

Song as an indicator of male parental effort in the sedge warbler

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Repertoire size has been found to be a sexually selected trait in a number of bird species, although the advantages of mating with a male who possesses a complex song remain unclear. We studied the potential role of song as an indicator of male parental effort in the sedge warbler *Acrocephalus schoenobaenus*. The male provisioning rate was used as a measure of male parental effort and was found to increase with nestling age and brood size. When controlling for chick age, brood size and other variables, we found a highly significant positive correlation between a measure of song complexity (repertoire size) and male parental effort. Both male parental effort and repertoire size were found to be positively correlated with chick weight when controlling for chick age. We found no correlation between a measure of song output (amount of song flighting) or territory size and parental effort. Repertoire size is known to be the most important cue in female choice amongst sedge warblers and we discuss the possible reasons for this. We suggest that, in choosing a male with a large repertoire, a female obtains not only indirect benefits but also direct benefits in the form of increased parental effort.

Keywords: song; parental effort; sexual selection; *Acrocephalus*

1. INTRODUCTION

Models dealing with the coevolution of female choice and male secondary sexual traits predict that females can obtain direct and indirect benefits from mating with males displaying exaggerated traits (Kirkpatrick & Ryan 1991; Andersson 1994). One potential direct benefit which may be indicated by male traits is the amount or quality of parental care provided (Hoelzer 1989). If the standard of male care is important for subsequent fledgling survival and reproductive success, females may select secondary sexual traits which indicate the quality of male parental care (Heywood 1989).

In birds, only a few species have so far been shown to possess reliable indicators of male parental care. Female red-winged blackbirds (*Agelaius phoeniceus*) prefer to mate with experienced males who have larger repertoires and provide more food at the nest. However, this decision appears to be affected by territory quality, as these males also defend larger territories (Yasukawa *et al.* 1980; Searcy & Yasukawa 1996). Similarly, female stonechats (*Saxicola torquata*) have been found to prefer males with higher song rates who later go on to make more provisioning visits to the nest (Greig-Smith 1982). Again it seems possible here that female choice may in part be based upon territory quality rather than song directly. Female choice for male traits which indicate foraging efficiency rather than territory quality has been demonstrated in the house finch (*Carpodacus mexicanus*) (Hill 1990). Females choose males on the basis of carotenoid-based plumage pigments which are accumulated in the diet. Brighter males are more successful foragers and also provide more food to their offspring (Hill 1990, 1991).

Theoretical mechanisms for the evolution of biparental care have received considerable attention since Trivers (1972) first suggested how such balanced cooperation

could be evolutionarily stable. For species with biparental care, the quality and quantity of male parental care is clearly of great importance to a female seeking a breeding partner. Some studies have suggested that withdrawing male parental care has a detrimental effect on chick survival (Mock & Fujioka 1990) or on the female by demanding a compensatory increase in her provisioning rate (Greenlaw & Post 1985; Møller 1988). A range of male removal experiments have consistently demonstrated the redundancy of male parental efforts (Gowaty 1983; Greenlaw & Post 1985; Wolf *et al.* 1988). Such studies have only investigated current reproductive effort, ignoring the possible detrimental effects on the long-term survival of the young and future reproduction of the female.

The evolution of mating systems with particular reference to provisioning behaviour in the genus *Acrocephalus* has been the subject of reviews by Leisler & Catchpole (1992) and Catchpole (1995). In brief, socially polygynous species specialize upon large, highly profitable insect prey and females often raise their broods without male assistance. Socially monogamous species such as the sedge warbler specialize on smaller, less profitable insects and male assistance is more important in raising broods successfully. This was tested by Duckworth (1992) by removal experiments in the socially monogamous reed warbler *Acrocephalus scirpaceus*. Females increased their provisioning rate to compensate for the lack of male parental effort and late broods were unsuccessful due to starvation of the young in the nest. This suggests that females in socially monogamous *Acrocephalus* species are more dependent upon male provisioning for maximizing their reproductive success than in closely related polygynously mating species.

Catchpole (1980) suggested that the evolution of song complexity in the genus *Acrocephalus* might well be related to female choice for high-quality males. From a series of field and experimental studies on the sedge warbler

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(Catchpole *et al.* 1984; Buchanan & Catchpole 1997) we now know that song complexity, as measured by repertoire size, is driven by female choice. Large repertoire sizes appear to be associated with an increased volume of the higher vocal centre (HVC), the song control nucleus associated with song development and production (Székely *et al.* 1996). If such neural development was associated with the ability to provide a higher standard of parental care, females choosing males with complex songs could be receiving direct benefits for their offspring. A recent study examining the relationship between song display and male parental effort in the European starling (*Sturnus vulgaris*) found no relationship between repertoire size and parental care (Mountjoy & Lemon 1997). As yet, no study has demonstrated that song complexity may be advertising superior parenting qualities to females who will obtain direct benefits in the form of extra food for their young. In this paper we test the hypothesis that male song complexity acts as a reliable indicator of the quality of future male parental effort. We therefore predict that males with larger repertoires should provision chicks at a higher rate than males with lower repertoires. We also predict that chicks fathered by such males should consequently fledge at heavier weights.

2. METHODS

Field observations were carried out at Wraysbury Lakes, Surrey, UK. Male sedge warblers were followed from their arrival at the field site from mid-April during 1995 and 1996. The vegetation consisted of low willow *Salix* sp. and bramble *Rubus* sp. scrub with access to nearby standing water from all territories. We caught both male and female sedge warblers using mist-nets as soon as possible after their arrival at the site and marked them with an individual combination of coloured leg rings. Pairing was indicated by the cessation of male singing activity accompanied by the appearance of a female in the territory. The success of males in obtaining a mate was monitored as part of a study examining the role of song in mate choice (Buchanan & Catchpole 1997).

(a) Song display

Prior to pairing, a 15-min sample of song was recorded for each displaying male within the first 5 h of daylight. This was recorded using a Marantz tape recorder and a Sennheiser microphone mounted on a parabolic reflector. Song analysis was carried out using a Kay DSP model 5500 sonograph (Kay Elemetrics Corp., Pine Brook, NJ, USA). The repertoire of the sedge warbler is comprised of a number of syllable types which are used to construct songs which are immensely variable in length and structure. The repertoire size of individual males was estimated from the total number of different syllable types within the first 20 uninterrupted songs from this recording. Sampling of syllable types has shown that the rate of appearance of novel syllable types reaches an asymptote at approximately ten songs (see Catchpole 1980). Analysis of recordings from the same male singing on consecutive days has shown that this measure of repertoire size has a repeatability of greater than 90% (Buchanan *et al.* 1999).

Male sedge warblers sing from either a perched position or in flight (song fighting). We quantified the amount of time spent song fighting by male sedge warblers during daily 10-min time-budgets in both 1995 and 1996. We used these results to calculate

the mean number of song flights and the mean time spent song fighting. Although the time spent song fighting varied between days, observations carried out on the same individual on the same day had greater than 90% repeatability (Buchanan *et al.* 1999). The amount of time spent singing was quantified in an earlier study, but was not found to relate to female choice (Buchanan & Catchpole 1997).

(b) Territory size

Territory boundaries were ascertained gradually by daily observations of boundary disputes and the song posts used for display. Territory size (m²) was measured in the field using these boundaries at the time of pairing. Any adults from 1995 returning to breed at the site in 1996 were excluded from the analysis.

(c) Parental effort

The breeding success of all adults was monitored by locating each nesting attempt and determining clutch size, brood size and fledging success. Parental provisioning rates were used as a measure of parental effort and were standardized by sampling provisioning rates at each nest between 07.00 and 11.00 seven days after chick hatching. During nest observations, the time of each visit as well as the identity of the parent was noted. No attempt was made to quantify the amount or quality of food delivered.

(d) Analyses

All data analysis was carried out on MINITAB or Statview 4.01 for the Macintosh. Parametric statistics were used only where the data were normally distributed or could be transformed to achieve a normal distribution. For comparative purposes and visual display, figures are shown as scatter plots showing untransformed data.

3. RESULTS

In 1995 14 nests were observed between 31 May and 20 July, and in 1996 11 nests were observed between 30 May and 5 August. All nests were observed for 84.6 ± 6.1 min (mean \pm s.e.; minimum period 1 h). Brood sizes were 4.9 ± 0.2 (range three to six) in 1995 and 3.5 ± 0.5 (range one to six) in 1996. Successful nests fledged 5.0 ± 0.2 chicks (range four to six chicks) in 1995 and 4.6 ± 0.3 chicks (range three to five chicks) in 1996.

In 1995 five nests were observed on multiple days in order to compare the parental provisioning rate with chick age. This clearly showed that the total provisioning rate increased rapidly with age (figure 1). As expected the total provisioning rates also increased with brood size (Spearman's rank correlation $r_s = 0.487$, $n = 25$ and $p = 0.017$) (figure 2a). Therefore, brood size was controlled for throughout the analysis by expressing the provisioning rate as the number of visits made to the nest per chick in the nest. There was also an effect of brood size on the total amount of provisioning provided to each chick, with chicks in larger broods receiving a smaller absolute number of provisioning visits ($r_s = -0.459$, $n = 25$ and $p = 0.025$). This effect appears to be due to an increased amount of absolute provisioning per chick ($r_s = -0.570$, $n = 25$ and $p = 0.005$) and the proportion of care ($r_s = -0.438$, $n = 25$ and $p = 0.032$) provided by the female at smaller brood sizes (figure 2b). However, the absolute amount of male provisioning per chick was not

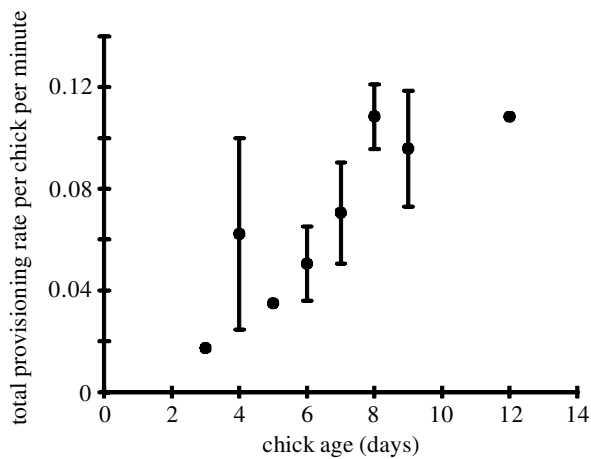


Figure 1. The relationship between the mean total provisioning rates per chick per minute at nests (\pm s.e.) ($n = 1-5$) and chick age (days after hatching).

significantly affected by brood size ($r_s = -0.286$, $n = 25$ and $p = 0.161$).

The combined mean provisioning rate of both parents was slightly higher in 1996 (1995, 3.15 ± 0.2 visits per chick per hour and 1996, 5.61 ± 0.5 visits per chick per hour). Considering 1995 and 1996 together, male provisioning accounted for approximately half of the visits to the nest ($52.2 \pm 3.4\%$). Male weight was calculated by regressing body weight against wing length to control for body size. There was a non-significant tendency for males with a smaller residual weight to make a lower percentage of the total provisioning visits ($r_s = 0.432$, $n = 17$ and $p = 0.08$).

When considering the results from 1995 and 1996 together, there was a highly significant correlation between the male provisioning rate per chick and male repertoire size ($r = 0.663$, $n = 20$ and $p < 0.001$) (figure 3). Taking each year separately this relationship held true in 1996 only (1995, $r_s = -0.08$, $n = 11$ and $p = 0.777$ and 1996, $r_s = 0.85$, $n = 9$ and $p = 0.017$). Considering 1995 and 1996 together, there were no significant relationships between male provisioning effort and either of the two other previously detected mate choice cues of song fighting ($r = 0.019$, $n = 21$ and $p > 0.05$) or territory size ($r = 0.108$, $n = 25$ and $p > 0.05$). There was also no significant relationship between male age and male provisioning effort (Kruskal–Wallis test, $H_2 = 1.05$, $n = 25$ and $p = 0.588$).

When combining both years, date appeared to act as a confounding variable, as there was both a positive correlation between the date of the provisioning observations and male provisioning visits per chick ($r = 0.456$, $n = 25$ and $p < 0.02$), and a strong positive correlation between the date of provisioning observations and repertoire size ($r = 0.717$, $n = 20$ and $p < 0.001$). When considering each year separately, date was not significantly related to male provisioning effort (1995, $r_s = 0.28$, $n = 14$ and $p = 0.307$ and 1996, $r_s = 0.478$, $n = 11$ and $p = 0.131$). However, overall, successful nests of high repertoire males occurred later in the season, as many early nesting attempts were unsuccessful due to poor development of the ground vegetation. There was significantly higher male provisioning effort for second nesting ($n = 15$) attempts compared to first attempts ($n = 10$) ($p = 0.024$, Mann–Whitney U -test).

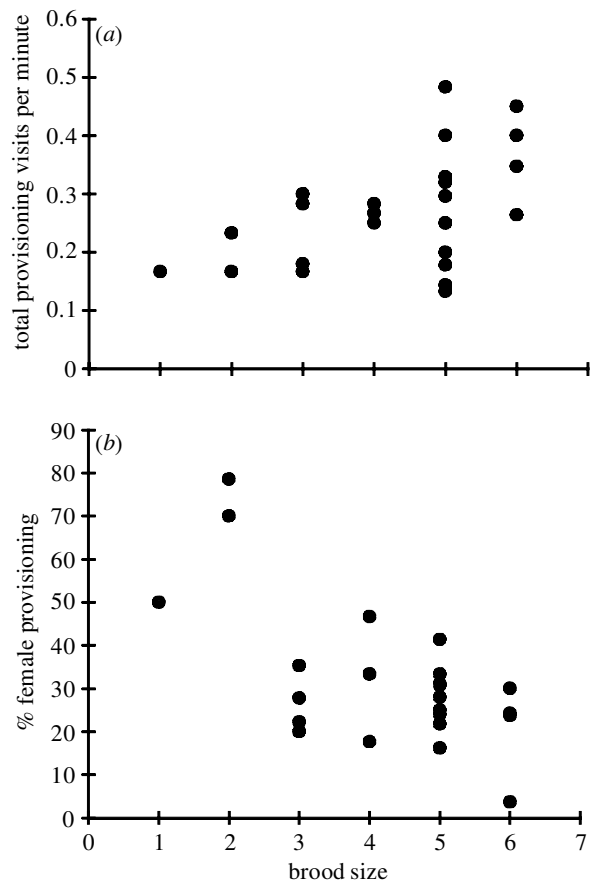


Figure 2. (a) The relationship between brood size and the amount of total provisioning visits made per minute to the nest. (b) The relationship between brood size and the percentage of provisioning effort provided by the female.

In addition, the minimum temperature on the day of the provisioning observation had a significant effect on the male provisioning rate per chick ($r = 0.479$, $n = 21$ and $p < 0.05$). A general linear model was then constructed to partition the variation in male provisioning due to each variable. Repertoire size and minimum temperature were entered as continuous variables whilst nesting attempt, date and year were entered as covariates. This model showed that nesting attempt, date and year had non-significant effects on the male provisioning rates, whilst the significant effect of repertoire size remained ($F_{1,18} = 5.63$ and $p = 0.033$). The minimum temperature had a non-significant effect on male provisioning effort ($F_{1,18} = 1.2$ and $p = 0.291$). This confirmed that, when controlling for all other variables, the only variable to act as a significant predictor of male provisioning effort was repertoire size.

There was no evidence that the male provisioning effort was correlated with any measure of reproductive success. Taking the nests successful in fledging some young only, there was no direct relationship between male provisioning per chick and the number of young fledged ($r_s = -0.165$, $n = 13$ and $p = 0.567$). In addition, there was no overall effect of the total provisioning rate on the number of young fledged ($r_s = -0.372$, $n = 13$ and $p = 0.198$).

In 1996 chicks were weighed whilst in the nest, although the age at weighing varied between broods. We regressed the mean chick weight of broods against age ($y = 2.88 + 0.925\text{age}$; $r^2 = 49.1\%$ and $p = 0.007$) and took

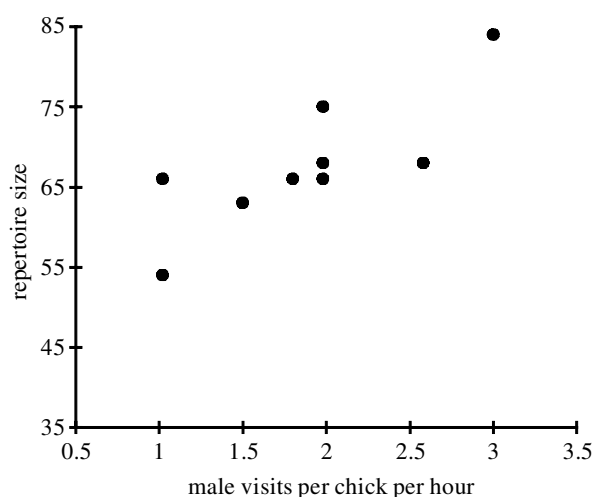


Figure 3. The relationship between the number of male provisioning visits per chick per hour and male repertoire size.

the residuals of this relationship as an expression of relative chick weight for a given age. Chicks in nests where males were making more provisioning effort had a higher residual weight ($r=0.738$, $n=11$ and $p=0.02$) (figure 4a). However, there was no effect of female provisioning effort per chick ($r=0.036$, $n=11$ and $p=0.91$). Furthermore, there was a significant relationship between male repertoire size and residual chick weight (figure 4b), suggesting that the higher quality of care provided by males with larger repertoire sizes may result in improved survival chances for their offspring.

4. DISCUSSION

Repertoire size has been found to be important for female choice in a number of songbird species particularly those within the genus *Acrocephalus* (Catchpole 1980, 1986; Catchpole *et al.* 1984; Catchpole & Leisler 1996). However, the potential benefits to females from mating with high repertoire males remain the subject of considerable speculation. To the best of our knowledge this is the first reported association between song quality and the quality of male parental care. This result appears to be robust as it remains when controlling for the potentially confounding effects of date, nesting attempt and daily temperature. The increase in male parental effort with date may in part be a reflection of a seasonal increase in food availability. However, other factors such as extra-pair mating opportunities may also play a role in determining the optimum level of male provisioning at the nest.

The relationship between male song complexity and parental effort was only found to be significant in one of the two years when analysed separately. This may be partly due to a decreased variance in male repertoire size in 1995 (coefficient of variation, CV = 8.3%), compared to 1996 (CV = 12.1%), masking any underlying relationship. Alternatively, it may be due to fundamental differences in parental care between the years. In 1995 males made fewer absolute provisioning visits per chick. The population density was particularly high in 1995 coupled with poor environmental conditions at the start of the season, suggesting that competition for limited food may have been particularly high in this year. It is also possible that

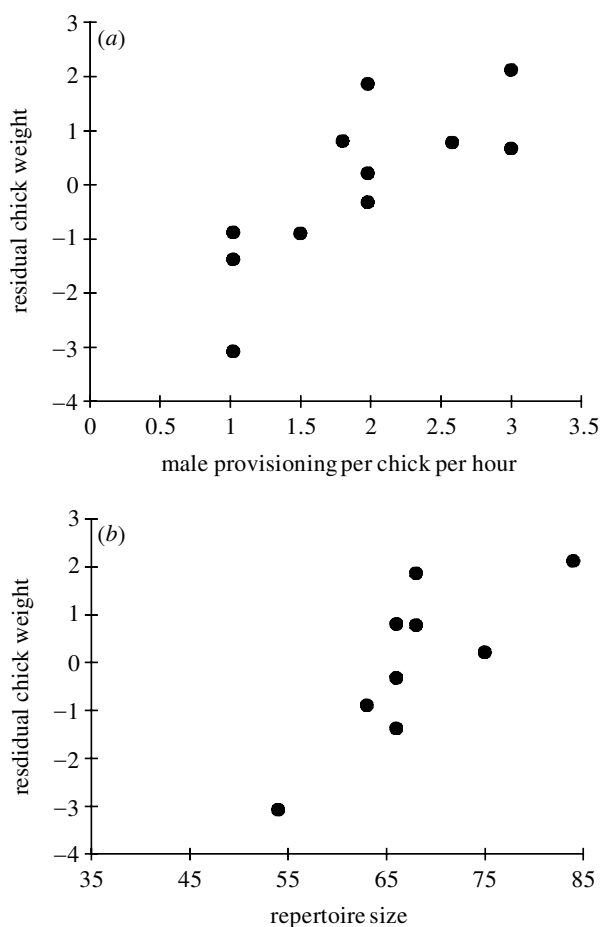


Figure 4. (a) The relationship between male provisioning effort per chick per hour and residual chick weight (controlling for chick age). (b) The relationship between male repertoire size and residual chick weight (controlling for chick age).

the higher population density had implications for the trade-off between parental care and increased chances of extra-pair copulations (Westneat *et al.* 1990). In contrast with our result, Mountjoy & Lemon (1997) failed to find any relationship between male repertoire size and parental effort in the European starling. There are a number of possible reasons for this including the possibility that interspecific differences in the mating systems could affect the degree of male parental effort. The redundancy of male parental care is likely to affect whether traits evolve as effective indicators of male parental care and, if so, we would predict that traits indicating male parental effort should only exist in species where female choice is associated, by necessity, with a high standard of care for the young.

Male parental effort will aid offspring success by increasing their weight or condition at fledging and these are known to be important predictors of post-fledging survival (Magrath 1991). Increased male effort is also likely to shorten the time the offspring are vulnerable in the nest and, thus, decrease the risk of predation, a significant factor in determining reproductive success. We found strong evidence that increased male provisioning was associated with heavier chick weights in the nest. Furthermore, we found a direct relationship between repertoire size and chick weight. This lends strong support to the argument that females benefit from mating

with large-repertoire males because their chicks are heavier and, therefore, more successful. Although it is possible that females increase their provisioning rate in relation to the attractiveness of their partner, no effect of female provisioning on chick weights was detected.

Relationships between song output and territorial quality have been reported in the literature (e.g. Davies & Lundberg 1984; Radesäter & Jakobsson 1989; Hoi-Leitner *et al.* 1993). It is therefore not surprising that there is some evidence that females use song output as an indicator of male or territorial resources (Greig-Smith 1982; Alatalo *et al.* 1990). There is also some indirect evidence that female red-winged blackbirds use repertoire size as an indicator of territorial resources (Searcy & Yasukawa 1996). In the case of the great reed warbler (*Acrocephalus arundinaceus*), Hasselquist (1998) also concluded that female choice for larger repertoire males is a consequence, at least in part, of territory quality. Older, more experienced males have the most complex songs and also claim the best territories. The great reed warbler is socially polygynous (Hasselquist 1998) and so territory quality may be of greater importance to nesting females.

In a parallel study on this population of sedge warblers, we found that territory size was an important cue for female choice (Buchanan & Catchpole 1997), suggesting that it may be indicative of the territorial resources available. However, in this study there was no indication that territory size was correlated with parental effort. Although there is some evidence that male sedge warblers increase their repertoire size with age (Birkhead *et al.* 1997), there is no evidence that older males provide more parental care. The amount of song fighting is also known to be a cue in female choice (Buchanan & Catchpole 1997), but there was no correlation with the level of male parental effort. This is surprising as song fighting is energetically expensive and, therefore, likely to reflect physiological condition. Instead we found that repertoire size was the most important cue in female choice.

In *Acrocephalus* warblers, the hypothesis that male repertoire size indicates genetic benefits to females has recently received some support. Hasselquist *et al.* (1996) found that, in the great reed warbler, extra-pair males had higher repertoires than the males whom they cuckolded. As females receive no direct benefits from parental care, their only benefits were the 'good genes' of the extra-pair males. Furthermore, the offspring of high repertoire males had increased viability, as demonstrated by higher rates of return to breed. In this species there was no evidence of a relationship between male parental care and repertoire size.

We have also studied the effects of haematzoan parasites on repertoire size and song fighting (Buchanan *et al.* 1999). Although parasitized males sang less than non-parasitized males in one year, in both years they had smaller repertoire sizes. Once again, repertoire size proved to be the more reliable indicator as well as the most important cue used in female choice and, by avoiding parasitized males, females may well be obtaining good genes for parasite resistance as first suggested by Hamilton & Zuk (1982).

The apparent paradox of why repertoire size is a more reliable, honest indicator may well be due to the neural

costs of acquiring and maintaining a complex song (Catchpole 1996). A comparative study of the size of the song control pathway in *Acrocephalus* warblers (Székely *et al.* 1996) showed that species with larger repertoires also have a larger main song control nucleus (HVC). In the sedge warbler, we have recently shown that males with larger repertoires also have a larger HVC (Airey *et al.* 2000). This area stores and produces the complex songs which are learned in the first year of life and this is when they are subject to the challenge and costs of parasite infection. Nowicki *et al.* (1998) suggested that song learning may be subject to nutritional stress during early development and Von Schantz *et al.* (1999) pointed out that the maintenance of HVC neurons may also be subject to physiological stress. Indeed, there is increasing evidence that post-hatching environmental factors may be more important than genetic effects in determining adult expression of sexual traits (Griffiths *et al.* 1999). The song-learning pathway may therefore reflect not only the genetic endowment but also the developmental history of the young male. In choosing a male with a large repertoire a female obtains direct benefits in the form of increased male parental care leading to heavier young with an increased chance of survival. Repertoire size might therefore be an honest indicator signalling both direct and indirect benefits to choosy females.

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