM retained to represent seasonal swan usage variations over the year included AREA, HISTORY plus PI250 in interaction with NB250 (Table 4). Drought of fishpond during the previous season (HISTORY) had a significant positive effect on swan usage. AREA and PI250 also had significant positive effects but the magnitude of their respective effect was lower than that of HISTORY. The interaction term between PI250 and NB250 had a significant negative effect, meaning that NB250 limited the positive relationship between PI250 and swan usage. Consequently high swan usage values were more likely to occur on fishponds dried during the summer preceding the season considered. To a lesser extent, fishpond area and fishpond with dense surrounding fishponds also increased the likelihood of observing high swan usage values throughout the year for a given fishpond.

Given the strong effect of fishpond HISTORY on swan usage, we pushed the analysis further to assess how this influenced swan usage between seasons. During winter, swan usage was three times higher on dried fishponds than on fishponds which remained flooded the previous summer. The difference was statistically significant (Mann–Whitney test: $W = 896$, $P = 0.0052$). During spring and summer, there was no difference in swan.days.ha^{-1} values between previously dried and previously flooded fishponds (spring Mann–Whitney test: $W = 1014.5$, $P = 0.59$ – summer Mann–Whitney test: $W = 1121.5$, $P = 0.67$). During autumn, swan usage was six times higher on previously dried fishponds, which was statistically significant (Mann–Whitney test: $W = 407.5$, $P = 0.0103$) (Fig. 3). There were no statistically significant differences detected in swan.days.ha^{-1} values between agricultural practices exerted on dried fishponds (non-cultivated, cultivated with maize or cultivated with other cereals) (winter $K-W$: $\chi^2 = 1.3$, df = 2, $P = 0.52$ – spring $K-W$: $\chi^2 = 4.24$, df = 2, $P = 0.12$ – summer $K-W$: $\chi^2 = 1.09$, df = 2, $P = 0.58$ – autumn $K-W$: $\chi^2 = 0.16$, df = 2, $P = 0.93$).

We did not detect a significant statistical effect of fishpond area on swan usage during winter, spring or autumn (winter: $F_{1,103} = 0.89$, $R^2 = -0.001$, $P = 0.35$; spring : $F_{1,92} = 2.34$, $R^2 = 0.01$, $P = 0.13$; autumn: $F_{1,105} = 2.62$, $R^2 = 0.02$, $P = 0.11$). However, fishpond area had a statistically significant and positive effect during summer ($F_{1,91} = 14.57$; $R^2 = 0.13$, $P = 0.0003$).

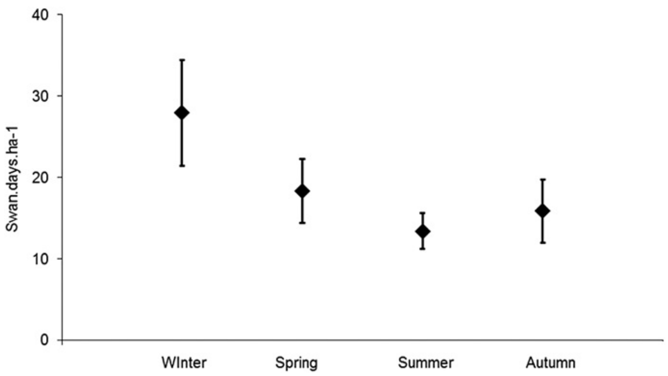

Fig. 2. Swan usage of fishponds from winter 2007/2008 to autumn 2008. Dots represent means and bars are standard errors.

4. Discussion

Our results provide new insights into the use of wetlands by waterbirds throughout the year. Among fishponds larger than 10 ha, the seasonal use patterns by mute swans were regular: a similar proportion of fishponds was heavily, moderately and lightly used in all seasons (Question 1). Nevertheless, swans did not use to the same extent individual fishponds year round (Question 2), possibly because of their own fluctuating ecological requirements (e.g. different social behavior according to breeding status) and habitat specific properties (Question 3).

4.1. Fishpond use patterns between seasons

The number of swans counted during the icing count period was close to the total number of swans estimated in the Dombes region (1000 swans according to Benmergui et al., 2005). A few fishponds should thus be used very intensively during severe winter, owing to the massive flocking of birds (including swan pairs) on the few wintering sites which were not entirely frozen. Despite a short cold spell, winter was generally mild during the monitoring period (2007/2008), a situation that may become increasingly common in the future owing to global warming (see Hughes, 2000). This may limit massive swan concentrations and their associated acute damages to a few ice-free flocking sites.

Swan pairs are known to remain on their breeding sites throughout the year (Scott, 1984). They possibly generate low to moderate fishpond use values in all seasons except during summer. The presence of cygnets in addition to their parents can lead to high use values – though lower than at flocking sites. The possible presence of flocks of non-breeders on the same fishponds throughout the year also demonstrates that such water bodies can provide valuable habitat over the long term for swans. However, the consequences of such a long and intensive use on ecosystem functioning deserve further work.

Table 4
Results of GLMM after a backwards-stepwise selection procedure of parameters at $P > 0.05$ to explain variations in seasonal swan usage on fishponds over the year. 'AREA' is for fishpond size (square meters). 'PIs' and 'NBs' are indices of isolation and number of fishponds within a radius of 250 m and 2000 m. 'HISTORY' represents the practice exerted on a fishpond the previous summer (flooded versus dried).

	Estimate	Standard error	Degree of freedom	t	P
Intercept	0.93	0.30	284	3.11	0.002
AREA	0.03	0.01	109	2.16	0.03
HISTORY	0.65	0.16	284	4.08	0.0001
PI250	7.5e – 06	3.43e – 06	109	2.17	0.03
NB250	0.02	0.06	109	0.35	0.73
PI250*NB250	−9.0e – 07	4.3e – 07	109	−2.16	0.03

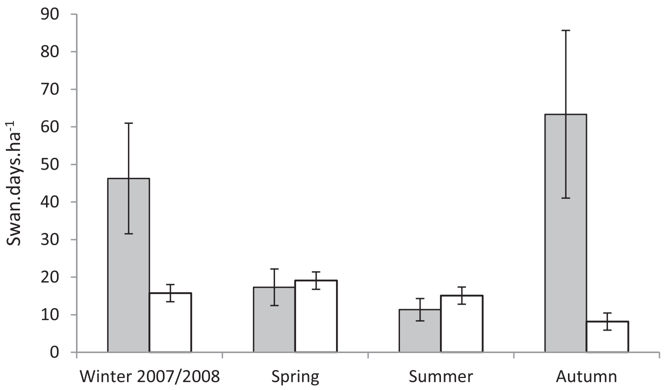

Fig. 3. Swan usage of fishponds from winter 2007/2008 to autumn 2008 depending on drought history. Gray columns are fishponds dried the previous summer, white columns are fishponds flooded the previous summer. Bars are standard errors.

4.2. Factors affecting seasonal swan usage

This study provides evidence that swan usage largely depends on previous agricultural practices on the fishpond. Greater use was indeed observed during autumn and winter after reflooding of dried fishponds. This result underlines the role of such temporarily dried wetlands for waterfowl. A similar role of harvested fields for wintering waterfowl has been shown in the Mississippi Alluvial Valley (e.g. rice fields in Stafford et al., 2006) and in the Central Valley of California. In the latter, waterfowl benefited from agriculture (waste rice) but also had a beneficial effect on rice cultivation by accelerating straw decomposition (Bird et al., 2000). Given that corn is harvested later in the season than other cereals in Dombes, and that corn seeds presumably have higher detectability and nutritional value (McNab and Shannon, 1974) than other cereals, we expected that cultivation types would further explain differences in winter swan usage on dried and cultivated fishponds. This however was not recorded. A rapid depletion of waste grains could explain the lack of such an effect. Furthermore, dried but non-cultivated fishponds may also grow a natural terrestrial vegetation which can produce non-negligible amounts of seeds available to birds once reflooded. Elphick (2000) even demonstrated that some non-cultivated sites (semi-natural habitats) were able to produce more seeds than crop remains in rice fields.

On the other hand, swan dependence on large sites demonstrates that usage does not only depend on drought history alone (i.e., management/agricultural practices), since large use values are also recorded on sites that remain flooded, if large enough, especially during summer. Such large sites may be necessary to host large moulting swan concentrations (e.g. in June). During the summer period (i.e. aquatic plant growth period), the vegetation and resources available in fishponds (in terms of quantity and quality) may play an additional role. Waterfowl abundance is indeed generally associated with high development of macrophyte beds in lakes (Mitchell and Perrow, 1998) and this resource should also affect waterfowl stay. In future studies, consideration of aquatic plant resource availability should help improve our understanding of waterfowl stay on fishponds, in addition to the parameters considered here. Finally the positive influence of the proximity index at a short distance (250 m) indicates a positive relationship between swan usage and the existence of a dense fishpond network. Such dense fishpond areas may be preferentially selected by swans because they provide an adjacent refuge alternative in case of disturbance or food depletion at the formerly selected fishpond.

4.3. Implications for wetland management and waterfowl populations

It is remarkable that the factors previously observed to drive swan presence on a fishpond (e.g. area or fishpond management, see Gayet et al., 2011c) were also those affecting swan use over the longer term here. This suggests that the effects of such factors are consistent enough not only to attract swans to a given site temporarily, but also to benefit the birds over extended periods. The latter is what wetland conservation managers are interested in, as those environmental conditions at sites repeatedly used by birds over the longer periods are more likely to later affect population dynamics. The similarity of results between this study of swan usage based on repeated surveys combined with a previous study of swan presence on fishponds (Gayet et al., 2011c) indicates that regular (but intermittent) sampling of bird numbers may provide managers with a reliable proxy of long term habitat use by mute swans. This type of intermittent sampling is easier and cheaper to conduct than more regular and frequent monitoring over extended periods as carried out in the present study.

Present conclusions however also apply to the wintering and breeding species of migratory waterfowl (especially herbivores) in the study area. Our results confirm the influence of some habitat features on the extent of usage of the waterbody by waterfowl (see Brown and Dinsmore, 1986; Paracuellos and Telleria, 2004). Depending on the biological stage of both the waterfowl and the freshwater habitats, some covariates such as fishpond spatial configuration and food resource do play an additive role on waterfowl stay. As a consequence, some fishponds of specifically high value to swans were repeatedly used over successive seasons. Swans may exert high grazing pressure on the food resources of such fishponds, and flocking was indeed observed over successive seasons on the same fishponds. Indirect consequences of extended swan usage (e.g. resource depletion, nutrient loading or transmission of disease) would also be likely to accumulate during the year on such repeatedly used waterbody.

In such disturbed and artificial environments, appropriate summer habitat management, sometimes including some sort of agricultural use, should be regarded as an opportunity to promote carrying capacity for wintering waterfowl through increased food availability. In such heterogeneous wetlands, habitat management dedicated to waterbirds should be focused to areas with an abundance and variety of waterbody, especially larger-sized waterbody clustered together. All fishponds in a network should not be flooded or dried the same year in order to enhance habitat suitability for wintering waterfowl. Since fishpond drought may lead to the aggregation of foragers in specific waterbody to consume crop remains, this may benefit the general fishpond ecosystems by decreasing the average waterfowl pressure on natural food resources.

The preferential use of previously dried fishponds by swans has a range of potential consequences. Swan consumption of waste grains may reduce the availability of a resource shared with fishes, which is bred by landowners, or shared with other waterfowl species. Despite wintering site fidelity over the long term, regular emptying and reflooding may lead swans to regularly switch between fishponds between years, thus preventing extended uses on the same preferred sites. The preference of swans for previously dried fishponds may therefore limit more intensive winter use of natural plants on previously flooded sites. This would be especially beneficial to plants at a dormant stage in winter, which are then less resistant to consumption by herbivores (Boege and Marquis, 2005). Summer-dried fishponds in the Dombes fishpond region should therefore play a similar role to that of sacrificed crops in some areas, which are used to deter swans from damaging other fields. In the same way, Gauthier et al. (2005) suggested that such use of arable lands by Snow Geese (*Anser caerulescens* L.) in Canada may prevent overgrazing of natural marshes. Even if temporary summer drainage may benefit waterbirds over the short term, it should be kept in mind that intensification of agricultural practices in wetlands at a large scale can on the contrary be quite detrimental to them (Duncan et al., 1999). Further work is required on the consequences of such practices on aquatic communities.

4.4. Conclusion

This study provides new knowledge for conservation managers. Habitat properties that drive annual use of man-made wetlands by waterfowl are clearly identified. They may hold for both resident and migratory species. In the perspective of creating valuable habitats for waterfowl, conservation managers can also consider these factors during the implementation of management strategies. In the context of waterfowl populations potentially having detrimental effects onto natural ecosystems and socio–economical activities, managers can consider these factors to locate and measure the likely consequences of the targeted wildfowl species. This knowledge should also allow considering the option of controlling concentrated and intensive use of selected sacrificed waterbody. Contrary to common belief, we demonstrated that extended use of some sites by waterbirds is not restricted to winter or summer, when birds are more gregarious, but can conversely occur throughout the year. This should generate very different consequences on the ecosystem functioning depending on the phenology of aquatic communities which interact with waterfowl.

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