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Fuelling rates of garganey (*Anas querquedula*) staging in the Camargue, southern France, during spring migration

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Abstract Most species of long-distance migratory birds put on energy stores to fuel their travels. However, recent studies have highlighted the potential costs associated with carrying too much fuel, either through increased predation risk or decreased flight efficiency. Consequently, it is now widely accepted that migratory birds should carry optimal rather than maximum fuel loads. Information from 372 garganey (*Anas querquedula*) ringed and recaptured at least once during the same spring in the Camargue, southern France, was used to document fuelling rates of individual ducks in relation to environmental variation and individual variation in condition. On average, garganey added very little fuel stores in the Camargue (mean gain per day = 0.33 g, less than 0.5% of mean body-mass in total over an average stay of 5 days). Fuelling rates were negatively correlated with body mass at capture, but it cannot be excluded that this pattern was a statistical artefact. Given their body-mass at ringing, garganey could potentially still fly long distances when they stop in the Camargue. It is therefore likely that the aim of their stay in southern France is more for resting than refuelling, a finding that may have implications for the proper management of stop-over sites.

Keywords *Anas querquedula* · Body condition · Camargue · Fuelling rates · Migration

Introduction

It is well established that energy stores of adult breeding birds are correlated with their breeding success. For example, females may produce more offspring if they manage to build larger energy stores before starting reproduction (e.g. Ebbinge and Spaans 1995), because they will be able to produce more eggs of better quality (Ankney et al. 1991; Esler and Grand 1994) and/or because they will be able to reduce the time spent feeding and hence maximise time allocation to territory establishment or nest attendance (Afton 1980; Gloutney and Clark 1991; Sandberg and Moore 1996). For males, an increase in energy stores may enable them to allocate more time to social display, possibly resulting in a higher dominance status and mating success (Wishart 1983; Holmberg et al. 1989; Sandberg and Moore 1996). In addition, heavier males may devote more time to mate guarding and provide more protection against predators, thus increasing the pair's breeding success (Sandberg and Moore 1996).

Storing large amounts of fat also has its drawbacks, as reviewed by Witter and Cuthill (1993); higher body-mass may hamper locomotion, especially for flight, as the mechanical power requirement of flight is an accelerating function of body-mass (e.g. Pennycuik 1975; Kvist et al. 2001). Heavier birds are also less manoeuvrable and have more difficulty in taking off (e.g. Witter et al. 1994) which, together with the fact that maintenance of higher body-mass requires longer feeding times (hence longer periods exposed), should increase predation risk (e.g. Lima 1986). As a consequence of the above trade-off, many studies, both theoretical (Lima 1986; McNamara and Houston 1990; Witter and Cuthill 1993) and empirical (e.g. Freed 1981; Rogers 1987; Witter et al. 1995; Gosler 1996; Schaub and Jenni 2000),

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have shown that birds aim at reaching an optimal body mass during migration stop-overs. This means that birds do not necessarily use stop-over sites as fattening places if they still have enough fuel for migration.

In the context of this trade-off between the costs and benefits of carrying extra fat stores, the fuelling rate on the staging areas may be a key determinant of the migration strategy. Fuelling rate affects the speed of migration and consequently the date of arrival at the breeding grounds, potentially a main determinant of breeding success (e.g. Duncan 1987; Alerstam and Lindström 1990; Lindström and Alerstam 1992; Klaassen and Lindström 1996; Blums et al. 1997). In addition, for large birds like ducks, body condition upon arrival at the breeding grounds may depend not only on the environmental conditions there, but also on their ability to build-up stores at wintering and migratory stop-over sites (e.g. McLandress and Raveling 1981; Tamisier et al. 1995; Klaassen et al. 2001; Klaassen 2002).

To date, fuelling rates of migrants have been mainly documented in passerines, waders, and a few geese (review in Lindström 1991, 2002). With the exception of mallard (*Anas platyrhynchos*; LaGrange and Dinsmore 1988), fuelling rates of dabbling ducks are unknown. This is unfortunate, since they face high levels of disturbance and massive reductions in habitats. Dabbling ducks are hunted in many countries and make use of wetlands as stop-over sites which, compared to most other habitats, are highly spatially segregated and heterogeneously distributed between their wintering and breeding areas. Over the past century, and at an ever-increasing rate, the quality of these sites has decreased, leading to increasing distances between suitable sites for the migrating waterfowl. Management of these wetlands and their inhabitants requires sound ecological knowledge of the species' annual cycle and knowledge of the course, extent and requirements of migratory fuelling (Bairlein 1998).

Garganey (*Anas querquedula*) are declining over most of their breeding range (Tomialojc et al. 1995), thus requiring special attention to the constraints affecting the species in spring and summer. Fuelling rates in (Western Palearctic) migrating dabbling ducks are generally difficult to ascertain because their breeding ranges are huge and the breeding, wintering and staging areas of different populations overlap greatly. Fortunately, this problem does not exist with garganey, which is a long-distance migrant. Birds from the European/West African population winter almost exclusively between 10° and 20°N, while they breed mainly in Russia, Ukraine and Belarus (Scott and Rose 1996; Schricke 2001). Many birds cross Western Europe through Spain, France and Italy in spring, but these countries serve mainly as staging areas since they host only a tiny fraction of the breeding population [under 1,000 pairs (Schricke 2001) whereas total population size is estimated at 2 million individuals (Scott and Rose 1996)]. In the Camargue, southern France, garganey traditionally stop during spring and autumn migration, but only

exceptionally do the birds winter or breed: a female with five young in 1990 was the first proof of breeding in the area since 1966, and the species has been recorded in the Camargue only twice (one individual each time) in November and January between 1990 and 1994 (Thibault et al. 1997).

In this paper, we use information from garganey ringed and recaptured within the same season over 13 years in the Camargue to document fuelling rates of individuals during spring migration. We analyse males and females separately, and study the environmental and individual factors that may affect these rates.

Methods

Study site

Garganey in the Camargue were caught at the Domaine de la Tour du Valat (43°30'N, 4°40'E) between March 1952 and May 1974 using standard dabbling duck automatic traps hidden in the vegetation (details of the Camargue technique in Bub 1991). Traps were baited with rice, which may lead to a slight over-estimation of bird weight at capture. However, this should not affect the results since the goal of the study was to calculate the rate at which individuals gain body mass rather than describing average body mass in the population. Using baited traps may also bias sampling towards food-stressed individuals (Dufour et al. 1993). However, in this case one would predict that the body mass of birds recaptured at least once would be lower than that of birds never caught again after initial ringing, which was not the case (see below).

Bird measurements

Ducks were sexed using plumage criteria and examination of the cloaca and bursa of Fabricius. Because garganey can be sexually mature at 1 year of age, the age of individuals often could not be ascertained in spring, and ages were consequently not distinguished in the analyses. A total of 2,447 individuals was ringed at the Tour du Valat between March 1952 and May 1974. The analysis was restricted to birds ringed during the period 1 February to 31 May each year, assumed to encompass the whole period of spring migration (Fig. 1). During this period, 1,978 birds were caught of

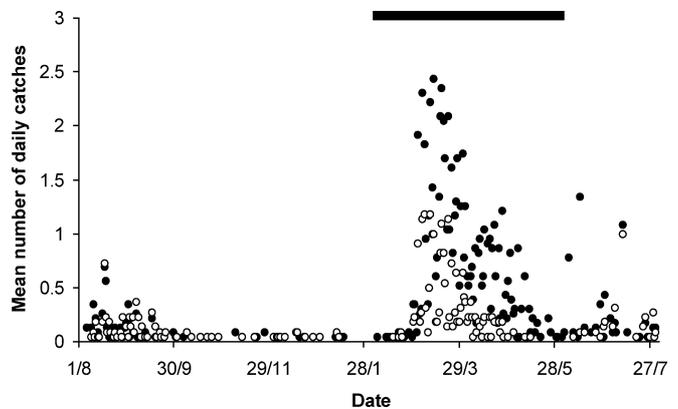


Fig. 1 Mean number of garganey (*Anas querquedula*) (black dots males, white circles females) ringed per calendar date (average of all years of ringing) at the Tour du Valat, 1952–1974. The horizontal bar at the top of the graph shows the limits of the season considered in the analyses, i.e. first catches between 1 February and 31 May

which 383 were recaptured at least once during the same spring. Data from the years when there was only one individual of a given sex (i.e. 1953 for males and 1954, 1956 and 1971 for females) were discarded from the analyses. In addition, body mass was not measured in three males at ringing and four males at last recapture. The dataset therefore consisted of 316 males caught between 1954 and 1966, and 56 females caught between 1957 and 1963 (Fig. 2). Most of these birds were recaptured only once or twice; 90% of the birds were caught less than 5 times during the same spring. The number of days between first catch and last recapture varied between 1 and 67 days (median: 7 days). Average time between successive captures was 5.2 days (± 5.3 SD, range: 1–38, $n=372$ individuals).

The fuelling rate of an individual might vary depending on whether it is 'early' or 'late' within the migration season. Also, the onset and end of the migratory season are likely to change from one year to another depending on environmental conditions. Therefore, we included in the analyses for each individual the number of days elapsed since the first arrival of migrants that year, rather than the calendar date. The first arrival of migrants was arbitrarily assumed to be the first day of a year when at least two garganey were caught simultaneously (which was always followed by more captures on the following days). This date of first arrival of migrants varied from 19 February (1960) to 18 March (1966), with no significant trend over years (Spearman rank correlation, $r_s = -0.55$, $P > 0.06$).

Birds caught were weighed to the nearest 1 g in both sexes. The frequency distributions of body masses did not differ between females caught only once and females subsequently recaptured during the same spring (Kolmogorov-Smirnov tests: females: $P > 0.10$; Fig. 3). In males, the P -value was just equal to the significance threshold ($P = 0.05$). Also average body mass did not differ significantly between females caught only once and females subsequently recaptured ($311.7 \text{ g} \pm 39.8 \text{ SD}$, $n=410$ and $316.1 \text{ g} \pm 37.2 \text{ SD}$, $n=56$; $t = -0.78$, $P > 0.40$). Although in males this difference was statistically significant and birds subsequently recaptured were heavier on average than birds that were ringed and never recaptured, this difference was only 6 g, or less than 2% of average body mass ($345.1 \text{ g} \pm 38.7 \text{ SD}$, $n=316$ and $339.3 \text{ g} \pm 39.0 \text{ SD}$, $n=1180$, respectively; $t = -2.39$, $P = 0.0171$). It could therefore not be concluded that the body mass of birds recaptured at least once was lower than that of birds never caught again, nor that use of baited traps biased the sample towards food-stressed individuals.

The flattened wing length at ringing was measured to the nearest 1 mm. Only 9 out of the 372 birds were still moulting when first caught. Moulting feathers in this case were small body feathers, not remiges. These birds were retained in the sample. Initially, we aimed to correct body mass for structural size to obtain a body condition index. However, in males there was only a weakly significant positive relationship between body mass and wing length ($r = 0.18$, $P < 0.05$). In females, the relationship was non-significant ($r = 0.12$, $P = 0.37$). Even when considering a potential effect of the

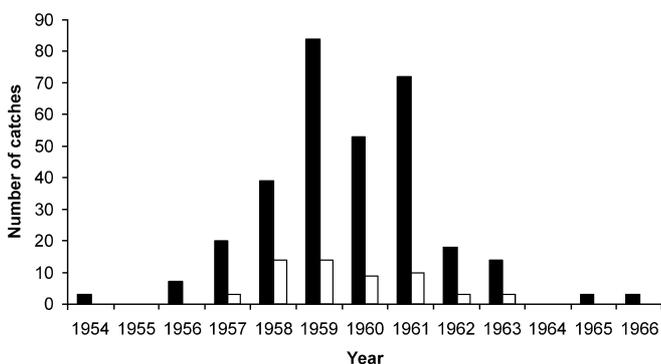


Fig. 2 Annual total number of garganey (black columns males, white columns females) caught and recaptured at least once at the Tour du Valat during the same spring

year of capture and of the number of days elapsed since arrival of first migrants in addition to wing length (to take into account potential time effects on the mass vs size relationship), models only explained 11% and 29% of variation in body mass of males and females, respectively. Because of these poor relationships, we considered it inappropriate to derive a body condition index from the residuals of the reduced major axis linear regression of body mass on wing length (Green 2001). Instead, body mass at ringing was considered to reflect body condition. Because of sexual size dimorphism (Fig. 3), analyses were carried out separately for males and females.

Data analyses

We first tested whether body mass differed between sexes and, for each sex, if body masses differed between years or showed a significant trend with time within the migration season, i.e. if body mass was significantly correlated with the number of days between the first arrival of migrants and ringing date. Body mass gain (in grams per day) between first and last capture was then computed for each individual. We tested if there was a significant difference in body mass gain between years, to analyse the potential effects of annual differences in the environment. Then, for each individual, the effects of day of capture (since first arrival of migrants), number of days between ringing and last recapture, initial body mass, and average temperature at the Tour du Valat between capture and last recapture were assessed through a backwards stepwise general linear model (threshold P -value 0.05). All analyses were run separately for the two sexes. Correlation matrices for the independent variables in the male and female GLM models are shown in Table 1. Temperature data were only available from 1 January 1959 onwards, except for March 1960, and hence for only 219 out of the 316 males, and 32 of the 56 females. All analyses were run with Statistica (Statsoft 2002).

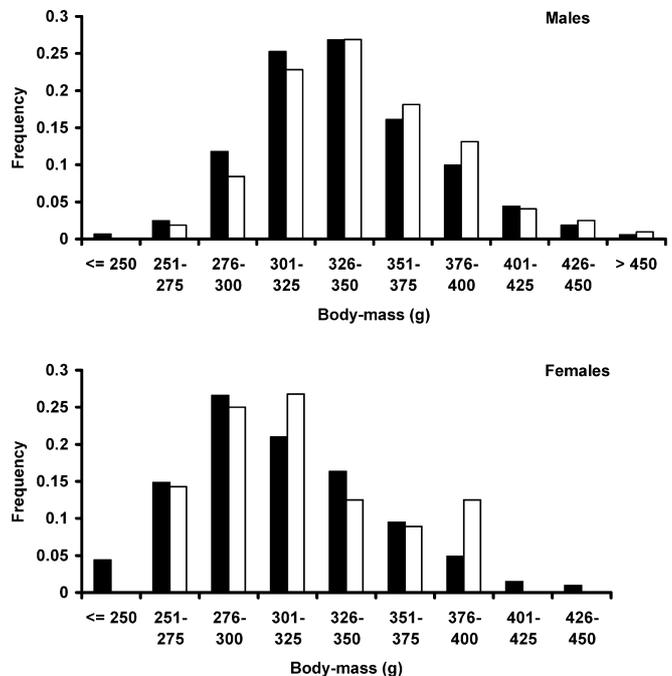


Fig. 3 Frequency distributions of body masses of female (bottom) and male (top) garganey ringed and recaptured (white columns) or ringed and not recaptured (black columns) at the Tour du Valat. For each sex and category (either ringed and recaptured or ringed and not recaptured), frequencies refer to the number of individuals in a given body-mass class as a proportion of the total number of individuals. See text for statistics

Table 1 Correlation matrices between the independent variables entered in the GLM model to explain variations of body mass change in male ($n=316$ individuals) and female ($n=56$) garganey (*Anas querquedula*). Significant correlations at $P<0.05$ are indicated by an asterisk. Abbreviations are: *DAY* number of days since arrival of first migrants; *NBDAYS* number of days between ringing and last recapture; *IBM* initial body mass at ringing; *TEMP* average temperature at the Tour du Valat between capture and last recapture. All correlations are Pearson coefficients. Note that due to missing values, sample size in correlations including temperature is 219 for males, and 32 for females

	DAY	NBDAYS	IBM
Males			
DAY			
NBDAYS	-0.06		
IBM	0.10	-0.15*	
TEMP	0.77*	0.28*	0.04
Females			
DAY			
NBDAYS	0.09		
IBM	0.25	-0.08	
TEMP	0.76*	0.43*	0.07

Results

Body mass

Males were heavier than females at ringing ($345.2 \text{ g} \pm 38.7 \text{ SD}$, $n=316$ and $316.1 \text{ g} \pm 37.2 \text{ SD}$, $n=56$, respectively; $t=5.22$, $P<0.0001$; Fig. 3).

The body mass of males at ringing did not show any significant trend with increasing number of days since arrival of first migrants ($r^2=0.01$, $df=314$, $P=0.068$; Fig. 4). A significant difference was observed between years of capture (ANOVA: $F_{10,305}=2.14$, $P=0.021$). However, year only explained 6.6% of male body mass variation and Bonferroni-adjusted t -tests showed that only the average values from two years differed significantly from one another ($P<0.05$): 1960 ($356.2 \text{ g} \pm 45.8 \text{ SD}$, $n=53$) and 1963 ($313.1 \text{ g} \pm 35.3 \text{ SD}$, $n=14$).

In females, body mass did not show a significant trend with increasing number of days since arrival of first migrants ($r^2=0.07$, $df=54$, $P=0.060$; Fig. 4), and did not differ significantly between years (ANOVA: $F_{6,49}=0.61$, $P=0.720$).

Fuelling rates

In males, fuelling rates differed significantly between years (ANOVA: $F_{10,305}=2.85$, $P=0.0021$). However, Bonferroni-adjusted t -tests showed that this was only due to a significant difference ($P<0.05$) between average values from two years: 1960 ($-4.0 \text{ g.day}^{-1} \pm 9.5 \text{ SD}$, $n=53$) and 1961 ($2.7 \text{ g.day}^{-1} \pm 8.9 \text{ SD}$, $n=72$). When only the 219 males for which temperature data were available were considered, and temperature was included in the first step of the GLM to explain variations in body mass gain, the final model at the end of the backwards

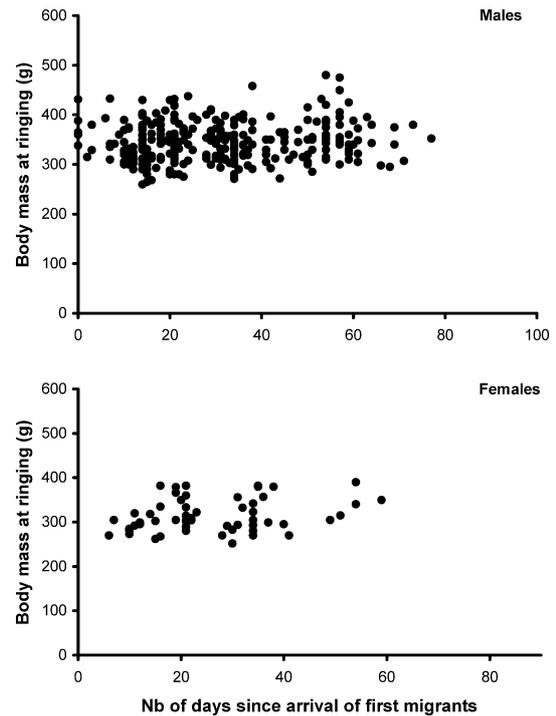


Fig. 4 Initial body mass of male (*top*) and female (*bottom*) garganey in relation to the number of days between their capture date and the date at which the first migrants arrived that year. Neither of the two regressions was significant (see text)

Table 2 Best fitting models of variation in individual body-mass gain (g day^{-1}). Only final models of backwards stepwise general linear models are presented (see Methods for complete list of dependent factors and variables used). Sample size was 316 males and 56 females

	Estimate \pm SD	F	df	P
Males				
Model		37.78	2	<0.0001
No. days since arrival of first migrants	-0.10 ± 0.02	17.66	1	<0.0001
Body mass at ringing	-0.08 ± 0.01	50.92	1	<0.0001
Females				
Model (body mass at ringing)	-0.06 ± 0.02	8.32	1	0.0056

stepwise procedure retained only the initial body mass and number of days since arrival of first migrants (final model: $F_{2,216}=28.65$, $P<0.0001$, $r^2=0.21$). The analysis was therefore re-run without including temperature, and considering all 316 males. The result of the backwards stepwise procedure was similar, as only the initial body mass and the number of days since arrival of first migrants were eventually retained (Table 2). This model explained 19.4% of the variance in body mass gain, of which 74% was explained by initial body mass alone. Males gained body mass when their initial condition at ringing was low, and lost body mass when their initial condition at capture was high (Fig. 5).

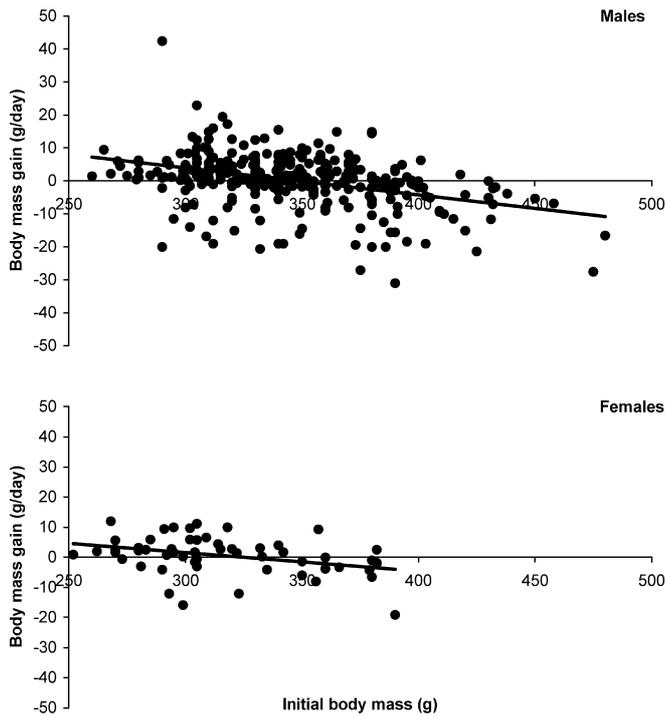


Fig. 5 Fuelling rates of male (*top*) and female (*bottom*) garganey in relation to their initial body mass at capture. Regressions were significant in both cases ($r^2=0.15$, $df=314$, $P<0.0001$ and $r^2=0.13$, $df=54$, $P<0.01$, respectively)

In females, no significant differences in fuelling rates were detected between years (ANOVA: $F_{6,49}=0.77$, $P=0.601$). When only the 32 females for which temperature data were available were considered, and temperature was included in the first step of the GLM to explain variations in body mass gain, the final model at the end of the backwards stepwise procedure retained only the initial body mass (final model: $F_{1,30}=5.25$, $P=0.0291$, $r^2=0.15$). The analysis was therefore re-run without including temperature, and considering all 56 females. The result of the backwards stepwise procedure was similar, as only the initial body mass was eventually retained (Table 2). This model explained 13.4% of the variance in body mass gain, with the same pattern of decrease in body-mass gain with increasing initial body condition at capture (Fig. 5).

Mean body-mass gain was close to nil in both sexes: $0.27 \text{ g}\cdot\text{day}^{-1} \pm 8.22 \text{ SD}$ ($n=316$) in males and $0.68 \text{ g}\cdot\text{day}^{-1} \pm 6.29 \text{ SD}$ ($n=56$) in females and did not differ significantly between sexes (t -test: $t=-0.34$, $P=0.737$). On average, the body mass of garganey during their stay in the Camargue hardly changed.

Discussion

Average body-mass changes

On average, garganey did not accumulate significant reserves in the Camargue: 0.33 g per day and therefore

less than 2 g for an average stay of approximately 5 days, i.e. less than 0.5% of average body mass. It remains possible that garganey do not put on weight in the Camargue because foraging conditions are poor. However, the fact that birds could have found food in the trap and that foraging is a minor activity for this species in the area in spring (J-Y. Pirot, unpublished data) does not support this hypothesis. Potential predation pressure was not measured, so it cannot be excluded that predation risk prevented birds from engaging in foraging activities. Further studies on available food stocks and behaviour of spring-staging dabbling ducks are currently being undertaken (C. Arzel, personal communication).

Stress linked to capture and manipulation has been found to affect fuelling rates of migratory birds, leading in some cases to body mass loss (e.g. Ens et al. 1990). There was no significant difference in average body-mass change between birds recaptured once, twice, 3 times, 4 times or 5 or more times (ANOVA: $F_{4,311}=1.66$, $P=0.159$). It is therefore unlikely that the lack of fattening observed in the birds resulted from the handling during capture. Another hypothesis could be that birds do not put on weight because they devote most of their time to non-foraging activities. In spring, social displays to acquire a mate or mate guarding by males would be good candidates for such activities. However, this is most unlikely since pair-bonds are very strong in this species, rape attempts are very rare and most (i.e. 97%) females are already paired at the end of winter (Cramp and Simmons 1977, and references therein). Behavioural observations in the Camargue in March (J-Y. Pirot, unpublished data) have shown that 100% of females were paired, and that courtship was very infrequent.

Of course, because garganey do not put on weight at the Camargue stop-over, the question arises as to why this site is not by-passed altogether during spring migration. Although some garganey may have passed through Spain before arriving in the Camargue, most had probably just crossed the Mediterranean Sea. Only three garganey ringed in the Camargue and one of 61 recovered garganey ringed in Britain were recovered in Spain between December and May (Owen et al. 1986). Furthermore, garganey are only occasionally observed in the Maghreb, and this species is consequently thought to migrate directly to southern Europe from sub-Saharan regions (Moreau 1967). Analysis of spring ringing recoveries ($n=189$) shows that the next stop-over sites after the Camargue are either other areas in France (28 recoveries) or northern Italy (100 recoveries), which in both cases is an easy flight over land from the Camargue (600 km between the Camargue and northern Italy). Assuming that the leaner birds captured in the Camargue were close to the starvation body mass of garganey (i.e. 220 g in females and 230 g in males), males and females with the average body mass recorded in this study still had 96 g and 115 g of body stores left at first capture, respectively. Assuming the energy content of these body stores was 30 kJ g^{-1} (Jenni and Jenni-Eiermann 1998), the flight speed of these birds is 14.1 m s^{-1}

(Bruderer and Boldt 2001) and, using Norberg (1996) to predict power requirements for flight, males and females arriving in the Camargue would on average still be capable of covering 2,005 km and 1,797 km, respectively.

The stop in the Camargue therefore does not appear to be used for fattening purposes by migrating garganey. Because of the very long flight from the sub-Saharan region before arriving in southern France and the short duration of their stay there, it is possible that resting is the main purpose of the Camargue stop. In addition, it is also possible that garganey try to optimise their migration overall, and do not skip the Camargue because the timing may be too early for flying directly to subsequent stop-overs (in terms of food availability or climatic conditions there), therefore making it more profitable to wait in southern France.

Inter-individual variation

When first caught in the Camargue, the body mass of garganey showed considerable variation, some birds being much heavier than others. Because the direct journey from south of the Sahara to southern France must require considerable amounts of energy, birds probably store large fuel stores before departure in order to buffer potential adverse effects of bad conditions encountered en route. We hypothesise that in fact some individuals had an easier journey than expected (because adverse desert winds are potentially a major threat, but their frequency is such that some birds may pass through without encountering any), and consequently arrived in the Camargue still with a large share of their initial stores.

Body-mass at ringing was the main factor explaining subsequent variation in fuelling rates, while annual variation in the environment or temperature experienced by the birds had no significant effect. Garganey arriving lean in the Camargue gained body mass, while fat birds initially lost mass. Several studies have shown that the fuelling rate at a migration stop-over decreases with individual body-mass (e.g. Klaassen and Lindström 1996; Fransson 1998; Schaub and Jenni 2000), for which extra resting metabolic and transport costs associated with an increase in fuel load may be held responsible (Klaassen and Lindström 1996). However, it would be premature in our case to conclude that this indicates that the fattest garganey deliberately lost mass to reduce the costs associated with carrying too much load (e.g. because this hampers flight ability and/or increases predation risk), because this pattern is likely to reflect only a mathematical artefact. Because fuelling rate is derived from initial body mass at ringing, a correlation between the two is likely to arise automatically for statistical reasons (part-whole correlation; Sokal and Rohlf 1995; see the application to mass loss in relation to initial mass in Gebhardt-Henrich 2000). Only if the result of the major axis regression between mass loss and initial body

mass differs significantly from 1 can one be sure that the relationship is due to biological effects in addition to statistical effects. In Camargue garganey, the slopes of the reduced major axis regressions were 1.04 and 1.09 in males and females, respectively. In males, the standard error of the slope was computed with software RMA (Bohonak 2002), and was equal to 0.05, therefore encompassing the value of 1. In females, the standard error could not be computed due to too small a sample size. However, for females the value of the slope was very close to 1, and therefore it cannot be concluded that the observed pattern has a biological explanation.

From a management point of view, it is often argued that the main value of stop-over sites for migrating birds is the ability to find the necessary food resources to refuel after a previous flight, and to prepare for the next. This study does not provide any insight into the foraging value of the Camargue for migrating garganey, but suggests that the main reason for this stop could be for resting after a long and hazardous journey. It is important to realise that management providing quietness and safety at stop-overs may be at least as important for this species as feeding opportunities.

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