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Short communication

The income–capital breeding dichotomy revisited: late winter body condition is related to breeding success in an income breeder

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Reproduction is a costly event for most organisms, and the trade-off between survival and short-term reproductive success of individuals is one of the most discussed topics in life-history theory. Previous research shows large variation in the way animals prepare for breeding. For example, Drent and Daan (1980) coined a dichotomy between 'capital' and 'income breeders'; the latter acquire the energy needed for reproduction locally in the breeding environment, whereas the former rely on body reserves stored long before breeding. Capital breeding strategies have been described in virtually all vertebrate groups: reptiles (reviewed by Bonnet *et al.* 1998), amphibians (Bull & Shine 1979, Elmberg 1991), fishes (e.g. Hendry *et al.* 1999), mammals (e.g. Festa-Bianchet *et al.* 1998, Beck *et al.* 2003) and birds (e.g. Drent & Daan 1980, Meijer & Drent 1999). In some large migratory birds, the relationship between the amount of energy stored by females and their subsequent breeding success may be so deterministic that it is possible to predict breeding output several thousand kilometres away by using body condition at spring stopovers (e.g. Ebbinge 1989 for Brent Geese *Branta bernicla*). The reason why it may be optimal for these birds to carry fat loads during spring migration, despite the costs of doing so (Witter & Cuthill 1993, Klaassen & Lindström 1996), is generally considered to be food shortage on the breeding grounds upon arrival (Ebbinge & Spaans 1995). Of course, income and capital breeding are the two extremes of a continuum of strategies (Meijer & Drent 1999), with smaller, migratory species least able to store and carry large energy reserves through migration (Klaassen 2002). For example, amongst the Anseriformes, ducks are typically income breeders, although some larger-bodied species rely partly on endogenous reserves (Esler & Grand 1994, Baldassarre & Bolen 2006), and geese are typically capital breeders, although some complement endogenous reserves with exogenous food acquired on the breeding grounds (Budeau *et al.* 1991, Bromley & Jarvis 1993, Gauthier *et al.* 2003, Arzel *et al.* 2006).

The Eurasian Teal *Anas crecca* is the smallest of all dabbling ducks wintering in western Europe (mean mass approximately 300 g; Fig. 1), and is thus probably unable to bring significant energy reserves to the breeding grounds. For example, Paquette and Ankney (1998) found that the time-budget of prebreeding and incubating females indicated a strong reliance on breeding area resources for reproduction.

In avian ecology, winter was long considered to be 'a waiting interval' between two breeding seasons, during which birds move south to avoid freezing conditions and food shortage at high latitudes (Weller & Batt 1988). However, recent work on dabbling ducks suggests that winter is a crucial part of the year, during which individuals restore reserves after autumn migration, form pairs and prepare for the next spring migration (e.g. Tamisier *et al.* 1995). Shifts between these phases are associated with a clear dynamic of body mass change, the latter increasing during the first, decreasing during the second (birds spend more time in social displays at the expense of feeding), and increasing again during the last, as paired individuals acquire a dominant status allowing them to feed more efficiently and store energy in preparation for spring migration (Tamisier *et al.* 1995, Guillemain *et al.* 2005a). Because of competition (for food, mates or breeding sites), ducks supposedly try to start each of the three 'wintering phases' as quickly as possible, so as eventually to leave on migration in the best possible condition (Tamisier *et al.* 1995). Indeed, a recent study showed that earlier-breeding Eurasian Teal use the best lakes and have higher breeding success (Elmberg *et al.* 2005), corroborating a general pattern of an inverse relationship between breeding success and breeding initiation in waterfowl (Duncan 1987, Bowler 2005).

Although a positive correlation between female body condition at nest initiation and reproduction has been demonstrated in Northern Shovelers *Anas clypeata*

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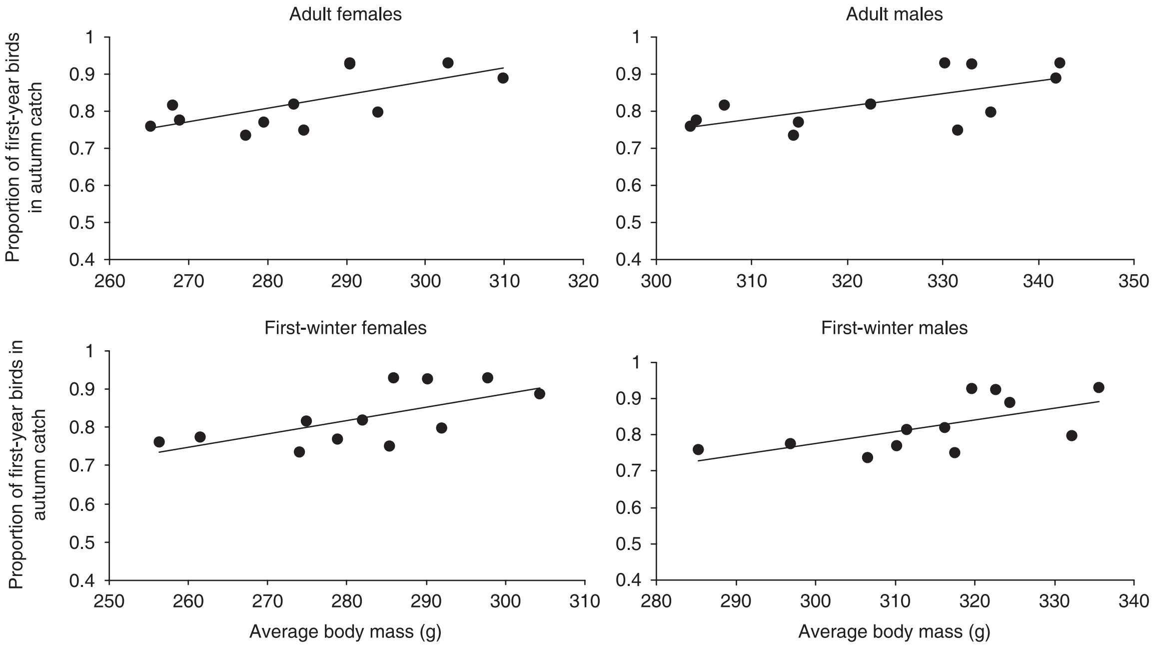

Figure 1. Annual proportion of first-year individuals in the autumn catch of Eurasian Teal as a function of average body mass late in the preceding winter. Data from Tour du Valat in the Camargue, France, from 1957 to 1968. All regressions are significant (see text). Note that two dots are superimposed on the graph for adult females with average body mass around 290 g.

(MacCluskie & Sedinger 2000), similar correlations between late winter body condition (reflecting successful strategic choices in winter) and subsequent breeding success have not been demonstrated in long-distance migratory dabbling ducks, and very rarely so in other income-breeding migrants (Marra *et al.* 1998, Newton 2004).

The aim of the present study was to determine if there is any relationship between average body condition at the end of winter and subsequent breeding success in a Eurasian Teal population. Given the fact that this species is very unlikely indeed to be a capital breeder, but nonetheless prepares for reproduction by pairing and increasing energy reserves before spring migration, this is a test of the hypothesis that wintering conditions and individual strategic choices in winter have carry-over effects (*sensu* Newton 2004) on fitness. It should be noted, though, that this study is merely a first step, as the data on which it is based are population-level data rather than individual data, the level on which strategic decisions are taken.

METHODS

We used the ringing dataset at the Station Biologique de la Tour du Valat in the Camargue, southern France, to examine the relationship between average body mass of Eurasian Teal caught between February and April the same calendar year and the proportion of first-year birds in the subsequent autumn catch (September–November). In doing so, we assumed that birds caught in spring and autumn belong to the same population. Previous analyses support this assumption; 12% of Eurasian Teal ringed in spring in the Camargue and recovered interannually in September–November (i.e. shot or found dead at least one season after the season of ringing), were within a 200 × 200-km square centred on Tour du Valat ('local' recoveries in Guillemain *et al.* 2005b). Recaptures of individuals ringed elsewhere were only occasional, because there were few other large-scale ringing operations elsewhere in Europe during this period, thus preventing us from determining with precision the proportion of individuals recaptured in autumn that came from other populations. However, Eurasian Teal wintering in western Europe are in any case very likely to form only one single large population (Guillemain *et al.* 2005c). Both sexes were included in the analysis because we were interested in the connection between individual condition by the end of winter and breeding success, not the relationship with female body stores only, as would be the case in a capital breeding species. For example, a male in better condition may be able to provide more mate guarding, allowing more efficient foraging for his female at migration stopovers, and hence earlier arrival at the breeding grounds. We ran separate analyses for adults and first-winter birds, as Eurasian Teal breed at one year of age. Note that we used the term 'first-winter birds' for individuals in their first winter and their second calendar year when ringed and weighed between

Table 1. Number of Eurasian Teal weighed in late winter and number of adults and first-year birds captured the following autumn at the Station Biologique de la Tour du Valat between 1957 and 1968 and included in the analysis.

	Late winter sample				Autumn sample	
Year	Adult females	Adult males	First-winter females	First-winter males	Adults	First-year birds
1957	23	172	268	316	118	1578
1958	133	496	1211	680	11	50
1959	98	309	363	179	99	1234
1960	70	374	206	37	74	589
1961	42	188	151	35	18	235
1962	72	146	127	45	225	714
1963	126	363	282	420	175	602
1964	37	76	43	49	48	190
1965	233	290	12	133	3	10
1966	19	50	33	36	8	24
1967	51	153	27	116	29	81
1968	75	76	77	133	28	124

February and April, while we kept the term 'first-year birds' for individuals caught during their first autumn. Body mass was used directly as a proxy for body condition because the relationship between body mass and body size (i.e. wing length) was non-significant except in adult females, where variation in wing length still only explained 0.3% of the variance in body mass (linear regression: $r^2 = 0.003$, $F_{1,1621} = 4.94$, $P = 0.0264$). Teal were caught with funnel traps as described in Bub (1991). The traps were not moved over the study period, and catching effort was fairly constant, the traps being in operation almost every day. A total of 59 187 individuals were ringed between January 1952 and February 1978, although the catch was especially large in the 10–12 years in the middle of this period (see below). We only used data from the main period of annual presence in the Camargue (September–April), but excluded data from December and January, as the sample from these months may be biased by cold conditions further north, obliging already lean birds to undertake a costly journey to the south of France (e.g. Ridgill & Fox 1990, Guillemain *et al.* 2005b). In addition, mid-winter samples may be biased because ducks of different sexes and ages are not equally likely to move south to the Camargue in response to cold weather. We only used data from those years in which > 100 individuals were ringed and weighed in late winter (February–April) and the proportion of first-year birds could be calculated the following autumn. We did not use any data from 1956, when the worst cold spell of the second half of the 20th century affected the Camargue for most of February, biasing the late winter sample in terms of both age and sex-ratios and average body mass of individuals. Other cold spells during the study period were at the most half as intense, as judged from Hellman indices (Ridgill & Fox 1990), and they mainly occurred in December and January (Leroy & Siguier 2003). Because of lower and more intermittent catching effort, data from 1969–78 were too scarce, either not reaching the threshold of 100 individuals weighed in late winter or preventing any reliable estimation of age-ratio in the autumn (i.e. a few or no individuals caught in one of the age classes). Our remaining sample therefore comprised 8651 individuals caught in late winter and 6267 individuals caught in autumn, from 1957 to 1968 (Table 1). The proportion of first-year birds was arcsine-transformed prior to the analyses (Sokal & Rohlf 1995), but actual proportions are presented in Figure 1 to facilitate reading.

RESULTS AND DISCUSSION

The annual proportion of first-year birds in the autumn catch was indeed significantly and positively correlated to mean body mass in the preceding late winter, whatever the sex or age of the birds (linear regressions: adult females: $y = -17.00 + 0.29x$, $r^2 = 0.45$, $P = 0.02$; adult males: $y = -24.29 + 0.28x$, $r^2 = 0.43$, $P = 0.02$; first-winter females: $y = -12.56 + 0.28x$, $r^2 = 0.42$, $P = 0.02$; first-winter males: $y = -16.99 + 0.26x$, $r^2 = 0.38$, $P = 0.03$, $df = 10$ in all cases; Fig. 1). Average annual body mass of all sex and age classes were intercorrelated, too (all six pairwise r^2 values > 0.73, all $P < 0.0004$). We thus conclude that in years when conditions allowed birds to build up body mass more prior to spring migration departure the proportion of first-year individuals returning in the autumn was larger.

Eurasian Teal are hunted in late summer and autumn in countries further north before reaching the Camargue, and fledged first-year birds suffer higher mortality rates than adults (a large share of it related to hunting, e.g. Fransson & Pettersson 2001, Devineau 2003). For example, the average proportion of first-year Eurasian Teal in the

September–November catch at Abberton Reservoir, England, was over 0.80 (recalculated from Fox *et al.* 1992). The proportion of first-year birds in the Camargue data set may therefore generally underestimate absolute breeding success, and especially so in good breeding years (which would be good hunting years in the north, with many 'naïve' juveniles in the population). However, this proportion was always over 0.70, which is intrinsically linked to the demographic parameters of this species: a short-lived duck with a high annual productivity (Devineau 2003). These patterns do not affect our main result, but simply suggest that the slope (not necessarily the strength of the correlation, if the hunt in the north is directly related to annual breeding success) of the relationship between late winter body condition and subsequent breeding success may be steeper than observed in the Camargue data. The pattern nonetheless appears to be highly significant biologically, given that variation in average late winter body mass explained approximately 40% of the variation in apparent recruitment, as recorded by the proportion of first-year birds in the autumn catch.

The relationship between late winter body condition of breeders and subsequent breeding success in Eurasian Teal as described here does not imply that the good condition of birds is directly responsible for larger clutches or better survival of young, as would be the case in a capital breeder. Rather, our analysis suggests that in years when Eurasian Teal undertake spring migration in good body condition they may be better placed to secure the necessary resources for successful breeding when they arrive on the breeding grounds: a carry-over effect (Newton 2004). The likely scenario is that during benign winters (milder, or when food abundance is higher) birds can build up larger reserves earlier, which may allow them to depart on migration earlier or in better condition, translating into earlier arrival at the breeding grounds, and hence higher breeding success (cf. Elmberg *et al.* 2005). Fox *et al.* (1992) indeed observed that body condition of Eurasian Teal in Britain declined during poor winter weather conditions. If so, income breeders, too, build up energy reserves well before reproduction, and the size of these stores and/or the date at which these are accumulated may subsequently affect breeding success, even if the reserves simply put the birds in a better position to secure resources on the breeding grounds (income breeding), rather then being available directly for the actual formation of eggs and young (capital breeding). Accordingly, we argue that future studies should not underestimate the role of energy reserves in supposed income-breeding species, even if this role is likely to be indirect. Our study also has profound conservation implications by demonstrating for the first time a link between wintering conditions (which land managers may partly affect) and population dynamics of a duck species, through breeding success. Accordingly, any management option or conservation policy that may favour foraging and fattening in dabbling ducks in late winter may have consequences later on at the population level, a result reinforcing the idea that these species need to be managed at the flyway scale (Arzel *et al.* 2006). In order to aid such management, the present results suggest that it may be possible partly to predict dabbling duck breeding success as early as by the end of the winter.

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