Stabilizing selection on body mass in the sociable weaver *Philetairus socius*

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The survival of small birds is often believed to increase with increasing body mass, despite some evidence that body mass is usually maintained below the physiological maximum and that there are costs associated with high body mass, such as increased energetic expenditure and predation risk. In this study, we used an eight-year dataset to investigate survival in relation to body mass in a wild population of sociable weavers (*Philetairus socius*), a savannah-dwelling passerine bird. We present evidence for strong stabilizing selection on body mass, verifying the prediction that body mass probably results from a trade-off between the risks of starvation at low mass and predation at high mass.

Keywords: body mass; *Philetairus socius*; predation risk; stabilizing selection; survival

1. INTRODUCTION

Survival is a key life-history trait in ecological and evolutionary theory, and thus it is important to know the factors that might affect it, and how. Among birds, body mass is often thought to influence survival, with the common assumption being that post-fledging survival increases with body mass (Perrins 1965; Gill 1995; Brown & Brown 1996). It is also believed that low body mass can reduce adult survival, for example, through an increase in the risk of starvation (Cuthill & Houston 1997) or the weakened immunocompetence of lighter birds (Møller *et al.* 1998). However, there are also costs associated with high body mass, stemming mostly from the disadvantages of carrying high fat levels (Lima 1986; Witter & Cuthill 1993; Cuthill & Houston 1997). These costs are usually expressed in terms of predation risk, either through increased foraging time and thus increased exposure to predators or through decreased flight manoeuvrability, or in terms of the higher energetic requirements of larger mass (Lima 1986; Witter & Cuthill 1993; Cuthill & Houston 1997). An important question, however, is not whether high body mass has costs, but whether they are of sufficient magnitude to be biologically interesting (Cuthill & Houston 1997). Several studies have investigated the possible costs of high body mass (e.g. Metcalfe & Ure 1995; Gosler *et al.* 1995; Kullberg *et al.* 1996; Gentle & Gosler 2001), although the link between high body mass and survival was indirect. An exception was a study on blue tits *Parus caeruleus*, in which Adriaensen *et al.* (1998) found that high fledgling body mass had a negative effect on survival in the presence of an avian predator but not in its absence.

If both low and high body mass have significant costs,

survival of both relatively lean and fat individuals should decrease, resulting in stabilizing selection on body mass (see also Endler 1986; Adriaensen *et al.* 1998). In fact, it has been suggested that stabilizing selection is a sort of selection that populations commonly experience (Endler 1986), but only a few studies have provided examples of it. In this study, we use a long-term dataset to investigate the relationship between mass and survival in adult and juvenile sociable weavers (*Philetairus socius*), a sedentary group-living passerine bird endemic to the arid savannahs of southern Africa. We present evidence for strong stabilizing selection on body mass and thus verify the prediction that body mass represents a trade-off, possibly resulting from the benefits of storing fat to avoid starvation and the benefits of being lighter and more agile to avoid predation.

2. MATERIAL AND METHODS

(a) *Study area and species*

The sociable weaver is a colonial, cooperatively breeding passerine that is endemic to southern Africa (Mendelsohn & Anderson 1997). Sociable weavers weigh *ca.* 26–32 g (mean 28.5 g), with the sexes being indistinguishable in the field. Males have a slightly longer tarsus, but there are no significant inter-sexual differences in mass (R. Covas, unpublished data). Sociable weavers feed on insects, seeds and other plant products, and forage predominantly on the ground but also in trees (Maclean 1973c). These weavers build a very large communal nest, usually on camelthorn trees (*Acacia erioloba*), in which they roost and breed. The nest mass is maintained and occupied by the whole colony throughout the year. At night, the birds roost in the chambers within the nest mass and may also return to the nest during the day to escape predators (R. Covas, personal observation).

The study took place at Benfontein Game Farm, near Kimberley, in the Northern Cape Province, South Africa (*ca.* 28°53′ S 24°49′ E). The vegetation consists of semi-arid open savannah and is dominated by *Stipagrostis* grasses and the camel-

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thorn tree *A. erioloba*. The area experiences low and unpredictable rainfall (average 431 ± 127 mm per year; Weather Bureau, Pretoria), occurring mainly during the summer. The daily temperature ranges are typically high, with cool to warm nights and hot days in summer (*ca.* 8–40 °C) and very cold nights and mild days in winter (*ca.* −8–25 °C).

(b) Field methods

We conducted a capture–mark–recapture study at Benfontein from July 1993 to November 2000. The study area contained 25 sociable weaver colonies; at 16–18 of these, we captured birds twice a year. During the first five years, the capture effort was constant throughout the year (i.e. one to two colonies were caught every month). From mid-1998 until the end of the study we concentrated our capture efforts on the one to two consecutive months at the beginning and end of the breeding period. The birds were captured with mist nets, which were placed before dawn around the nesting tree. We generally caught 70–100% of the colony residents. The birds were individually ringed with a numbered metal ring (from SAFRING; University of Cape Town). We measured mass (to the nearest 0.5 g), wing length (to the nearest 0.5 mm) and tarsus length (to the nearest 0.1 mm; only measured regularly in the last three years). The age of juvenile weavers was estimated through the development of the black patch on the face and throat (Maclean 1973*a*). Birds were designated as adults if they were older than four months upon capture and as juveniles if they were younger than four months. Individuals were sexed using a test based on two CHD (chromo–helicase–DNA-binding) genes that are located on the avian sex chromosomes (Griffiths *et al.* 1998). Only individuals caught from 1998 onwards were sexed.

(c) Statistical methods

We estimated annual survival probabilities and tested for significant differences between different classes of birds using the general methods of Lebreton *et al.* (1992). We used the program MARK (Cooch & White 1998; White & Burnham 1999) to generate the maximum-likelihood estimates of survival and recapture probabilities. MARK computes survival and recapture parameters using an information matrix derived from recapture histories and, by testing the fit of different statistical models, it provides a way to test different biological hypotheses (Lebreton *et al.* 1992). We use the general notation of Lebreton *et al.* (1992), in which the annual survival probability is denoted by ϕ and the recapture probability by p. The subscripts indicate whether parameters in a model are time-dependent (e.g. ϕ_t, p_t), are constant over time (e.g. ϕ, p), are group-specific (e.g. ϕ_g, p_g) or exhibit group- and time-specific interaction (e.g. $\phi_{g \bullet t}$, p_t).

We assessed whether our dataset met the assumptions inherent in the general capture–mark–recapture framework using the program RELEASE (Burnham *et al.* 1987) under the ϕ_t and p_t model. We found no evidence of transients, as shown by Test 3.SR ($\chi^2_5 = 7.72$, $p = 0.17$) and Test 3.SM ($\chi^2_3 = 1.60$, $p = 0.66$), or trap dependence, as shown by Test 2.CT ($\chi^2_3 = 3.91$, $p = 0.27$) in RELEASE, which allowed application of the Cormack–Jolly–Seber mark–recapture models and their refinements to our data. This also meant that corrections for overdispersion were not necessary.

We tested and selected among different models by examining the Akaike Information Criterion (AIC; Akaike 1973; Lebreton *et al.* 1992; Burnham & Anderson 1998). MARK provides a calculated AIC value for each model (corrected for small sample size relative to the number of parameters estimated; AICc) and

those with the lowest values are the most parsimonious. The AICc is used to select among different models; the currently accepted convention (Burnham & Anderson 1998) is that models with AICc that differ by two or less are indistinguishable, statistically. In general, for model selection and hypothesis testing, we relied on 'AICc weights', a measure of a model's relative probability of being the best model for the data, compared with alternative models (Burnham & Anderson 1998). The potential effects of covariates on survival were assessed by comparing models that did and did not incorporate an effect of the covariate. If a model with a covariate provided a better fit than one without it, we concluded that survival was affected by that covariate. We do not present results of the fits of all models tried; rather, in the tables we show only the five models with the lowest AICc and that are relevant to the hypotheses being tested. The number of estimable parameters in our models was given by MARK.

Due to the fact that sociable weavers are unpredictable, aseasonal breeders, the time intervals in between our capture occasions were not constant. MARK allows analysis of unequal time intervals between successive capture occasions; for the eight capture occasions, corresponding to the eight breeding periods that occurred between July 1993 and January 2001, we used seven time intervals of 0.67, 2, 0.92, 1.2, 0.58, 1.4 and 0.67 years, respectively. Each interval was defined as the time from the start of the non-breeding period until the end of the successive breeding period. However, all survival and recapture probabilities reported here are annualized ones, that is, for a 12-month period, allowing comparison with other studies. Although some birds were caught during non-breeding periods, these captures were not used in constructing individual encounter histories; a bird had to be caught during a breeding period to be designated as surviving until that period. As a continuous covariate, we used body mass in grams, taken each time a bird was captured and averaged over all captures for individuals that were caught multiple times. We also tested whether there was a higher-order (i.e. nonlinear) relationship with mass as a covariate.

3. RESULTS

Juvenile mass was related to survival in a nonlinear way. A model incorporating mass and mass^2 as covariates (model 2; table 1) was a better fit (three to four times more plausible) than models with solely mass or without a mass effect, using our sample of birds first ringed and weighed as juveniles ($N = 435$). There was no improvement by using models with age-dependent survival, consistent with other analyses showing no age-related effects on survival (R. Covas, C. R. Brown, M. D. Anderson and M. Bomberger Brown, unpublished data). This indicates that the apparent effect of juvenile mass is expressed across age classes and is not confined only to the juvenile's first year of life (and is consistent with the similar results for adult body mass; see next paragraph). The best-fitting and most parsimonious model, model 2 (table 1), yielded a regression equation describing a curvilinear relationship between juvenile mass and survival, which is plotted in figure 1*a* over the observed range of the juvenile masses. This illustrates a strong disadvantage for birds that are lighter or heavier than the mean and indicates a high level of stabilizing selection on body mass.

We found a similar relationship with adult body mass. Using all birds for which we had body masses measured as

Table 1. *Models to assess the effect of juvenile body mass on survival probabilities in sociable weavers.*

(Mass was a continuous covariate and some models incorporated both mass (subscript m) and mass^2 (subscript m^2) as predictors. The age classes used were the first year and all older ages combined.)

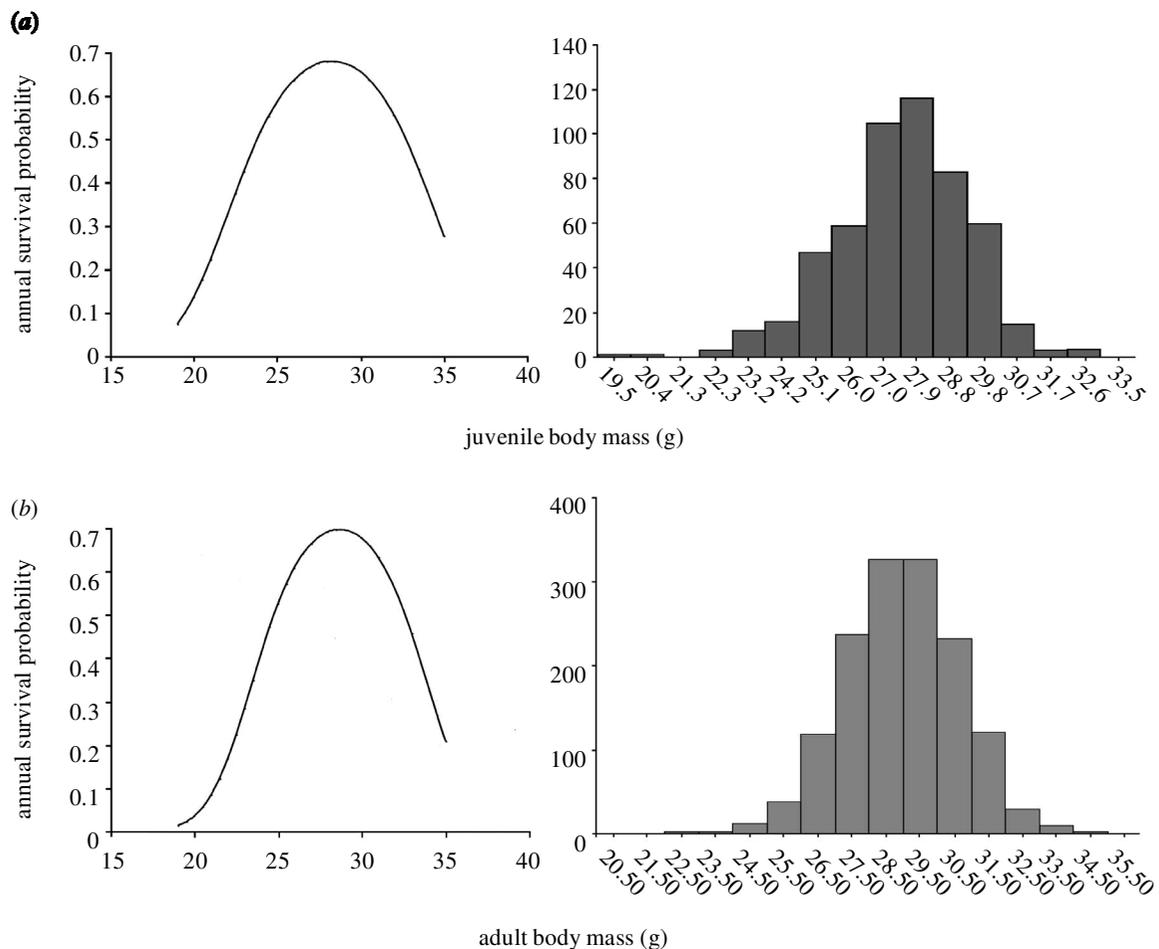| model	AICc	AICc weight	number of estimable parameters	deviance
(1) $\phi_{m+m^2\bullet a}$, p_t	916.5	0.2629	12	891.9
(2) ϕ_{m+m^2}, p_t	917.0	0.2112	9	898.6
(3) $\phi_{m+m^2\bullet t}$, p_t	917.6	0.1538	21	873.8
(4) ϕ_m, p_t	919.4	0.0619	8	903.1
(5) ϕ, p_t	919.5	0.0596	7	905.2

Figure 1. Relationship between body mass and annual survival in sociable weavers (as estimated from the models (tables 1 and 2) with mass + mass^2 as covariates) for (*a*) juveniles and (*b*) adults, with histograms showing the distribution of the body masses (juveniles: 27.9 g ± 2.0, $N = 435$; adults: 28.7 g ± 2.2, $N = 977$). Note the same scale for each.

adults (and using an average value for each bird weighed multiple times; $N = 977$), we found that a model with survival constrained as a function of mass + mass^2 provided the best fit (model 6; table 2). In the case of adults, this nonlinear relationship was statistically much stronger than in the juveniles; AICc weights indicated that the model with mass as a curvilinear covariate was several hundred times more plausible than models with mass as a linear covariate or without an effect of mass (table 2). For neither adults nor juveniles was there any time-dependent interaction of body mass on survival (tables 1 and 2), indicating that the curvilinear relationship held across years. The regression equation predicted by model 6 described a strong effect of adult mass on survival over the range of observed

mass values (figure 1*b*). As in juveniles, there appeared to be strong stabilizing selection on adult body mass.

Using a smaller sample of birds of known sex ($N = 171$) captured over a shorter time span (the final three capture occasions of the study), we found no evidence that the survival pattern detected for adults (figure 1*b*) varied with sex. A model with mass as a curvilinear constraint on survival with the sexes treated separately ($\phi_{t\bullet m+m^2}$, p_t) did not provide a better fit (AICc = 306.7) to the data than a model with the sexes treated identically (ϕ_{m+m^2}, p_t; AICc = 305.3). In fact, the AICc weights indicated that the model with the sexes treated identically was about twice as plausible as the one with the sexes separated (AICc weights of 0.1557 versus 0.0775).

Table 2. Models to assess the effect of adult body mass on survival probabilities in sociable weavers.
(Mass was a continuous covariate, and some models incorporated both mass (subscript m) and mass^2 (subscript m^2) as predictors.)

model	AICc	AICc weight	number of estimable parameters	deviance
(6) $\phi_{m + m^2}, p_t$	1921.7	0.8826	9	1903.6
(7) $\phi_{m + m^2 \cdot v}, p_t$	1926.2	0.0927	23	1879.3
(8) $\phi_{m \cdot v}, p_t$	1929.2	0.0017	17	1894.7
(9) ϕ_m, p_t	1935.0	0.0011	8	1918.9
(10) ϕ, p_t	1936.0	0.0007	7	1921.9

Survival seemed to be related primarily to mass *per se* and not to other correlates of mass, such as overall body size. In this population of sociable weavers, mass was only weakly related to two common indices of skeletal size, *viz.*, tarsus and wing length ($r^2 = 0.09$, $p < 0.001$, $N = 187$ birds; $r^2 = 0.05$, $p = 0.01$, $N = 220$ birds, respectively).

4. DISCUSSION

Our study showed a strong survival disadvantage for birds that are lighter or heavier than the mean, indicating stabilizing selection on body mass. To our knowledge, this is the first long-term study on a natural population showing such an effect on both adult and juvenile birds. Furthermore, our study shows stabilizing selection acting throughout the years studied, and not occurring as a result of alternating years of opposing directional selection, as was found in other studies (e.g. Gibbs & Grant 1987). Our result was obtained in a sedentary, southern-temperate population, showing that even moderate variations in body mass (i.e. 10% around the mean) can have a significant effect on survival. This result was probably due to body mass and not to a confounding effect of skeletal body size, as, in our population, mass was only weakly related to wing and tarsus lengths. It is also possible that the increased mortality at high body-mass levels could reflect heavier birds being the ones with greater propensity for dispersal. This, however, is unlikely because sociable weavers are highly sedentary and only 6.9% of the birds ringed ($N = 2094$) were recaptured at other colonies. Moreover, we monitored 18 colonies out of 25, thus many of the birds that dispersed were recaptured. There was also no significant difference in mass between philopatric and emigrant birds in this population (R. Covas, unpublished data).

In general, light birds have low fat reserves and face higher risk of starvation due to unpredictability of foraging success (Lima 1986; Cuthill & Houston 1997). For example, birds at high latitudes can experience long, cold nights or snowstorms that make food inaccessible. Our study species inhabits an area where climate is relatively mild and prolonged bad weather is rare, although cold nights often occur in winter. Sociable weavers cope with the energy demands of cold weather in part through roosting in the communal nest structure and by huddling (White *et al.* 1975). Still, it seems probable that part of that energy demand will be supplied by body reserves, such that birds with low fat reserves incur a cost, especially whenever cold weather lasts for several days (e.g. Brown & Brown 1998). Low fat reserves might also reflect disease,

high parasite loads (Brown & Brown 1996; Marsden 1999) or weakened immune function (Møller *et al.* 1998), all of which may negatively affect survival.

Despite the costs associated with low body-mass values, birds normally maintain a mass that is below maximal levels, indicating there are also costs associated with high mass levels (Witter & Cuthill 1993). These have received less attention. The costs of high body mass in birds have been suggested to result mainly from mass-dependent metabolic expenditure and predation risk (see reviews in Witter & Cuthill 1993; Cuthill & Houston 1997). Metabolic expenditure costs should arise because increased mass is believed to make flight energetically more costly (particularly when wing load increases), and periods of inactivity might also involve higher energetic expenditure associated with the maintenance of an increase in tissue (reviewed in Witter & Cuthill 1993). Furthermore, increased energetic expenditure will normally be associated with an increase in time spent feeding or feeding intensity, which is associated with an increased predation risk (Lima 1986; McNamara & Houston 1990) or decrease in time available for other important activities such as territory defence or plumage maintenance. However, empirical work measuring these costs remains scarce and we know of no study linking an increase in body mass with higher energetic expenditure and decreased survival.

Predation risk is expected to place a limit on high body mass because leaner birds should be more agile in escaping predators (Lima 1986; McNamara & Houston 1990). Several studies of captive birds have investigated agility, showing that fatter birds have lower take-off speed and manoeuvrability (e.g. Metcalfe & Ure 1995; Kullberg *et al.* 1996). Studies in the wild have also found evidence for a trade-off between body mass and predation risk. For example, Gosler *et al.* (1995) found that great tits *Parus major* became significantly heavier when sparrowhawks *Accipiter nisus* were absent from the area due to pesticide poisoning, and became lighter when the hawks reoccupied the area. In a recent experiment, Gentle & Gosler (2001) showed that great tits adjusted their fat reserves to the perceived predation risk, carrying significantly reduced fat under high predation risk. To our knowledge, the only study directly linking body mass to survival was that of Adriaensen *et al.* (1998), who showed that the shape of the curve describing fledgling survival as a function of body mass changed from a monotonically increasing relationship in predator-free plots to a curve with an optimum around the mean in the presence of sparrowhawks. We too found impaired survival at low and high body mass, but in our case this persisted across all years of the

study (as we found no time-dependent effect of mass on survival). The same trend in both age classes was expected as, in this sedentary species, juvenile birds are subjected to the same factors that affect mass and survival in adults (see also Adriaensen *et al.* 1998); furthermore, survival is not age-dependent in the sociable weaver (R. Covas, C. R. Brown, M. D. Anderson and M. Bomberger Brown, unpublished data). Like some of the results of Adriaensen *et al.* (1998) on blue tits, our results on juvenile weavers contradict the often accepted view that post-fledging survival always increases with mass. Predation might explain why heavier birds had higher mortality in our study, as sociable weavers inhabit open savannah areas where predation by raptors in general is probably high (Du Plessis *et al.* 1995). Furthermore, predation by the gabar goshawk *Micronisus gabar* is known to be important in this species (Maclean 1973*b*; Marsden 1999; R. Covas and M. D. Anderson, personal observation).

In conclusion, we verified the theoretical predictions that the costs and benefits of both low and high body mass should lead to stabilizing selection for intermediate mass and that this trade-off probably leads to the body masses observed in the field.

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