

## What is the spatial unit for a wintering teal *Anas crecca*? Weekly day roost fidelity inferred from nasal saddles in the Camargue, southern France

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Dabbling ducks generally use distinct day roost and nocturnal habitats, the set of which constitute their 'functional unit'. The rate at which these birds may switch between day roosts has never been quantified. Using resightings of nasal-saddled birds and capture-recapture modelling in the Camargue, southern France, we estimated the weekly probability that a teal *Anas crecca* switches from one day roost to another one nearby (transition probabilities). We also estimated the probability that a teal survives and remains in our study area, consisting of four neighbouring roosts (apparent survival). Birds were highly faithful to one specific water body if they remained in our study area (i.e. weekly rate of switching between roosts was only about 2-6%), but the probability that an individual remained within one of the four roosts from one week to the next (local weekly apparent survival rate) was only 60-70%. Intensive search efforts led to a 60% detection probability. Low local apparent survival coupled with very high site fidelity within the system suggests that two distinct strategies may coexist, i.e. frequent movement between distant winter quarters vs very high fidelity to the very same local wetland. Such strategies may be used successively by the same individuals, or may alternatively represent distinct bird categories (i.e. transients vs residents). In any case, these different strategies suggest that habitat management procedures need to be considered at both local and flyway scales simultaneously. The former may ensure that sites repeatedly used by the same individuals can provide adequate conditions to birds when they remain in a given winter quarter, while the latter will ensure transient birds find appropriate sites within the network of distant wetlands they may use as successive wintering quarters during a season.

**Key words:** *Anas crecca*, capture-mark-recapture, nasal saddles, roost fidelity, teal, transience

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Habitat selection by wintering dabbling ducks is typically considered to reflect their use of 'functional units': birds gather on one roost during the day for social and comfort activities, and disperse at night into the associated surrounding foraging areas (Hughes & Green 2005). In its formal definition, the functional unit of a dabbling duck thus consists of one day roost to which individuals are faithful, and a limited number of nocturnal foraging areas around this roost, whose use may depend upon, for instance, flooding conditions and relative food availability. To our knowledge, the fact that wintering dabbling ducks distribute themselves and partition their activities in general accordance with the functional unit principle has always been supported by studies dealing with wintering duck habitat selection (e.g. Tamisier & Tamisier 1981, Cox & Afton 1996, Duncan et al. 1999, Guillemain et al. 2002, Legagneux et al. 2009a). However, other studies also suggest that, despite following this general pattern, some individuals may nonetheless move within their winter quarter and therefore switch between day roosts separated by distances of several kilometres (Guillemain et al. 2002, Legagneux et al. 2009b). The aim of our study was to quantify the extent to which such switches between day roosts occur, by means of resightings of nasal-saddled teal *Anas crecca*. Such definition of the scale at which habitat selection occurs in wintering ducks may obviously be useful in terms of wetland management policies. The rate at which ducks move locally between water bodies may also have a key influence on the rate at which such birds disperse pathogens (e.g. Highly Pathogenic Influenza A viruses) between marshes over short distances (Jourdain et al. 2007, Lebarbenchon et al. 2009, Brochet et al. in press).

## Methods

A total of 118 teal were captured with baited funnel traps at the Rendez-Vous marsh in the Tour du Valat, Camargue, southern France ( $43^{\circ}30'N$ ,  $04^{\circ}40'E$ ), from 9 October 2007 to 11 January 2008, and released in the same place (Fig. 1). These consisted of 66 females (21 adults, 44 first-year birds and one individual of unknown age) and 52 males (23 adults, 26 first-year birds and three of unknown age). Individuals of unknown age were discarded from the analysis. All birds were fitted with

individually-coded plastic nasal saddles of the type described by Rodrigues et al. (2001), whose lack of deleterious effect to dabbling ducks was demonstrated by Guillemain et al. (2007). Marked teal were then searched for daily over the three main duck day roosts of the Tour du Valat estate, namely the Rendez-Vous (11 ha), the Garcines (2.2 ha) and the Saint-Seren (69 ha) marshes, as well as on 5 ha of the nearby Salin de Badon marsh (see Fig. 1). These sites are shallow (< 1 m depth in most parts) freshwater wetlands, permanently flooded in winter, and are all protected areas that are either closed to the public (the three at Tour du Valat) or only open to a limited number of visitors (Salin de Badon). The distance between our four study sites range from 800 m to ca 5 km. Although these are not the only teal roosts in the area, they were the main roosts where teal were both abundant and could be observed regularly without disturbance (all sites have hides from which observations were performed, except Garcines). A minimum of one hour was spent searching for marked teal at each of the roosts, almost every day of the week (Monday–Friday) from when the first teal was caught until 21 March, i.e. over 24 successive weeks. Presence/absence of each bird in each day roost was then coded for each week. A bird using several roosts in the course of one week was considered as having switched when at least one roost was different between two consecutive weeks. When a bird was observed on one roost a given week and on several roosts the next week, we assumed that it had switched to the most distant roost (observations on nearer roosts were assumed to have been made while the bird was moving between the most distant roosts). Information about marked birds reported as seen or shot by hunters elsewhere (there was no hunting on any of the four day roosts) was also collected, but was too scarce to be used in the analyses. We thus relied on a multistate capture-recapture modelling procedure including four different states, corresponding to the four day roosts where teal could be observed alive: Rendez-Vous (i.e. the ringing site), Saint-Seren, Salin de Badon and Garcines. Survival, recapture/resighting and transition probabilities were estimated separately for each age/sex group, i.e. first-year females, adult females, first-year males and adult males. Since data were relatively sparse, we applied constraints for modelling transition probabilities. We modelled transitions from the ringing site A differently than from transitions of roost sites B, C

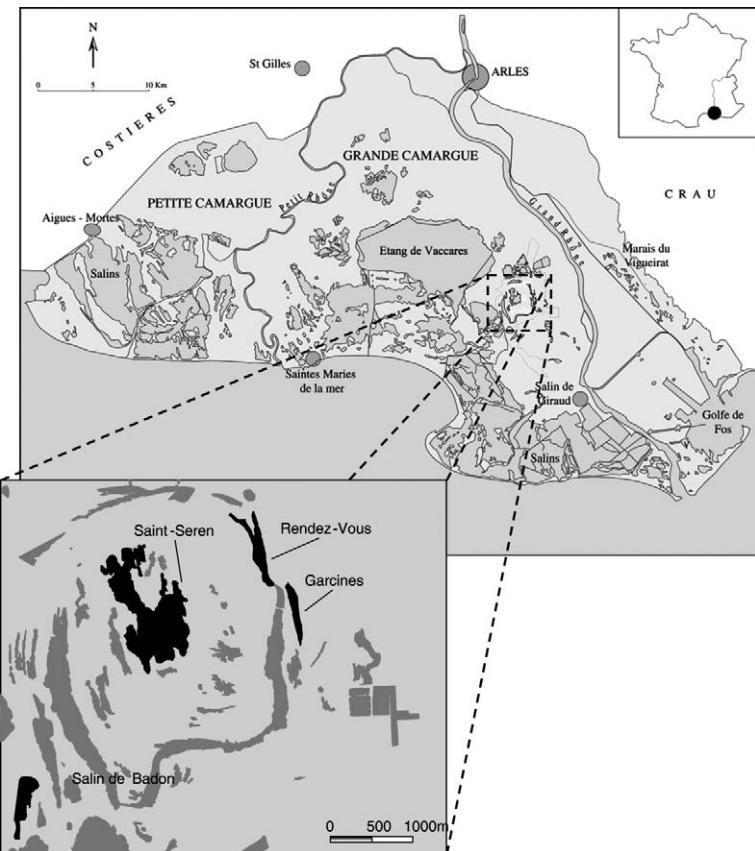


Figure 1. The study area showing the position of the Camargue in France (top right), the Camargue area as a whole (centre) and a detailed view of the local wetlands (dark grey) and four study sites (black) (bottom left). Individual maps provided by Tour du Valat.

and D, but transitions from B, C and D were modelled as being equal.

Because the rate of movements between roost sites may vary across the season, or according to body condition, we examined the month of ringing and bird body mass at the time of ringing in addition to the age.sex structure mentioned above. Since marked birds were searched for by the same observer (JF), following the same protocol on all sites, we modelled resighting probabilities as constant, and independent of any covariate.

Apart from the age.sex interaction, which was modelled as a group structure, we considered additive models only. Given our covariates (age, sex, month and mass at ringing), and data sparseness, interactions made little biological sense and would have led to overparameterisation. We therefore used the preceding criteria to build 55 *a priori* models, and we carried out our model selection using Akaike's Information Criteria with small sample size correction ( $AIC_c$ ; Burnham & Anderson 2002), as implemented in program MARK (White & Burnham 1999).

## Results

The results of the model selection process are presented in Table 1. All six best ranking models ( $AIC_c$  weight  $> 0.01$ ) included the effect of month of ringing on both survival and transition probabilities (estimate  $= 0.1 \pm 0.027$  SD). The best- $AIC_c$  model accounted for  $\sim 56\%$  of  $AIC_c$  weight. According to this model, the weekly probability to move from ringing site A to one of the other roost sites (estimate  $\pm$  SE:  $0.019 \pm 0.005$ ) was lower than the weekly probability to leave roosts B, C or D for site A ( $0.062 \pm 0.018$ ). Both these transition probabilities were constant across age and sex classes.

Because data for birds seen or shot elsewhere could not be used, permanent emigration to areas outside our study area was not included in the models. For all individuals, local weekly survival was  $0.705 \pm 0.044$  on the ringing site and  $0.604 \pm 0.092$  on roosts B, C and D. Weekly recapture probabilities on ringing site A were modelled as independent of any covariate and were estimated to  $0.375 \pm 0.032$ . Similarly, weekly resighting proba-

Table 1. Top ranking models obtained from model selection. S: survival probabilities, P: capture/resighting probabilities,  $\Psi$ : transition probabilities. Age: probability varies between first year and adult individuals. Sex: probability differs between males and females. np: number of parameters in the model.

Model	AIC <sub>c</sub>	$\Delta AIC_c$	AIC <sub>c</sub> weight	Likelihood	np
S <sub>month</sub> P $\Psi_{month}$	1453.8	0.00	0.561	1.000	7
S <sub>age + month</sub> P $\Psi_{sex + month}$	1456.8	3.00	0.125	0.223	11
S <sub>month</sub> P $\Psi_{sex + month}$	1457.0	3.17	0.115	0.205	9
S <sub>sex + month</sub> P $\Psi_{month}$	1457.6	3.79	0.084	0.150	9
S <sub>age + month</sub> P $\Psi_{age*sex + month}$	1458.7	4.89	0.049	0.087	12
S <sub>month</sub> P $\Psi_{age*sex + month}$	1459.3	5.43	0.037	0.066	13
S <sub>month</sub> P $\Psi$	1461.8	7.99	0.010	0.018	7

bilities were modelled as constant over time and independent from any covariate, and were equal to  $0.619 \pm 0.086$ .

## Discussion

Our study highlights two general patterns: wintering teal show a low apparent survival at their winter quarter, but a high site fidelity to their day roost if they survive and remain within the same winter quarter.

From one week to the next, local apparent survival rate was 70% at the ringing site and 60% at the three other study marshes, for all age and sex classes. This suggests that many birds either die or leave the area each week, in accordance with results obtained in earlier studies. Pradel et al. (1997) indeed demonstrated a high turnover within wintering teal populations before the 1970s, which was confirmed by more recent work in the Camargue and in the Loire Estuary (Western France) by A. Caizergues, M. Guillemain, C. Arzel, O. Devineau, G. Leray, D. Pilvin, M. Lepley, G. Massez & V. Schricke (unpubl. data). A large share of the wintering birds may thus be considered as transients, spending only short periods of time within each of several wintering quarters. Alternatively, these results may indicate a very high mortality rate, even at a weekly scale. While apparent survival, to our knowledge, has never been quantified with such temporal precision (mostly because visual marking has seldom been used in dabbling ducks so far), such high transience may explain how teal hunting bags can be so high compared to bird counts. At the scale of France, the most recent estimate of the annual teal bag is over 330,000 individuals (Mondain-Monval & Girard 2000), while the total winter count was under 100,000 (Deceuninck 2004). For the

Camargue only, the annual teal hunting bag is estimated to be around 25,000 individuals (J-Y. Mondain-Monval, pers. comm.), while winter counts vary between years from ca 30,000 to 50,000 individuals (Kayser et al. 2008).

Within the local network of day roosts, teal remaining in the area appeared to be highly faithful to one particular marsh, since the weekly transition probability from the ringing site to another marsh was only about 2%. This corroborates earlier studies relying on radio-tracking techniques, suggesting that ducks repeatedly come back to the same roost day after day (e.g. Tamisier & Tamisier 1981, Cox & Afton 1996, Guillemain et al. 2002, Le-gagneux et al. 2009a). Another conclusion from our study is that teal are unlikely to simply have moved to surrounding marshes when they are not detected at their traditional day roost, but should rather be considered as having left the wintering quarter overall, or being dead. An alternative explanation to that result would be the effect of trap-dependence (in this case, trap-happiness). Indeed, on ringing site A, teal were captured using a baited trap and transition rates (i.e. low transition rate from A to B, C and D, higher transition from B, C and D to A) could indicate that teal tended to go back to the ringing site to find an easy food source. Although we did not test specifically for trap-dependence, we believe its effect to be relatively weak, because the higher transition rate from B, C and D to A is only based on resightings, not trap recaptures at any of the sites. It is possible that site A was more attractive than the other sites for some unknown reason (e.g. safety or roost quality), including the attraction of the trap or trapping bait, but this would need further work to ascertain.

In terms of propagule or disease transport (e.g. Lebarbenchon et al. 2009, Brochet et al. 2009) the above results suggest that teal are relatively unlikely

to act as efficient local vectors from one day roost to another adjacent day roost directly. The potential for indirect dispersal via nocturnal areas remains to be tested, but should be relatively higher, given the fact that individuals in the Camargue disperse short distances to feed at night around their day roosts (Guillemain et al. 2008), i.e. interconnectivity via birds from nearby roosts should be relatively frequent at night. In fact, ring recoveries from one nearby nocturnal foraging area suggest it was used equally by teal from different day roosts (A-L. Brochet, unpubl. data). It is also possible that the stability of our study wetlands, in terms of regular freshwater availability and low human disturbance, may have contributed to the high site faithfulness recorded here for teal. Dabbling ducks may be more likely to move between roosts or use them sequentially over time when these have more variable environmental conditions (e.g. Kloskowski et al. 2009 for changing diurnal distribution in variable wetlands in southwestern Spain), or are submitted to higher disturbance.

Finally, our study suggests that wintering teal may rely on two distinct strategies, i.e. frequent movement between distinct wintering quarters versus, on the contrary, very high fidelity to the same local day roost day after day. Such strategies may possibly be used successively by the same individuals or, as suggested elsewhere (i.e. French Atlantic Coast sites; A. Caizergues, M. Guillemain, C. Arzel, O. Devineau, G. Leray, D. Pilvin, M. Lepley, G. Massez & V. Schricke, unpubl. data), represent two distinct categories of individuals: resident and transient birds. Our results do not allow us to distinguish between these two possibilities, but suggest that birds may benefit from the protection of wetland sites at two different geographic scales. Because they repeatedly use the same sites when they remain within a winter quarter, they would directly benefit from the identification and protection of these water bodies. However, because they also frequently leave their winter quarters, presumably for other large wetland complexes within their wintering range, they would also benefit from adequate protection and management of a network of sites, so as to let transient birds find adequate conditions while they travel between regions or even countries during the winter period.

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