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What type of lean ducks do hunters kill? Weakest local ones rather than migrants

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An earlier study in western France showed that birds shot around protected areas had a lower body mass than birds remaining in nature reserves, but it was impossible at that time to distinguish whether shot birds were leaner because they were exhausted and ignorant migrants, or whether there was simply a body-condition bias making the leaner individuals of the area more likely to be shot. To test these hypotheses, we used body mass at ringing from close to 5,000 teal *Anas crecca* in the Camargue, southern France. Distinguishing between 'resident' birds recaptured alive in the same protected area at least once during the month following ringing, 'locally shot birds' hunted in the Camargue and 'migrants' hunted out of the Camargue area during the same period, we could not detect any significant difference between the average body mass of 'residents' and 'migrants', whereas locally shot birds were generally lighter. This suggests that migration is not the reason why hunters generally shoot lean ducks around nature reserves. Conversely, these results support the idea that some mechanisms, maybe linked to competition and dominance relationships between birds in protected areas, make the leaner teal more likely to get killed by hunters. Whatever the mechanism involved, this pattern suggests that carrying capacity was reached in the protected areas, a situation calling for appropriate habitat management.

Key words: *Anas crecca*, body condition bias, body mass, migration

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In an earlier study, we documented a significant difference in body mass between heavy 'resident' dabbling ducks *Anas* sp. remaining in protected areas at night, and leaner ducks shot by hunters in marshes surrounding protected areas in western France (Guillemain et al. 2002). This was consistent with the general 'body condition bias' reported in other studies, describing the fact that hunted ducks often have a lower body mass than ducks in protected areas (Heitmeyer et al. 1993). At the time of our study, two non-necessarily mutually exclusive hypotheses were proposed to explain the observed patterns.

First, birds shot outside reserves could be leaner individuals that would roost in protected areas during daylight hours, but would for some reason be more likely to be shot at dusk, at night or at dawn by hunters than heavier congeners. Among the mechanisms behind this pattern, heavier birds in protected areas could potentially be dominants that force weaker birds at dusk to fly over or use hunted areas as nocturnal feeding grounds (for the day-night distribution of dabbling ducks and their daily time-budget, see Tamisier 1976, 1978; dominance relationships would be less acute during the day when birds flock together mostly for non-foraging activities). Earlier studies suggested that the nocturnal use of protected areas by dabbling ducks was indeed positively related to feeding opportunities inside the reserves (Cox & Afton 1997). Analysis of plasma testosterone levels suggested that dominant ducks remain in protected areas more than subordinate ducks (H. Fritz, M. Poisbleau, C. Moreau, L. Denonfoux, M. Guillemain & O. Chastel, unpubl. data; experimental work showed that testosterone levels and dominance score were indeed significantly related in dabbling ducks; see Poisbleau et al. 2005). In breeding shelduck *Tadorna tadorna*, Ingold (1991) demonstrated that dominant individuals indeed were able to exclude subordinates from the best feeding areas. Hepp & Hair (1984) suggested that differences in dominance rank between wintering male and female dabbling ducks could be held responsible for the exclusion of females from the preferred feeding zones, and so did Choudhury & Black (1991) in pochard *Aythya ferina*. Similarly, Paulus (1983) suggested that dominant paired gadwall

Anas strepera gained better access to food resources than subordinate single individuals. An alternative mechanism could be more simply that leaner individuals are less efficient foragers that would have to spend more time in food-rich feeding areas at night exposed to hunters (similarly to less efficient oystercatchers *Haematopus ostralegus* spending more time in pastures where the risks of predation and parasitism are higher; see Caldow et al. 1999).

The second hypothesis proposed to explain differences in body condition between birds in protected areas and birds shot at night in western France was that hunted birds in the evening or at night could be exhausted migrants just arriving to the area, unaware of the potential danger, whereas more resident, experienced individuals would remain in protected areas throughout the 24-hours cycle. The average lower body mass of shot birds could be due to these migrants arriving with their fat reserves depleted.

In the earlier study in western France, available data made it impossible to properly test the two hypotheses. This was unfortunate, as the two alternatives do not have the same management implications: if killed birds are leaner simply because they are naïve migrants, then little can be done. Conversely, if hunters kill leaner birds because these individuals have difficulties meeting their daily energy requirements in the favoured protected area, whatever the mechanism behind this pattern, then this suggests that the carrying capacity of the reserve may be too low for the total number of birds present in the area, a situation that may sometimes be changed by appropriate management (e.g. Anderson & Smith 1999).

In our study, we used bird measurements at ringing combined with subsequent known fate of the individuals to test whether ducks shot around protected areas are lean because they are the weakest local individuals forced to use risky areas or, alternatively, whether they are more likely to be migrating birds. To do so, we used the teal *Anas crecca* ringing database from the Saint Seren Nature Reserve at Tour du Valat in the Camargue, southern France, and we distinguished between: 1) birds recaptured at least once in the same protected area during the 30 days following ringing, and termed them 'residents', 2) birds shot locally in the

Camargue during the 30 days following ringing, termed 'locally shot', and 3) birds shot outside the Camargue area during the 30 days following ringing, considered to be travelling when ringed, and hence termed 'migrants'. We compared the initial body mass of the three bird categories at ringing, expecting the following:

- 1) If ducks shot around reserves are lean mostly because they are weaker local birds, then locally shot birds should have a lower body mass than both residents and migrants.
- 2) If ducks shot around reserves are lean mostly because they are migrants, then residents and locally shot birds should both be heavier and have similar body mass.
- 3) If individuals that have to move (migrants or weaker local birds) incur more costs without distinction, then both locally shot birds and migrants should have a lower body mass than residents.

Method

Teal were caught with dabbling duck funnel traps in the 1,071-ha Saint Seren protected area in the Domaine de la Tour du Valat in the Camargue, southern France (43°30'N, 04°40'E), between January 1952 and February 1978 (for details on the Camargue technique, see Bub 1991:103). Ducks were sexed and aged using plumage criteria as well as inspection of the cloaca and the bursa of Fabricius. A total of 59,187 teal were captured and ringed. Among these, 4,913 were captured between August and March (the period during which hunting occurred in the Camargue marshes in the earlier part of the study), were sexed, aged, weighed (to the nearest g), had their wing length measured (to the nearest mm), and were either recaptured alive at the same place, shot locally in the

Table 1. Number of teal of each sex and age class which, during the 30 days after ringing at Saint Seren, were either recaptured alive at least once ('residents'), hunted in the Camargue ('locally shot') or hunted elsewhere ('migrants').

	Residents	Locally shot	Migrants
Females			
Adults	274	53	66
First-years	1485	147	160
Males			
Adults	924	103	85
First-years	1287	164	165

Camargue (average distance travelled = 12.1 km ± 0.9 SE) or shot further away during the 30 days following ringing (average distance travelled = 349.7 km ± 17.2 SE), and they constituted the total sample size of this study (Table 1). Birds both recaptured and shot during the 30 days after ringing (90 individuals) were not included in the analyses.

We used General Linear Models (GLMs), and always first included wing length as a covariate in the models; i.e. we looked at the potential additional effect of bird type (i.e. residents, locally shot or migrants) to explain differences in body mass between bird types given the potential effect of body size. Models were run separately for males and females, first-year birds and adults. Earlier studies have documented that body mass of wintering birds cycles throughout the season (e.g. Tamisier et al. 1995). We therefore also included a 'period' factor in the analyses, distinguishing birds weighed in early season (August–November), mid-season (December) or late season (January–March), following the classification given in Guillemain et al. (2005). 'Period' too, like wing length, was included first in the GLMs so that we looked at additional effects of bird type. Because we wanted to know whether some birds genuinely use hunted areas more because they are lean or, alternatively, whether they get lean because they use hunted areas, we included the interaction period*bird type in a first running of models. A significant effect of this interaction would suggest that the difference between the body mass of the three bird types changes across time, i.e. would support the idea that birds get leaner and leaner as they repeatedly use hunted areas if the difference between resident birds and birds shot locally increases over periods. When the interaction was not significant, it was removed from the models and the GLMs were re-ran.

Results

In the first running of models, the interaction period*bird type never had a significant effect in any sex and age class (GLMs: all partial $F < 1.8$, all $P > 0.13$). The results of subsequent models excluding this interaction are presented in Table 2. In all cases, wing length always had a highly significant positive effect, contributing by itself for at least 68.0% of the explained variance in body mass, after ratios of partial F values. Body mass also differed significantly between periods of the season in all sex and age classes, and estimates for the effect of body mass revealed

Table 2. Results of GLM analyses of teal body mass depending on wing length (in mm), period of weighing (early, mid or late season) and bird type ('resident', 'locally shot' or 'migrant'). Estimates with different letters differ from each other. Estimates for the different bird types were computed for mid-season, and estimates for the different periods of the season were computed for resident individuals.

	R ²	Estimates	df	F	P
First-year females (N = 1792)					
Complete model	0.09		5	33.61	< 0.0001
Wing length		2.156	1	120.3	< 0.0001
Period		early: -111.8A; mid: -95.1B; late: -100.4C	2	14.8	< 0.0001
Bird type		res.: -95.1A; loc.: -107.2B; mig.: -93.9A	2	9.1	0.0001
First-year males (N = 1616)					
Complete model	0.08		5	26.55	< 0.0001
Wing length		2.028	1	85.4	< 0.0001
Period		early: -79.6A; mid: -61.2B; late: -59.6B	2	20.5	< 0.0001
Bird type		res.: -61.2A; loc.: -68.0B; mig.: -65.2AB	2	3.1	0.0446
Adult females (N = 393)					
Complete model	0.11		5	9.56	< 0.0001
Wing length		2.583	1	24.61	< 0.0001
Period		early: -170.4A; mid: -169.4A; late: -188.3B	2	9.73	0.0001
Bird type		res.: -169.4; loc.: -179.6; mig.: -173.6	2	1.87	0.1557
Adult males (N = 1112)					
Complete model	0.08		5	18.29	< 0.0001
Wing length		1.901	1	55.74	< 0.0001
Period		early: -44.1A; mid: -20.8B; late: -38.1A	2	11.03	< 0.0001
Bird type		res.: -20.8A; loc.: -34.9B; mig.: -27.6AB	2	6.82	0.0011

a general tendency for December (i.e. mid-season) birds to be heavier than birds caught during the other periods, though this was not always significant in the different sex and age classes. In all cases except adult females, bird type also explained a significant part of the variance in body mass (see Table 2). In all sex and age classes, the pattern was the same, though not always significant; locally shot birds were leaner than residents, while the difference between locally shot teal and migrants, though always in the same direction (i.e. migrants being heavier than locally shot birds), was only significant in first-year females. The body mass of migrants never differed significantly from the body mass of residents (see tests of estimates in Table 2).

Discussion

As already observed in western France (Guillemain et al. 2002), the body mass of teal shot around the protected area of Saint Seren was significantly lower than that of 'resident' individuals in this hunting-free site for all sex and age classes, except adult females for which the pattern was nonetheless the same. The Camargue data do not suffer from potential biases linked to the way birds were collected (captures in traps versus shot birds; e.g. Heitmeyer et al. 1993), as in

the present case we always compared body mass at ringing, between individuals with different known fates afterwards. One could argue that migrants may subsequently have a lower body mass when shot away from the Camargue, due to the energy cost of flight from the ringing site to there, and therefore that the lack of difference between residents and migrants would be an artefact. However, this would imply that migrants had their full body reserves when ringed, which there is no reason to believe. Conversely, we assumed that migrants could have just arrived in the area or be just ready to leave with full 'fuel tanks' when caught and ringed, as they would be when shot elsewhere.

The difference between body mass of teal from the different bird types was observed when taking into account the relationship with wing length (i.e. bird type explained a significant additional part of the variance in body mass). This indicates that differences between resident, locally shot and migrant teal body mass reflected an opposition between lean and fatter birds rather than small versus larger birds. In the same way, we observed cyclic changes in teal body mass throughout the season as we did previously (Guillemain et al. 2005), but bird type had a significant additional effect on this factor, too.

Using ringing data allowed us to identify a class of 'migrant' birds, which was a prerequisite for testing the

earlier hypotheses about why the body mass of shot birds was lower. We could not detect a significant difference between the average body mass of resident and migrant birds, which was similar in all sex and age classes. Furthermore, migrants tended to be heavier than locally shot birds, though the tests of the estimates in the GLM procedure only reached significance for first-year females. This result suggests that the low body mass of ducks shot around protected areas, both in the Camargue and probably in western France (Guillemain et al. 2002), was not due to hunters being more likely to kill exhausted migrants. Conversely, it seems that the leaner local birds were for some reason more likely to be shot, which accords with the body condition bias in hunted ducks recorded previously (e.g. Heitmeyer et al. 1993). The fact that residents in the protected area were heavier than birds shot in the surrounding hunted zones is also consistent with earlier results showing a positive relationship between duck body mass and annual survival rate (e.g. Haramis et al. 1986, Pace & Afton 1999, but see, however, Krementz et al. 1989).

The initial test of the interaction bird type*period, aiming at testing whether the difference between body mass of resident, locally shot and migrant birds varied across season (which could indicate that some individuals gradually get leaner because of their repeated use of unprotected areas) never provided significant results. This indicates that it is because some birds are lean that they move to hunting areas more (or stay longer there) and not the reverse, leading to the described body condition bias in shot birds.

In conclusion, our study supports the hypothesis that some local mechanisms are making leaner individuals more at risk of being hunted than their fatter congeners. How exactly this mechanism is working will require further work: at present, it is not possible to determine e.g. whether leaner teal are forced out of protected areas by more dominant birds in better body condition, or whether leaner birds simply have to spend more time foraging exposed in hunted areas than fatter birds, which could meet their energy requirements more easily. However, whichever mechanism involved, our study suggests that, when it comes to feeding, carrying capacity may be reached in protected areas at night. Cox & Afton (1997) suggested that the nocturnal foraging opportunities of protected areas may limit their use by dabbling ducks, to the point that fewer birds could use these reserves as the habitats gradually get depleted throughout winter. As suggested earlier (Guillemain et al. 2002), the results of our study support the idea that managing

protected areas for dabbling ducks not only as day-roosts, but also at least partly as nocturnal foraging grounds (e.g. Anderson & Smith 1999), may be beneficial to wintering populations of dabbling ducks.

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