

Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice

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Females of many songbird species show a preference for mating with males that have larger song repertoires, but the advantages associated with this preference are uncertain. We tested the hypothesis that song complexity can serve as an indicator of male quality because the development of the brain regions underlying song learning and production occurs when young birds typically face nutritional and other stresses, so that song reflects how well a male fared during post-hatch development. A key prediction of this hypothesis is that variation in nestling condition should correspond to variation in the adult song repertoires of individuals. We used data from a long-term study of the great reed warbler (*Acrocephalus arundinaceus*) to test this prediction, correlating two measures of nestling development with subsequent repertoire size of males. We found that the length of the innermost primary feather, a standard measure of development, significantly predicted first-year repertoire size. The relationship between repertoire size and body mass was nearly significant, in spite of the large variance inherent in this measure. These data support the idea that song may provide females with information about a male's response to developmental stress, which in turn is expected to correlate with indirect or direct benefits she might receive.

Keywords: sexual selection; female choice; song repertoire; nutritional stress; *Acrocephalus arundinaceus*

1. INTRODUCTION

Female mating preferences are known to be influenced by male singing behaviour in many songbird species (reviewed in Searcy & Andersson 1986; Andersson 1994; Catchpole & Slater 1995; Searcy & Yasukawa 1996). Such female preferences could evolve if, by mating with males that have preferred song characteristics, females obtain either direct benefits, such as better parental care or access to a better territory, or indirect benefits in the form of 'good genes' for her offspring (Kirkpatrick & Ryan 1991). The fact that females in some species choose males based on song therefore suggests that song might serve as an indicator of male phenotypic or genotypic quality.

For a trait to be a useful indicator, however, there must be a mechanism that ensures its honesty (Grafen 1990*a,b*). Generally, this mechanism is thought to involve the cost of producing the trait (Zahavi 1975; Grafen 1990*a*; Johnstone & Grafen 1993). Consider song output, for example. How much a male sings, measured as the duration of songs or the rate at which songs are delivered, has been found to influence female mate choice in several species (e.g. Alatalo *et al.* 1990; Eens *et al.* 1991; Kempenaers *et al.* 1997). The cost of producing the preferred trait seems clear in this case: increasing song output requires added expenditure of time or energy, thus, high song output may be an honest indicator of a male's condition (Greig-Smith 1982) or the food resources of his territory (Radesäter & Jakobsson 1989). It is not so obvious what costs might ensure honesty of other features of song known to be preferred by females. In many species, for example, females have been shown to prefer males with larger song repertoires (e.g. Yasukawa *et al.* 1980;

Catchpole *et al.* 1984, 1986; Searcy 1984; Baker *et al.* 1986; Hasselquist *et al.* 1996; Hasselquist 1998). In what way could it be more costly to sing multiple song types or syllable types, as compared to fewer types, if the units are of the same duration and delivered at the same rate?

Nowicki *et al.* (1998) recently outlined a hypothesis for how song could function as an indicator of male quality based on developmental costs associated with song learning (see also Catchpole 1996; Buchanan 2000; Doutrelant *et al.* 2000). This hypothesis suggests that song features influenced by learning may honestly indicate quality because the brain structures that underlie song learning and production develop during a period early in life when, as nestlings or young fledglings, songbirds are likely to experience developmental stress, especially due to undernourishment. Individuals differing either in the magnitude of stress they experience or in their response to a given level of stress will vary in phenotypic development in general and in brain development in particular. Variation in brain development, in turn, will translate into variation in song learning and production abilities among males. In this way, a male's songs may be an honest indicator of how well he developed in the face of nutritional or other stresses experienced early in life. Males better able to express preferred song traits will be phenotypically superior, and their phenotypic superiority may reflect genotypic superiority as well.

A key prediction of the 'nutritional-stress hypothesis' is that variation in the condition of young males should be reflected in their adult songs, in features that are used by females in mate choice. We provide here the first direct test of this prediction, using data from the polygynous great reed warbler (*Acrocephalus arundinaceus*), a species in which song repertoire size is known to be an important factor in mate choice. Male great reed warblers with

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larger song repertoires attract more females as social mates (Catchpole 1986; Hasselquist 1998) and also obtain more extra-pair copulations (Hasselquist *et al.* 1996). In laboratory experiments, females perform more copulation solicitation displays in response to playback of larger song repertoires (Catchpole *et al.* 1986). Males with larger repertoires occupy superior territories (Hasselquist 1998), therefore females pairing with these males may obtain direct benefits in the form of better resources. Offspring sired by males with larger repertoires are more likely to survive to breeding age (and this relationship is not confounded by male parental abilities because nestling mass does not covary with the male parent's repertoire size), suggesting that females may also obtain indirect benefits in the form of 'good genes' by mating with such males (Hasselquist *et al.* 1996; Hasselquist 1998). Thus, repertoire size both influences female choice in great reed warblers and correlates with potential direct and indirect benefits. If the nutritional-stress hypothesis is correct then differences in the condition of nestlings or young fledglings should correlate with differences in their adult song repertoires.

To test this prediction, we used data from a long-term field study of the great reed warbler population at Lake Kvismaren, near Örebro, Sweden (for background information on this population, see Bensch & Hasselquist 1991; Hasselquist *et al.* 1995; Bensch 1996; Bensch *et al.* 1998; Hasselquist 1998). About 15% of birds born in this population return to breed there (Bensch & Hasselquist 1991; Hasselquist 1995); this proportion is relatively high compared to many migratory songbird populations, thus making it possible to obtain a reasonable number of individuals measured both as nestlings and as adults. We used two measures as estimates of nestling growth and developmental condition: body mass and the length of the innermost primary wing feather. We asked how well these measures predict the size of individual male's song repertoires as adults in their first year.

2. METHODS

(a) *Nestling measurements*

Nests were located by observing male mate-guarding or female nest-building behaviours, and were checked at one- to four-day intervals until the expected hatch date approached, when they were checked daily. Over 95% of all nests were found during nest building; thus we have accurate estimates of egg-laying, hatching and fledging dates for almost all young in the population. Nestlings were individually marked using aluminium and coloured leg rings between eight and ten days of age. More detailed descriptions of the field methods can be found in Bensch & Hasselquist (1991), Hasselquist *et al.* (1995), Bensch *et al.* (1998) and Hasselquist (1998).

Body mass of nestlings was measured to the nearest 0.1g using a Pesola spring balance (Pesola AG, Baar, Switzerland). The length of the innermost primary feather was measured to the nearest 1mm using a ruler inserted between the outermost secondary and innermost primary feather. Each nestling was measured only once because of the increased risk of predation associated with approaching and disturbing nests. A single-point measurement of body mass provides a relatively inaccurate estimate of nestling growth and condition because weight gain in songbirds is nonlinear and typically involves an overshoot and

recession (O'Connor 1975, 1978; Ricklefs 1984). Also, it is difficult in the field to account for variance associated with the timing of the measurement relative to when the individual most recently passed a faecal sac. Primary-feather growth rate is also commonly used to estimate nestling growth and has been shown in several studies to be an accurate measure of nestling developmental rate (e.g. O'Connor 1978; De Steven 1980; Ricklefs 1984). Feather growth rate tends to be more linear than weight gain (Ricklefs 1984; Quinney *et al.* 1986), so single-point measurements may more accurately reflect an integrated measure of growth and development than single-point body-mass measurements. Feather growth has also been shown to reflect nutritional condition in a number of species, both during nestling development (Price 1985; Quinney *et al.* 1986; De Steven 1980) and during adult moult (for reviews, see Grubb 1989, 1995).

Nestlings were measured between eight and ten days after hatching. It was necessary to adjust measurements to account for the time offset from a standard measurement day (relative to the age of the earliest-hatched chick in a nest) and the time of day, because individuals were not all measured at exactly the same time relative to hatching. The standardized mass and feather lengths were calculated from regressions based on data obtained from all male chicks hatched in the population between 1987 and 1999 for which the relevant data had been recorded (standardized mass, $n = 579$; standardized feather length, $n = 555$). The sex of the chicks was determined by molecular methods (see Westerdahl *et al.* 1997). The estimated mass and feather length at a standard measurement time of 11.00 on the ninth day after hatching were calculated for each bird using the regressions of mass and feather length on age to correct the observed values for that bird. Mathematically, this adjustment is equivalent to adding (or subtracting) the residuals from the regressions for a given bird to the expected mass and feather length at 11.00 on day 9 (25.0g and 19.4mm, respectively). The difference in feather lengths between siblings within a brood was taken as an indirect measure of hatching asynchrony (with a difference of 4.6 mm approximately corresponding to an offset of one day in hatching date).

We investigated whether these two measures of nestling condition (standardized mass and feather length) were correlated with, first, survival rate to adulthood, second, adult tarsus length (measured following Alatalo *et al.* (1984)) and, third, lifetime reproductive success. We assumed that male offspring that survived the first winter were those that were recorded on breeding grounds in any subsequent year. When analysing lifetime reproductive success, we excluded the males hatched in 1995 and later because some individuals in these cohorts were still alive. Before statistical analyses, lifetime reproductive success was square-root transformed to improve normality. All statistical analyses were performed using SYSTAT 5.0 (Wilkinson 1992) except logistic regressions, which were conducted in SAS 6.12 (SAS 1990).

(b) *Song-repertoire measurements*

At least 4–5 min of mate-attraction song (for description, see Hasselquist & Bensch 1991) were recorded from all males included in this study, using a Sony TC-D5M recorder and a Telinga parabolic microphone (Telinga, Tobo, Sweden). Sound spectrograms ('sonograms') were made using either a Kay Elemetrics 5500 DSP Sona-graph (Kay Elemetrics, Pine Brook, NJ, USA), Canary v.1.2 sound analysis software (Cornell Bio-acoustics Program, Ithaca, NY, USA; Charif *et al.* 1995) or Signal v.3.1 sound analysis software (Engineering Design, Belmont,

Table 1. Relations between two measures of nestling condition (standardized mass and standardized feather length) and three correlates to fitness in male great reed warblers

fitness correlate	standardized mass	standardized feather length
survival to recruits ^{a,b}	positive, $n = 578$, $\chi = 2.59$, $p = 0.11$	negative, $n = 559$, $\chi = 0.01$, $p = 0.9$
tarsus length ^{a,c}	positive, $b = 0.162$, $n = 71$, $F = 20.8$, $p < 0.001$	positive, $b = 0.045$, $n = 63$, $F = 5.64$, $p = 0.021$
lifetime reproductive success ^{c,d} (total number of young) ^{1/2}	positive, $b = 0.245$, $n = 51$, $F = 5.01$, $p = 0.029$	positive, $b = 0.089$, $n = 41$, $F = 1.91$, $p = 0.17$

^aIncludes hatch years 1987–1998.

^bLogistic regression.

^cLinear regression.

^dIncludes hatch years 1987–1994.

MA, USA; Beeman 1999), with a frequency resolution (i.e. ‘filter bandwidth’) of 195 Hz and a time resolution of 5 ms in all cases.

Repertoire size was determined by visual inspection of the sonograms by one of us (D.H.) without knowing the identity of the male being analysed. Great reed warblers sing variable songs (or ‘strophes’) composed of different combinations of highly stereotypic syllables that are usually repeated several times in sequence before the bird switches to a different syllable type. We used the number of distinct syllable types sung by each male as the measure of his repertoire size, a measure typically used for *Acrocephalus* warblers (e.g. Catchpole 1983, 1986; Hasselquist *et al.* 1996). Repertoire size was estimated as the cumulative number of syllable types observed over 150 syllable-type switches; this number of syllable-type switches was generally observed over the course of approximately 20–25 song strophes. Previous work has shown that estimates of repertoire size in this species reach an asymptote far earlier, after only 10–12 strophes (Catchpole 1983, 1986).

Song repertoire size of males when one year old is highly correlated with their age-standardized song repertoire size averaged over their whole lives ($r = 0.666$, $p = 0.003$, $n = 18$; this analysis excludes males that were recorded only in their first year). In previous studies we have shown that our measure of age-standardized song repertoire size predicts aspects of fitness in male great reed warblers (total number of lifetime offspring recruits and offspring survival from nestling to breeding age; Hasselquist *et al.* 1996; Hasselquist 1998).

3. RESULTS

(a) Standardizing body-mass and feather-length measurements

Body mass increased significantly with both age at weighing (slope: 1.95 g d^{-1} , $t = 7.50$, $p < 0.001$) and time of day (slope: 0.15 g h^{-1} , $t = 4.31$, $p < 0.001$), which together explained 10.8% of the variation in body mass. The length of the innermost primary feather also increased with age at measurement (slope: 4.63 mm d^{-1} , $t = 9.26$, $p < 0.001$) and time of day (slope: 0.19 mm h^{-1} , $t = 2.94$, $p = 0.003$) and these two factors explained 14.3% of the variation in feather length. We used the residuals from these models to construct the standardized measures of body mass (standardized mass) and feather length (standardized feather length). These two measures of condition were highly correlated ($r = 0.74$, $p < 0.0001$). Standardized body mass was not related to the hatching date of the brood (that is, when the brood was hatched within a season; $r = -0.05$, not significant) whereas

standardized feather length decreased with hatching date ($r = 0.098$, $p = 0.019$).

(b) Regression of nestling mass and feather length on adult phenotype

Neither measure of nestling condition was related to individual survival through the first winter (table 1). However, both standardized mass and standardized feather length were significant predictors of adult tarsus length (table 1), a reliable measure of structural size (Rising & Somers 1989) and the only factor that tends to predict male arrival date, which is a critical fitness factor in great reed warblers (Hasselquist 1998). Moreover, standardized mass was significantly correlated with lifetime reproductive success. The relationship between standardized feather length and lifetime reproductive success was positive, although not significantly so (table 1). However, because complete data on lifetime reproduction is only available for birds belonging to cohorts up to 1994, the sample size is small and the statistical power for this analysis is low. To conclude, both measures of nestling condition we examined are significant predictors of some variables correlated with fitness.

(c) Regression of repertoire size on standardized nestling mass and feather length

There is a statistically significant positive relationship between first-year repertoire size and standardized nestling feather length ($F_{36,1} = 5.234$, $p = 0.028$, figure 1). There is also a positive relationship between standardized nestling body mass and first-year repertoire size, with the regression closely approaching statistical significance ($F_{42,1} = 3.792$, $p = 0.058$, figure 2). That is, feather length significantly predicts repertoire size, while body mass almost does so.

We also tested whether these relationships were confounded by other factors that may influence nestling condition or repertoire size. Date of hatching, a variable that is strongly related to survival through the first winter in great reed warblers (Bensch 1996), did not correlate with song repertoire size ($r = -0.02$, $n = 45$, not significant). Similarly, time of hatching in the within-brood hatching sequence (inferred from the within-brood differences in feather length) did not correlate with song repertoire size ($r = -0.18$, $n = 29$, not significant). Males raised in nests of secondary females did not differ in song repertoire size compared to males raised in nests of primary females ($F_{1,42} = 0.06$, not significant).

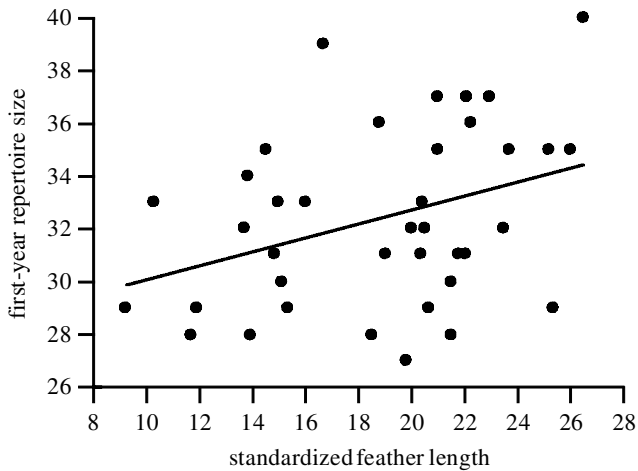


Figure 1. The relationship between standardized nestling primary-feather length and subsequent first-year repertoire size of individual males. Feather length was standardized to a constant post-hatch measurement date and time, as described in §2; $n = 38$, $r^2 = 0.127$, $p = 0.028$.

4. DISCUSSION

Our results demonstrate that the size of a male great reed warbler's song repertoire corresponds to aspects of his developmental condition as a nestling, and thus provide evidence for a mechanism by which song may serve as a reliable indicator of a male's phenotypic or genotypic quality. One of our measures of nestling development, the length of the innermost primary feather, significantly predicted the repertoire size of first-year males (figure 1). The relationship between repertoire size and body mass, our other measure of nestling development, was nearly significant (figure 2), in spite of the large variance inherent in this measure. Thus, these data suggest that by choosing to mate with a male that has a larger song repertoire, a female is choosing a male that fared better on average in post-hatch development. The nutritional-stress hypothesis (Nowicki *et al.* 1998) proposes brain development as the mechanism connecting nestling condition and song repertoire size: larger brains enable young songbirds to learn better or more, but are costly to build (Catchpole 1996). Those parts of the brain associated with song learning and production develop during the nestling and early fledging phase when young songbirds are most likely to be subject to nutritional stress, making song learning a potentially sensitive indicator of post-hatch development (Nowicki *et al.* 1998). To the extent that the response of an individual to developmental stress depends on heritable factors, females might derive indirect benefits by choosing males on the basis of song. Whether or not this is the case, females may derive direct benefits if variation in brain development correlates with other aspects of a male's phenotype that affect his ability to provide parental care, defend a territory and so forth.

We do not know for certain that the differences among nestlings we observed in the field were directly caused by differences in nutritional stress. Both feather growth and body mass have been shown to reflect the amount of food a nestling receives (O'Connor 1978; De Steven 1980; Ricklefs 1984; Price 1985; Quinney *et al.* 1986; Grubb

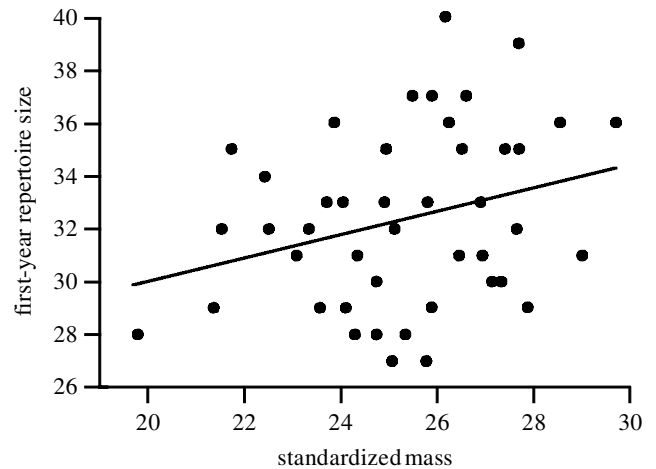


Figure 2. The relationship between standardized nestling body mass and subsequent first-year repertoire size of individual males. Mass was standardized to a constant post-hatch measurement date and time, as described in §2; $n = 44$, $r^2 = 0.083$, $p = 0.058$.

1995) but other stressors, such as parasite load, may also affect an individual's ability to mobilize the resources it has available for growth and development. In a comparative study of 38 species, Møller *et al.* (2000) found a positive relationship between song repertoire size and the mass of the spleen (a component of the immune system), suggesting that birds with stronger immune function may be able to devote more resources to brain development, at least across species. Similarly, Buchanan *et al.* (1999) recently demonstrated in sedge warblers (*A. schoenobaenus*) that individual males infected with parasitic blood protozoans have smaller song repertoires than males who are free from infection. The incidence of blood parasites (mainly *Haemoproteus*) in our great reed warbler population is about 20% in adults (O. Östman, D. Hasselquist and S. Bensch, unpublished data). In young birds up to eight weeks of age, however, none of the 99 birds examined were infected by blood parasites (Östman *et al.* 2001), suggesting that blood parasite load during the song-development period is unlikely to be a source of the variation we observed. Regardless of which stressor or combination of stressors are responsible for the observed effect, our data directly demonstrate a link between nestling condition and song repertoire size within individuals, which in turn provides a mechanism by which song can be a meaningful indicator of some aspect of male quality.

For species such as the song sparrow (*Melospiza melodia*) or the swamp sparrow (*M. georgiana*), in which the song repertoire does not change after the first year (Marler & Peters 1989), repertoire size may serve primarily as an indicator of nestling condition. The repertoires of male great reed warblers continue to change throughout adulthood, however, generally increasing with age (Hasselquist 1994, 1998). This fact suggests that the song repertoires of older males may also reflect factors affecting condition later in life. Effects of stress on adult condition, for example, may help to explain the correlation between parasite levels and repertoire size observed in adult sedge warblers by Buchanan *et al.* (1999). Nutritional status on overwintering grounds is another example of a factor that could affect the expression of an individual's repertoire on

an annual basis, similar to the annual condition dependence observed for plumage characters in some cases (Hill 1999). Even if adult condition further influences repertoire size, the condition during the nestling phase may determine a 'set point', in the form of a constraint on neural capacity, that sets an upper bound on the amount that an individual's song repertoire may change over his lifetime, and thus the effect of nestling condition that we observed may continue to be reflected in the size of a male's repertoire throughout his lifetime.

Our results suggest that males with larger repertoires developed better as nestlings, but what is the benefit to females of choosing to mate with such males? The possibility that female great reed warblers obtain indirect genetic benefits from this preference is supported by the observation that females only engage in extra-pair copulation with males having larger repertoires than their social mate (Hasselquist *et al.* 1996) and the fact that offspring of males with larger song repertoires are more likely to survive and be recruited into the breeding population (Hasselquist *et al.* 1996; Hasselquist 1998). If all males in a population are exposed to the same level of stress, then those with generally superior genotypes are expected to develop better on average (Williams 1966, p. 184). It is likely that heritable differences in response to stress reflect more specific genetic differences associated with immune function (Westneat & Birkhead 1998; Buchanan 2000) or physiological systems counteracting oxidative stress (Von Schantz *et al.* 1999).

Whether or not females receive indirect benefits from their preference for males with large repertoires, phenotypic differences among males resulting from stress experienced early in life can persist through adulthood (e.g. Boag 1987; Richner *et al.* 1989) and, for social mates, these phenotypic differences will probably translate into differences in the abilities of males to provide direct benefits in the form of territory defence and parental care. For example, Buchanan & Catchpole (2000) recently demonstrated a correlation between repertoire size and parental effort in male sedge warblers, consistent with this view. A potential difficulty for any indicator mechanism is the requirement that the expression of the trait being assessed be closely coupled to the expression of the trait that actually provides the female with some benefit. In the case of song, it may be that the most relevant trait affecting direct benefits is brain development itself, with little need to postulate coupling with other aspects of the phenotype. By assessing the outcome of song learning, the female may gain accurate information about critical cognitive abilities such as spatial navigation and memory, which in turn affect behaviours such as territory defence, predator avoidance and the ability to find food.

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REFERENCES

- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1984 High frequency of cuckoldry in pied and collared flycatchers. *Oikos* **42**, 41–47.
- Alatalo, R. V., Glynn, C. & Lundberg, A. 1990 Singing rate and female attraction in the pied flycatcher: an experiment. *Anim. Behav.* **39**, 601–603.
- Andersson M. 1994 *Sexual selection*. Princeton University Press.
- Baker, M. C., Bjerke, T. K., Lampe, H. U. & Espmark, Y. 1986 Sexual response of female great tits to variation in size of males' song repertoires. *Am. Nat.* **128**, 491–498.
- Beeman, K. 1999 *'Signal' 3.1 user's manual*. Belmont, MA: Engineering Design.
- Bensch, S. 1996 Female mating status and reproductive success in the great reed warbler: is there a potential cost of polygyny that requires compensation? *J. Anim. Ecol.* **65**, 283–296.
- Bensch, S. & Hasselquist, D. 1991 Territorial infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *J. Anim. Ecol.* **60**, 857–871.
- Bensch, S., Hasselquist, D., Nielsen, B. & Hansson, B. 1998 Higher fitness for philopatric than for immigrant males in a semi-isolated population of great reed warblers. *Evolution* **52**, 877–883.
- Boag, P. T. 1987 Effects of nestling diet on growth and adult size of zebra finches (*Poephila guttata*). *Auk* **104**, 155–166.
- Buchanan, K. L. 2000 Stress and the evolution of condition-dependent signals. *Trends Ecol. Evol.* **15**, 156–160.
- Buchanan, K. L. & Catchpole, C. K. 2000 Song as an indicator of male parental effort in the sedge warbler. *Proc. R. Soc. Lond. B* **267**, 321–326.
- Buchanan, K. L., Catchpole, C. K., Lewis, J. W. & Lodge, A. 1999 Song as an indicator of parasitism in the sedge warbler. *Anim. Behav.* **57**, 307–314.
- Catchpole, C. K. 1983 Variation in the song of the great reed warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. *Anim. Behav.* **31**, 1217–1225.
- Catchpole, C. K. 1986 Song repertoires and reproductive success in the great reed warbler *Acrocephalus arundinaceus*. *Behav. Ecol. Sociobiol.* **19**, 439–445.
- Catchpole, C. K. 1996 Song and female choice: good genes and big brains? *Trends Ecol. Evol.* **11**, 358–360.
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird song: biological themes and variations*. Cambridge University Press.
- Catchpole, C. K., Dittami, J. & Leisler, B. 1984 Differential responses to male song in female songbirds implanted with oestradiol. *Nature* **312**, 563–564.
- Catchpole, C. K., Leisler, B. & Dittami, J. 1986 Sexual differences in the responses of captive great reed warblers (*Acrocephalus arundinaceus*) to variation in song structure and repertoire size. *Ethology* **73**, 69–77.
- Charif, R. A., Mitchell, S. & Clark, C. W. 1995 *Canary 1.2 user's manual*. Ithaca, NY: Cornell Laboratory of Ornithology.
- De Steven, D. 1980 Clutch size, breeding success, and parental survival in the tree swallow (*Iridoprocne bicolor*). *Evolution* **34**, 278–291.
- Doutrelant, C., Blondel, J., Perret, P. & Lambrechts, M. M. 2000 Relationship between song repertoire size and male quality in blue tit. *J. Avian Biol.* **31**, 360–366.
- Eens, M., Pinxten, R. & Verheyen, R. F. 1991 Male song as a cue for mate choice in the European starling. *Behaviour* **116**, 210–238.
- Grafen, A. 1990a Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546.
- Grafen, A. 1990b Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* **144**, 473–516.

- Greig-Smith, P. W. 1982 Song-rates and parental care by male stonechats (*Saxicola torquata*). *Anim. Behav.* **30**, 245–252.
- Grubb Jr, T. C. 1989 Ptilochronology: feather growth bars as indicators of nutritional stress. *Auk* **106**, 314–340.
- Grubb Jr, T. C. 1995 Ptilochronology: a review and prospectus. In *Current ornithology*, vol. 12 (ed. D. M. Power), pp. 89–114. New York: Plenum Press.
- Hasselquist, D. 1994 Male attractiveness, mating tactics and realized fitness in the polygynous great reed warbler. PhD dissertation, Lund University, Lund, Sweden.
- Hasselquist, D. 1995 Demography and lifetime reproductive success in the polygynous great reed warbler. *Jpn. J. Ornithol.* **44**, 181–194.
- Hasselquist, D. 1998 Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* **79**, 2376–2390.
- Hasselquist, D. & Bensch, S. 1991 Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. *Behav. Ecol. Sociobiol.* **28**, 187–193.
- Hasselquist, D., Bensch, S. & Von Schantz, T. 1995 Low frequency of extra-pair paternity in the polygynous great reed warbler. *Behav. Ecol.* **6**, 27–38.
- Hasselquist, D., Bensch, S. & Von Schantz, T. 1996 Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**, 229–232.
- Hill, G. E. 1999 Mate choice, mate quality, and carotenoid-based plumage coloration: a review. In *Proceedings of the 22 International Ornithological Congress* (ed. N. Adams & R. Slotow), pp. 1654–1668. Durban, South Africa: University of Natal Press.
- Johnstone, R. A. & Grafen, A. 1993 Dishonesty and the handicap principle. *Anim. Behav.* **46**, 759–764.
- Kempnaers, B., Verheyen, G. R. & Dhondt, A. A. 1997 Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol.* **8**, 481–492.
- Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.
- Marler, P. & Peters, S. 1989 Species differences in auditory responsiveness in early vocal learning. In *The comparative psychology of audition: perceiving complex sounds* (ed. R. Dooling & S. H. Hulse), pp. 243–273. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Møller, A. P., Henry, P.-Y. & Erritzøe, J. 2000 The evolution of song repertoires and immune defence in birds. *Proc. R. Soc. Lond. B* **267**, 165–169.
- Nowicki, S., Peters, S. & Podos, J. 1998 Song learning, early nutrition and sexual selection in songbirds. *Am. Zool.* **38**, 179–190.
- O'Connor, R. J. 1975 Initial size and subsequent growth in passerine species. *Bird-Banding* **46**, 329–340.
- O'Connor, R. J. 1978 Structure in avian growth patterns: a multivariate study of passerine development. *J. Zool. Lond.* **185**, 147–172.
- Price, T. 1985 Reproductive responses to varying food supply in a population of Darwin's finches: clutch size, growth rates and hatching synchrony. *Oecologia* **66**, 411–416.
- Quinney, T. E., Hussell, D. J. T. & Ankney, C. D. 1986 Sources of variation in growth of tree swallows. *Auk* **103**, 389–400.
- Radesäter, T. & Jakobsson, S. 1989 Song rate correlations of replacement territorial willow warblers *Phylloscopus trochilus*. *Ornis Scand.* **20**, 71–73.
- Richner, H., Schneiter, P. & Stirnimann, H. 1989 Life-history consequences of growth rate depression: an experimental study on carrion crows (*Corvus corone corone*). *Funct. Ecol.* **3**, 617–624.
- Ricklefs, R. E. 1984 Components of variance in measurements of nestling European starlings (*Sturnus vulgaris*) in southeastern Pennsylvania. *Auk* **101**, 319–333.
- Rising, J. D. & Somers, K. M. 1989 The measurement of overall body size in birds. *Auk* **106**, 666–674.
- SAS 1990 Version 6.11. Cary, NC: SAS Institute, Inc.
- Searcy, W. A. 1984 Song repertoire size and female preferences in song sparrows. *Behav. Ecol. Sociobiol.* **14**, 281–286.
- Searcy, W. A. & Andersson, M. 1986 Sexual selection and the evolution of song. *A. Rev. Ecol. Syst.* **17**, 507–533.
- Searcy, W. A. & Yasukawa, K. 1996 Song and female choice. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 454–473. Ithaca, NY: Cornell University Press.
- Von Schantz, T., Bensch, S., Grahm, M., Hasselquist, D. & Wittzell, H. 1999 Good genes, oxidative stress and condition-dependent sexual signals. *Proc. R. Soc. Lond. B* **266**, 1–12.
- Westerdahl, H., Bensch, S., Hansson, B., Hasselquist, D. & Von Schantz, T. 1997 Sex ratio variation among broods of great reed warblers *Acrocephalus arundinaceus*. *Mol. Ecol.* **6**, 543–548.
- Westneat, D. F. & Birkhead, T. R. 1998 Alternative hypotheses linking the immune system and mate choice for good genes. *Proc. R. Soc. Lond. B* **265**, 1065–1073.
- Wilkinson, L. 1992 *SYSTAT: the system for statistics*. Evanston, IL: SYSTAT.
- Williams, G. C. 1966 *Adaptation and natural selection*. Princeton University Press.
- Yasukawa, K., Blank, J. L. & Patterson, C. B. 1980 Song repertoires and sexual selection in the red-winged blackbird. *Behav. Ecol. Sociobiol.* **7**, 233–238.
- Zahavi, A. 1975 Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**, 205–214.