Biodivers Conserv (2007) 16:3633–3651
DOI 10.1007/s10531-007-9160-z

ORIGINAL PAPER

Ecotourism disturbance to wildfowl in protected areas: historical, empirical and experimental approaches in the Camargue, Southern France

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Received: 29 September 2006 / Accepted: 30 January 2007 / Published online: 7 March 2007

Abstract Ecotourism is becoming very popular, especially in protected areas where wildlife concentrate and is easier to observe, but the consequences of associated disturbance have seldom be quantified other than in the short-term, making the sustainability of this activity untested. We combined a historical, an empirical and an experimental approach to assess the long-, medium- and short-term consequences of disturbance to wintering wildfowl (*Anatidae*) in a wetland of international importance in the Camargue, Southern France. In the short-term, disturbance made teal (*Anas crecca*) move away temporarily from observation blinds without leaving the waterbody. Wildfowl fed more after disturbance, disrupting their normal resting activities. In the medium-term, waterbodies with more tourists did not host fewer birds: conversely the most heavily disturbed one hosted the highest wildfowl density. In the long term, wildfowl numbers were not related with the number of visitors. When practiced with appropriate guiding of people, and where appropriate facilities are provided to limit human disturbance as done here, ecotourism may not affect wintering wildfowl other than reversibly in the very short term. The legitimate demand of the public for access, even in fragile protected areas, may therefore be sustainable under some conditions.

Keywords *Anas crecca* · *Anatidae* · Camargue · Ecotourism · Human disturbance · Protected areas · Sustainability · Teal · Wildfowl · Winter

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Introduction

Though its impact on long-term wildlife population dynamics is often difficult to establish (e.g. Cayford 1993; Béchet et al. 2004), recreational human disturbance is well-known for its immediate influence on animal behaviour and distribution (e.g. Boyle and Samson 1985; Davidson and Rothwell 1993; Triplet et al. 2003; Blanc et al. 2006). Among these activities, leisure hunting has early been identified as a major source of disturbance (e.g. Madsen and Fox 1995; Harradine 1998; Madsen 1998a; Tamisier et al. 2003). To counterbalance the negative effects of hunting disturbance, hunting-free refuges or reserves have been set-up in most countries, whose benefits have been clearly illustrated by massive redistributions of individuals from hunted to these non-hunted areas (e.g. Owen and Williams 1976; Guillemain et al. 2002; Mathevet and Tamisier 2002). Elegant experimental work by Madsen (1998b) demonstrated that hunting ban by itself could be sufficient to induce displacement of waterbirds, a result that was not confounded by potential improvement in the carrying capacity of sites linked with reserve management as in earlier studies.

Because they host large concentrations of wildlife, protected areas are also very attractive to ecotourists, which themselves can become a source of disturbance within reserves (Blanc et al. 2006). For the manager, a trade-off between the protection of wildlife and the demand of the public therefore arises (e.g. Dahlgren and Korschgen 1992; Johns 1996). Because reserves are often located on public land, because visits can be a non-negligible source of income and because they can also be the basis for public environmental education, ecotourism in protected areas is generally considered as a legitimate activity, but requires adequate policy and/or management. So far, the incidence of ecotourism disturbance in protected areas has mostly been considered in the short-term, through the immediate disruption of behaviour or escape flights of animals (relatively short-term ‘‘effects’’ of disturbance, as opposed to longer-term ‘‘impacts’’, Robinson and Pollitt 2002; see also e.g. Klein 1993; Burger and Gochfeld 1998; Mathers et al. 2000). The duration of the effect of disturbance, in terms of time taken by the animals to come back to their initial behaviour, has received less attention (see however Lott and McCoy 1995), and the longer-term incidence of ecotourism on habitat use by animals within a reserve has seldom been analysed (Gill et al. 2001). Proposed management measures to mitigate disturbance are often the creation of buffer zones between people and wildlife, the building of designated paths, fences or observation hides, and the limitation of visitor numbers (e.g. Klein 1993; Carney and Sydeman 1999; Finney et al. 2005). Most reserves have such infrastructures or guide small groups of tourists during visits, assuming that this allows preventing completely or at least limiting potential impact on wildlife. However, the consequences of ecotourism under these conditions has seldom been tested (with the exception of Ikuta and Blumstein (2003) concerning the efficiency of fenced areas to protect wildlife), while most protected areas propose visits for schools or to the broader public for the reasons outlined above.

The aim of the present study was to combine historical, empirical and experimental approaches to determine if the use of hidden paths and blinds to observe the birds, combined with a limitation of tourist numbers and a strict guiding of people are indeed appropriate measures allowing the development of ecotourism within a protected area while still providing suitable quiet wintering conditions to waterbirds, namely Anatidae (dabbling ducks *Anas* spp. and greylag goose *Anser anser*). Ducks and geese are quarry species in many countries (e.g. Mooij 2005, for the European Union), and are known to react strongly to the creation of reserves (e.g. Owen and Williams 1976; Guillemain et al. 2002; Mathevet and Tamisier 2002). These large concentrations of wildfowl are then very popular with the public.

The study was conducted at the Marais du Vigueirat in the Camargue, Southern France. The Camargue is the most important wintering area for wildfowl in France, being of international importance for many species (i.e. in January 2005, for all six dabbling ducks (*Anas* spp.) that winter in western Europe except Pintail *Anas acuta*, Deceuninck et al. 2006). The Marais du Vigueirat are one of the most important Camargue day-roosts for wildfowl, especially dabbling ducks. They gradually became protected from hunting, and free public visits got banned in most of their area over the last 20 years (Mathevet and Tamisier 2002), while guided tours in observation hides and paths hidden to the birds through adequate management (tree hedges) and infrastructures (observation blinds) were developed instead.

Combining 15 years of duck counts at three distinct waterbodies of the site and censuses of the number of tourists at each of these over 10 years, the first aim of this study was, through a historical long-term approach, to determine if any sign of potential limitation of duck numbers could be attributable to the development of ecotourism at the scale of the site and, more precisely, if waterbodies visited more often over a long period were eventually hosting fewer birds than more quiet ones.

The second objective was to rely on traditional empirical methods to determine the effect of tourist visits on the average spatial distribution, numbers and behaviour of wildfowl at three waterbodies with contrasted average frequency of visitor disturbance over a wintering season, on days without such visits, trying to determine if ecotourists have lasting effects in the medium-term.

The third objective, combining real guided visits and experimental disturbance, was to determine the short-term effect of ecotourism on wildfowl distribution and behaviour at the most heavily disturbed waterbody of the site, trying to determine how long it takes for birds to come back to their initial distribution and activities after having been disturbed, if such disturbance arose with guided tours in observation blinds.

Methods

Study sites

The Marais du Vigueirat are a 1,000 ha estate gradually bought since 1982 from private landowners by the Conservatoire de l'Espace Littoral et des Rivages Lacustres, the French national body in charge of pre-empting coastline to prevent its urbanisation and ensure its protection in the long-term (Mathevet and Tamisier 2002). The Marais du Vigueirat are located in Arles in the Camargue, Southern France (43°40'N 04°38'E). The Camargue is the most important wetland for wintering Anatidae in France (see above), and within the Camargue the Marais du Vigueirat is a site of international importance for wintering wildfowl (regularly more than 20,000 wintering individuals; G. Massez personal communication). Because they frequently host more than 10,600 wintering teal *Anas crecca* (the Ramsar threshold for that population, Delany and Scott 2002) on a rather small area, the Marais du Vigueirat are also of international importance for that species alone, and are the most densely used wetland by teal in France. It is however important to note that duck numbers at the Marais du Vigueirat built up at the expense of other traditional Camargue day-roosts (Mathevet and Tamisier 2002). This suggests that birds potentially have the choice between roosts within the Camargue, a prerequisite for studying the potential impact of ecotourism (which would be meaningless if birds had no other option than to rest at the Marais du Vigueirat whatever their level of disturbance). Fourty-five percent of teal wintering in the Camargue spend the daylight hours in unprotected day-roosts (Tamisier and Dehorter 1999). Though 26% of these use one single estate where hunting pressure is relatively low, hunting in itself may therefore not be the major factor affecting teal selection of a day-roost (see also Brochet 2006).

The three main waterbodies of the Marais du Vigueirat were considered in the analyses. These have the same broad characteristics in terms of surrounding vegetation (mostly reedbeds, *Juncus* spp. and *Tamarix* sp.), steepness of the banks (always very low) and depth (generally <1 m in deepest parts), but mostly differ in size (Fangassier 55 ha, Baisse des Oies 15 ha and Rizières 3 ha) and their degree of use by tourist visits: Fangassier is an unvisited sanctuary, Baise des Oies is sometimes visited while Rizières is always used by guided tours (see the results section). Because of these contrasted sizes, only bird numbers per waterbody transformed into density per hectare were used in the analyses.

Wildfowl and tourist censuses—''Historical'' approach

Ducks and geese have been counted monthly by the managers of the reserve during winter (September–January included) at the three sites from September 1989 to January 2005. There were only four missing counts: October and November 1989, November 1991 and December 2003. Species considered in this study were greylag goose, teal, mallard *Anas platyrhynchos*, shoveler *A. clypeata*, gadwall *A. strepera*, pintail and wigeon *A. penelope*. Earlier studies have demonstrated that susceptibility to disturbance, often measured as flight initiation distance, can be a species-specific trait (e.g. Blumstein et al. 2003; Blumstein 2006; Fernández-Juricic et al. 2006). In addition to running the analyses for all wildfowl together (teal included), we therefore also analysed the consequences of disturbance for teal alone, because teal is often considered to be one of the most susceptible wildfowl species to disturbance (e.g. Tuite et al. 1984 for *A. crecca crecca*; Pease et al. 2005 for green-winged teal *A. crecca carolinensis* in North America) and is also the main species for which the area is important internationally. Annual average teal numbers represented 56% of average total wildfowl counts at the three waterbodies over the 1989–2005 period.

The full dataset was first used to determine potential trends in average annual numbers of wildfowl or teal over years at the scale of the Marais du Vigueirat, pooling data from the three sites each month and averaging monthly data per wintering season. During those years when some counts were missing the average over remaining available monthly data was used instead. Count data satisfied the normality criterion (non-significant Kolmogorov–Smirnov tests at $P = 0.05$) and were analysed with polynomial regression due to non-linearity of the trend over years.

We then used an ANOVA to compare average annual bird densities (nb ha^{-1}, which also were normally distributed) between the three sites, once for teal and once for all wildfowl together. Bonferroni-adjusted *t*-tests at $P < 0.05$ were used for post-hoc pairwise comparison when appropriate. This was done using data from September 1991 onwards only, the date at which major management works ceased. After this date the three wetlands looked like they do today, while their appearance may have been slightly different in 1989–1990.

The total annual number of visitors in winter (September–March included) was also computed for the three sites together, and was normally distributed. Potential trend over years was analysed as before, as were correlations between the number of visitors and the number of teal or all wildfowl together. Due to relatively smaller sample sizes than for bird counts, the average annual number of visitors was then compared with Mann–Whitney *U* test between Baisse des Oies and Rizières (there were no visitors in Fangassier).

Distribution and behaviour of the birds—empirical approach

The distribution and behaviour of the birds on days without disturbance was studied 1 day per week (only weekdays, Saturdays and Sundays were never considered) at each waterbody using scan sampling (Altmann 1974) from week 11–15 October 2004 to week 7–11 March 2005, except when meteorological conditions (heavy wind, or cold conditions when waterbodies were taken in ice) made it impossible. As opposed to sites open to the public with free access, where the number of people is generally greatest on Saturdays and Sundays (e.g. Evans and Warrington 1997), the number of tourist visits here is relatively similar between weekdays and weekends, often limited to one guided tour per day, sometimes two tours on weekends. In total, data were available for 22 weeks at Baisse des Oies, 19 weeks at Fangassier and 18 weeks at Rizières. Scan samples were taken every hour from 09:00 to 16:00 approximately. During each scan, the behaviour, species and position of each bird on the waterbody was recorded. The position was determined after a set of fixed poles erected at 100 m from the hide (distance measured with a range finder, ca. 10 poles per waterbody) before the beginning of the study. Birds were thus assigned to one of the two possible distance classes: 0–100 m or >100 m. Behaviour was distinguished into five main categories: foraging (whatever the foraging method used, from dabbling to upending), comfort (resting and preening), movement (swimming, walking or flying), vigilance (either immobile or overtly vigilant, with the head raised), plus other less common behaviours (comprising essentially agonistic behaviours and sexual displays). Pooling data from all individuals of a scan sample also provided the total number of birds at each waterbody. Because total count data were normally distributed after non-significant Kolmogorov–Smirnov tests, we used ANOVAs to compare average densities of teal and all wildfowl between waterbodies. Replicates were weekly averages, that is we averaged data from all scan samples of each weekly disturbance-free study day per site to avoid pseudoreplication.

We then compared the proportion of birds >100 m between sites to determine if they were more regularly further away at some waterbodies. The proportions of birds engaged in each of the four main behaviour categories (Foraging, Comfort, Movement and Vigilance) were then compared between waterbodies. In both cases (analyses of distribution and of behaviour), analyses were performed first for teal alone, then for all wildfowl together. Here too data were averaged per study day to avoid pseudoreplication. Proportions were not normally distributed and an arcsin-transformation (Sokal and Rohlf 1995) did not solve the problem, so proportions were analysed using non-parametric Krukal–Wallis analysis of variance to perform comparisons between waterbodies, followed by Mann–Whitney pairwise comparisons where appropriate. Percentages are used in the text, tables and figures to ease reading.

Confounding factors

Studies of disturbance often suffer from not considering potentially confounding factors that may affect subject animals' behaviour and distribution (Gill and Sutherland 2000; Gill et al. 2001). We here considered two main confounding factors: food availability and predation risk.

Winter food of teal and mallard, the other most abundant wintering dabbling duck at the Marais du Vigueirat, mostly consist of seeds of natural plants (this is also the case, though to a lower extent, for other dabbling duck species; Green et al. 2002). We therefore sampled seeds at each of the three waterbodies, with 10 replicates per class of distance (0–50 m, 50–100 m, >100 m), once at the beginning (November 2004) and once at the end of the season (February 2005). Two replicates from Fangassier could not be analysed properly, reducing sample size to 58 there. Each replicate was a core of sediment 10 cm long, 7.2 cm in diameter. Samples were sieved (mesh size 0.3 mm, the minimum inter-lamellae distance in a dabbling duck bill, i.e. the smallest size of particles a dabbling duck can retain when filtering the sediment for food, Thomas 1982) and hand-sorted in the laboratory under a binocular microscope. Seeds were then counted per species and the total dry weight per replicate for each species was determined after a reference table (Arzel et al. in press). We compared the average biomass densities of seeds (g dry weight m^{-2}) between the two sampling occasions per site with Student's *t* tests, then used ANOVAs to compare average biomass densities between the three waterbodies. Biomass densities were Log-transformed prior to these analyses, which allowed meeting the normality criterion (non-significant Kolmogorov–Smirnov tests).

Diurnal predation risk was measured as the frequency of fly-overs by raptors, mostly Marsh Harrier *Circus aeruginosus*. Each study day the occurrence of any of such predators was continuously recorded, from morning to evening (see also Fritz et al. 2000). This was measured on all days (i.e. with or without human disturbance) to increase sample size, considering that since both human visits and raptor patrols were discrete and short-termed events, human disturbance should not affect the average daily frequency of fly-overs significantly. In total, sample sizes (i.e. number of daily frequencies) were 42 at Rizières, 26 at Fangassier and 31 at Baisse des Oies. Average frequencies were compared between sites with ANOVAs and post-hoc tests when appropriate, again after Log-transformation, which normalized the data (non-significant Kolmogorov–Smirnov tests).

Short-term effects of tourist visits—empirical and experimental approaches

The aim of this last part of the study was to determine, on days with tourist visits, the immediate effect of these on the total number, behaviour and distribution of the birds, and whether these potential effects lasted for some time. This short-term analysis was conducted at Rizières, the most regularly disturbed of the three sites. In order to do so, on days with disturbance the frequency of scan sampling was increased to one every 15 min during 2 h after the visit, which lasted 10 min approximately. All visits at this hide were guided by a member of the reserve staff, and arrangements were taken so that visits were generally around 11:00. One shortcoming of many field studies of disturbance is that the observer relies on incidental disturbance events, i.e. these cannot be manipulated (Cayford 1993). This was the case in our study, where there were only 16 study days with visits at Rizières over the winter. We therefore relied on an experimental approach in addition to real tourist visits to increase sample size. On 7 days with no tourist visits at Rizières (never more than 1 day per week), we played a cassette where the background noise of a group of people in a closed room was recorded. We adjusted the sound level so that is was similar to the ear to the average noise made by a tourist visit, and played the cassette for exactly 10 min, the cassette player being in the hide and facing the waterbody through an opened window, therefore apparently similar conditions to a real visit. Only the noise made by people was simulated, since real tourist visits were in hides, therefore probably hardly visible to the birds. We first compared the effects (in terms of bird numbers, behaviour and distribution, as described above) of cassette plays and visits to ensure the former simulated the latter adequately and, since no significant difference but one was observed (see the results section), then pooled the two under a ''disturbed day'' heading and compared the data with those from days without disturbance.

To measure the immediate effect of visits, we compared the average proportion of teal and all wildfowl engaged in each of the four main behaviour categories (Foraging, Comfort, Movement, Vigilance) as well as average bird numbers and distribution (i.e. proportion of individuals >100 m) during the scan samples 15 min after visits or cassette play and the 11:00 scan samples of days without visits.

To measure the time taken by birds to come back to their initial distribution and behaviour, we then compared the average numbers, behaviour and distribution of birds over all scans within 1 h after visits or cassette play with the average of 11:00 and 12:00 scan samples of days without visits (that is data from the two scan samples of each disturbance-free day were averaged, these average daily values then constituting the replicates for the tests). The same was then done for 2 h after visits or cassette play and 11:00, 12:00 and 13:00 scan samples of days without visits.

Total teal or all wildfowl numbers did not follow a normal distribution at this time scale for this site, nor did the proportion of individuals in the two classes of distance or behaviour (Kolmogorov–Smirnov tests, all $P < 0.05$). The effect of the visits (real guided one or simulated) on bird numbers, distribution and behaviour was thus analysed using Mann–Whitney pairwise comparisons. Percentages are used in the text, tables and figures to ease reading.

Results

Wildfowl and tourist counts

Changes in both teal numbers and the total number of wildfowl at the three waterbodies across time were well fitted by type II polynomial regressions: numbers

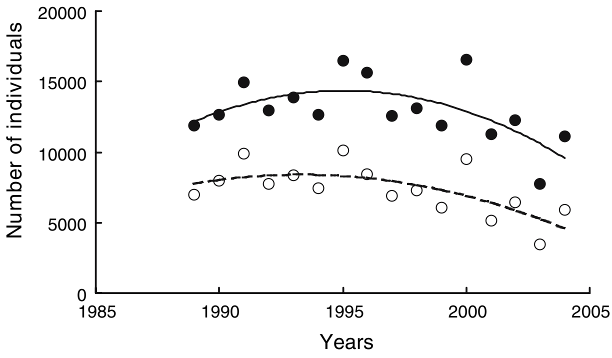

Fig. 1 Changes in teal (white circles, dotted curve) and all wildfowl (black dots and black curve) total numbers across years at the three waterbodies (years refer to the beginning of each wintering season, i.e. 1989 is for winter 1989–90). Equations of regressions are $Y = -33.49X^2 + 356.65X + 7449$ and $Y = -59.77X^2 + 842.56X + 11394$ for teal and for all wildfowl, respectively)

increased slightly from the beginning of the counts until the middle of the 1990s, and decreased since then ($r^2 = 0.47$, df = 13, $P = 0.0166$ and $r^2 = 0.42$, df = 13, $P = 0.0299$ for teal and for all wildfowl, respectively; Fig. 1). The average density of teal did not differ significantly between the three waterbodies ($F_{2,39} = 3.22$, $P < 0.0506$), due to large variances, though Rizières tended to have a slightly higher number of teal per hectare than the two others (Fig. 2). When all wildfowl were considered together, the density of birds per hectare differed between the three waterbodies ($F_{2,39} = 9.93$, $P = 0.0003$; Fig. 2), and Bonferroni-adjusted *t*-tests showed that it was significantly higher at Rizières than at Baisse des Oies or Fangassier.

Like bird numbers, changes in the average annual number of winter tourists over years since 1995 were well fitted by a type II polynomial regression ($r^2 = 0.81$, df = 7, $P = 0.0029$; Fig. 3). This time the maximum numbers were recorded around year 2000. As a consequence, neither the average annual number of teal nor the average number of all wildfowl together were significantly correlated with the average number of visitors (Spearman rank correlations: $r_s = -0.55$ and $r_s = -0.43$, respectively, both P values >0.05). The mean number of visitors per winter at Rizières was

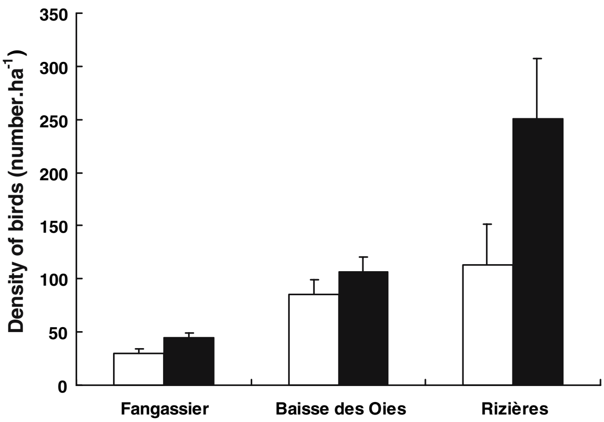

Fig. 2 Average densities of teal (white columns) and all wildfowl (black columns) at the three waterbodies between winter 1991–92 and winter 2004–05. Vertical bars show standard errors, in all cases the number of data is $n = 14$. See text for statistics

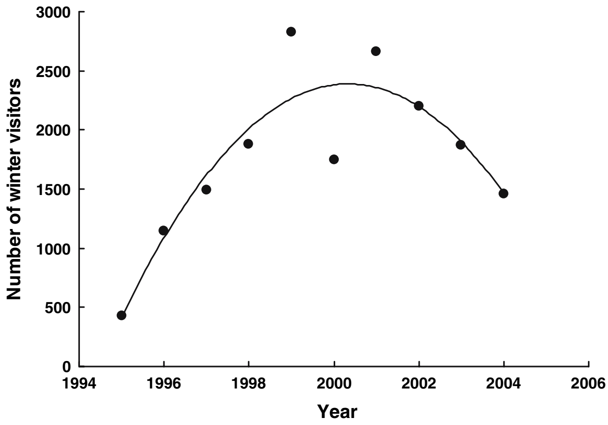

Fig. 3 Changes in the average annual number of winter visitors at Marais du Vigueirat from 1995–96 to 2004–05. Equation for the regression is $Y = -69.12X^2 + 876.17X - 387.52$

1748.2 (± 224.6 SE, n = 10), which was significantly higher than the number at Baisse des Oies (866.6 ± 96.4 SE, n = 10, Mann–Whitney: Z = –2.87, P = 0.0041). Fangassier is a sanctuary that is never visited.

Confounding factors

The average biomass density of seeds did not differ between the two sampling occasions at any of the three waterbodies (t tests: all t absolute values <1.43, all $P > 0.16$). When data from the two sampling occasions were thus pooled, no significant difference could be detected between mean seed biomass densities of the three waterbodies ($F_{2,175} = 0.41$, $P = 0.6641$). On average at the three study sites seed biomass density was 4.97 ± 0.34 g dry weight m^{-2} SE (n = 178). It is true that the power of the test was low (0.1164), so it is likely that potential differences remained undetected due to large variance. However, average seed biomass densities were 4.21, 5.90 and 4.82 g dry weight m^{-2} at Baisse des Oies, Fangassier and Rizières, respectively. Potential differences between sites, if they existed, were thus of limited magnitude and, further, the most heavily disturbed site (Rizières) had an intermediate seed biomass density between the two other waterbodies. It is therefore unlikely that food availability confounded any potential effect of human disturbance on bird behaviour and distribution.

Conversely, the average frequency of fly-overs by raptors was markedly different between the three ponds ($F_{2,96} = 19.03$, $P < 0.0001$), Bonferroni-adjusted post-hoc t-tests indicating that all pairwise comparisons were significant ($P < 0.05$): raptor fly-overs were less frequent at Rizières than at Baisse des Oies, and less so at Baisse des Oies than at Fangassier (Fig. 4).

Average distribution and behaviour throughout a winter

Like for historical data above, Rizières hosted a higher average density of all wildfowl together than Baisse des Oies and Fangassier during winter 2004–05, and there were no significant differences for average densities of teal alone (Table 1). Data for 2004–05 were therefore similar to those over the last 15 years.

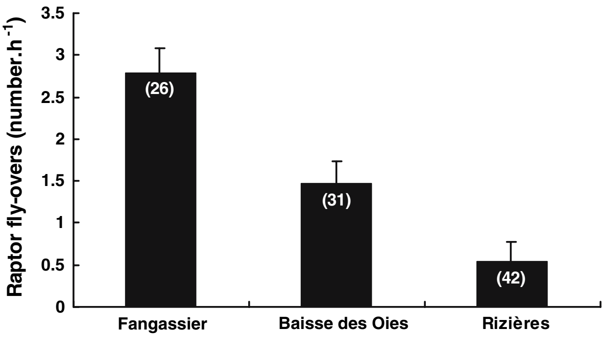

Fig. 4 Average frequency of fly-overs by raptors at the three waterbodies from October 2004 to March 2005. Vertical bars show standard errors, numbers in brackets are sample sizes. All three average values differ significantly from each other (see text)

Table 1 Average densities of teal alone or all wildfowl together at the three waterbodies during winter 2004–05

Fangassier	Baisse des Oies	Rizières	ANOVA	
(n = 19)	(n = 22)	(n = 18)	F	P value
Teal density (number ha^{-1})				
12.7 ± 3.1	8.9 ± 2.8	13.2 ± 3.1	0.66	0.5227
Density of all wildfowl (number ha^{-1})				
17.9 ± 5.8 A	18.9 ± 5.4 A	46.5 ± 6.0 B	7.72	0.0011

Values are means ± SE, values with different letters differed significantly after Bonferroni-adjusted post-hoc t-tests

Teal did not make the same use of the area at the three waterbodies, as illustrated by the significant difference in the relative use of the area further than 100 m away from the hide (Kruskal–Wallis: $H_{2,57} = 14.56$, $P < 0.0001$): Fangassier: 97.07 ± 4.16% SE, n = 19; Baisse des Oies: 94.66 ± 3.87% SE, n = 22, Rizières: 62.59 ± 4.53% SE, n = 16. Pairwise comparisons showed that the relative use of the area >100 m away from the hide did not differ between Fangassier and Baisse des Oies (Mann–Whitney: Z = –0.10, P = 0.9167), but was higher at these sites than at Rizières (both Z values >3.25, both P < 0.0012). Birds therefore relied more on the areas closer to the hide at Rizières than at the two other sites. However, given the differences in size between the three waterbodies, the zone >100 m does not always represent the same percentage of the total area: it actually represented 46.2% of total pond area at Rizières, 89.6% at Baisse des Oies and 92.8% at Fangassier. Based on the comparison of the relative use by teal compared to the relative area it represented (comparison of a single observation with the mean of a sample, Sokal and Rohlf 1995 p. 228), no significant selective use of the area >100 m could be detected at any of the three waterbodies (all t absolute values < 0.87, all P > 0.05). Birds therefore apparently distributed according to relative available area, i.e. did not avoid areas closer to the observation blinds.

For all wildfowl together too the relative use of the area >100 m from the hides differed between the three waterbodies (Kruskal–Wallis: $H_{2,59} = 30.19$, $P < 0.0001$). Pairwise comparisons showed that the proportion of birds >100 m did not differ significantly between Fangassier and Baisse des Oies (97.54 ± 3.04% SE, n = 19 and 97.38 ± 2.82% SE, n = 22, respectively; Mann–Whitney: Z = 0.80, P = 0.4252),

Table 2 Average percentage of time (± SE) spent in the four main behaviour categories by teal or all wildfowl together during winter 2004–05

	Fangassier	Baisse des Oies	Rizières	Kruskal–Wallis	
				H	*P* value
Teal alone					
	(*n* = 18)	(*n* = 20)	(*n* = 16)		
Foraging	7.2 ± 1.8 B	9.3 ± 3.1 B	40.1 ± 7.6 A	10.91	0.004
Comfort	49.9 ± 6.0 A	37.6 ± 4.4 A	21.8 ± 5.9 B	10.97	0.004
Movement	33.9 ± 5.6	38.1 ± 4.9	23.0 ± 5.4	5.72	0.057
Vigilance	8.6 ± 2.3	13.8 ± 5.2	14.5 ± 7.6	2.24	0.325
All wildfowl					
	(*n* = 19)	(*n* = 22)	(*n* = 18)		
Foraging	16.5 ± 2.3 B	17.8 ± 2.2 B	34.6 ± 5.6 A	10.03	0.006
Comfort	50.0 ± 4.1	42.8 ± 2.1	44.8 ± 5.7	4.03	0.133
Movement	26.0 ± 3.0 A	30.6 ± 1.8 A	13.9 ± 2.7 B	17.76	<0.001
Vigilance	7.2 ± 1.8	7.9 ± 1.7	6.4 ± 1.6	1.20	0.547

Results of Kruskal–Wallis analyses of variance are indicated. Values with different letters differed significantly ($P < 0.05$) after Mann–Whitney tests. Numbers in brackets are sample sizes

while values from these two sites were both higher than at Rizières (55.51 ± 3.12% SE, $n = 18$, both $Z > 4.66$, both $P < 0.0001$). However, as above based on the comparison of the relative use by wildfowl compared to the relative area it represented, no significant selective use of the area >100 m could be detected at any of the three waterbodies for all wildfowl together (all t absolute values <1.62, all $P > 0.05$). Wildfowl therefore simply distributed according to available area, not to the position of observation blinds.

Statistics concerning the average time-budget of either teal alone or all wildfowl together are presented in Table 2. In both cases birds spent significantly more time foraging at Rizières than at the other sites, at the expense of comfort activities for teal and at the expense of movement behaviours for all wildfowl together. The average proportion of time spent vigilant did not differ significantly between waterbodies in either teal or all wildfowl.

Short-term effects of tourism disturbance

At Rizières, days with no disturbance, with a guided visit and with the cassette recording being played were first compared with regards to the total number of individuals, the proportion of individuals >100 m from the hide and the proportion of time spent foraging, in comfort, in movement or vigilant, in teal alone then for all wildfowl together, either 15 min, 1 h or 2 h after the disturbance event (or comparable periods of the day on days without disturbance). There were no significant difference ($P > 0.05$) between the three types of days for any of the measured variables or, if some difference was observed, post-hoc pairwise tests did not reveal that data after visits differed significantly from data after playing of the cassette. Data from days with visit and days with a cassette play were therefore pooled under the general ''disturbed day'' heading below to ease the analysis of the effects of disturbance in general.

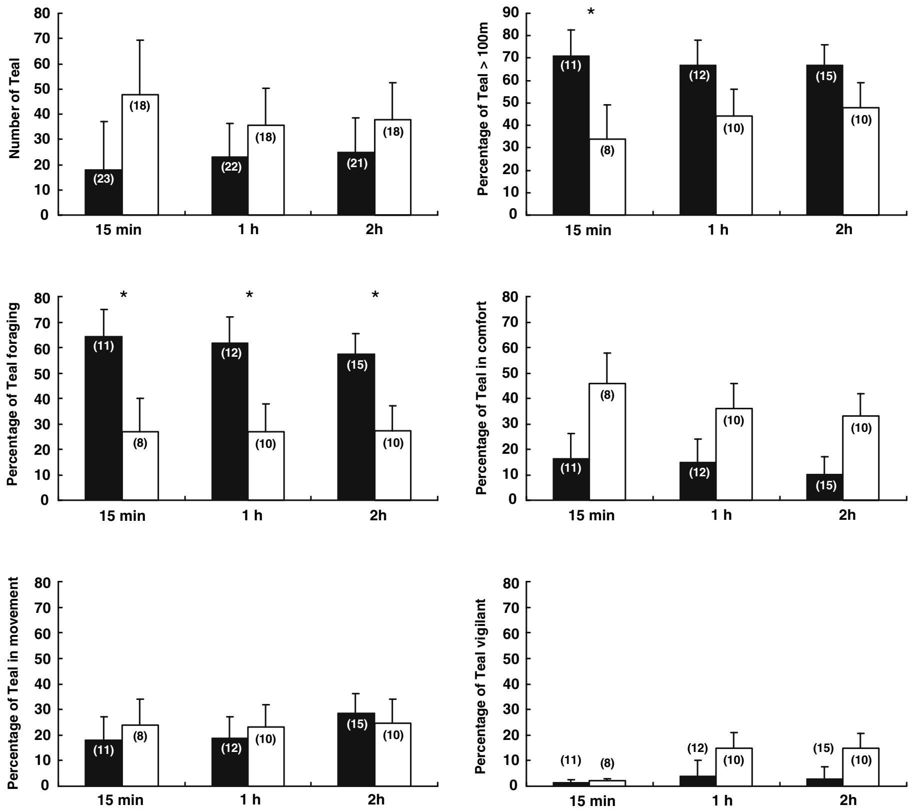

Fig. 5 Average numbers, distribution and behaviour of teal at Rizières on days with (black) and without (white) disturbance. Vertical bars show standard errors, numbers in brackets are sample sizes. Stars represent statistically significant differences after Mann–Whitney tests

For teal alone, there was no significant difference between the number of birds on the waterbody on days with or without disturbance, either 15 min after disturbance or during the following 1 or 2 h. About 15 min after disturbance, there were more individuals >100 m and birds fed more (Fig. 5). When the periods of 1 h or 2 h after the disturbance event were considered instead, the difference in distribution was no longer significant, but teal still fed more on disturbed than on undisturbed days (Fig. 5).

For all wildfowl together, disturbance did not cause a change in total number of birds present or their distribution over the waterbody, neither at 15 min nor during the 1 or 2 h after disturbance, though at 15 min the proportion of birds >100 m was almost significantly higher on days with disturbance ($Z = 1.88$, $P = 0.0603$). Large variance was probably the reason why no significant difference could be detected between days with and without disturbance concerning total bird numbers. Concerning behaviour, birds fed more (though for 1 h the difference was marginally significant: $P = 0.0851$), spent less time in comfort and more time in movement (except for movement at 15 min: $Z = 1.30$, $P = 0.1973$) on days with disturbance than on days without (Fig. 6).

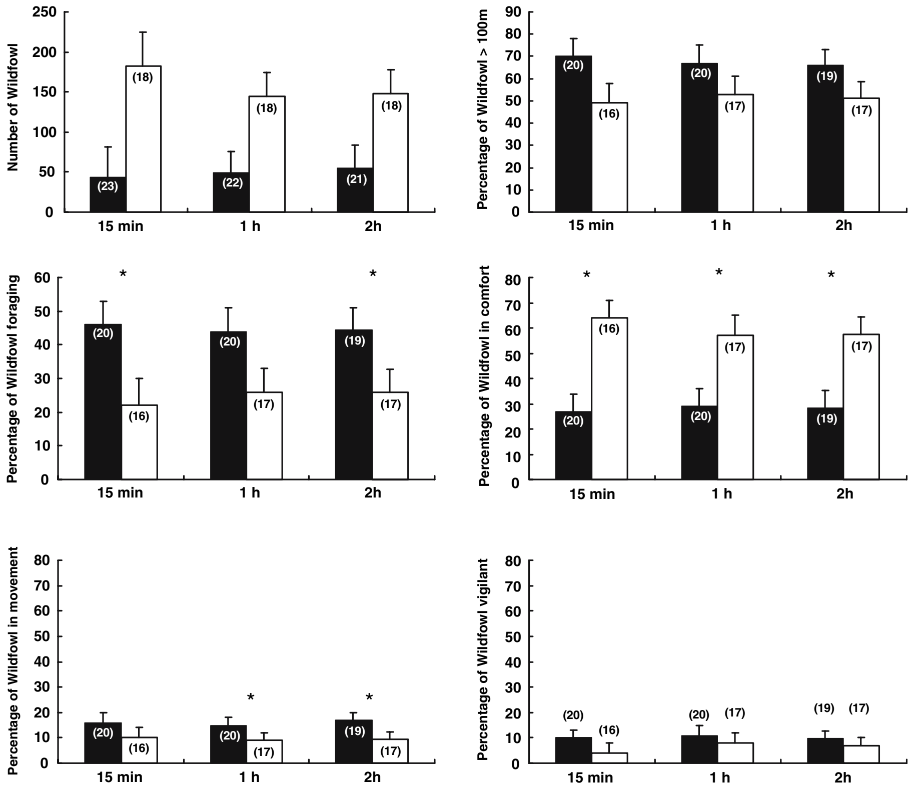

Fig. 6 Average numbers, distribution and behaviour of all wildfowl together at Rizières on days with (black) and without (white) disturbance. Vertical bars show standard errors, numbers in brackets are sample sizes. Stars represent statistically significant differences after Mann–Whitney tests

Discussion

Short-term effects of disturbance: distribution and behaviour of birds after tourist visits

When disturbance occurred, be it real visits or experimental cassette display, teal reacted initially by moving away from the hide for 15 min, then came back to their initial distribution within 1 h, while no birds left the waterbody. This highlights the fact that these ducks probably got accustomed to disturbance to some extent, or that the cost of moving elsewhere was too high. A similar pattern was recorded for all wildfowl species together, though the difference in distribution between days with or without disturbance at 15 min was just above the significance threshold. It is interesting to note that teal reacted more than other wildfowl, as observed in other studies (e.g. Tuite et al. 1984; Pease et al. 2005). These results also support the idea that though the level of susceptibility to disturbance may strongly differ even between closely-related species (Burger and Gochfeld 1998; Rodgers and Schwikert 2002 for waterbirds; Fernández-Juricic et al. 2001 for urban birds), local conditions determine which species of a community are the more likely to react to disturbance (e.g. classification of waterbird species the most affected by disturbance in Platteeuw and Henkens 1997 as opposed to that in Tuite et al. 1984). In both teal and all wildfowl, a clear effect of disturbance was observed on time-budget, that lasted for a few hours at least: after a disturbance event birds fed more than during corresponding periods of the day when free from disturbance, mostly at the expense of comfort activities (though the difference did not reach the significance threshold in teal alone). The reason why it is feeding activities (rather than vigilance) that increased in the time-budget of disturbed birds is unclear: in many cases an opposite trend of decreased feeding time is recorded following disturbance (Owens 1977; Lott and McCoy 1995; Burger and Gochfeld 1998; White et al. 1999; Duchesne et al. 2000). However, these studies were mainly dealing with animals that were initially foraging before being disturbed, i.e. their main activity was disrupted, as were the comfort activities of our ducks and geese. Disturbance therefore clearly affected, potentially negatively, the behaviour of the birds at our study site. It cannot be excluded that teal and other wildfowl at Marais du Vigueirat increased feeding time after disturbance in order to try to compensate for energy loss related with involuntary movement, just like Mute Swans *Cygnus olor* do as described by Madsen (1998a). However, this would only hold if ducks and geese were able to maintain feeding efficiency after being disturbed, which remains to be proved and would need further work.

To conclude about short-term effects of disturbance, it is clear that ecotourists do have an effect on wildfowl behaviour, and for some species also on their local short-term distribution, even if at our study sites visitors are briefed and guided, and remain in designated facilities. Ducks and geese therefore apparently did not fully habituate to human disturbance at Marais du Vigueirat, even at the most frequently disturbed of the reserve waterbodies.

Medium-term effects of disturbance: distribution and behaviour throughout a winter

The average density of wintering teal alone did not differ between the three waterbodies, while for all species together Rizières hosted the highest density of birds. It is remarkable that Rizières is also the lake with the highest frequency of tourist visits: in the medium term, tourist visits as practiced in Marais du Vigueirat therefore do not seem to prevent the use of wetlands by ducks and geese. Within waterbodies, the distribution of birds was not skewed towards the most distant areas from the hides neither but, conversely, birds appeared to be regularly distributed over the two classes of distances. It is to our knowledge the first time these patterns of distribution (lack of differences between lakes with contrasted disturbance regimes and within lakes in relation to distance from the disturbance source) are demonstrated: on the contrary, abandonment of disturbed wetlands by waterbirds (Evans and Warrington 1997; Madsen 1998b; Marsden 2000; Evans and Day 2002) and more generally under-use by wildlife of areas closer to human activities (Owens 1977; Madsen 1985; Keller 1991; Klein et al. 1995; Gill 1996; Larsen and Madsen 2000; Evans and Day 2001; Lafferty 2001; Taylor and Knight 2003; Finney et al. 2005) are the most commonly documented situations. It is true that visitors are few even at Rizières (13 people per day on average over the last 5 years), and that tourists there are briefed and guided, and remain in hidden paths and observation blinds, which is likely to reduce disturbance. Tourist disturbance can be much higher and much less regulated at other sites elsewhere, and can therefore potentially have there more serious effects than those described here. As an example for comparison, when testing the effect of varying levels of disturbance on birds flight initiation distances, Webb and Blumstein (2005) used an area where the average instantaneous number of visitors was up to 24 people. However, this was precisely the aim of our work: while most managers suggest that reducing the number of visitors and providing adequate guiding and facilities should be promoted to reduce disturbance, actual disturbance under these conditions had to our knowledge never been tested. Our results suggest that while in the short-term visits may still impact birds distribution and behaviour (see above), such ecotourism policies are indeed a valuable option allowing to prevent medium-term disturbance to wintering wildfowl.

Average time-budgets, on the other hand, differed markedly between the three waterbodies, and surprisingly the main difference was a twice (all wildfowl) or four times (teal alone) higher proportion of time spent foraging at Rizières compared to Baisse des Oies or Fangassier, while Rizières was the most frequently disturbed of the three wetlands on average (time-budgets in this case being recorded on disturbance-free days only). One may consider that this higher tendency to feed at Rizières, at the expense of comfort or movement activities, may therefore be a remnant effect of higher average disturbance (just like foraging is more frequent at Rizières after tourist visits). However, it cannot be excluded that differences in average time-budget are simply reflecting better foraging conditions at Rizières: if this was the case, it is however not through higher food availability, which was observed not to differ between the three study sites. A possible explanation may be linked with the fact that the frequency of disturbance by Marsh Harrier was markedly lower at Rizières, and that this lower predation risk allowed ducks and geese engaging in feeding behaviour more easily, while foraging may globally be a risky activity (especially so for these birds when they forage with the eyes underwater, Guillemain et al. 2001). This hypothesis cannot be properly tested at present, but would be consistent with the marginally significant negative relationship between average daily proportion of time spent foraging by teal and average daily frequency of fly-overs by Marsh Harriers on the 15 days when both could be computed at Rizières (Spearman rank correlation: $r_s = -0.44$, $P = 0.085$). The lower average frequency of fly-overs by raptors at Rizières probably has nothing to do with the frequency of tourists there, but is most likely to be related with the relatively low number of wildfowl present: earlier studies have shown that these raptors patrol less often over waterbodies with fewer ducks and geese (Fritz et al. 2000), as was the case here for Rizières.

Long-term effects of disturbance: wildfowl and tourist counts

Both the annual number of wildfowl (or teal alone) and the average number of tourists visiting the Marais du Vigueirat were well fitted by type II polynomial regressions, but the period of maximum in the curves differed, occurring 5 years earlier for birds than for tourists. The study by Mathevet and Tamisier (2002) demonstrated that the massive increase in wildfowl numbers (especially ducks) at the Marais du Vigueirat during the second half of the 1980's was due to the protection status acquired by the site by that date. Another more recent study showed that trends in teal and all wildfowl at the Marais du Vigueirat were then strongly correlated with numbers of these birds at the scale of the whole Camargue delta (Blanc 2005) during the 1990–2005 period, so that the patterns observed in Vigueirat were linked with more general factors than just the local number of tourist visits, plus potentially other local management or environmental factors (N. Hecker, personal communication). The reason why the number of visitors also decreased in recent years (i.e. mostly since year 2000) is purely artificial, and is linked with new law regulations over the work of nature guides and wardens, that lead the site to be deliberately closed to the public each year in December and January since year 2000.

In the long-term, there was therefore no apparent contradiction between the development of ecotourism as practiced here and the increasing attractivity of the site for wildfowl (though it is impossible to determine the carrying capacity itself and whether the development of the ecotourism activity impacted the rate of increase in wintering bird numbers). However, the effect of ecotourism at Marais du Vigueirat seems to be limited, since contrary to our expectations the most frequently visited waterbody also had the highest (for all wildfowl together) or a similar (for teal) bird density than the other ones.

Conclusion

Short-term negative effects of human disturbance on animals have been described on many occasions for various species and environmental systems (Boyle and Samson 1985; Dahlgren and Korschgen 1992; Cayford 1993; Klein 1993; Tamisier et al. 2003; Triplet et al. 2003; Blanc et al. 2006). However, without neglecting the ethical problem that disruption of wildlife behaviour may represent, it is clear that conservationists should especially be concerned by those disturbances that affect population dynamics in the long term, rather than by those constraining the behaviour of some individuals for only short periods (e.g. Cayford 1993). However, linking a disturbance event with breeding success and survival several months or years later may be challenging, even more so in migrating animals for which these events may occur several thousands of kilometres apart. In addition to modelling, which may be another way out in this domain (e.g. Gill and Sutherland 2000), long-term studies such as the one we partly relied on may help establishing such links, since one may believe that the use of an area whose disturbance conditions directly affect individual survival and breeding success may decrease over time if animals behave optimally and have alternative options, like here in the Camargue where suitable wetlands are numerous.

Combining different methods allowed us considering the consequences of tourist visits within a protected area at different time and spatial scales: though a traditional short-term with/without disturbance analysis would have suggested that ecotourism as practiced in Marais du Vigueirat does have an effect on wildfowl behaviour and distribution, our results show that there are no visible carry-over effects in the medium or long term. Such a test of the consequences of ecotourism in a protected area shows that if some precautions are taken in terms of limiting the number of visits, guiding of people and provision of adequate facilities, then the opening to visitors can be a sustainable activity within nature reserves.

Acknowledgements We would like to thank all those who helped during the collection of data at Marais du Vigueirat, especially Grégoire Massez, Jean-Baptiste Noguès, Mathieu Chambouleyron, Jeanne Marques, Kevin Durque and Patrice Noble. We are grateful to Nathalie Hecker and Jean-Laurent Lucchesi for their support and for their help with historical data, and Dan Blumstein and an anonymous referee for their constructive comments on an earlier version of this manuscript. This study received funding from the Agence de l'Eau Rhône-Méditerranée-Corse.

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