ORIGINAL ARTICLE

Variation in home-range size and movements of wintering dabbling ducks

**Pierre Legagneux · Christine Blaize ·
Franck Latraube · Jérôme Gautier ·
Vincent Bretagnolle**

Abstract Despite a long historical record of radio-tracking analyses, basic home-range information is still lacking for most common waterfowl species, especially during the winter. We investigated how dabbling duck home ranges and daily foraging movements are influenced by extrinsic (site, temperature, date) and intrinsic factors (species, sex, age). We radio-tagged and monitored 125 individuals of three duck species (mallard *Anas platyrhynchos*, Eurasian teal *A. crecca crecca* and northern pintail *A. acuta*) in three French wetlands over four winters. Home-range sizes for a given species varied greatly among our study sites. Moreover, species differed according to home-range structure and distance traveled to reach their foraging grounds (teal had a more patchy home range and traveled farther distances than mallards). Foraging distances increased with temperature and time (over the winter season), but this effect differed among species, suggesting that they behave differently in response to food depletion and/or cold weather. The commuting behavior (i.e., the decision to leave the roost at night for foraging) differed among species and season. Teals were more risk-prone because they were more likely to leave the roost at night. In our study, ducks foraged at distances of 1–2 km from roosts, whereas distances of 2–48 km have been recorded in North America. We suggest that food supply, hunting pressure or population density may account for these inter-continental differences.

Communicated by F. Bairlein.

P. Legagneux (✉) · C. Blaize · F. Latraube · V. Bretagnolle
Centre d'etudes biologiques de Chizé, Villiers en Bois, France
e-mail: legagneux@cebc.cnrs.fr

J. Gautier
Réserve Naturelle des marais de Moëze-Oléron,
17780 Saint Froult, France

Introduction

Studies on movement patterns are essential to our understanding of social or spatial organization by individuals within animal populations (e.g., Cantoni 1993; Bodin et al. 2006), inter- as well as intra-species relationships and space use overlap (e.g., McLoughlin et al. 2000; Redpath 1995), or habitat selection (Aebischer et al. 1993). Furthermore, understanding the factors that determine the spatial distribution of animals is fundamental not only to theoretical science, but also to applied aspects such as conservation and wildlife management decisions (Gittleman and Harvey 1982; Mace et al. 1983; Mathevet and Tamisier 2002). For instance, wildlife managers need to understand movements and spatial use of target species, especially highly mobile ones (Sinclair 1983; Webb and Shine 1997; Jiguet et al. 2000), to adjust the size of protected areas to their ecological needs (Kramer and Chapman 1999; Madsen 1998a, b).

The home range of an animal is defined as the area explored by an individual during its normal activities (i.e., food gathering, mating and caring for young, Burt 1943; Powell 2000). Many factors are known to directly affect spatial organization (i.e., home-range size and shape) by animals (reviews in Mace et al. 1983; Rolando 2002), such as age, sex, breeding status, body condition, habitat structure, or weather conditions. However, home ranges are primarily driven by the underlying distribution of food resources (Brown 1975; Schoener 1983). To characterize individual home ranges, precise locations collected over a

minimum time window are necessary (review in Kenward 2001a). Since the 1970s, the use of small radio-transmitters fitted to wild animals have been responsible for an impressive number of studies on a great diversity of animals (Kenward 2001b). At the same time, statistical tools have improved (see Powell 2000; Kernohan et al. 2001) to allow detailed and accurate home-range analyses.

Ducks (Anatidae) are robust and heavy birds (Madge and Burn 1988; Kear 2005). They can thus be easily fitted with radio-transmitters to study habitat use (Pietz et al. 1995) and were among the first birds to be fitted with radio tags (Eliassen 1960 on mallard, *Anas platyrhynchos*). Early waterfowl research focused mainly on understanding spatial occupation by duck on the breeding grounds (e.g., Nudds and Ankney 1982; Håland 1983; Rotella and Ratti 1992), and this remains an active field (Clark and Shutler 1999; Mack et al. 2003; Mack and Clark 2006). In addition, ducks have been radio-tracked in North America during the breeding season to estimate survival rates (e.g., Pietz et al. 2003; Devries et al. 2003). However, ducks, as long-distance migrants (Scott and Rose 1996; Guillemain et al. 2005), are known to use very distinctive habitats and have different ecological requirements in winter compared to the breeding season, with presumably completely different spatial use due to divergent energy (reproduction *vs.* survival) and social requirements. In winter ducks are known to use separate habitats (roosting sites used during the day and foraging sites at night: McNeil et al. 1992; Tamisier and Dehorter 1999; Cox and Afton 1996); this is termed commuting behavior. However, despite long-term radio-tracking records, basic home-range information (both size and spatial characteristics) is still lacking for the most common waterfowl species, especially during the non-breeding season. Although several studies have provided information on habitat use and movements for Nearctic populations (e.g., Jorde et al. 1984; Frazer et al. 1990; Cox and Afton 1996; Cox et al. 1998; Fleskes et al. 2002) and Palearctic populations (Tamisier and Tamisier 1981; Guillemain et al. 2002), none have estimated home-range size, inter-individual variation or studied the effects of environmental factors on home-range characteristics of wintering duck species.

Our objectives were three-fold: first, by using complementary methods, we describe movement patterns and spatial use (home range shape and size, distance traveled) for dabbling ducks during winter in France. We studied three species (mallard *Anas platyrhynchos*, Eurasian teal *A. crecca crecca*-hereafter teal-and northern pintail *A. acuta*-hereafter pintail-and three contrasting study sites over 4 years to estimate whether home ranges were affected by site, species and annual differences. Because these species occupy the same site during winter, their ecological needs should be similar (Baldassare and Bolen 2006), and thus we predicted that different species in the same study site should differ less with regard to space use than the same species in different study sites. In other words, the available resources in a given site should result in less variation within than among sites. Secondly, we investigated to what extent sex and age of tracked birds may affect space use. We expected juvenile ducks, likely to be inexperienced, to have greater home ranges and/or to travel greater distances. In contrast, we expected no differences between sexes, as dabbling ducks are already paired in winter. Thirdly, we investigated to what extent environmental factors affect space use and foraging by dabbling ducks; more specifically, we expected ducks to reduce energy expenditure (i.e., distance traveled) when temperature falls, but also in wet weather as resource availability increases with water level. We also predicted that commuting behavior would differ between early and late winter due to food (mainly seed) depletion. We expected dabbling ducks to forage close to roosting sites early in the season and either to change roosting site and/or increase traveling distance as food resources decline around the roosting site.

Methods

Study areas

Data were collected from November to March during four consecutive winters (2001–2002 to 2004–2005), referred as years 01, 02, 03 and 04 respectively. Three different areas were studied (see Fig. 1).

The "Réserve Naturelle de l'Estuaire de la Seine" (4,000 Ha, 49°17′N, 00°16′E), hereafter named "Seine," is strongly influenced by human activities, including the presence of a large industrial harbor (Le Havre), factories and a motorway. The Seine landscape is comprised of a large and continuous reed bed (1,461 ha), marsh areas (3,140 ha), mudflats (597 ha) and about 200 ponds used for hunting (total 86 ha). Two capture sites were used: the "Réserve Naturelle" itself and another nature reserve, "La Grand'mare," to the east (Fig. 1).

The second study site, the Brenne (central France, 46°45′N, 01°14′E; hereafter named "Brenne") covers 80,000 ha made up of woods, wet meadows and more than 2,000 lakes (8,000 ha) constituting a mosaic of habitats, much of which is managed for fish farming and wildfowling. Three protected lakes were used to capture ducks: the Réserve Naturelle de Chérine, Plessis and Massé. In Brenne, hunters artificially increase resource availability on lakes (through adding grain to attract ducks: up to 1,200 kg of wheat per lake has been recorded over one winter, P. Legagneux, unpublished data).

Fig. 1 Map of the three study sites (Seine estuary, Brenne lakes and Moëze marshes) used in France to trap (capture sites, i.e., protected areas, are shown in *grey*) and radio-track dabbling ducks during four consecutive winters (2001–2005)
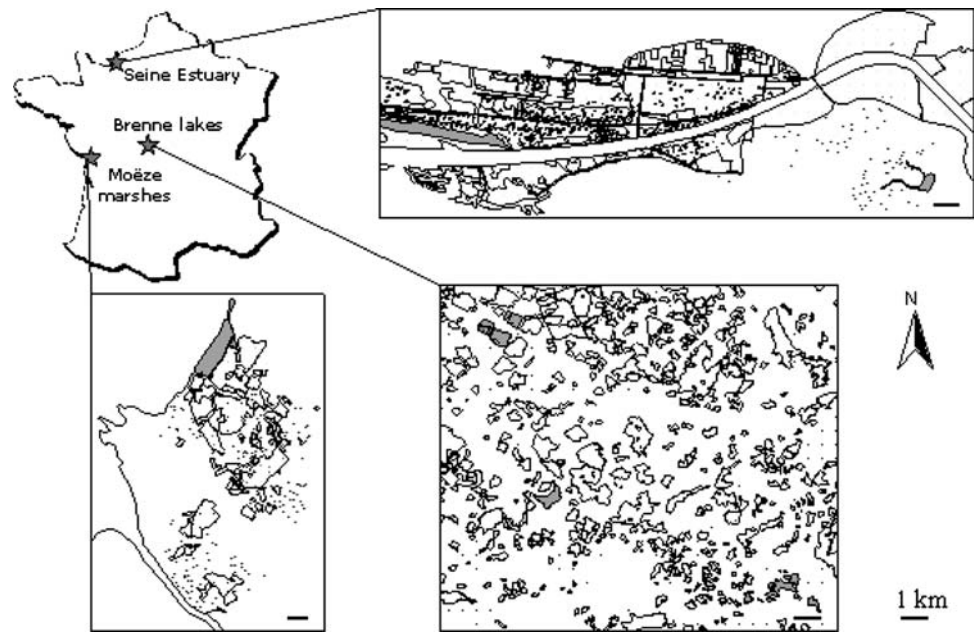
The third study site is the Moëze marshes (12,000 Ha; hereafter named "Moëze") in western France (45°55′N, 01°04′W); bounded by two estuaries, this region is comprised of wet meadows (9,900 Ha) used mainly for grazing and crops (1,400 Ha). A single capture site was used: the Réserve Naturelle des Marais de Moëze-Oléron (214 ha).

The first two sites were studied during winters 01, 02 and 03, Moëze only during the final winter (04). Meteorological data were available at http://www.ncdc.noaa.gov for the cities of Le Havre, Châteauroux and La Rochelle (all less than 30 km from their respective study sites). For

each study day, minimum and maximum temperatures, as well as total precipitation, were available.

Capture, marking and radio-tagging

Ducks were caught using either a funnel trap or clap net (Bub 1991), both at night and during the day. A total of 125 dabbling ducks was caught over the 4 years from November to February (Table 1). Birds were ringed, sexed and aged (as adults or juveniles) using wing feathers and molt data (Baker 1993). Each bird was fitted with a 9-g

Table 1 Summary of the statistics (mean and SE) on the tracking dataset according to species, study site and year

Species	Site	Year	n of fixes	SE	Days tracked	SE	Roost fidelity (%)	Home ranges C_{part}	SE	Core area (Ha)	SE	MCP (Ha)	SE	n (HR)	Distances Dist (m)	SE	n (Dist)
Teal	Brenne	02	20.1	2.8	30.7	7.0	100	0.4	0.20	22.8	8.7	555.1	867.2	4	762	63	7
		03	43.0	9.7	18.0	5.7	66.7	0.1	0.02	31.1	2.5	212.2	30.7	5	8,447	3,028	6
	Seine	02	15.0		55.5	10.5	100								3,840	289	1
		03	13.5	3.2	33.5	5.9	100	0.1	0.04	162.7	25.8	1,631.6	646.2	5	2,281	139	12
	Moëze	04	39.8	5.3	40.3	4.8	46.2	0.2	0.11	82.4	11.1	895.4	609.8	12	1,008	193	13
Mallard	Brenne	01	26.0	5.0	38.5	9.8	62.5	0.5	0.17	10.8	2.1	184.7	147.7	7	495	127	8
		02	26.0	5.0	70.6	11.5	61.5	0.4	0.14	19.0	3.5	496.2	861.3	8	1,216	135	13
		03	27.1	3.6	61.4	6.0	47.4	0.3	0.10	40.4	10.0	1,257.3	1,915.1	15	1,287	245	19
	Seine	02	15.5	2.1	44.8	4.1	100	0.7	0.12	41.7	6.	221.0	242.8	7	682	52	15
		03	18.6	3.4	46.1	8.0	94.4	0.4	0.13	84.1	15.7	326.6	162.7	8	1,139	278	18
Pintail	Moëze	04	24.1	3.8	22.2	3.1	77.8	0.3	0.13	66.7	8.9	556.1	663.5	7	1,263	281	9

Roost site fidelity is the percentage of individuals that used only one roost during the whole winter. The sample size (n) differs relative to the type of variable (distances vs. home-range, see "Methods" for details). The core area (ha) is calculated with nearest cluster neighbor analysis (Kenward et al. 2003). Mean distances between roosting and foraging sites are also provided

VHF radio-transmitter (TW3, Biotrack®, UK; 2–4% of birds' body mass). Radio tags were tail-mounted and glued. This attachment technique does not appear to disturb animals (Pietz et al. 1995) as transmitters are situated on an extension (tail) of the animal's body; not on the back, which is known to increase loading costs (Pietz, personal communication) and time spent on comfort movements (Garrettson et al. 2000). Due to both statistical (number of transmitters fitted, see below) and logistical constraints, our study is based on an unbalanced sample size (i.e., species and sites), e.g., only nine pintails were tracked in Moëze. Therefore, species and site comparisons do not necessarily involve all sites and species. Only mallard and teal could be compared among all study sites.

Radio tracking

Each bird was located two or three times per week both during day and night in winter 01. The number of radio locations was increased in following winters to up to four or five times per week (Table 1). Radio-tracking surveys were conducted from mid-November to mid-March. Terrestrial radio-tracking was done using hand-held Yagi antennas with three elements and a Yaesu FT-817 receiver. Birds were located by triangulation (White and Garrott 1990), from at least two bearings taken within 10 min of each other. As Brenne has more than 2,000 lakes, location accuracy was limited to the lake (lakes larger than 5 ha being divided into sectors). All locations were plotted onto a GIS (ArcView 3.2, Environmental Systems Research Institute, Inc., Redlands, CA).

Aerial surveys were conducted at night to relocate birds that were temporarily lost using ground-based telemetry to determine if those birds had deserted the study area. Following predetermined transects covering the whole study area (see Seddon and Maloney 2004), 30 aerial surveys were performed in the three study sites with two directional antennas fixed below the aircraft and directed towards the ground. All tag frequencies were scanned throughout each survey (which usually lasted about 1 h) and GPS waypoints (GARMIN 12) were taken in association with signals received. The flight and all locations were reproduced onto the GIS. The accuracy of this method was tested with transmitters left on the ground with a known position. Error between estimated and exact locations was 781 m ± 175 SE, $N = 8$. Among the 2,920 locations collected during this study, 95.6% were obtained by terrestrial survey.

Analysis of radio-telemetry data

Because of their commuting behavior, dabbling duck locations during radio-tracking follow a bimodal (day, night) pattern. In addition, many areas within home ranges are not used, i.e., between roosting and foraging sites. This is a typical situation of multinuclear cores, for which the use of nearest-neighbor clustering analysis is recommended (Kenward et al. 2001). Moreover, this method requires a smaller sample size than density estimation methods, such as kernel methods (Hodder et al. 1998; Kenward et al. 2001).

To estimate individual home-range characteristics, we further used the following spatial approaches and methods:

1. *Minimum convex polygon* (MCP), i.e., the smallest polygon which can be drawn around a set of locations, providing an indication of the maximum extent of the total area (100% of fixes were used).
2. The *core area* delineates polygons where activity is concentrated (based on apparent discontinuities in utilization plots). To detect the core area (i.e., the percent of locations included in the clusters calculation), rather than choosing a particular core size for all the individuals, we followed Barg et al. (2005) and calculated for each individual the home-range size at each 5% increment of locations (from 20 to 90%). We then extracted the difference in area between the successive 5% and deduced the core area as the area bounded by the greatest difference of the two consecutive 5% of locations.
3. *Partial area* (C_{part}) of core area cluster polygons, is the area of the separate clusters divided by the area of a single polygon that would include all clusters (Hodder et al. 1998; Walls et al. 1999). This gives an index of patchiness, ranging from 1 (for a single nucleus) to 0 (patchy or fragmented range: see Kenward et al. 2003).
4. The *distance traveled* is the distance between night (foraging habitat) and day (roost) locations. In cases where locations were not available for consecutive days and nights, we used the closest (in time) night and day locations. Ducks rarely make additional flights at night (Tamisier and Tamisier 1981; Cox and Afton 1996; personal observation); thus, the distances calculated represent half of the daily minimum distance traveled.

Commuting decisions were analyzed by investigating if the foraging location (night) was outside or inside the roosting area. For each tracked individual, the ratio of nights spent outside the roost provided an index of whether ducks commuted or not. To investigate whether commuting decision varied among study sites and species, we performed a logistic mixed-effect model (with year and individuals as random factors and study site, species and date as fixed factors) on the nights spent inside or outside the roost.

Statistical analysis

To determine the minimum number of locations needed per individual, we calculated the home ranges (core area

and MCP) for all individuals and tested for the effect of the number of locations on the estimated size of home ranges. Starting by using all individuals (number of fixes per bird >4), we built a linear model of the core area or MCP as a function of the number of fixes. We incremented the minimum number of fixes per individual one by one and plotted the P-value of the linear model against the number of fixes, until the relationship was no longer significant ($P > 0.05$). Home ranges were analyzed using Ranges6 (Kenward et al. 2003). Means are reported $\pm$ SE. Both home-range sizes and traveled distances were $\log_{10}$ transformed for statistical analyses (see Walls and Kenward 1995). Normality of the variables was assessed with Kolmogorov-Smirnov tests. We tested for the effect of age (adults vs. juveniles), sex, year and study site on home-range size by using general linear mixed models (GLMM). Year was considered as a random factor in these analyses because we could not control for this effect. In addition, given that a variable number of distances was available per individual [9.7 ± 2.8 distances (mean $\pm$ SE), $n = 125$], we also considered individuals as a random effect when analyzing traveled distances, which resulted in giving the same weight to each individual and avoiding pseudo-replication among individuals (Pinheiro and Bates 2000).

Twenty-two candidate models were considered, including all combinations of the tested factors and their possible interactions, and a null (intercept only) model. For this and subsequent analyses, we used Akaike's information criterion as the principal basis for selecting among competing models (Burnham and Anderson 1998). We used an estimation method set to the maximum likelihood rather than the restricted maximum likelihood to ensure that the test compared likelihood based on the same data (Venables and Ripley 2002). We used the freeware R 2.5.0 for all statistical analyses. All the statistical tests were considered significant within the level of $\alpha = 0.05$.

Results

Methodological issues

A total of 125 different dabbling ducks (73 mallards, 39 teals and 9 pintails) was used in this analysis ($N = 1,217$ distances, Table 1). The effect of the number of locations on the core area ceased when more than 15 locations were obtained per individual ($F_{1,82} = 2.58$, $P = 0.11$). Therefore, 43 individuals with fewer locations were excluded from the home-range analyses (Table 1). Home-range size estimated by using MCP remained totally unaffected by the number of fixes ($F_{1,110} = 0.056$, $P = 0.81$ for all individuals).

All locations collected for each individual were biologically independent from each other, because ducks could easily explore their entire home ranges (i.e., move between roosting and foraging sites) in less than 60 min, our shortest time lag between two consecutive locations. The 82 birds in the home-range analyses were tracked during almost 2 months on average (58 days $\pm$ 3 SE), mainly during January–February with a mean of 31.7 locations ± 1.5 SE per individual (see Table 1). The mean % of locations retained per bird to calculate the core area was 72.1% $\pm$ 1.6 SE.

Space use and movement patterns: comparison between species and study sites

Neither core area nor MCP was affected by species, age or sex (GLMMs, all $P > 0.5$). However, space use was quite variable depending on individuals: some used a single foraging location and a single roosting site (the capture site), while others used several foraging sites and/or several roosts (see Fig. 2). This was also variable according to sites; in the Seine, 46 of 47 (97.87%) ducks used a single roost during the winter, while in Brenne and Moëze, these figures were respectively 59.6% ($N = 57$) and 59.1% ($N = 22$). Pintails tracked in Moëze showed high site fidelity to the nature reserve (77.8%, see Table 1), which was used both by day and night by all except three individuals that eventually foraged on hunting ponds 8 km from the site after the hunting season had closed. As expected, we found a positive relationship between MCP and mean foraging distances for all species ($F_{1,25} = 108.5$, $P < 0.0001$, $r^2 = 0.82$ for teals; $F_{1,45} = 19.8$, $P < 0.0001$, $r^2 = 0.31$ for mallard; and $r_s = 0.82$, $N = 7$, $P = 0.03$ for pintail).

Teal core areas were marginally larger than mallard core areas (t-value $= -1.75$, $P = 0.08$). In contrast, teal traveled larger distances to reach their foraging areas than did pintail or mallard (Table 2; Fig. 3). Compared to mallard, teal showed a more fragmented use of space (lower Cpart value, Wilcoxon rank sum test on arcsine-transformed data, $W = 1,392.5$, $P = 0.019$). As teal showed a higher roost site fidelity through the winter (83.1 vs. 73.4% for mallards), the patchiness was thus related to a greater number of foraging sites.

MCP was not affected by any of the tested factors (time in days), temperature, species, age, sex or study site, all P-values > 0.2), but core areas varied according to study site ($F_{2,72} = 21.94$, $P < 0.0001$, Fig. 4). Analyses were repeated on teal and mallard separately (providing higher sample sizes). In teal, core areas, MCP and daily distances varied according to study site ($F_{2,21} = 23.56$, $P < 0.0001$; $F_{2,21} = 10.17$, $P < 0.001$ and $F_{2,36} = 13.79$, $P < 0.0001$ respectively). For instance, core areas were twice as large

Fig. 2 Selected examples of winter home ranges (core areas and MCP) calculated for a male teal in Brenne in 2002–2003 (**a**), a female pintail in Moëze in 2004–2005 (**b**) and a female mallard in the Seine in 2002–2003 (**c**)
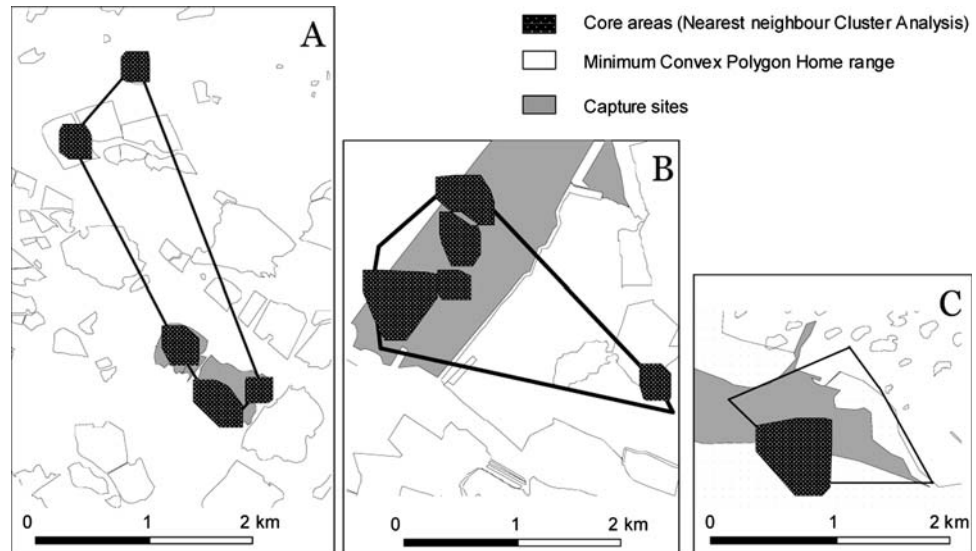

Table 2 Model selection from linear mixed models on the daily distance traveled by wintering ducks in France

Models	Df	AIC	ΔAIC
MaxT × species × date + site	**21**	**4,115.99**	**0.00**
MaxT × species × date + site + age	22	4,117.70	1.71
MaxT × species × date + site + sex	22	4,117.75	1.76
MaxT × species × date + site + sex + age	23	4,119.48	3.48
MinT × species × date + site	21	4,120.87	4.88
MaxT × species × date + site + sex × age	24	4,121.42	5.43
Species × date + site	13	4,123.66	7.66
MaxT + species × date + site	14	4,125.09	9.10
Site × date + species × MaxT	16	4,125.17	9.17
MaxT × species + date + site	14	4,148.88	32.88
MaxT + species + date + site	11	4,151.10	35.10
MaxT + species + date + site + sex + age	13	4,154.68	38.69
MaxT + species	8	4,161.34	45.34
Species	7	4,161.98	45.99
MaxT + species + date	9	4,163.08	47.09
Site	6	4,169.35	53.36
Null model	4	4,181.08	65.09

Year and individual were treated as random factors to account for potential pseudoreplication. Degree of freedom (Df), Akaike information criterion (AIC) and ΔAIC are presented. The most parsimonious model (shown in *bold*) included a triple interaction among the maximum daily temperature (MaxT), studied species (species) and time (date in Julian days) as well as an effect of study site. The other factors such as age and sex were included in the model selection, but not retained in the most parsimonious model

Fig. 3 *Box plots* of the distances traveled in meters for mallards, pintails and teals wintering in Seine (in *black*), Moëze (in *grey*) and Brenne (in *white*)

Fig. 4 Mean home-range sizes in ha (+SE) for teal and mallard in Brenne (*white columns*), Moëze (*grey columns*) and Seine (*black columns*). *Core* represents the core area calculated with nearest-neighbor cluster analysis, and MCP is the maximum convex polygon

in Seine as in Moëze and six times greater in Brenne. Similarly, MCP and foraging distances were twice as large in Seine compared to Moëze and four times greater in Brenne (Fig. 5). In mallard, only the core area differed between study sites ($F_{1,41} = 16.87$, $P < 0.0001$), as it was
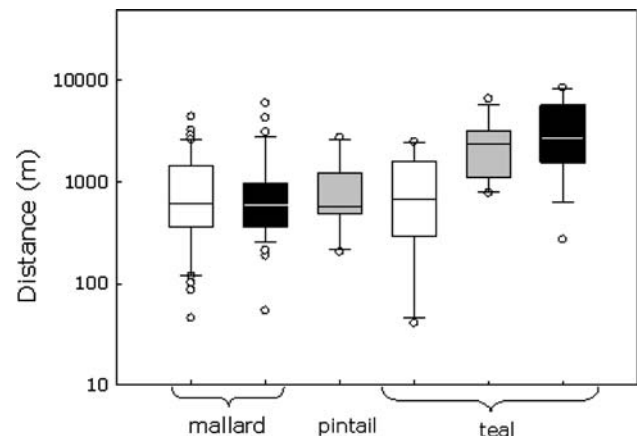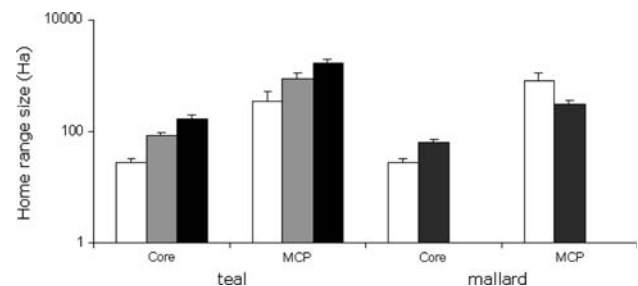
not significant for MCP ($F_{1,41} = 0.24$, $P = 0.63$) nor traveled distance ($F_{1,71} = 1.44$, $P = 0.23$; Fig. 3).

The decision to spend the night outside the roost was affected by date ($F_{1,1067} = 9.21$, $P = 0.0025$), species

Fig. 5 *Scatter plots* and *trendlines* illustrating the correlations between log-transformed distance traveled (in meters) and maximum daily temperature (°C) or date (in Julian days) for three wintering dabbling duck species radio-tracked in France from 2001 to 2005. All the linear regressions are significant (all $P < 0.02$), R^2 is provided for each relation. These relationships illustrate the triple interaction between temperature, species and time (Table 2)
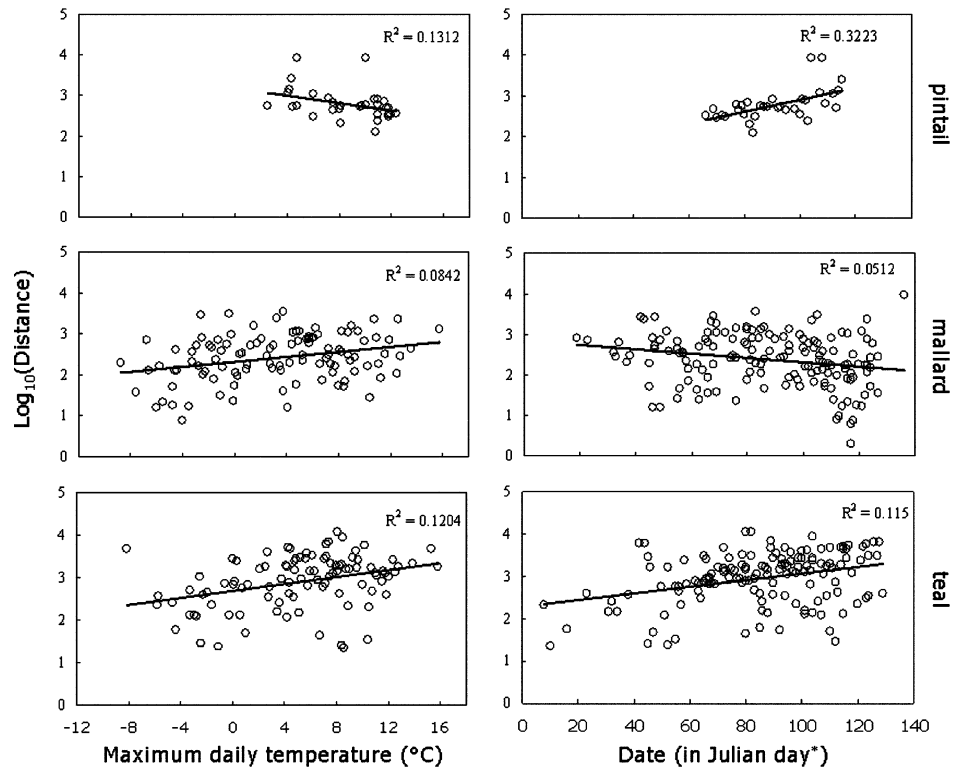
($F_{2,119} = 10.57$, $P = 0.0001$) and their interaction ($F_{2,1067} = 26,55$, $P < 0.0001$) but not by study site ($F_{2,117} = 1.74$, $P = 0.18$). Mallards choose to stay more at roosts at night than to move to distinct nocturnal foraging habitats ($t_{45} = -6.84$, $P < 0.0001$): 74.8% of the decisions taken by mallards were to stay. The same pattern was found for pintail ($t_7 = -5.93$, $P = 0.001$). Conversely, in teal, the two decisions were balanced ($t_{25} = 0.039$, $P = 0.97$), i.e., teal were equally likely to stay or to leave their roost site at night.

Effects of the environment on duck movements

As we found that the behavioral decision to leave the roost or not was affected by date (see above), we tested the effects of additional environmental factors (e.g., temperature or precipitation) on the distance traveled. The best-fitting model showed that the traveled distance varied according to study site (fixed factor) and significant interactions among maximum daily temperature, species and date (Table 2). More precisely, the distance traveled was affected by maximum, but not by minimum daily temperature (GLMM, $F_{1,1089} = 0.96$, $P = 0.33$) nor daily precipitation (GLMM, $F_{1,737} = 0.02$, $P = 0.88$). Interaction terms suggested that species reacted differently to temperature according to date (Fig. 5). Teal increased foraging distance with date and daily maximum temperature, but mallard did so only for

increasing temperature, while pintail did so only in relation to date.

Discussion

Sex, age and species effect on space use

We detected no sex or age effect on home-range size for any of the species studied. The lack of difference between sexes was expected, because at the time of our study (late winter), most individuals were already paired (Tamisier et al. 1995; Baldassare and Bolen 2006). The lack of an age effect is however surprising, because we had expected to find larger home ranges in juveniles that presumably have to explore and familiarize themselves with a new site. While this non-age effect could be due to a small sample size, it is also possible that, because our birds were caught in mid winter (i.e., at least 1 month after their arrival), they may have already learned about potential foraging grounds. Since dabbling ducks are gregarious in winter and traveled in small flocks (McNeil et al. 1992), this behavior may also explain the lack of age effect and may reveal a non-age-stratified population in winter. Because all our study species belong to the same guild, and have a similar feeding regime (granivorous to a large extent in winter, see Thomas 1982), we expected little difference among species. However,

distance traveled and home-range size and shape did differ among species. For instance, teal traveled farther and had more patchy home ranges than mallard or pintail, in accordance with the latter two species using their roost sites for foraging more often than teal. The teal is a much smaller species (350 g in average) than mallard or pintail (ca. 1,106 and 805 g, respectively: Madge and Burn 1988). Indeed, considering their smaller size, teals have relatively larger daily requirements than mallards and may therefore need to travel greater distances to feed on abundant and high-quality resources. Moreover, because dabbling ducks mainly feed on seeds during winter (e.g., Thomas 1982; Tamisier and Dehorter 1999) and typically forage in small flocks at night (Tamisier and Tamisier 1981; McNeil et al. 1992), food depletion may be a more likely mechanism of competition than interference at the end of the winter as the resources are not renewed (Bonis et al. 1995). It is also possible that smaller species were excluded by larger ones due to dominance hierarchies (e.g., Harper 1982; Poisbleau et al. 2005), leading smaller species to leave nature reserves and travel farther to find their food resources (Guillemain et al. 2002). Whatever the mechanism involved in the decision to leave the roost, teal appear to be a more risk-prone species since they leave their roosting (and usually protected) site more often than other dabbling duck species.

Temperature, study site and season effects

Severe weather conditions (i.e., low temperatures and/or high winds) affect the behavior of wintering ducks of Nearctic populations in the reduction of high-energy activities (Brodsky and Weatherhead 1985; Longcore and Gibbs 1988; Cox and Afton 1996). Indeed, we found that maximum daily temperature, rather than precipitation or minimum daily temperature, influenced distance traveled

(for example, teal and mallard increased their foraging distances in relation with maximum daily temperature). In addition, we found that time (days), through interaction with temperature, also affected daily distance traveled. During cold spells (i.e., negative temperatures at day and night), ducks reduced their energy expenditure by staying at their roost during both day and night (Gauthier-Clerc et al. 1998), enhancing gregarious behavior (see Longcore and Gibbs 1988; Ridgill and Fox 1990) and reducing deterioration in body condition during harsh environmental conditions (Owen and Cook 1977; Baldassare et al. 1986; Boos et al. 2002). The negative relation observed for pintail is more puzzling because pintail were tracked during days with positive temperatures. It is however possible that seasonal factors were involved (enhancement of movement due to pre-migratory behavior).

More interestingly, we found that study site was the main factor accounting for home-range variation. This was particularly true for teal where home-range sizes and travel distances were different for each site. We found that teals wintering in Brenne had smaller home ranges and traveled less than those of the two other study sites, and this appears to be the case at other French sites (Table 3) that have been studied. Brenne may be a particular case as hunters artificially increase resource availability on lakes. Smaller home ranges and movements by teal in Brenne may therefore result from an adjustment of their behavior in relation to higher food availability. We also found that in the Seine, teal used the same roost throughout the winter, while in the other study sites individuals were able to use different roosting sites. This was clearly related to roosting site availability, restricted in the Seine to only two places. In mallard, only the core area differed between Brenne and the Seine. Although separated by 500 km and despite these two study sites having largely different habitats

Table 3 Mean flight distances reported for wintering dabbling ducks between day roosts and nocturnal foraging habitats

Location	Species	Distance (km)	N	Density (ducks/ha)	Area	Authority
Nearctic	A. platyrhynchos	2.2–20	17	0.7[a]	Nebraska	Jorde et al. (1983)
Nearctic	A. acuta	17.4–48.8	108	6.5[b]	Louisana	Cox and Afton (1996)
Palearctic	A. platyrhynchos	1.0	67	2.2[c]	Brenne and Seine	This study
Palearctic	A. acuta	1.5	9	1.0[c]	Moëze	This study
Palearctic	A. penelope	2.8	9	1.1[d]	Saint Denis Du Payré	Fritz et al. (in preparation)
Palearctic	A. crecca	2.1	27			
Palearctic	A. crecca	1.7	21	2.0[b]	Camargue	Tamisier and Tamisier (1981)
Palearctic	A. crecca	2.2	36	1.8[c]	Brenne, Moëze and Seine	This study

[a] Density calculated from Jorde et al. (1983)

[b] Densities reported from Tamisier and Dehorter (1999)

[c] Density calculated from Legagneux et al. (unpublished data)

[d] Density calculated from Duncan et al. (1999) and Meunier and Joyeux (personal communication)

(continental lakes vs. estuary), home ranges (MCP) were of the same magnitude. Moreover, mallard is known to be more sedentary than teal in France, the latter being a typical migrating bird (Guillemain et al. 2005). In addition, reared mallard are released each year before the hunting season (Mondain-Monval and Girard 2000), and this could enhance sedentary behavior. Distance traveled increased in both pintail and teal as the season advanced. This result is in accordance with our findings on the behavioral decision showed by these species, being more likely to leave their roost at night later in the season. This could be related either to environmental or physiological changes that occur during the winter. First, resource availability may be involved because the amount of available food decreases through the winter due to seed depletion (e.g., Guillemain et al. 2000) forcing individuals to travel more or to leave the roost to find a suitable feeding habitat. Alternatively, hunting may also be a cause as duck select safe sites (Cox and Afton 1997; Tamisier and Dehorter 1999). In the present study, hunting ceased on 31 January each year (day 91 in Fig. 5), which corresponds to the median of our survey and may thus explain why teal and pintail traveled greater distances at the end of the winter. Conversely, mallard did not show these behavioral changes and may therefore suffer less from food depletion and/or hunting pressure.

Comparison between Nearctic and Palearctic duck movements

Because of the different methods that have been used to estimate home ranges and the limited number of studies on space use by duck in winter, we restricted our comparisons to night flight distances. We found that the distances traveled between roost and foraging sites in our study were similar to those of earlier studies of Palearctic duck (mean distance traveled between 1 and 4 km), but smaller than the distances traveled by North American ducks (between 2.2 and 48.8 km: Table 3). We suggest this may be explained by differences in duck densities between European and North American sites, leading presumably to different levels of competition (Table 3). The highest foraging distances were found for pintail (Cox and Afton 1996), which also showed the highest density (6.5 ducks/ha, while the average is 1.8 for Palearctic sites). Alternatively, ducks tracked in North America roosted in large wetlands, e.g., >6,000 ha for Lacassine pool (Cox and Afton 1996), or rivers where feeding sites are more distant from the roost than at our French sites, where nature reserves (i.e., the roosting sites) are small (200 ha in average in this study) and included as part of a broader wetland network. For a given size area and duck density, more patchy environments such as our study sites would provide more fringe habitats (boundaries) and thus may increase resource availability.

Zusammenfassung

Variation in der Größe des Aktionsgebietes und den Bewegungen überwinternder Gründelenten

Trotz einer langen historischen Dokumentation von Radiotelemetrie-Analysen gibt es nach wie vor keine grundlegenden Informationen über Aktionsgebiete für die meisten der weitverbreiteten Wasservogelarten, insbesondere für den Winter. Wir haben untersucht, inwieweit die Aktionsgebiete und täglichen Nahrungssuchbewegungen von Gründelenten durch extrinsische (Standort, Temperatur, Datum) und intrinsische Faktoren (Art, Geschlecht, Alter) beeinflusst werden. Wir haben 125 Individuen dreier Entenarten (Stockente *Anas platyrhynchos*, Krickente *A. crecca crecca* und Spießente *A. acuta*) in drei französischen Feuchtgebieten über vier Winter mit Radiosendern versehen und überwacht. Die Größe der Aktionsgebiete einer gegebenen Art schwankte stark zwischen unseren Untersuchungsgebieten. Überdies unterschieden sich die Arten in der Struktur ihrer Aktionsgebiete und in der Entfernung, die sie zurücklegten, um ihre Nahrungsgebiete zu erreichen (Krickenten hatten ein fleckenhaftes Aktionsgebiet und legten größere Entfernungen zurück als Stockenten). Die zur Nahrungssuche zurückgelegten Entfernungen nahmen mit Temperatur und fortschreitender Zeit (über die Wintersaison) zu, doch dieser Effekt unterschied sich zwischen den Arten, was darauf schließen lässt, dass sie unterschiedlich auf eine Erschöpfung der Nahrungsressourcen und/oder Kälte reagieren. Das „Pendelverhalten" (d.h. die Entscheidung, den Schlafplatz nachts zur Nahrungsaufnahme zu verlassen) unterschied sich zwischen Arten und Jahreszeiten. Krickenten waren einem stärkeren Risiko ausgesetzt, weil sie mit höherer Wahrscheinlichkeit nachts ihren Schlafplatz verließen. In unserer Studie suchten die Enten 1–2 km vom Schlafplatz entfernt nach Nahrung, während in Nordamerika Entfernungen von 2–48 km erfasst wurden. Wir vermuten, dass Nahrungsangebot, Jagddruck oder Populationsdichte diese interkontinentalen Unterschiede bedingen könnten.

References

Aebischer NJ, Robertson PA, Kenward RE (1993) Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325

Baker K (1993) Identification guide to European non-passerines. British Trust for Ornithology

Baldassare GAR, Bolen EG (2006) Waterfowl ecology and management, 2nd edn. Malabar, Krieger Publishing Co

Baldassare GAR, Whyte RJ, Bolen EG (1986) Body weight and carcass composition of nonbreeding Green-winged Teal on Southern High Plains of Texas. J Wild Manage 50:420–426

Barg JJ, Jones J, Robertson RJ (2005) Describing breeding territories of migratory passerines: suggestions for sampling, choice of estimator, and delineation of core areas. J Anim Ecol 74:139–149

Bodin C, Benhamou S, Poulle M-L (2006) What do European badgers (Meles meles) know about the spatial organisation of neighbouring groups? Behav Proc 72:84–90

Bonis A, Lepart J, Grillas P (1995) Seed bank dynamics and coexistence of annual macrophytes in a temporary and variable habitat. Oikos 74:81–92

Boos M, Zorn T, Le Maho Y, Groscolas R, Robin J-P (2002) Sex differences in body composition of wintering mallards (Anas platyrhynchos): possible implications for survival and reproductive performance. Bird Stud 49:212–218

Brodsky LM, Weatherhead PJ (1985) Variability in behavioural response of wintering Black Ducks to increased energy demands. Can J Zool 63:1657–1662

Brown JL (1975) The evolution of behaviour. New York

Bub H (1991) Bird trapping and bird banding. A handbook for trapping methods all over the word. Cornell University Press, New York

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information–theoretic approach. Springer, New York

Burt WH (1943) Territoriality and home-range concepts as applied to mammals. J Mamm 24:346–352

Cantoni D (1993) Social and spatial organisation of free-ranging shrews, Sorex coronatus and Neomys fodiens (Insectivora, Mammalia). Anim Behav 45:975–995

Clark RG, Shutler D (1999) Avian habitat selection: pattern from process in nest-site use by ducks? Ecology 80:272–287

Cox RR, Afton AD (1996) Evening flights of female northern pintails from a major roost site. Condor 98:810–819

Cox RR, Afton AD (1997) Use of habitats by female northern pintails wintering in south western Louisiana. J Wild Manage 61:435–443

Cox RR, Afton AD, Pace RM (1998) Survival of female northern pintails wintering in southwestern Louisiana. J Wild Manage 62:1512–1521

Devries JH, Citta JJ, Lindberg MS, Howerter DW, Anderson MG (2003) Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. J Wild Manage 67:551–563

Duncan P, Hewison AJM, Houte S, Rosoux R, Tournebize T, Dubs F, Burel F, Bretagnolle V (1999) Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. J Appl Ecol 36:11–23

Eliassen E (1960) A method for measuring the heart rate and strocke/pulse pressures of birds in normal flight. Årbock Universitet Bergen. Mathematisk Naturvitenskapelig 124:184–193

Fleskes JP, Jarvis RL, Gilmer DS (2002) Distribution and movements of female northern pintails radiotagged in San Joaquin valley, California. J Wild Manage 66:138–152

Frazer C, Longcore JR, MacAulay DG (1990) Home-range and movements of postfeldging American black ducks in eastern Maine. Can J Zool 68:1288–1291

Garrettson PR, Rohwer FC, Moser EB (2000) Effects of backpack and implanted radiotransmitters on captive blue-winged teal. J Wild Manage 64:216–222

Gauthier-Clerc M, Tamisier A, Cezilly F (1998) Sleep-vigilance trade-off in green-winged teals (Anas crecca crecca). Can J Zool 76:2214–2218

Gittleman JL, Harvey PH (1982) Carnivore home-range size, metabolic needs and ecology. Behav Ecol Soc 10:57–63

Guillemain M, Houte S, Fritz H (2000) Activities and food ressources of wintering teal (Anas crecca) in a diurnal feeding site: a case study in Western France. Rev Ecol (Terre et Vie) 55:171–181

Guillemain M, Fritz H, Duncan P (2002) Foraging strategies of granivorous dabbling ducks wintering in protected areas of the French Atlantic coast. Biodiv Cons 11:1721–1732

Guillemain M, Sadoul G, Simon G (2005) European flyway permeability and abmigration in teal Anas crecca, an analysis based on ringing recoveries. Ibis 147:688–696

Håland A (1983) Home-range use and spacing in mallard Anas platyrhynchos broods. Ornis Scand 14:24–35

Harper DGC (1982) Competitive foraging in mallards: 'Ideal free' ducks. Anim Behav 30:575–584

Hodder KH, Kenward RE, Walls SS, Clarke RT (1998) Estimating core ranges: a comparison of techniques using the common buzzard. J Rapt Res 32:82–89

Jiguet F, Arroyo B, Bretagnolle V (2000) Lek mating systems: a case study in the Little Bustard Tetrax tetrax. Behav Proc 51:63–82

Jorde DG, Krapu GL, Crawford RD (1983) Feeding ecology of mallards wintering in Nebraska. J Wild Manage 47:1044–1053

Jorde DG, Krapu GL, Crawford RD, Hay MA (1984) Effects of weather on habitat selection and behavior of mallards wintering in Nebraska. Condor 86:258–265

Kear J (2005) Introduction. In: Kear J (ed) Ducks, geese and swans. Oxford University Press, Oxford, pp 5–13

Kenward RE (2001a) A manual for wildlife radio tagging. Academic Press, London

Kenward RE (2001b) Historical and practical perspectives. In: Millspaugh JJ, Marzluff JP (eds) Radio tracking and animal populations. Academic Press, San Diego, pp 3–12

Kenward RE, Clarke RT, Hodder KH, Walls SS (2001) Density and linkage estimators of home-range: nearest-neighbor clustering defines multinuclear cores. Ecology 82:1905–1920

Kenward RE, South AB, Walls SS (2003) Ranges6 v1.2 : For the analysis of tracking and location data (Online manual). Anatrack Ltd, Wareham

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JP (eds) Radio tracking and animal populations. Academic Press, San Diego, pp 125–166

Kramer DL, Chapman MR (1999) Implications of fish home-range size and relocation for marine reserve function. Envir Biol Fish 55:65–79

Longcore JR, Gibbs JP (1988) Distribution and numbers of American Black ducks among the Maine coast during the severe winter of 1980–1981. In: Weller MW (ed) Waterfowl in winter. University of Minnesota Press, Mineapolis, pp 377–389

Mace GM, Harvey PH, Clutton-Brock T (1983) Vertebrate home-range size and energetic requirements. In: Swingland IR, Greenwood PJ (eds) The ecology of animal movement. Clarendon, Oxford, pp 32–53

Mack GG, Clark RG (2006) Home-range characteristics, age, body size, and breeding performance of female mallards (Anas platyrhynchos). Auk 123:467–474

Mack GG, Clark RG, Howerter DW (2003) Size and habitat composition of female mallard home-ranges in the prairie-parkland region of Canada. Can J Zool 81:1454–1461

Madge S, Burn H (1988) Wildfowl. An identification guide to the ducks, geese and swans of the world. Kent London

Madsen J (1998a) Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. J Appl Ecol 35:386–397

Madsen J (1998b) Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. J Appl Ecol 35:398–417

Mathevet R, Tamisier A (2002) Creation of a nature reserve, its effects on hunting management and waterfowl distribution in the Camargue (southern France). Biodiv Conserv 11:509–519

McLoughlin PD, Ferguson SH, Messier F (2000) Intraspecific variation in home-range overlap with habitat quality: a comparison among brown bear populations. Evol Ecol 14:39–60

McNeil R, Drapeau P, Goss-Custard JD (1992) The occurrence and adaptive significance of nocturnal habits in waterfowl. Biol Rev 67:381–419

Mondain-Monval J-Y, Girard O (2000) Le canard colvert, la sarcelle autres canards de surface. In: Landry P, Migot P (eds) Enquête nationale sur les tableaux de chasse à tir. Saison 1998/1999. Faune Sauvage Cahiers Techniques, Paris, pp 124–132

Nudds TD, Ankney CD (1982) Ecological correlates of territory and home range size in North American dabbling ducks. Wildfowl 33:58–62

Owen M, Cook WA (1977) Variations in body weight, wing length and condition of Mallard Anas platyrhynchos and their relationship to environmental changes. J Zool 183:377–395

Pietz PJ, Brandt DA, Krapu GL, Buhl DA (1995) Modified transmitter attachment method for adult ducks. J Field Ornith 66:408–417

Pietz PJ, Krapu GL, Brandt DA, Cox RR (2003) Factors affecting gadwall brood and duckling survival in Prairie Pothole landscapes. J Wild Manage 67:564–575

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Springer, New York

Poisbleau M, Fritz H, Guillemain M, Lacroix A (2005) Testosterone and linear social dominance status in captive male dabbling ducks in winter. Ethology 111:493–509

Powell RP (2000) Animal home-ranges and territories and home-range estimators. In: Boitani L, Fuller TK (eds) Research techniques in animal ecology: controversies and consequences. Columbia University Press, pp 65–110

Redpath SM (1995) Habitat fragmentation and the individual: tawny owls Strix aluco in woodland patches. Ecology 64:652–661

Ridgill SC, Fox AD (1990) Cold weather movements of waterfowl in Western Europe. IWRB Special Publication 13, Slimbridge

Rolando A (2002) On the ecology of home-range in birds. Rev Ecol (Terre et Vie) 57:53–73

Rotella JJ, Ratti JT (1992) Mallard brood movements and wetland selection in southwestern Manitoba. J Wild Manage 56:508–515

Schoener TW (1983) Simple-models of optimal feeding-territory size—a reconciliation. Am Nat 121:608–629

Scott DA, Rose PM (1996) Atlas of Anatidae populations in Africa and Western Eurasia. Publ. No 41. Wetlands International, Wageningen

Seddon PJ, Maloney RF (2004) Tracking wildlife radio-tag signals by light fixed-wing aircraft. Department of Conservation Technical Series, Department of Conservation, Wellington, vol 30, pp 1–23

Sinclair ARE (1983) The function of distance movements in vertebrates. In: Swingland IR, Greenwood PJ (eds) The ecology of animal movement. Oxford University Press, Oxford, pp 240–258

Tamisier A, Dehorter O (1999) Camargue, canards et foulques. Centre Ornithologique du Gard, Nîmes

Tamisier A, Tamisier M-C (1981) L'existence d' unités Fonctionnelles démontrée chez les sarcelles d'hiver en Camargue par la biotélémétrie. Rev Ecol (Terre et Vie) 35:563–579

Tamisier A, Allouche L, Aubry F, Dehorter O (1995) Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species. Wildfowl 46:76–88

Thomas GJ (1982) Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. J Zool 197:131–172

Venables WN, Ripley BD (2002) Modern applied statistics with S, 2nd edn. Springer, New York

Walls SS, Kenward RE (1995) Movements of radio tagged buzzards Buteo buteo in their first year. Ibis 137:177–182

Walls SS, Mañosa S, Fuller RM, Hodder KH, Kenward RE (1999) Is early dispersal enterprise or exile? Evidence from radio-tagged Buzzards. J Avian Biol 30:407–415

Webb JK, Shine R (1997) A field study of spatial ecology and movements of a threatened snake species, Hoplocephalus bungaroides. Biol Con. 82:203–217

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego