



Serins with intermediate brightness have a higher survival in the wild

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More ornamented individuals are supposed to signal their superior quality and health, however the development of larger ornaments or brighter plumages can affect their survival probabilities. The survival of male serins *Serinus serinus* in relation to the color characteristics of carotenoid-derived breast coloration was analyzed in a six-year capture–recapture study in northeastern Spain. A total of 210 males were individually marked generating 340 captures, between 1997 and 2003. The model with the best fit indicated a quadratic relationship between brightness of carotenoid-derived coloration and survival, independent of time and age of the birds, so that individuals with intermediate plumage brightness survived longer. Hence, results stress that plumage color in male serins is under stabilizing natural selection, with reduced survival both in drabber and brighter individuals. While lower condition of drabber individuals can explain their lower survival, brighter birds can suffer more from predation risk or from a higher investment of resources into mate attraction and/or reproduction.

There is often a relationship between male sexual ornaments and survival (Jennions et al. 2001), because only high quality males can produce the showiest ornaments. However, the most high quality males may invest more heavily in sexual displays and consequently die younger (Hunt et al. 2004). Plumage ornaments often reflect aspects of male quality such as condition, resistance to parasites, foraging ability, social dominance or quality of parental care (Andersson 1994, Hill 1999, 2002, Møller et al. 1999, Senar et al. 2002). Some aspects of plumage may be positively related to survival (e.g. parasite resistance, condition, etc., Badyaev et al. 2001), however conspicuous coloration is also expected to incur in survival costs. Indeed, recent empirical work has shown that brightly ornamented species or individuals are more often captured by birds of prey, negatively selecting on plumage brightness (Promislow et al. 1992, 1994, Götmark and Hohlfält 1995, Slagsvold et al. 1995, Dale and Slagsvold 1996, Götmark 1997, 1999, Huhta et al. 1998, 2003, Rytönen et al. 1998, Montgomerie et al. 2001).

Most studies have specifically tested the predictions that male plumage characteristics are related to survival, that more ornamented individuals are more exposed to predation or invest more in reproduction and die young. However, it follows from these two different processes that plumage coloration may be under balancing selection, at least if plumage coloration reflects aspects of male quality related to survival.

In spite of the plethora of papers studying ornamental plumage coloration (see previous references), no single work has provided data supporting stabilizing selection on this character. This contrasts with data from morphological studies (reviewed by Kingsolver et al. 2001), although this is probably the result of a bias, in that researchers studying sexual selection are traditionally concerned with finding out a “benefit” through mate choice for characters under study. To date, all studies on plumage coloration have tested for a positive relationship between plumage brightness and survival (Hill 1991, Nolan et al. 1998, González et al. 1999, Hórak et al. 2001). Only Gregoire et al. (2004)

reported stabilizing selection on beak coloration when examining the costs of early development of adult like coloration in young blackbirds (*Turdus merula*).

In this paper, we explicitly test for stabilizing natural selection on plumage coloration, focusing on the yellow carotenoid-based coloration of the serin *Serinus serinus*. In this species, we previously found a significant stabilizing selection on body mass, also most probably constrained by predation risk (Conroy et al. 2002). Male serins treated with insecticide to remove ectoparasites had brighter plumage after molt (Figuerola et al. 2003), confirming that male coloration is a condition-dependent trait. Analyses were carried out taking advantage of the recent developments in capture-recapture methodology (Williams et al. 2002). This approach not only controls for the confounding effect of recapture rate, which can highly bias results (Lebreton et al. 1993), but also allows testing of possible selective forces operating over continuous characters, by including individual covariates in the models (Kingsolver and Smith 1995, White and Burnham 1999). In this study, we show that stabilizing natural selection operates over bird coloration, due to a lower survival of both less and more brightly colored individuals.

Methods

Serins were trapped from November 1997 to February 2003 in the suburban area of Barcelona in northeastern Spain. The study area consisted of orchards, small woods dominated by pine, *Pinus halepensis*, and gardens. Birds were trapped at least weekly at baited feeders using Yunick platform traps, clap-nets and mist-nets, and marked with numbered aluminium bands (Senar 1988). Age (first-year or adult birds) was determined according to Svensson (1984), based on the extent of wing partial moult. Male serins present a conspicuous carotenoid-based coloration on the breast and head produced by the deposition of carotenoids in the developing feathers (Stradi et al. 1995a, 1995b). General yellowish plumage coloration was measured with a Minolta CR200 colorimeter (Anonymous 1994) using a standard D65 light flash (Figuerola et al. 1999a). Color in the visible human spectra was characterized according to its hue, chroma and brightness. Bird vision differs from those of humans, and plumage of many bird species presents emissions in the UV portion of the spectra (Eaton 2005), but yellow colours derived from carotenoids largely lack in emission in the UV portion of the spectra (Goodwin 1973, Gross 1987, Moss and Weeden 1999), or it is a by product of carotenoid coloration so that visible and UV peaks are highly correlated (MacDougall and Montgomerie 2003). Hue corresponds to wavelength and is

expressed in degrees of a circle starting with red, continuing through yellow, green and blue and completing the circle again with red. Chroma (also called intensity or saturation) corresponds to color purity on a scale from 0 for white to 100 for pure color. Brightness (also called lightness) corresponds to physical light intensity on a scale from 0 for black to 100 for white. The repeatability of three color variables (estimated from intra-class correlation) was high (brightness, $r_i = 0.90-0.99$, $p < 0.001$; chroma, $r_i = 0.95-1.00$, $p < 0.001$; hue, $r_i = 0.80-0.98$, $p < 0.001$, $n = 10$ individuals measured twice; Figuerola et al. 1999a). Color measurements were taken at crown, breast and belly and a principal components analyses (PCA) was done for each color component to summarize the measurements obtained from the three body areas studied. The first component of each of these analyses was used as an index of coloration. The first principal component summarizing brightness described 51.6% of variance in the three body areas (factor loadings for crown = 0.60, breast = 0.67, belly = 0.44). The first principal component for chroma described 80.4% of variance (crown = 0.55, breast = 0.61, belly = 0.58) and the first principal component for hue described 59.8% of variance (crown = 0.60, breast = 0.65, belly = 0.47).

We used capture-recapture models to estimate survival of marked individuals between seasons. Only captures occurring between November and February were included in the analyses, so as to estimate the probability of a bird alive in one wintering season being still alive at the start of the next wintering season. Survival analysis was based on Cormack-Jolly-Seber models (CJS). We used program MARK (White and Burnham 1999) to model local survival rates, and to analyze the influence of individual covariates and their interactions on local survival (White and Burnham 1999).

Model selection started from a fully parameterized model where both survival and recapture probability varied according to age and time. Models incorporating age dependent effects allowed parameters estimated from birds captured as young to be different from adults only during the year after first capture. The adjustment of the CJS model to the data was assessed by the Release program goodness-of-fit (Burnham et al. 1987). Test 2 of Release tests if recapture probability at time i is the same for all marked individuals present at time i . The goodness-of-fit of the models was also tested using a parametric bootstrap approach. The parameter estimates from the model were used to simulate data according to the assumptions of CJS models (individuals were independent and no over-dispersion of data occurred). This process was repeated 1000 times and the deviance of each model was calculated to determine whether the deviance of the

observed model exceeded that of the simulated data. The overdispersion parameter ($c\text{-hat}$) was calculated as the ratio between mean deviance of simulated models and deviance of the observed model (Cooch and White 2004). We found no evidence of significant overdispersion ($c\text{-hat} < 1.20$), and thus no evidence for deviation of the assumption that fates of the individuals were independent of each other (Anderson et al. 1994). For this reason, results were not adjusted for overdispersion (ideally $c\text{-hat}$ should be 1.00). In this case, this makes the presented results conservative because $c\text{-hat}$ adjusted results further supported the conclusions of this paper (unpubl.).

Analyses were restricted to males because data for females were too sparse to allow model testing and simplification. Model simplification started by analyzing the factors affecting recapture probability by constructing models with variation between age and time, and the age $\times$ time interaction. In a second step of model simplification, we analyzed age and time variation in survival. Finally, using the capture and survival simplified model, we tested the possible relationship between survival and individual coloration. We further tested the robustness of our conclusions by comparing the fit of models with coloration dependent survival against models with coloration dependent recapture rate. We used small sample size adjusted Akaike's information criterion (AICc) for model selection. AICc is considered a simple, effective and objective means for model selection (Burnham and Anderson 1998). Models with lower AICc are assumed to best fit the data with the least possible number of parameters. Models with AICc values differing by less than 2 were considered equivalents. In these cases we chose the model with the fewest parameters as that best explaining the data (Burnham and Anderson 1998), and the used likelihood ratio test (LRT) to determine whether this decision resulted in a significant loss of fit (Lebreton et al. 1992). However, to test the robustness of our conclusions on coloration and survival, effects of coloration were tested with all the different equivalent models, according to the AICc criteria. Given that no qualitative change occurred, the results for these alternative models are not presented. Additionally, the same final model was selected according to the nested AICc and the LRT criteria (Lebreton et al. 1992).

Results

Data showed a good fit to a general CJS model (Release tests: Test 2, $\chi^2 = 0.71$, 3 DF, $p = 0.87$). Bootstrap goodness-of-fit test also indicated that the model including age and time effects ($\phi_{\text{age} \times \text{time}} P_{\text{age} \times \text{time}}$) had a good fit ($p = 0.30$).

Table 1. Model selection for age and time effects on recapture (A) and survival probability (B). Models are ranked according to its AICc values. Differences of less than two in AICc indicate not significant differences between models. ϕ : survival probability, P: recapture probability, age: parameters for first year and adult birds are not forced to be the same, time: parameters are allowed to change between capture occasions, +: only main factors included in the model, $\times$: main factors and its interaction included in the model.

Model	AICc	Parameters	Deviance
(A) Recapture			
$\phi_{(\text{age} \times \text{time})} P_{(\text{constant})}$	194.93	11	171.49
$\phi_{(\text{age} \times \text{time})} P_{(\text{age})}$	195.48	12	169.77
$\phi_{(\text{age} \times \text{time})} P_{(\text{age} + \text{time})}$	200.03	15	167.35
$\phi_{(\text{age} \times \text{time})} P_{(\text{time})}$	200.48	14	170.15
$\phi_{(\text{age} \times \text{time})} P_{(\text{age} \times \text{time})}$	202.86	18	162.97
(B) Survival			
$\phi_{(\text{age})} P_{(\text{constant})}$	186.39	3	180.27
$\phi_{(\text{constant})} P_{(\text{constant})}$	186.79	2	182.73
$\phi_{(\text{age} + \text{time})} P_{(\text{constant})}$	188.80	7	174.20
$\phi_{(\text{time})} P_{(\text{constant})}$	190.09	6	177.65
$\phi_{(\text{age} \times \text{time})} P_{(\text{constant})}$	194.93	11	171.49

When modeling recapture probability, two models were similarly supported by AICc (Table 1). The lowest AICc was for the model with constant recapture rate P_{constant} , while some support was also found for the model assuming differences in recapture rate among first year and adult birds P_{age} . Removal of age effects on recapture parameter did not result in a significant loss of fit of the model (LRT test, $\phi_{\text{age} \times \text{time}} P_{\text{constant}}$ vs $\phi_{\text{age} \times \text{time}} P_{\text{age}}$, $\chi^2 = 1.73$, 1 DF, $p = 0.19$).

The model with less parameters P_{constant} was used to model survival probability, although as already commented, no qualitative change in results occurs when using models with P_{age} . When modeling survival probability, two different models were similarly supported by AICc (Table 1): $\phi_{\text{age}} P_{\text{constant}}$ and $\phi_{\text{constant}} P_{\text{constant}}$. The removal of age effects had no significant effect on the fit of the model ($\chi^2 = 2.46$, 1 DF, $p = 0.12$), and consequently the model with fewer parameters was used to model individual covariate effects on survival. The ($\phi_{\text{constant}} P_{\text{constant}}$) model had a good fit to CJS assumptions (Bootstrap goodness-of-fit test, $p = 0.32$). Survival was estimated at in 0.39 ± 0.08 and recapture probability at 0.23 ± 0.08 , with no differences between ages and years.

A second order polynomial relationship between survival and plumage brightness was found when analyzing the relationship between survival and individual coloration (Fig. 1). The model including brightness and squared brightness as covariates presented the lowest AICc and fitted the data better than the model assuming homogenous survival among individuals, as judged by the LRT test ($\phi_{\text{constant}} P_{\text{constant}}$ vs $\phi_{\text{brightness}} P_{\text{constant}}^2$, $\chi^2 = 8.99$, 2 DF, $p = 0.01$).

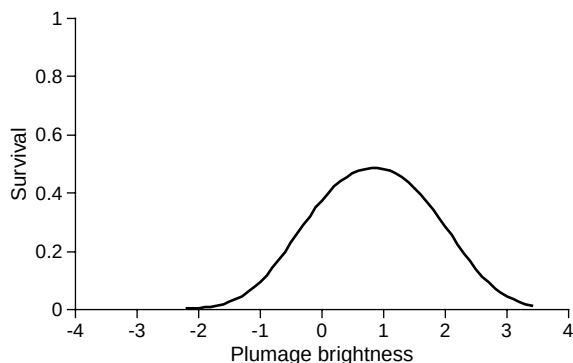


Fig. 1. Survival probability of serins (ϕ) in relation to plumage brightness (model $\phi_{(\text{brightness brightness}^2)} P_{(\text{constant})}$). Mean plumage brightness for the population ($\pm$ SD) estimated from a principal components analysis of the brightness at crown, breast and belly was $0.45 \pm 1.16\%$ (range -2.74 – -3.39).

According to this model, an individual's expected survival was:

$$\text{Logit } (\phi) = -1.0022839 + 1.2509081 \times \text{brightness} - 1.3252688 \times \text{brightness}^2$$

where brightness corresponds to the centered and standardized values ((brightness-mean brightness)/SD). None of the other models with individual co-variants improved the fit of the model (Table 2).

Discussion

It has been widely hypothesized that ornamental plumage coloration represents a balance between sexual selection and natural selection and that the combination of these factors shape the expression of this character (Darwin 1871). Our study clearly shows a higher survival of intermediate colored individuals. However, the overall pattern of selection on plumage color in male serins will be the result of the combined action of sexual selection and the stabilizing force of natural selection: i.e. on how plumage brightness is related to offspring production. Consequently, until no information will be available on the relationship between male coloration and offspring production we can not infer the shape of overall fitness in relation to coloration but just conclude that survival favours individuals with intermediate coloration

The lower survival rate of less brightly colored individuals may be because these individuals harbour more parasites and are in a poorer state of health as has been shown in several other avian species (Figuerola et al. 1999b, Lindström and Lundström 2000, Saks et al. 2003). They would hence be more susceptible to illness and/or starvation and therefore to mortality. In a

previous study, we demonstrated that male serins treated with an insecticide to remove ectoparasites developed a brighter plumage after molt (Figuerola et al. 2003). The fact that, in many species of birds, females select for these more brightly colored and hence healthier individuals is widely recognized (Zuk 1992, Hill 1999, 2002).

Different experiments have shown that birds with more access to carotenoids in their diet produce brighter plumages (Hill 2002). Access to carotenoids have also been shown to increase survival of nestlings (McGraw et al. 2005) and immune function of adult birds (McGraw and Ardia 2003, Alonso-Alvarez et al. 2004). Bright individuals have also been shown to have higher immune responses and better condition than drab individuals (Saks et al. 2003). Why, then, the brighter individuals present low survival rates than individuals with intermediate colorations? The lower survival rate of brightly colored birds could be the result of several factors, for instance, plumage brightness dependent dispersal given that permanent emigration from the area is treated by models as death. However, models incorporating brightness dependent recapture probability had a worse fit than models assuming constant recapture probability for all individuals suggesting that our results are not an artifact of a relationship between dispersal and plumage coloration. It could also be that bright individuals invested more in reproduction (Senar et al. 2002, Siefferman and Hill 2003; but see Møller 1994 and Duckworth et al. 2003 for results in the completely opposed direction), and hence, the reduced survival could reflect the costs of reproduction (Gustafsson et al. 1995). Several papers have shown how brightly colored individuals can be more conspicuous to predators and consequently suffer from increased predation risk (Götmark and Høglfält 1995, Slagsvold et al. 1995, Dale and Slagsvold 1996, Götmark 1997, 1999, Huhta et al. 1998, Rytönen et al. 1998, Montgomerie et al. 2001). However, increased mortality could also be due to other factors

Table 2. Models testing the relationship between individual covariates and survival. The models incorporating brightness as a covariate of recapture probability were used to test the hypothesis of a relationship between plumage brightness and dispersal.

Model	AICc	Parameters	Deviance
$\phi_{(\text{brightness brightness}^2)} P_{(\text{constant})}$	181.95	4	173.74
$\phi_{(\text{constant})} P_{(\text{constant})}$	186.79	2	182.72
$\phi_{(\text{chroma})} P_{(\text{constant})}$	186.80	3	180.67
$\phi_{(\text{constant})} P_{(\text{brightness})}$	187.45	3	181.33
$\phi_{(\text{brightness})} P_{(\text{constant})}$	187.92	3	181.79
$\phi_{(\text{hue})} P_{(\text{constant})}$	188.32	3	182.20
$\phi_{(\text{chroma chroma}^2)} P_{(\text{constant})}$	188.81	4	180.60
$\phi_{(\text{hue hue}^2)} P_{(\text{constant})}$	189.54	4	181.33
$\phi_{(\text{brightness})} P_{(\text{brightness})}$	189.58	4	181.37

that increase predation risk, like a higher conspicuousness because of the frequent song flights, typical of this species (Mota 1999). Although we do not have a direct measure of predation risk in our study area, sparrowhawks and great grey shrikes have frequently been observed hunting Serins in open areas frequented by our birds (pers. obs.). More interestingly, and according to the widely recognized starvation–predation risk trade-off (Witter and Cuthill 1993, Cuthill and Houston 1997), we previously demonstrated that body mass is also under stabilizing selection in this Serin population (Conroy et al. 2002). However, body mass and plumage brightness are unrelated in our sample ($F_{1,197} = 1.00$, $p = 0.32$), suggesting that selection on coloration is not an indirect effect of selection on body mass. Adriaensen et al. (1998) nicely demonstrated that the patterns of selection on blue tit body mass shifted from directional to stabilizing when sparrowhawk were present in the area. Similar results have been found for the great tit (Gosler et al. 1995).

In the future, there is a need to assess the generality of stabilizing natural selection on bird coloration and the role of predation and breeding effort in explaining differences in the intensity and direction of selective forces operating over bird coloration. Further studies analyzing the relationship between plumage coloration and survival in localities and species differing in susceptibility to predation and/or mating and parental care systems can greatly improve our understanding of the factors regulating the expression of sexual ornaments.

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