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Senescing sexual ornaments recover after a sabbatical

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Somatic deterioration in ageing animals may arise from allocation of resources to reproduction at the expense of repair and maintenance. Thus, accumulated reproductive effort is likely to progressively limit the expression of sexual ornaments at older ages. We analysed the effect of age and reproductive effort on the sexual attractiveness (foot colour) of male blue-footed boobies. Using a long-term dataset, we found that, as animals age and accumulate reproductive events, the expression of foot colour deteriorates. In addition, after non-breeding events males displayed more colourful feet compared with males that reproduced the year before, suggesting that sabbatical years facilitate recovery. Our results indirectly support the idea that allocation of resources to reproduction limits sexual attractiveness and that animals could cope with the negative effects of senescence on sexual ornaments by skipping some breeding events.

Keywords: senescence; sexual signals; reproductive effort

1. INTRODUCTION

Senescence, the progressive loss of function in ageing animals, is believed to be universal in age-structured populations and probably owing to accumulated somatic deterioration (Kirkwood & Austad 2000). According to life-history theory, iteroparous organisms invest in reproduction at the expense of their somatic maintenance and future reproductive output (Stearns 1992). In wild animals, recent evidence suggests that reproduction accelerates senescence (e.g. Reed *et al.* 2008), yet the mechanisms underlying age-specific rates of reproduction remain poorly understood (Zera & Harshman 2001). The reproductive success of animals is strongly influenced by sexually selected traits and these are costly to produce (Andersson 1994). Experimental manipulations of parental effort in birds demonstrate its negative effect on future sexual displays (Gustafsson *et al.* 1995; Griffith 2000; Siefferman & Hill 2005). Thus, the capacity to invest in sexual traits may be constrained in ageing animals (Torres & Velando 2007) by somatic deterioration owing to the accumulated negative effects of reproductive effort.

In the blue-footed booby, foot colour is a sexually selected trait that strongly affects several components of reproductive success (Torres & Velando 2003; Velando *et al.* 2006a). Foot colour depends on the combined effects of carotenoids (zeaxanthin) and structural collagen arrays (Velando *et al.* 2006a). Older males display duller feet (Torres & Velando 2007), which to some extent may explain male reproductive senescence after 10 years of age documented by Velando *et al.* (2006b). Furthermore, older males deal less well with the oxidative costs of self-maintenance which constrain their ability to mobilize a high flux of pigments into foot colour (Torres & Velando 2007). Blue-footed boobies have a long period of biparental care, roughly 45 days of incubation and a four-month rearing period (Torres & Drummond 1999). Because reproductive effort increases oxidative stress (Alonso-Alvarez *et al.* 2006), we predicted that in the blue-footed booby an accumulation of breeding events should negatively affect foot colour. Further, to diminish the effects of reproductive effort on foot colour, individuals may take advantage of sabbatical years (i.e. non-breeding events, a common strategy in long-lived birds) to recover (Wooler *et al.* 1989).

2. MATERIAL AND METHODS

The study was carried out in the blue-footed booby colony at Isla Isabel, Nayarit, Mexico from January to March 2004 and 2005. During the courtship period, 70 males in 2004 and 39 males in 2005 were haphazardly captured in the Costa Fragata study area and their foot colour was measured by taking three measures on the foot web using a spectrophotometer (MINOLTA CM-2600d). We analysed the chroma of foot colour as the proportion of reflectance between 460 and 620 nm (range of highest visual sensitivity; hereafter, green chroma), variability possibly owing to pigment deposition (Velando *et al.* 2006a). All captured birds had been banded in earlier years in the course of a long-term study and their reproductive histories were known (see Drummond *et al.* 2003; Kim *et al.* 2007). In our sample, 84 males had been ringed at fledging, so their ages were known, and 24 males were ringed when they first nested in the study area. The latter males could not be aged precisely but their recent reproductive histories were known, so they were used only in the analysis that did not include age.

The effect of previous breeding effort on foot colour of known-age males was analysed using general linear models (PROC GENMOD, SAS). The initial model included year (2004, 2005), age, body mass, breeding effort (measured as the number of previous breeding attempts), and whether the bird reproduced or skipped reproduction in the year before the study. Breeding effort was later excluded from model because it was highly correlated with age. Similar results were found if the total number of fledglings produced was used as an indicator of breeding effort. Only experienced breeders (with more than one previous breeding attempt; i.e. that had had the chance to skip a breeding year) were used in this analysis. All main factors and two-way interactions were included in the initial model and final models were obtained by backward elimination. Laying date was recorded in 48 males in 2004 and 30 males in 2005. Foot colour was not correlated with laying date ($r = 0.03$, $p = 0.80$) or the elapsed time between capture and laying date ($r = 0.02$, $p = 0.98$), so these variables were not included in the analyses, but similar results were achieved in the subset when they were included. Because foot colour is a condition-dependent trait (Velando *et al.* 2006a), the body mass of skipping and non-skipping males was compared; the model included male age and year.

3. RESULTS

Male foot colour during courtship declined with age ($r = -0.49$, $p < 0.001$; figure 1a) and with breeding effort ($r = -0.53$, $p < 0.001$; figure 1b), and these relationships did not differ between years (age * year $F_{1,80} = 0.019$, $p = 0.89$; breeding effort * year, $F_{1,104} = 0.56$, $p = 0.45$). After controlling for breeding

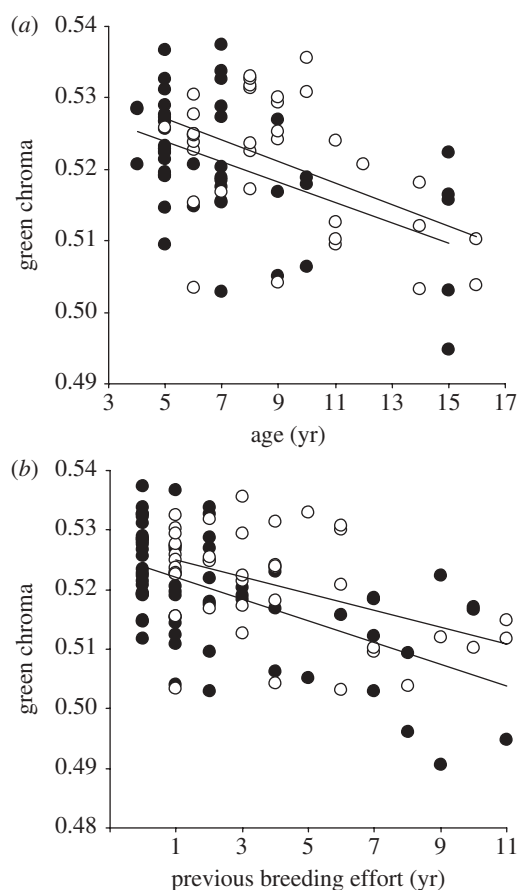


Figure 1. Male foot colour and (a) age and (b) breeding effort (number of previous breeding attempts). Filled circles, 2004; open circles, 2005.

effort, age was not significant ($F_{1,80} = 0.97$, $p = 0.33$), owing to the strong correlation between both variables ($r = 0.91$, $p < 0.001$); thus, breeding effort was excluded from the analysis of foot colour.

The expression of foot colour differed between the 2 years sampled ($F_{1,60} = 7.40$, $p = 0.009$), and skipping the previous year had a strong effect on foot colour ($F_{1,60} = 7.70$, $p = 0.007$; figure 2). Green chroma was greater in 2005 than 2004 and skipping males displayed more attractive foot colour (higher green chroma) than non-skipping males (figure 2), independently of age (age: $F_{1,60} = 17.89$, $p < 0.001$, age * skipping: $F_{1,59} = 0.61$, $p = 0.44$) and body mass ($F_{1,59} = 0.24$, $p = 0.63$).

Male body mass was not affected by age ($F_{1,61} = 0.14$, $p = 0.71$) or year ($F_{1,61} = 2.28$, $p = 0.14$), and skipping males did not differ in body mass from non-skipping males ($F_{1,61} = 0.02$, $p = 0.89$). In addition, we found no evidence that skipping males differed from non-skippers in their previous breeding experience ($F_{1,62} = 2.33$, $p = 0.13$), or accumulated number of fledglings produced prior to the skipping year ($F_{1,62} = 2.19$, $p = 0.14$).

4. DISCUSSION

We found that the sexual attractiveness of blue-footed boobies decreases with age and reproductive effort. In our cross-sectional study, as male boobies age and accumulate reproductive events, their foot colour

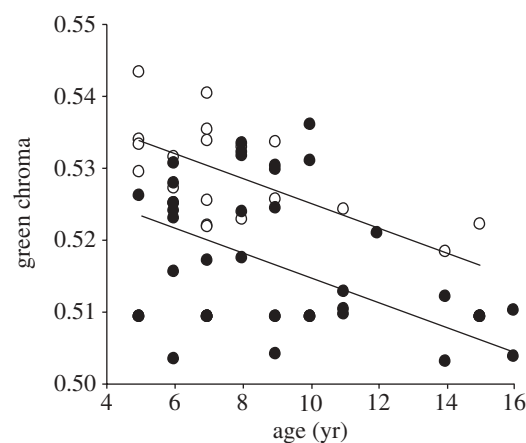


Figure 2. The effect of age and skipping a breeding event on male foot colour (controlling for year). Open circles and upper line, skipping males; filled circles and lower line, non-skipping males.

during courtship deteriorates. The effects of reproductive effort could not be separated from other intrinsic (not measured) effects of somatic deterioration through life, but the comparison between skipping and non-skipping males suggests that either reproductive effort in 1 year constrain expression of foot colour in the following year, or males strategically invest in enhanced coloration following a skipping event. Alternatively, skipping males may have displayed brighter foot colour because they were higher quality birds, but this is unlikely because skippers and non-skippers did not differ in body mass or previous reproductive effort and success. Sabbaticals might allow boobies to recover from reproductive effort and display brighter feet.

Studies of three short-lived birds have shown that an experimental increase in reproductive effort depresses the expression of sexual signals in the next breeding season (Gustafsson *et al.* 1995; Griffith 2000; Siefferman & Hill 2005). Interestingly, the costs of reproductive effort are reflected in signals of different species with different mechanisms of colour production: structural (Gustafsson *et al.* 1995), melanin-based (Griffith 2000) and carotenoid-structural-based (this study). Although seldom considered, postponed depression of sexual signals could be a widespread cost involved in the trade-off between present and future reproduction. In the blue-footed booby, reduced foot colour probably prejudices male success, affecting mate choice, probability of being cuckolded (Torres & Velando 2003) and female investment in eggs (Velando *et al.* 2006a; Dentressangle *et al.* 2008).

Our results suggest that reproductive effort may affect the mechanisms of colour production. In the blue-footed booby, foot colour honestly reflects individual condition (Velando *et al.* 2006a) and the capacity to cope with induced oxidative stress (Torres & Velando 2007). Age-associated decline in the expression of sexual signals may result, at least in part, from the accumulation of damage, such as oxidative damage (Alonso-Alvarez *et al.* 2006), owing to reproduction. Hence, costs of reproductive effort (oxidative and/or others) probably constrain the ability of blue-footed boobies to mobilize pigments into webs.

Trade-offs in life-history traits vary through life, and individuals may adopt different reproductive strategies as they age (Yoccoz *et al.* 2002). Senescence may affect male breeding strategy by diminishing the attractiveness of older males (Torres & Velando 2007). Because individuals that skip a breeding event avoid costs of reproduction (Stearns 1992), skipping has been interpreted as an adaptive strategy to maximize lifetime reproductive success (Wooller *et al.* 1989). Alternatively, sabbaticals may result in a net decrease in lifetime reproductive success if individuals take a sabbatical simply because they are unable to attract a female and invest in offspring. Blue-footed boobies that skipped the previous breeding event were able to produce a better sexual signal, suggesting that skipping may be an adaptive male strategy, particularly for older males with dull feet. The age-related costs and benefits of skipping need exploring to determine whether skipping is an adaptive breeding strategy in the blue-footed booby.

In conclusion, our results suggest that as blue-footed boobies age and accumulate reproductive events their foot colour deteriorates. The fact that, independently of age, non-skipping males displayed duller foot colour in the following year compared to skipping males supports the idea that accumulated effects of reproductive effort over the lifetime are partly responsible for the progressive loss of foot colour. Thus, limitations in somatic performance of ageing animals, as expressed by sexual signals, may arise from the costs of reproductive effort (Williams 1966), as predicted by the disposable-soma model of ageing (Kirkwood & Austad 2000). Interestingly, the recovery of attractiveness after skipping a breeding event suggests that some animals could mitigate the negative effects of senescence by resting.

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