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The importance of protected areas as nocturnal feeding grounds for dabbling ducks wintering in western France

Matthieu Guillemain*, Hervé Fritz, Patrick Duncan

Centre d'Etudes Biologiques de Chizé — CNRS UPR 1934, 79360 Beauvoir-sur-Niort, France

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Abstract

We studied the diurnal and nocturnal habitat use of wintering dabbling ducks (*Anas* spp.) in two protected areas of an internationally important winter quarter in western France. The waterbodies of the reserves are heavily used by ducks during daylight hours, and 3–55% of these birds used the reserves at night: >50% of shoveler (*A. clypeata*), 20% of granivorous ducks (mallard *A. platyrhynchos*, teal *A. crecca* and pintail *A. acuta*), and lower numbers of herbivores (wigeon *A. penelope* and gadwall *A. strepera*). Radio-tracking showed that some ducks used the reserves by day and by night, and that some of them may switch from one protected site to another: radio-tagged birds were located in one of the two protected areas for 76% of the days and 81% of the nights they were sought, with granivores switching from waterbodies to wet grasslands within a reserve between the two periods. Such resident individuals may be 'experienced' wintering ducks, avoiding surrounding unprotected feeding habitats at night, while birds that leave the reserves at night may be subdominants and/or 'naïve' individuals from a transient migratory sub-population. This study suggests that management of nature reserves should combine day-roosts with significant areas of nocturnal feeding grounds, since in protected areas both habitats may be successively used by wintering dabbling ducks across the 24-h cycle.

Keywords: Winter; Dabbling ducks; Nature reserves; Habitat use; Management

1. Introduction

Most wetlands have undergone major changes during the last few decades, despite growing public demand for wildlife conservation and the ratification of the Ramsar convention by many countries. In Europe the principal change has involved habitat loss, especially through drainage for agriculture (e.g. Thomas, 1976; Owen and Thomas, 1979; Poslavski and Shirekov, 1990; Williams, 1990a, 1990b; Handrinos, 1992; Tamisier and Grillas, 1994; Madsen, 1998). These processes have created a new landscape: a matrix of transformed agricultural landscapes enclosing protected, mostly small, areas. Agricultural fields can attract waterbirds when they provide abundant food (Thomas, 1981; Jorde et al., 1983; Van Roomen and Madsen, 1992; Baldassarre and Bolen, 1994), but the main consequences of agricultural development for waterbirds are negative: loss of habitat increases competitive interactions between individuals and mortality rates (e.g. Goss-Custard and West, 1997). Some birds avoid transformed habitats by modifying their migration routes (Dolman and Sutherland, 1995); nonetheless habitat loss in wetlands generally has severe consequences for waterbird populations (e.g. Goss-Custard and Sutherland, 1997; Weller, 1999). In dabbling ducks (Anatidae), major winter quarters have been abandoned, and large scale redistributions of birds have been reported after wetland transformation (e.g. Pirot and Fox, 1990; Poslavski and Shirekov, 1990; Williams, 1990c; Duncan et al., 1999).

The conservation management of wildfowl habitat, especially for *Anas* species, is difficult since most dabbling ducks are intercontinental migrants and use contrasting, spatially distinct habitats by day and by night in their winter quarters. The birds generally flock and rest on large waterbodies during daylight hours, and disperse to feed at night into smaller wetlands. Such systems of day-roosts and foraging habitats have been termed 'functional units' of dabbling ducks (Tamisier, 1976, 1978).

* Corresponding author at present address: Centre for Ecology, Hydrology — CEH Dorset, Winfrith Technology Centre, Winfrith Newburgh, Dorchester, Dorset DT2 8ZD, UK. Tel.: +44-1305-213-500 (switchboard).

E-mail address: magu@ceh.ac.uk (M. Guillemain).

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During the 1970s most of the internationally important winter quarters were marine (Appendix A). Since then several small, newly protected non-marine areas have become very important sites for these birds. For instance, in Charente Maritime the 35,000 ha Marais Littoraux et Côtiers now contain four nature reserves (total area of 400 ha, protected since the 1980s), in inland marshes and coastal lagoons (fresh or brackish, non-tidal) which are currently used by some 15,000 ducks in January (Deceuninck et al., 1999 and pers. comm.). Overall the crude density of ducks is ca. 0.4 birds ha^{-1}, similar to densities in the nearby wintering area, the western part of the Marais Poitevin, 50 km to the north (15,000–20,000 ducks on 40,000 ha, Duncan et al., 1999, Des Touches, pers. comm.). Crude densities in western France are thus of the same order as those in the Camargue, the most important winter quarter for ducks in France (ca. 2 birds ha^{-1} on 145,000 ha, Tamisier and Dehorter, 1999), but both are much lower than those recorded in the Pacific and Atlantic coasts of America (8–12 birds ha^{-1}, Baldassarre and Bolen, 1994). Nonetheless, the Charente-Maritime wetlands are internationally important for dabbling ducks (>10,000 individuals), and specifically for shoveler and teal.

The protected areas of Charente-Maritime are surrounded by intensive agriculture, and wildfowling takes place both by day and night. This poses particular problems for the conservation and sustainable use of waterbirds, and one major aim of the management of the reserves is to maintain, or create, good feeding habitats within the protected areas (e.g. Salamolard, 1993). There have, however, been few studies of the use of space in these ecological islands (but see Guillemain et al., 2000a, 2000b, 2000c).

The aim of this paper is to test the prediction that, unlike many other wintering areas, most or all of the birds stay in the protected areas at night. We use duck counts in two protected areas of Charente-Maritime by day, by night and of birds leaving the reserves in evening flights. Radio-marked individuals were followed to determine whether individual ducks specialise, i.e. by remaining in the reserves at night, or by leaving them for feeding habitats in the marshes around, and we describe the types of habitats they use within the reserves at night. The results are discussed in relation to the functional unit principle, and we draw conclusions for the management of nature reserves for these waterbirds.

2. Methods

2.1. Study sites

We studied use by ducks of two protected sites of the Marais littoraux et côtiers de Charente-Maritime (Western France, 45°60′ N, 01°00′ W), an area where agricultural drainage has reduced and fragmented the original grazed wet grasslands (Fig. 1). Both sites encompass non-marine day-roosts, surrounded by potential feeding habitats both inside and outside each reserve: these two sites are likely to be distinct functional units for wintering dabbling ducks. The two reserves differ greatly in their structure: the Reserve Naturelle des Marais d'Yves (hereafter 'Yves'), 185 ha, is located on the coast and consists of a brackish waterbody (24 ha), several small ponds (<1 ha) and surrounding wet grasslands. Adjoining this reserve is a 2000 ha marine reserve where hunting is prohibited. The Réserve de Chasse of the Cabane de Moins, near Breuil-Magné (hereafter 'Breuil'), 128 ha, is 6 km south-east of Yves. It contains two fresh waterbodies (28 and 7 ha) in an area of wet grasslands. The reserves of Yves and Breuil were created in 1981 and 1989, respectively.

2.2. Duck counts

The managers of each site counted ducks weekly over the whole reserve area (including the 2000 ha marine hunting reserve at Yves) from September to March during the winters 1995–1996 to 1997–1998, on the same day at Yves and Breuil. We used these data, first, to test for differences between years in the average number of ducks per species and site. The maximum sample size for each species at each site each year was the number of weeks between September and March (i.e. 30), but poor weather prevented some counts being made, reducing the sample sizes. Variations in duck numbers across weeks at each site were similar between years, but average numbers of ducks differed, so we described the phenology of duck numbers using regression models of the proportion of individuals in a week relative to the maximum number of individuals recorded in any count that winter. Polynomial regression models were used to fit the data when the pattern of wintering was obviously non-linear across weeks. We always selected the simplest model; second-order polynomial regressions fitted the data very well in all cases, and were chosen in preference to third or fourth order regressions. The analysis was run on arcsine-transformed average proportions each week over the three winters. The data are non-independent since the analyses are based on successive weekly counts. Consequently, little reliance can be placed on the P values, but the regressions were used only to assess the overall pattern of wintering.

2.3. Diurnal and nocturnal use of the reserves by ducks

In addition to the complete counts performed by the managers of each site, we counted ducks between 07:00 and 18:00 on another day each week from September 1996 to March 1997 and September 1997 to November

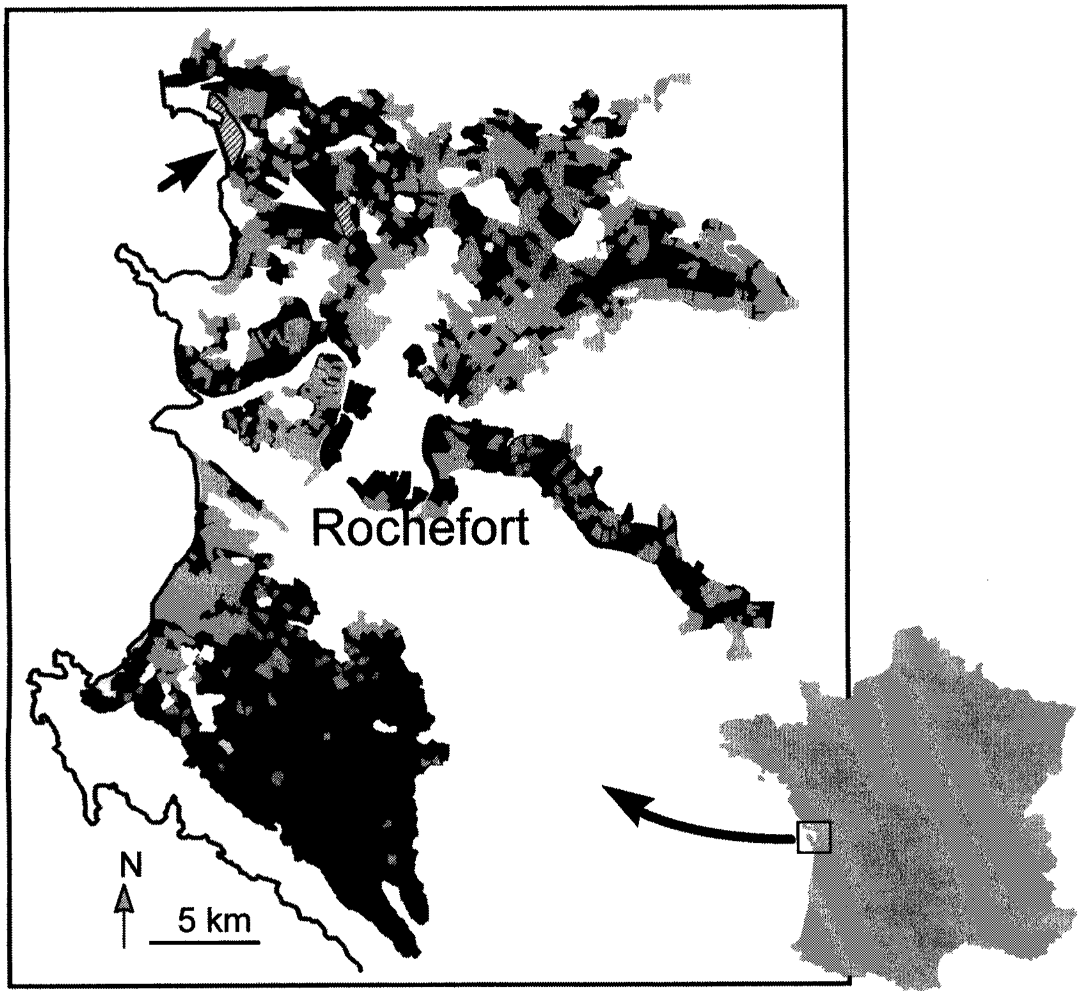

Fig. 1. Wet grasslands (black) and croplands (grey) in the Marshes of Rochefort in 1990. Map after DNP (1990). Dashed areas and arrows show the two study sites (black arrow: Yves, white arrow: Breuil).

1997, with 1–2 counts per day at Breuil and 1–7 counts per day at Yves using a ×20 telescope.

These diurnal numbers were compared with the number of ducks leaving the reserves at dusk in evening flights, and with the numbers of birds found in the reserves at night. The diurnal counts were made from well positioned permanent hides and are assumed to be accurate; the night counts were done 2–3 h before dawn and 2–3 h after dusk by observers using a ×4 binocular image intensifier (Thomson Optronique UGO). The image intensifier allowed birds to be assigned to species, but the observers had to be closer than during daylight hours. In order to compensate for this and to cover the same area (i.e. the whole protected area) during day and night counts, observers walked on a fixed circuit across each reserve for nocturnal counts (Gibbons et al., 1996). This method is likely to lead to underestimation of nocturnal duck numbers, which we expect to be slight (<10%) as these reserves are small, the observers knew them very well and lights from surrounding towns improved visibility considerably. Conversely, the evening counts of flying birds are likely to have a larger error than nocturnal counts: poor visibility at dusk (the image intensifier could not be used at this time of the day) certainly led to an underestimation of the number of birds leaving the reserves. It was sometimes impossible to distinguish between species: duck numbers in evening flights were, therefore, summed over all species in the analyses.

For the days when diurnal and nocturnal duck counts were both available, we computed the average daily numbers of ducks by day and by night for each species, and assessed the proportion of ducks using the reserve at night relative to diurnal numbers.

2.4. Radio-tracking

In order to study the movements and habitat use of individual birds we captured and radio-marked dabbling ducks at Yves and Breuil during the winter 1997–1998, using a 25 m^2 hoop-net at night at both sites, and a cannon-net (Bub, 1991) fired by day onto a islet in the main waterbody of Yves on January 20th, 1998. No bait was used for the cannon-net, and only small amounts for the hoop-nets.

Twenty-one ducks (of which 15 were trapped with the cannon-net) were fitted with radio-transmitters (Biotrack TW4, 3.5 g glued and bound to the central rectrices) and plastic patagial tags (Anderson, 1963). The transmitter was considered as lost when a bird was seen without its equipment or the transmitter stayed at the same place for longer than 48 h. Of the 21 radio-tagged individuals, one was found dead at Breuil three days after capture, one was shot between Yves and Breuil 5 days after capture, and the signal of three individuals was lost. Analyses were restricted to the 16 remaining individuals (of which 11 were caught with the cannon-net); one kept its transmitter until the end of the study period (15 March, 1998), while other individuals were tracked for 6–66 days (see Table 4).

After the first duck catches, in December, we first searched for the tagged birds in the Marshes of Rochefort (both in the reserves and in surrounding, unprotected areas) during 1 week using 30 sites which allowed complete coverage of the area. The ducks were all located inside the reserves, both during daylight hours and during the night, not outside them. We subsequently restricted the tracking survey to the reserves, where we tried to locate each bird by ground telemetry at least once each day and each night. In addition, we used a Cessna 172 for 10 nocturnal surveys of the whole Marshes of Rochefort, spread over the study period, which allowed us to check for birds not detected in the reserves. No bird was ever contacted outside the reserves by ground or aerial tracking. Data from air and ground tracking were pooled and analysed together.

In order to avoid pseudoreplication, average individual values were used in the analyses, for which the number of 'observations' is thus always $n=16$. For each individual we calculated search effort (i.e. number of tracking days or nights relative to the number of days it kept its transmitter) and search efficiency (i.e. number of days or nights it was located relative to the number of days it was sought). We assessed the fidelity of ducks to their functional unit by computing: (1) the daily fidelity to the roost (i.e. percentage of cases a bird used the same roost during two successive days); (2) the daily fidelity to the nocturnal feeding habitat (i.e. percentage of cases a bird used the same nocturnal habitat during two successive nights); and (3) the daily fidelity to the combination of roost and feeding habitat. When a bird could not be found in a reserve, it was considered that it had left it (Tamisier and Tamisier, 1981). This rule led to conservative estimates of the fidelity of the birds to their functional units. We also studied the day/night distribution of birds within the reserves, comparing diurnal and nocturnal use of the main roost and the surrounding ponds and wet grasslands; the two large waterbodies of Breuil were considered as being the main roost at this site.

3. Results

3.1. Patterns of duck numbers across the winter

Patterns of duck numbers across the winter are shown for each of the six species in Fig. 2. In species where average numbers differed between years, larger numbers were recorded in 1995–1996 than in 1996–97 or 1997–98 (Table 1). The number of mallard at Yves was maximal in early winter, and the numbers relative to the maximum count (hereafter 'relative number') decreased linearly from September to March ($r^2=0.80$, $F_{1,28}=113.57$, $P<0.0001$; Fig 3). There were two obviously distinct periods at Breuil: the relative number did not show any particular trend with time between early September and late January (weeks 1–21; $F_{1,19}=0.01$, $P=0.93$), and subsequently decreased ($r^2=0.92$, $F_{1,7}=86.26$, $P<0.0001$; Fig. 3).

The number of teal was low at both sites in early and late winter, and reached a maximum in late December/early January. Patterns of relative numbers of teal were very similar across the winter at the two reserves: they fitted a second order regression (Yves: $R^2=0.50$, $F_{2,27}=13.51$, $P<0.0001$; Breuil: $R^2=0.58$, $F_{2,27}=18.59$, $P<0.0001$; Fig. 3). The relative numbers of pintail (*A. acuta*) at Yves also fitted a second order regression with the maximum numbers of individuals in the middle of winter ($R^2=0.54$, $F_{2,27}=15.93$, $P<0.0001$), while relative numbers of pintail at Breuil increased at the end of winter ($R^2=0.59$, $F_{2,27}=19.25$, $P<0.0001$; Fig. 3).

Gadwall numbers increased linearly at Yves throughout the winter ($r^2=0.47$, $F_{1,28}=78.83$, $P<0.0001$), while at Breuil the numbers peaked in mid-winter (second order regression, $R^2=0.41$, $F_{2,27}=9.34$, $P<0.001$; Fig. 3). Wigeon numbers at Yves were also at their maximum in mid-winter ($R^2=0.37$, $F_{2,27}=7.76$, $P<0.003$). This species was not observed at Breuil in the first month of the season, and relative numbers of wigeon at Breuil fitted a second order regression with a maximum in the last part of winter ($R^2=0.65$, $F_{2,23}=21.83$, $P<0.0001$; Fig. 3).

Numbers of shoveler showed a similar pattern at the two sites, with linear increases from September to March (Yves: $r^2=0.84$, $F_{1,28}=152.47$, $P<0.0001$; Breuil: $r^2=0.42$, $F_{1,28}=20.28$, $P<0.0001$; Fig. 3).

3.2. Nocturnal use of the reserves

The number of ducks recorded in evening flights represented 40.9% of the number of individuals counted during daylight hours at Yves (±8.0 S.E., $n=26$ weekly data over the 1996–1997 and 1997–1998 winters), and

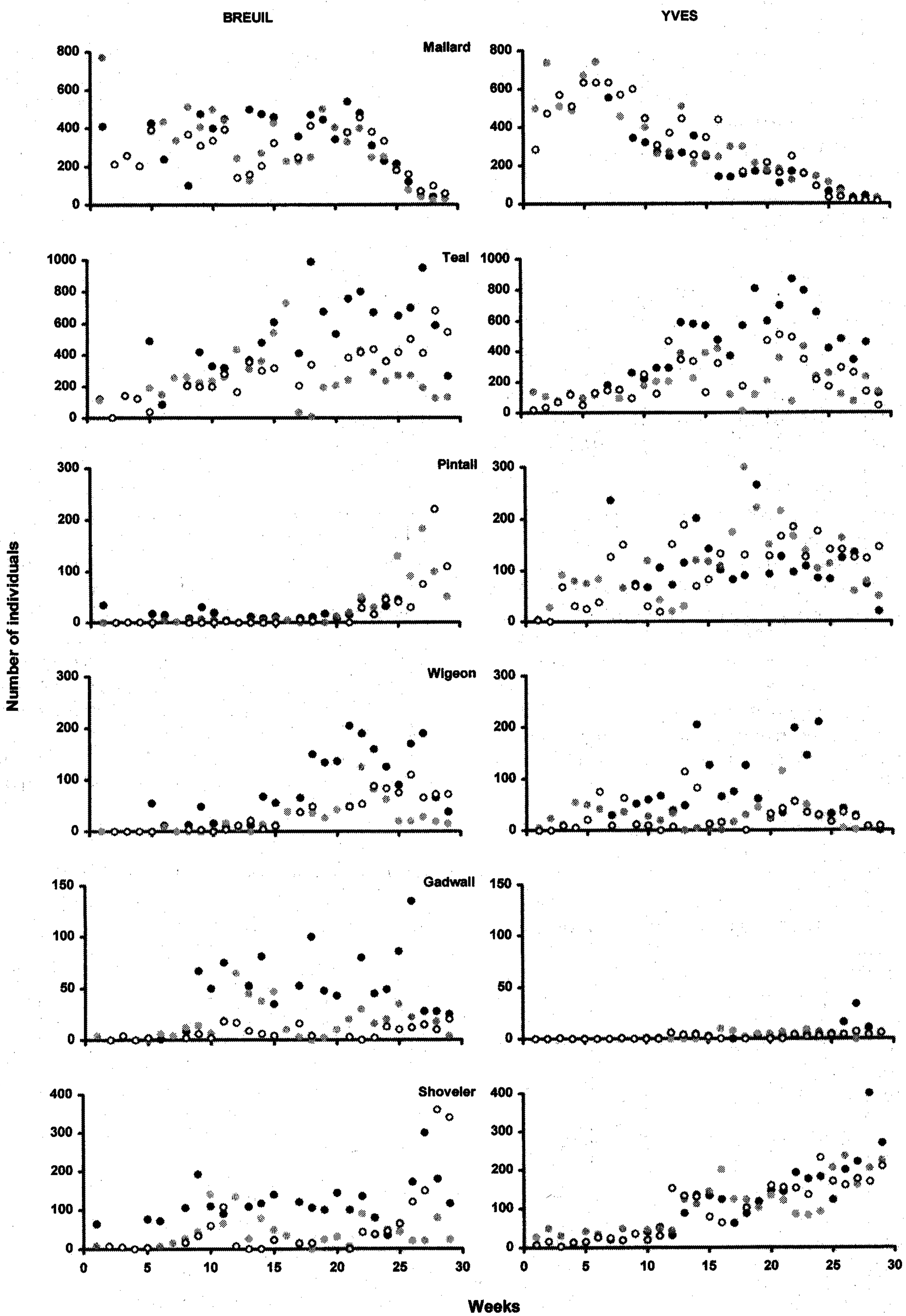

Fig. 2. Numbers of dabbling ducks across the winter at Yves and Breuil in the winter 1995–1996 (black), 1996–1997 (grey) and 1997–98 (white).

43.0% (±11.3 S.E., $n=16$) at Breuil. For the period when years could be compared (i.e. September to November), the percentage of ducks counted in evening flights relative to the diurnal number of birds did not differ significantly between 1996 and 1997 at Yves (respectively: 39.7%±9.1 S.E., $n=11$ and 58.6%±18.7 S.E., $n=9$; Mann–Whitney: $U=41.00$, $P=0.52$). At Breuil, evening flights represented 52.4% of diurnal numbers between September and November 1996 (±14.6 S.E., $n=11$). These results show that a large proportion of the birds left the reserves in the evening.

We recorded larger numbers of individuals during diurnal than during nocturnal counts in the six species at the two sites (Fig. 4). The average percentage of birds remaining in these reserves at night are given in Table 2; about half the shoveler remained, which was higher than for the other species. Few pintail used Yves at night (4%), and many of them left at dusk for the adjoining mudflats. At Breuil 13% remained, which was of the same order as for mallard, 10% at Breuil and 25% at Yves. A large percentage of teal remained in the two reserves, 27 and 31%. The percentage of the herbivorous species that remained was low, but only very small numbers used these reserves, so no firm conclusions can be drawn. About a fifth of the dabbling duck, therefore, remained in the reserves: 14.5% (±1.8 S.E., $n=30$) at Breuil, and 20.6% (±4.1 S.E., $n=26$) at Yves, and there was no change over the winter season in the proportion remaining at night. Both reserves were therefore used at night by considerable numbers of ducks. The average nocturnal duck densities were only 0.6 ducks ha^{-1} in both reserves, across the seasons (Table 3).

3.3. Radio-tracking survey

During the period that they kept their transmitter the 16 tagged ducks were sought on 81% of the days and 83% of the nights (Table 4). We located each bird, on average, in 76% of cases during daylight hours and 81% of cases during the night. A total of 995 locations were obtained (Fig. 5).

The day/night distributions of ducks fitted the functional unit principle, since at least 60% of the birds used the same reserve during successive days and successive nights, and made the same day/night and night/day movements between habitats (Table 5). However, not all birds remained in the same reserve throughout the radio-tracking survey, since the shoveler and two teal used both Yves and Breuil. These birds made successive stays in the two reserves, which were each used both during daylight hours and during the night (Fig. 6).

At Breuil, the distribution of the tagged birds was significantly biased towards waterbodies rather than ponds and wet grasslands, both during daylight hours (93.8% of locations ±3.3 S.E., $n=5$; $\chi^2=70.00$, $P<0.0001$; Table 6) and during the night (94.1% of locations ± 4.0 SE, $n=5$; $\chi^2=98.00$, $P<0.0001$; Table 6). At Yves, the shoveler was always found in the large waterbody, both during daylight hours and during the night. In contrast, the two radio-tracked mallard (which remained at Yves throughout the study period) were almost always located in the same small pool with a *Scirpus* fringe (79.2 and 80.6% of diurnal, and 88.5 and 86.8% of nocturnal searches).

One pintail sometimes used the marine reserve adjoining the study site (by day and by night, see

Table 1
Average numbers of ducks counted at the two study sites between September and March during the winters 1995–1996 and 1996–1997 (mean±SE)[a]

	1995–1996 (Breuil: $n=23$; Yves: $n=22$)	1996–1997 (Breuil: $n=27$; Yves: $n=28$)	1997–1998 (Breuil: $n=24$; Yves: $n=28$)	ANOVA	
Breuil					
Mallard	330±34	300±35	255±25	$F_{2,71}=1.33$	NS
Teal	512±51 A	252±29 B	252±29 B	$F_{2,71}=13.17$	***
Pintail[b]	20±3	30±9	25±10	$F_{2,67}=0.33$	NS
Wigeon	87±14 A	25±6 B	34±7 B	$F_{2,71}=12.86$	***
Gadwall	49±7 A	17±3 B	7±1 B	$F_{2,71}=23.26$	***
Shoveler	119±11 A	41±7 B	71±21 AB	$F_{2,71}=7.59$	***
Yves					
Mallard	191±27	291±41	310±41	$F_{2,75}=2.52$	NS
Teal	485±45 A	187±22 B	212±28 B	$F_{2,75}=25.60$	***
Pintail	114±12	105±13	99±11	$F_{2,75}=0.31$	NS
Wigeon	76±14 A	26±5 B	26±5 B	$F_{2,75}=11.91$	***
Gadwall	5±2	3±1	2±1	$F_{2,75}=2.60$	NS
Shoveler	136±19	108±12	95±14	$F_{2,75}=1.86$	NS

[a] Columns with different letters in capitals differed significantly (Bonferroni-adjusted *t*-tests)
[b] Numbers of pintail peaked with >2500 individuals in the first 2 weeks of March 1996. Data from this exceptional period were not included in the analysis.
***$P<0.001$.

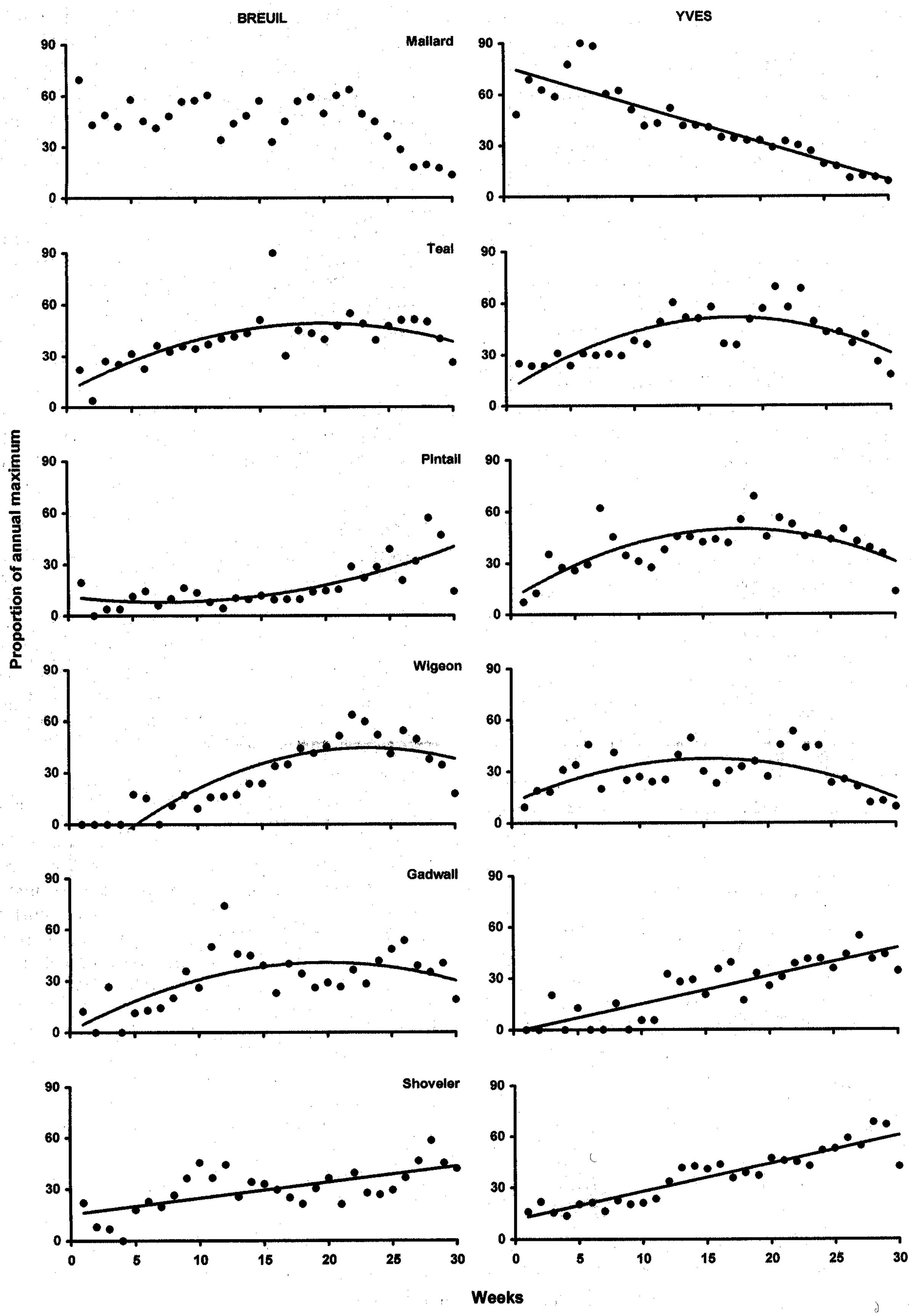

Fig. 3. Proportion of maximum annual number of individuals across the winter at Yves and Breuil. Each dot represents an average weekly value over the winters 1995–1996, 1996–1997 and 1997–1998. See text for statistics.

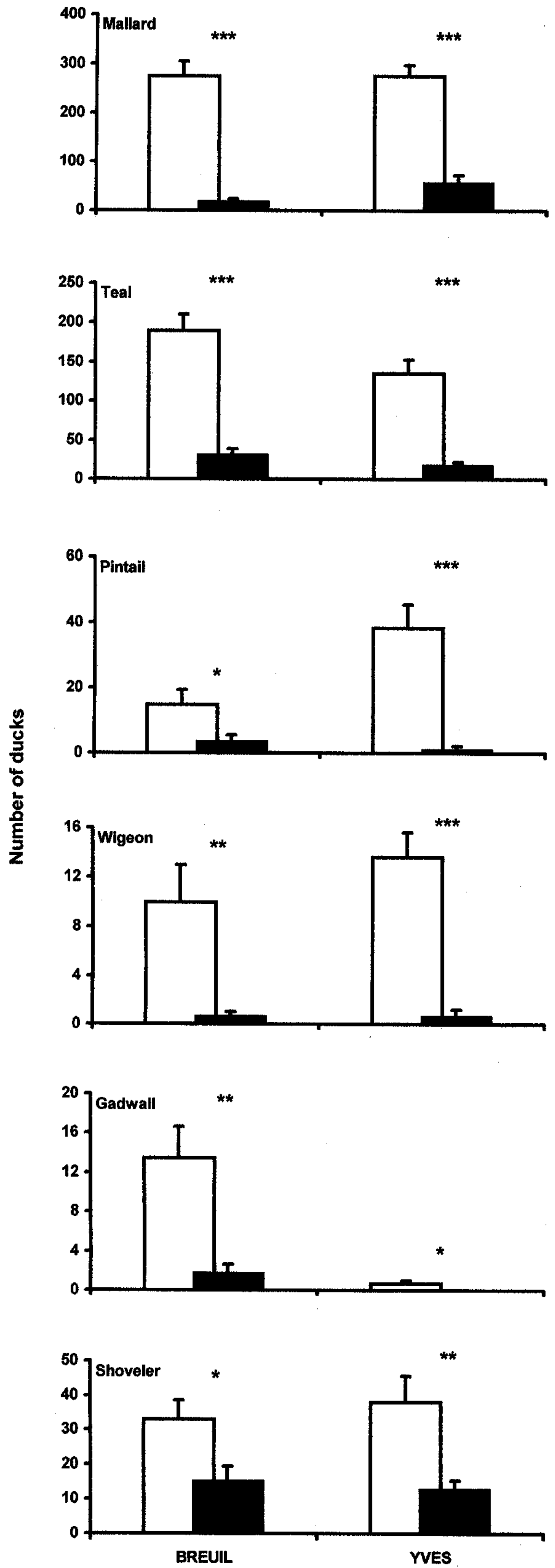

Fig. 4. Numbers of dabbling ducks during daylight hours (white columns) and during the night (black columns) at Yves and Breuil. Columns are means, vertical bars show standart errors. Sample sizes are $n=30$ at Breuil and $n=27$ at Yves. Stars show the results of Student's t-tests: *$P<0.05$, **$P<0.01$, ***$P<0.0001$.

Table 6). The other eight birds (teal and pintail) which remained at Yves throughout the radio-tracking survey never left the study site. The distribution of these birds over the main waterbody and surrounding ponds and wet grasslands differed significantly between daylight hours and the night ($\chi^2=234.88$, d.f. = 1, $P<0.0001$; Table 6): the main waterbody was largely used during daylight hours (62.7% of locations on average over the eight individuals ±6.8 S.E., vs. 37.3% ±6.8 S.E. in surrounding ponds and wet grasslands of the reserve), while most nocturnal locations were in ponds and wet grasslands (95.3% ±3.3 S.E. of locations on average over the eight individuals, vs. 4.7%±3.3 S.E. in the main waterbody of the reserve).

4. Discussion

4.1. Habitat use by wintering dabbling ducks

The nocturnal counts showed that both reserves were used at night by a large proportion of the ducks, especially shoveler, of which about half remained in the reserves during the night; at a nearby site of international importance for this species, over half the birds also feed at night on their day roost (Guillemain et al., 2000b). The same pattern, although less pronounced, was also observed in granivorous species: granivores, as predicted in Section 1, used the reserves extensively at night rather than dispersing into surrounding, unprotected wetlands as they generally do (Tamisier, 1976, 1978).

However, not all birds remained in the reserves at night, as the observations of evening flights showed that many of them left the reserves they used during daylight hours at dusk, at least 40% and probably more than half (since counts of birds in the evening flights are likely to be underestimates). Conversely, most radio-tracked individuals specialised in the use of protected areas, being present there most days and nights.

The tagged individuals showed ca. 60% fidelity to their functional unit, although this is likely to be an

Table 2
Nocturnal use of the reserves of Yves and Breuil relative to diurnal numbers (over the whole season, September–March; mean% ±S.E., sample size in brackets[a])

	Yves	Breuil
Mallard	25.4±6.7 (27)	9.6±1.8 (30)
Teal	31.2±8.5 (27)	26.7±8.8 (30)
Pintail	4.1±3.0 (23)	13.3±4.3 (27)
Shoveler	54.9±17.4 (25)	38.6±8.7 (30)
Wigeon	4.4±3.0 (24)	3.5±1.5 (17)
Gadwall	0 (9)	13.2±5.7 (22)

[a] Sample sizes differ between species because of weeks when no individuals of a given species was observed at a given site.

Table 3
Nocturnal duck densities at Yves and Breuil during the winters 1996–1997 and 1997–1998[a]

	Breuil	Yves	Mann–Whitney	
09/1996–03/1997	0.64±0.06 (22)	0.30±0.08 (17)	U=337.00	***
Min.	0.26 (Nov. 28th)	0.11 (Sept. 6th)		
Max.	1.21 (Oct. 31st)	1.44 (Nov. 1st)		
09/1997–11/1997	0.43±0.23 (8)	1.02±0.21 (10)	U=14.00	*
Min.	0.05 (Oct. 1st)	0.20 (Nov. 21st)		
Max.	2.03 (Nov. 20th)	2.33 (Sept. 23rd)		

[a] Values are indicated in ducks per ha of reserve area (mean±SE, sample size in brackets, range in italics). Differences between years for a given site as for the comparison of nocturnal numbers in text.
*P <0.05.
***P <0.001.

underestimate as we considered undetected birds had left their functional unit (see Tamisier and Tamisier, 1981). We failed to detect birds on 24% of days and 19% of nights, scattered over the study period, which regularly interrupted the data series. Radio-tags are unlikely to have prevented birds from flying, since observed individuals showed no signs of discomfort, and moved several kilometres between reserves (see Giroux et al., 1990; Cox and Afton, 1998, and review in Calvo and Furness, 1992).

The tagged individuals seldom used the ponds and wet grasslands of Breuil during the night. This was expected for gadwall and shoveler, which usually feed in open water (e.g. Thomas, 1982). Why the teal remained in the main waterbodies during the night at Breuil is not known. Except for two radio-tracked mallard which used approximately the same part of the reserve during daylight hours and during the night, the day/night distribution of most birds which used the reserve of Yves throughout the 24-h cycle was consistent with classical observations of duck habitat use (i.e. large waterbodies were used during daylight hours, and dispersal into small ponds and wet grasslands at night). However, a major difference between our results and the functional unit principle was that most of the tagged birds remained in feeding grounds immediately adjacent to their day-roost, and thus remained in the protected area throughout the 24-h cycle.

The results from the nocturnal bird counts and from the radio-telemetry appear to be conflicting, as the former show that many birds leave the reserves at night while tagged individuals almost always stayed in protected areas. The land around the two reserves have been transformed, especially through drainage for agriculture (see also Duncan et al., 1999 for data on wetland loss in a nearby site, the Marais Poitevin). Dabbling ducks use agricultural fields and dry lands for feeding in other areas (e.g. Thomas, 1981; Jorde et al., 1983; Baldassarre and Bolen, 1984), but they face major constraints in

Table 4
Technical data on the tracking of 16 ducks in the reserves of Yves and Breuil during the winter 1997–1998

Individual			Radio-tracking survey					Radio-tracking efficiency			Last observation[e]	
Species	Sex	Code[a]	Date and site of capture		Days with transmitter	Days searched[b]	Nights searched[b]	Days located[c]	Nights located[c]	Number of locations[d]	Type	Date
Mallard	M	MAL1	04/12/97	Yves	29	23 (79%)	16 (55%)	23 (100%)	15 (94%)	74	Visual	08/01/98
	M	MAL2	04/12/97	Yves	66	42 (64%)	35 (53%)	31 (74%)	34 (97%)	130	Visual	11/03/98
Teal	M	TEA1	06/12/97	Breuil	6	6 (100%)	6 (100%)	6 (100%)	6 (100%)	20	Visual	15/03/98
	M	TEA2	20/01/98	Yves	14	12 (86%)	11 (79%)	12 (100%)	10 (91%)	40	Telemetry	03/02/98
	M	TEA3	20/01/98	Yves	19	16 (84%)	16 (84%)	9 (56%)	16 (100%)	54	Visual	08/03/98
	M	TEA4	20/01/98	Yves	23	19 (83%)	20 (87%)	13 (68%)	8 (40%)	32	Hunted	12/02/98
	F	TEA5	20/01/98	Yves	23	19 (83%)	19 (83%)	13 (68%)	13 (68%)	52	Telemetry	12/02/98
	F	TEA6	20/01/98	Yves	20	16 (80%)	17 (85%)	13 (81%)	15 (88%)	51	Telemetry	09/02/98
	F	TEA7	20/01/98	Yves	20	16 (80%)	17 (85%)	11 (69%)	12 (71%)	35	Telemetry	09/02/98
Pintail	M	PIN1	20/01/98	Yves	36	26 (72%)	33 (92%)	19 (73%)	31 (94%)	126	Visual	15/03/98
	M	PIN2	20/01/98	Yves	8	6 (75%)	6 (75%)	6 (100%)	3 (50%)	10	Visual	15/03/98
	M	PIN3	20/01/98	Yves	29	24 (83%)	26 (90%)	11 (46%)	22 (85%)	67	Visual	15/03/98
	F	PIN4	20/01/98	Yves	52	37 (71%)	47 (90%)	27 (73%)	39 (83%)	126	Visual/Telemetry	15/03/98
	F	PIN5	20/01/98	Yves	14	12 (86%)	11 (79%)	5 (42%)	9 (82%)	25	Telemetry	03/02/98
Soveler	F	SHO1	05/12/97	Breuil	12	12 (100%)	12 (100%)	12 (100%)	8 (62%)	51	Hunted	04/01/98
Gadwall	F	GAD2	15/01/98	Breuil	49	35 (71%)	46 (94%)	22 (63%)	37 (80%)	102	Visual	15/03/98[f]

[a] Codes as follows: MAL: mallard, TEA: teal, PIN: pintail, SHO: shoveler, GAD: gadwall; 1: individual 1, 2: individual 2, etc.
[b] Values in brackets are search effort, i.e. number of days a birds was searched relative to the number of days it kept its transmitter.
[c] Values in brackets are search efficiency, i.e. number of days a bird was located relative to number of days it was searched.
[d] Individual birds were located several times per day, both during daylight hours and during the night.
[e] The study ended on March 15th, 1998.
[f] This individual was observed at Breuil the following winter.

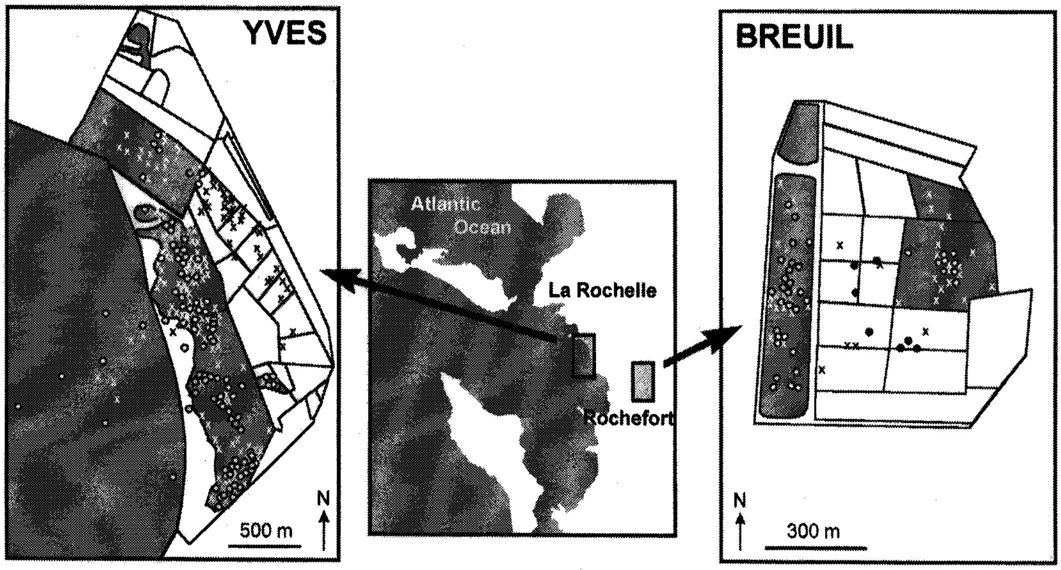

Fig. 5. Locations of radio-tracked ducks. Dots are diurnal, crosses nocturnal locations. $n=995$ locations; note that neighbouring locations were sometimes indicated by the same dot or cross. Grey areas are waterbodies and the Atlantic ocean, the white area is land, i.e. wet grasslands.

such habitats: unbalanced diet (Jorde et al., 1983), limited access to free water (Thomas, 1981; Guillemain et al., 1999), and hunting (both by day and by night in this region). Staying in the reserves at night may thus be more profitable to ducks, if (1) these are valuable foraging habitats, due to management of vegetation and water levels, (2) remaining in the immediate surroundings of day-roosts reduces energy costs associated with flying movements, and (3) remaining in reserves allows the birds to avoid potentially risky feeding areas.

The situation we observed is very similar to that described by Goss-Custard et al. (1996) and Caldow et al. (1999) for oystercatcher (*Haematopus ostralegus*) in England: some oystercatcher remain on mussel beds throughout the 24-h cycle, while others use cultivated fields at high tide (i.e. when food is difficult to access), where the risk of predation, parasitism and accidents is higher. The birds that used the two types of habitats successively (which is analogous to the ducks that left the reserves at night) were those with lower feeding efficiency on mussel beds and/or which were subdominants. It is possible that wintering dabbling ducks using unprotected marshes around the reserves during the night were either subdominant, less efficient at foraging, or both. It could be that competitive interactions between dabbling ducks are intense within the protected areas, and that dominant individuals exclude others from the reserves at night. Dominance hierarchies are well-known in dabbling duck populations (e.g. Harper, 1982), and we observed agonistic behaviours in ducks during this study. The comparison of body masses of ducks trapped in reserves of Charente-maritime during two successive winters with birds shot at night outside the protected areas shows that those in the reserves were heavier (Table 7), which is consistent with this hypothesis. The differences in body masses between trapped and shot ducks were not due to birds eating bait in the traps, since 12/13 pintail were caught in the unbaited cannon-net, and the body mass of teal trapped in baited traps (32/41), did not differ significantly from the body mass of teal caught with the cannon-net (four females and five males) which was fired over a non-baited roosting area (Mann–Whitney: males: $U=33.50$, $P=0.48$; females: $U=25.00$, $P=0.62$). These results are preliminary, especially as the duck capture area was small and the number of individuals weighed was small in some of the duck species. However, the differences between the body-masses of trapped and shot birds are considerable, suggesting that individuals may indeed come from two distinct sub-populations with contrasted ecological constraints.

Although it has long been considered that wintering duck populations are composed of individuals arriving at their wintering quarters in autumn and leaving them at the end of winter, Pradel et al. (1997) have demonstrated a rapid turn-over in the population of teal wintering in the Camargue, with some birds staying <10 days. This is consistent with the fact that the number of

Table 5
Fidelity of ducks to their functional unit in the reserves of Yves and Breuil[a]

Day n/ Day $n+1$	Night n/ Night $n+1$	Day n/ Night n	Night n/ Day $n+1$
61.75±6.83	66.44±6.78	61.19±5.66	59.06±6.15

[a] Values expressed as the percentage of cases in agreement with the functional unit principle (average over 16 individuals±SE), i.e. same site used during two successive days or two successive nights, same day/night or night/day travels.

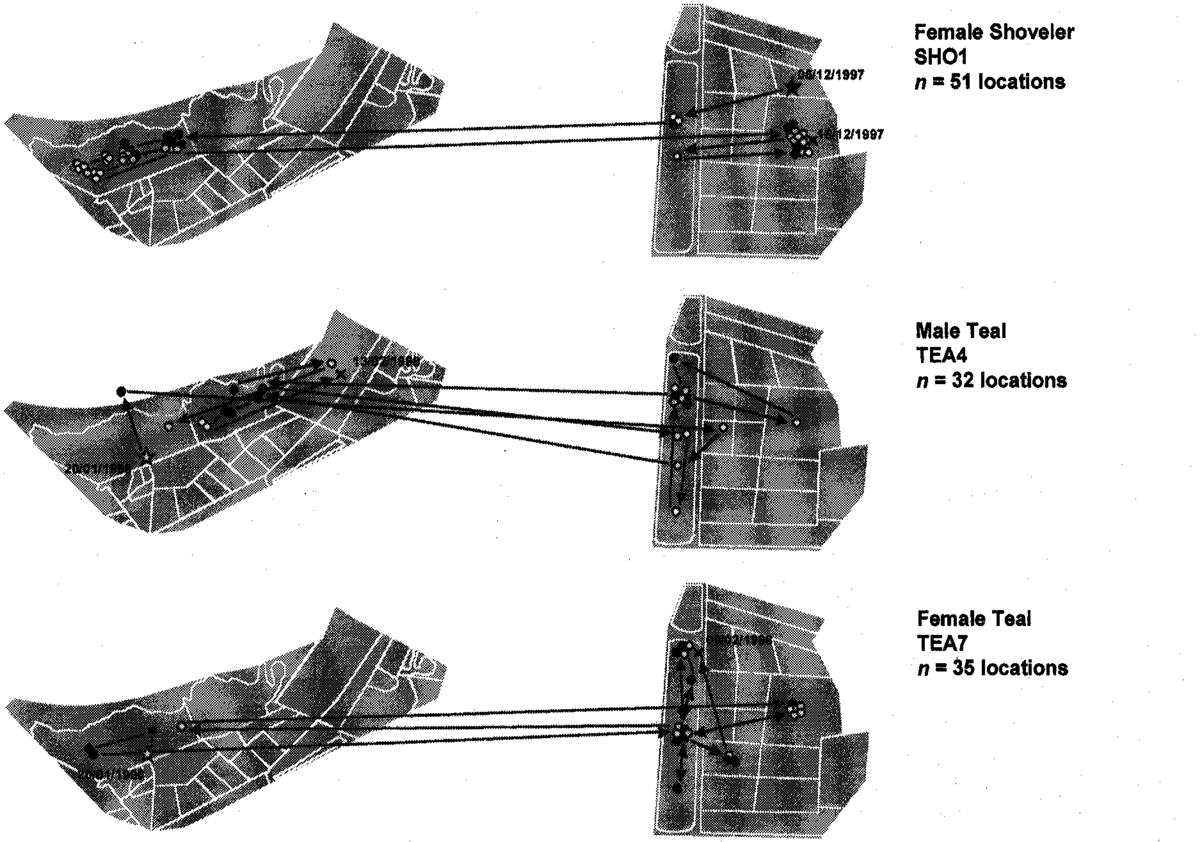

Fig. 6. Tracking locations of the three radio-equipped dabbling ducks which used both the reserve of Yves and the reserve of Breuil. White dots are diurnal, black dots nocturnal locations. Stars show the catching points, crosses show the last location of each bird.

Table 6
Distribution of radio-marked dabbling ducks within the reserves of Breuil and Yves[a]

Individual[b]	Breuil				Yves			
	Roost		Ponds and Grasslands		Roost		Ponds and Grassslands	
	Day	Night	Day	Night	Day	Night	Day	Night
GAD1	23	67	5	7				
TEA1	8	12	0	0				
TEA4	14	4	1	0	1	0	4	8
TEA7	15	12	1	3	2	0	0	2
SHO1	10	3	0	0	25	13	0	0
MAL1					10	3	38	23
MAL2					12	9	50	59
TEA2					15	6	3	16
TEA3					9	0	7	38
TEA5					7	1	14	30
TEA6					18	0	1	32
PIN1					26	3	13	82
PIN2					3	0	1+2 Sea	3+1 Sea
PIN3					8	0	8	51
PIN4					23	3	17	83
PIN5					3	0	2	20

[a] Values are the number of locations for each individual over the two types of habitat during the two periods of the 24-h cycle.
[b] Codes as in Table 4.

ducks shot during a winter is generally larger than the total number of wintering individuals counted during waterfowl censuses (Landry et al., 1986; Tamisier, pers. comm.), which is only possible if the number of ducks is regularly renewed. Data from our study sites, especially from Yves, accord with this idea: in teal, pintail, wigeon and gadwall, all migratory species, the number of individuals is maximal in mid-winter (which is usual, e.g. Tamisier and Dehorter, 1999) in spite of the fact that these species are hunted throughout the autumn and winter. In contrast, mallard is the only species whose numbers gradually decreased across the winter, and this is the least migratory of the ducks wintering in France (Rüger et al., 1987; Monval and Pirot, 1989): the mallard present in the area at the end of the breeding season may be gradually killed, while the numbers of other species are renewed by the arrival of migratory individuals. The gradual increase in shoveler numbers at Yves and Breuil is likely to be the consequence of another pattern, a redistribution from the sewage works of Rochefort across winter (Guillemain et al., 2000a).

There may, therefore, be two sub-populations of wintering ducks coexisting in our study sites: 'wintering' ducks sensu stricto and transient 'migratory' individuals. Patagial tags showed that some individuals

Table 7
Body masses of teal and pintail caught during ringing operations in protected areas[a] and shot[b] at night outside the reserves

Species	Sex	Caught in protected area	Shot	Mann–Whitney U-test
Teal	Male	363.2±12.5 (22)	326.5±7.6 (50)	751.00*
	Female	329.5±11.7 (19)	294.8±4.9 (84)	1159.50**
Pintail	Male	1031.4±30.9 (7)	810.8±48.2 (16)	99.00**
	Female	951.7±49.4 (6)	705.5±34.9 (11)	62.00**

[a] Ducks caught in protected areas are the 16 radio-tracked individuals + ducks trapped at night throughout the winters 1997–1998 (Dec–Jan) and 1998–1999 (Oct–Feb).
[b] Shot ducks were provided from local hunters and were killed from September to February of four successive winters (1995–1996 to 1998–1999).
*$P<0.05$.
**$P<0.01$.

stayed in the reserves for several months, and the radio-tracking survey suggests that the birds using the reserves at night are always the same. Tagged birds may thus be from this 'wintering' sub-population of individuals, which never leave the reserves throughout the 24-h cycle. Conversely, the evening flights of ducks leaving the reserves may be composed of naïve migratory birds which have high mortality rates in unprotected nocturnal feeding habitats, but are replaced by new arrivals. The fact that ducks shot outside the reserves have lighter body masses than birds caught in the protected areas (Table 7) is consistent with this hypothesis.

The results from evening flight counts, nocturnal duck counts and radio-telemetry are thus complementary rather than conflicting, as they may simply reflect to two coexisting duck sub-populations. It may be surprising that almost all the birds we radio-tracked were apparently from the 'wintering resident' sub-population, but this is likely to be due to the catching methods used: hoop-nets were located in wet grasslands of the reserves, which automatically limited the individuals we could capture to those using the reserves at night. In the same way, the cannon-net was launched during daylight hours on a small islet close to the main hide of Yves, which could have restricted the sample we captured to those birds which were confident enough to approach the hide. Improvements of catching methods will be necessary to avoid such biases and be able to radio-track individuals from the two sub-populations. In addition, our tracking survey took place late in the season, while nocturnal movements of ducks may vary across winter. More data from birds caught earlier in the winter are required to test the hypotheses proposed in the present study.

4.2. Implications for wildfowl conservation

The creation of non-marine nature reserves with large areas of fresh water has been associated with major changes in habitat use by wintering dabbling ducks on the French Atlantic coast during the last few decades: the birds have switched from marine to inland day-roosts in Britain (Owen and Williams, 1976) and in France, especially in Charente-Maritime. Here in the 1990s, the marine Baies Charentaises were almost completely deserted by ducks, which nowadays flock in the non-marine Marais littoraux et côtiers de Charente-Maritime and the Reserve Naturelle de Moëze-Oleron (Appendix). A consequence of this change is a high density of ducks on small sites during daylight hours: 20–30 ducks ha^{-1} in the day-roosts of Yves and Breuil. This could have major consequences for the birds, through food depletion and increased interference competition (e.g. Zwarts, 1976; Goss-Custard and West, 1997) as well as increased predation since the location of duck flocks is more predictable nowadays (Fritz et al., 2000). However, these potential costs may be counterbalanced by benefits which arise from the quality of the habitat (e.g. safe access to freshwater during daylight hours, Guillemain et al., 1999), social interactions (e.g. easier mate selection in large concentrations of individuals) and/or reduced individual predation risk through dilution or the 'many-eyes' effect (see Krebs and Davis, 1993).

In addition to documenting the heavy use of non-marine reserves during daylight hours, the results of this study show that wintering ducks do not necessarily go far from their day roosts to feed at night, as many birds remained in feeding areas close to the roosts. The management of these non-marine reserves to combine predictable large areas of shallow water in autumn and winter for roosts and, in addition, adequate nocturnal foraging habitats was therefore successful.

Nonetheless, the number of ducks remaining in the reserves at night was limited: nocturnal densities of ducks at Yves and Breuil were 0.6 duck ha^{-1} on average, which may be slightly underestimated but is of the same order as the crude density of ducks in January in the whole wetland system of Charente-Maritime. This suggests that protected areas, where almost all ducks concentrate during daylight hours, are not used at night any more heavily than the surrounding, unprotected marshes. Further, nocturnal duck density is much lower than in the freshwater marshes of the Camargue (up to

15 ducks ha^{-1}, Tamisier and Dehorter, 1999), suggesting that feeding conditions in the protected areas of Charente-Maritime are poor. This may be the consequence of competition for limited food supplies: few data on seed densities are available, but seed densities in one freshwater pond of Yves (4–17 kg ha^{-1}, Guillemain et al., 2000c) were much lower than in comparable freshwater wetlands of the Camargue (ca. 50–380 kg of seeds ha^{-1}, Tamisier pers. comm.). If this is so then management for higher seed densities should increase the nocturnal carrying capacity of these protected areas.

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Appendix A. ***Important***[a] sites for wintering dabbling ducks in the 1970s and the 1990s. M = marine areas (e.g. estuaries, bays, mudflats), N = non-marine areas (e.g. rivers, inland lakes and marshes); P = protected (at least partially), U = Unprotected. Important sites indicated in **bold type**

Departement	Site	Type	Area (ha)	1967–1979[b]	1992–1999[b]
English Channel/North Sea					
Somme	Baie de Somme / Littoral Picard	M + N	22,000	**P**	**P**
Calvados	Estuaire de la Seine / Marais Vernier	M + N	20,000	**P**	**P**
Manche	Baie des Veys	M	20,000	**P**	**P**
Atlantic coast					
Finistère	Yffiniac-Morieux	M	2000	P	**P**
Morbihan	Golfe du Morbihan	M	12,000	**P**	**P**
	Estuaire de la Vilaine	M	2800	**U**	**P**
Loire-Atlantique	Estuaire et Marais de la Loire	M + N	25,000	**P**	**P**
	Lac de Grandlieu	N	6000	**U**	**P**
	Presqu'île Guérandaise	M + N	2000	P	**P**
	Etangs du Nord Loire-Atlantique	N	400	U	**P**
Vendée	Baie de Bourgneuf	M + N	70,000	**P**	**P**
	Marais d'Olonne/Réserve de Chanteloup	N	1500	**P**	**P**
	Littoral Vendéen	M	8000	U	U
Charente-Maritime	Baie de l'Aiguillon (*Marais Poitevin*)	M	100,000	**P**	**P**
	Baies Charentaises	M	150,000	**P**	P
	Marais littoraux et côtiers de Charente-Maritime	N	400	U	**P**
	Réserve Naturelle de Moëze-Oléron (continental part)	N	210	U	**P**
Gironde	Bassin d'Arcachon	M	15,000	**P**	**P**
	Etang de Carcans-Hourtin	N	6600	P	**P**
Landes	Marais d'Orx	N	800	U	**P**
Mediterranean coast					
Hérault	Etangs et Salins du Languedoc	N	20,000	**P**	P
Bouches-du-Rhône	Camargue	N	142,500	**P**	**P**
Haute-Corse	Etang de Biguglia	N	1600	**U**	P

[a] A site was considered as being 'important' if it hosted > 1% of the flyway population of at least one species for at least 1 year during the period considered. Threshold numbers of individuals for a site to be considered important after Scott (1980) for the 1970s and Scott and Rose (1996) for the 1990s.

[b] Data after Scott (1980) for the 1970s, and after Rocamora (1993, 1994, 1995) and Deceuninck et al. (1995, 1997, 1998, 1999 and pers. comm.) for the 1990s.

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