Female choice and annual reproductive success favour less-ornamented male house sparrows

Simon C. Griffith¹*, Ian P. F. Owens² and Terry Burke³

¹Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, S-752 36 Uppsala, Sweden (simon.griffith@zoologi.uu.se)

²Department of Zoology, University of Queensland, St Lucia, QLD 4077, Australia

³Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK

Theories of sexual selection usually assume that female preferences for male ornamental traits are fixed and always likely to favour the largest or most extravagant sexual ornaments. This is not, however, always necessary or likely, particularly in resource-based monogamous systems. Here we show that in a closed population of house sparrows, small-badged males were preferred by females as both social and genetic mates and produced a higher number of viable offspring. Previous studies of other house sparrow populations have shown females to prefer large-badged males. Given the likely trade-offs operating between different male behavioural and morphological traits, we propose that female choice is a flexible adaptive strategy through which females can select those males likely to supply the male-acquired benefits that are locally most important.

Keywords: reproductive success; *Passer domesticus*; mate choice; direct benefits; sexual selection; female choice

1. INTRODUCTION

Why should females prefer males with elaborate ornaments? The 'good genes' hypotheses predict that the sexual ornaments of males will reflect favourable genes that can be passed onto their offspring: either genes for increased viability (Williams 1966; Hamilton & Zuk 1982), or genes for increased attractiveness (Fisher 1930). Alternatively, the 'direct benefit' hypotheses (Heywood 1989; Hoelzer 1989; Kirkpatrick & Ryan 1991) predict that male ornaments will reflect tangible benefits that females will acquire as a result of their preference.

Fundamentally, both the 'good genes' and the 'direct benefit' models predict a positive relationship between the reproductive success of a male and the size of his sexual ornaments (including being preferred by females; reviewed in Jennions & Petrie (1997)). The relationship is positive in all but one of the empirical studies reporting a significant relationship between the expression of a sexual trait and some measure of reproductive success (reviewed in Andersson (1994) and Johnstone (1995)). The single exception to this apparently general rule is the finding by Sætre *et al.* (1997) that female pied flycatchers (*Ficedula hypoleuca*) prefer the dullest brown males where they breed in sympatry with the collared flycatcher (*F. albicollis*), presumably to avoid the costs of hybridization. Although this unique example seems to be a special case, there are several other reasons why females might be predicted to not

always prefer the most ornamental or dominant males (reviewed in Qvarnström & Forsgren (1998)).

Here we present results from a study on an ecologically isolated population of the house sparrow (*Passer domesticus*), which enabled a thorough examination of female preference and reproductive success in relation to the male ornamental trait. These results are discussed along with those from several independent studies of sexual selection in the same species. The house sparrow is a socially monogamous, sexually dimorphic passerine. Whereas the female is a typical dull brown bird, the male displays several plumage traits, the most conspicuous of which is a melanin-based black throat patch or 'badge'. It is this trait that has been the focus of previous work on sexual selection in this species.

Owing to the unique nature of our study population we were able to measure the reproductive success of all individuals accurately. The population lived on an island and the lack of natal dispersal allowed us to assess the production of viable offspring by breeding individuals. The scarcity of natural breeding sites and the birds' acceptance of artificial nest-boxes allowed us to monitor every breeding attempt and identify those individuals that failed to breed. Additionally, molecular techniques revealed a very low level of extra-pair paternity within this population (less than 1% (Griffith *et al.* 1999)), which means that only within-pair reproductive success needs to be considered. These unique features of our population allowed us to monitor total annual reproductive success precisely and so test the predicted relationship between reproductive success and the size of the sexual ornament.

* Author for correspondence.

2. METHODS

(a) Population

This study was conducted during October 1995 to January 1997 on Lundy island, 20 km off the south-west coast of England (51.11°N, 4.40°W). The highly sedentary nature of the house sparrow (Paradis *et al.* 1998) results in an almost negligible movement in and out of this population. Adult birds were caught on multiple occasions throughout the study and all adults in the population were colour-banded with unique colour combinations in addition to a metal ring supplied by the British Trust for Ornithology. Morphological measurements were taken on several occasions throughout the study (following the method of Svensson (1984)), all of which were found to be highly repeatable within a single annual adult moult.

When the badge of the house sparrow is first produced in the autumn moult, the black badge feathers have substantial buff tips that conceal the black area: this is only fully revealed in the spring through abrasion of the tips (Veiga 1996). The size of the badge will therefore increase throughout the year and at any time before the spring the 'visible' badge size of a male will be primarily related to the extent of abrasion.

In our study, individuals were caught opportunistically throughout the calendar year, necessitating a measure robust to the extent of abrasion. Therefore we measured the 'hidden' length of the badge; this being the length (in millimetres) from the base of the bill down the chest to the point on the breast at which the black feathers ceased to grow from the skin. This measure was found to be highly repeatable between different measurements taken throughout the year ($r^2 = 0.755$, $F_{12,13} = 7.78$, $p < 0.001$; calculated by the method of Falconer (1960)) and is significantly related to the visible length of the badge during the breeding season ($r^2 = 0.47$, $n = 47$, $p < 0.001$). Owing to the loose nature of the skin horizontally, the 'hidden' width was found to have poor repeatability, so precluding any attempt to quantify badge area. We checked the validity of using the badge length in millimetres as our measurement of badge size by using a regression model to estimate the extent of variation in badge area (Møller 1987) that is explained by badge length. On the basis of 48 males caught during the summer, when badge area was easiest to measure, badge length explained 70% of variation in badge area ($r^2 = 0.82$, $n = 48$, $p < 0.001$).

Where they have been used, the validity of using parametric analyses was confirmed by testing data and residuals from regressions for departures from normality by using the Lilliefors test. All analyses were conducted with SYSTAT v. 5.2 (SYSTAT, Evanston, IL, USA).

(b) Measurement of reproductive success

During the 1996 breeding season (April to August) all possible nest sites were monitored every two days for signs of nesting. Once egg laying had begun, close monitoring of each nest began and continued until fledging. Chicks were measured, ringed and colour-banded at 12 days old. For each breeding pair, the first-egg date was calculated as the number of days from 1 May until the first egg was laid. In addition, clutch size, number of eggs that hatched and the number of fledglings produced were determined. This last was the number of chicks ringed on day 12 minus the number of corpses found in the empty nest after day 18 (house sparrow chicks usually fledge between day 15 and 17). The bodies of chicks that died after day 12 are too large and unwieldy for adults to remove through the nest-box hole.

Figure 1. The relationship between the badge size of a male and his annual production of fledglings. For illustrative purposes the four polygynous males are represented by square symbols. $y = -0.691x + 27.451$; $r^2 = 0.17$; $n = 40$; $p < 0.01$.

In addition to the quantitative estimates of reproductive success (as outlined above), the measurements of each 12-day-old chick's tarsus length and mass were used to investigate the possibility of a trade-off between quantity and quality of offspring. A further measurement of offspring quality was provided by the analysis of those offspring retrapped subsequent to fledging. During the period 3–10 January 1997, more than 80% of all living individuals in the population were caught (as shown by an extensive visual survey performed in parallel (S. C. Griffith, unpublished results)). We have no reason to suspect that this sample of birds was not a random sample of all offspring surviving at this time.

The limited amount of habitat suitable for breeding house sparrows and the nature of the population allowed us to monitor all possible breeding sites and individuals throughout the breeding season. Although several pairs made at least one attempt to breed within a partly inaccessible roof or wall cavity, 95% (99 out of 105) of all breeding attempts took place in nest-boxes. The inaccessibility of two nests resulted in the exclusion of one male from some parts of the analysis. All females made at least one breeding attempt. However, owing to a slight male skew in the adult population, seven males remained unpaired. These males established and displayed at a nest site throughout the season but failed to attract a female.

3. RESULTS

(a) Comparison of badge size with reproductive output

On the basis of single-linear-regression models there was no relationship between pair male badge size and the date on which a female laid her first egg ($r^2 = 0.01$, $n = 33$, $p = 0.52$), or the number of eggs produced by a female ($r^2 = 0.02$, $n = 28$, $p = 0.51$). Within the whole sample of males, including those unpaired and breeding polygynously, there was a non-significant tendency for large-badged males to have fewer eggs in total than small-badged males ($r^2 = -0.08$, $n = 39$, $p = 0.09$). There were significant negative relationships between the size of a male's badge and the number of chicks in his nest

Table 1. Coefficients of variation ($\pm$ s.e.m.) from separate multiple regression models between male traits and four measures of reproductive success

(Whole-model values are r^2 , (n) and the associated p . Sample sizes are unequal owing to the inaccessibility of one nest early in the rearing cycle and the exclusion of non-breeders from the analysis of the first-egg date.)

index of reproductive success	morphological variable of male				
	tarsus length	wing chord	mass	badge length	whole model
first-egg date (log)	0.03 (0.06)	-0.01 (0.03)	-0.01 (0.03)	-0.01 (0.03)	0.03 (33) (n.s.)
number of eggs	-0.77 (1.60)	0.50 (0.71)	-0.55 (0.73)	-1.00 (0.57)	0.11 (39) (n.s.)
number of chicks	-2.70 (1.11)*	0.58 (0.49)	-0.10 (0.51)	-1.03 (0.40)**	0.27 (39)*
number of young fledged	-1.58 (0.70)*	0.38 (0.31)	-0.02 (0.32)	-0.71 (0.25)**	0.29 (40)*

* $p < 0.05$; ** $p < 0.01$.

Figure 2. The mean badge size ($\pm$ s.d.) of the groups of males which were unpaired, monogamously paired or polygynously paired (sample sizes are shown above bars).

($r^2 = -0.13$, $n = 39$, $p = 0.02$) and the number of offspring that he fledged ($r^2 = -0.17$, $n = 40$, $p < 0.01$) (figure 1). Multiple regression models that included other male morphological variables (tarsus length, wing length and body mass) confirmed that the relationships reported above were not due to interactions between such variables and badge size (table 1).

Within the population, the breeding status of males was as follows: unpaired (17.5%, 7 out of 40), monogamously paired (72.5%, 29 out of 40) and polygynously paired (10%, 4 out of 40). Female choice for small-badged males as partners was revealed by the significant difference between the mean badge size of the three groups of male: unpaired, monogamous and polygynous (Welch ANOVA $F = 3.99$, d.f. = 2, $p = 0.05$). As illustrated in figure 2, there was a tendency for unpaired males to have larger badges than paired males (unpaired t -test, $t = 1.71$, d.f. = 38, $p = 0.09$). The difference between the badge size of polygynous and unpaired males was significant, these two groups presumably reflecting the extremes of female choice (unpaired t -test, $t = 2.51$, d.f. = 9, $p = 0.03$). Of course, if we account for the fact that we have done three independent comparisons, p would have to be less than 0.02 to meet the 5% level of significance.

Table 2. Values of r^2 and the associated p from single linear regression between male badge size and the total number of offspring that they produced against measures of mean offspring quality

(Residual mass is a measure of offspring weight accounting for skeletal size. Some studies have shown this to be a measure of offspring quality in passerine birds (see, for example, Alatalo *et al.* 1990; Tinbergen & Boerlijst 1990).)

index of offspring quality		male reproductive variable	
		no. of offspring	badge size
nestling ($n = 30$)	tarsus (mm)	0.06 (n.s.)	0.01 (n.s.)
	mass (g)	0.07 (n.s.)	0.01 (n.s.)
	residual mass (g)	0.01 (n.s.)	0.01 (n.s.)
post-fledging	tarsus (mm)	0.02 (n.s.)	0.02 (n.s.)
	mass (g)	0.03 (n.s.)	0.05 (n.s.)
	residual mass (g)	0.02 (n.s.)	0.09 (n.s.)

The observed relationship between badge size and the breeding status of a male was a major component of the overall relationship between badge size and reproductive output. For example, for fledgling production, three out of the top four most productive males bred polygynously, whereas seven out of the eight males in the population which produced no fledglings were unpaired. Despite this, the negative relationship between badge size and reproductive output was maintained after the exclusion of either polygynous males ($r^2 = 0.19$, $n = 36$, $p < 0.01$), unpaired males ($r^2 = 0.11$, $n = 33$, $p = 0.05$) or both together, leaving just the monogamously paired males ($r^2 = 0.14$, $n = 29$, $p = 0.04$).

(b) Comparison of badge size with offspring quality

There were no relationships between badge size or the number of offspring produced by a male and our measurements of mean offspring quality (tarsus length, mass and the residuals of a regression between these two) (table 2). Not surprisingly, there was a strong relationship between the initial number of fledglings produced by a male and the number of survivors recorded four months after fledging ($r^2 = 0.39$, $n = 31$, $p < 0.001$). Together, these results indicate that males that produced fewer offspring were not necessarily producing better offspring. Therefore,

Table 3. *Summary of the relationship between badge size and aspects of sexual selection in six populations of the house sparrow*

(Abbreviations used: LB, large-badged males; SB, small-badged males; BS, badge size. A dash denotes aspects that have not been reported by a given study.)

population	male–male competition	female preference	offspring production	references
Denmark	LB dominant, held more nest sites	LB preferred in mate choice trial; LB paired earlier; SB likely to remain unpaired	positive	Møller (1987, 1988, 1989, 1990)
Spain	LB dominant, held more nest sites	no effect of BS on pairing date	no overall relationship	Veiga (1993, 1995)
New Mexico, USA	no relationship between BS and nest site acquisition	no preference for BS observed	positive	Kimball (1995, 1996, 1997)
Norway	LB dominant in male–male contests	—	—	Solberg & Ringsby (1997)
Spain and UK	—	no effect of BS on female choice of EP mates	—	Cordero <i>et al.</i> (1998)
Lundy, UK	—	SB likely to be polygynous; LB likely to remain unpaired	negative	this paper

the finding of a significant negative relationship between badge size and the number of survivors (four months after fledging) was to be expected (Spearman's rank correlation coefficient = -0.34 , $n = 40$, $p = 0.03$).

4. DISCUSSION

Contrary to the expectations of most models of sexual selection (reviewed in Andersson (1994)), we found that male sparrows with the largest badges (i.e. the most 'showy' males) did not have the highest annual reproductive success. In fact, badge size was negatively correlated with all measurements of reproductive success in this population of house sparrows: small-badged males produced significantly larger numbers of surviving offspring.

As this was a correlative study it is difficult to identify the exact cause underlying the higher reproductive success of small-badged males. Although there was a slight tendency for these males to be paired with females that laid a larger clutch, they also produced significantly more surviving offspring, which suggests that they were more successful during the whole post-zygotic phase of reproduction. This could be accounted for by these males' being better parents themselves (Heywood 1989; Hoelzer 1989), or, assuming a female preference for small-badged males in this population, a differential allocation effect (Burley 1986), whereby small-badged males pair with better females or with females willing to invest more highly in reproduction.

We also found evidence that badge size was correlated with whether or not a male was monogamously or polygynously mated, with small-badged males being more likely to be polygynous. Once again, this relationship is the opposite to that predicted by most models of sexual selection. Considering that female house sparrows have been shown to suffer from reduced paternal help when paired polygynously (Veiga 1990), and the presence of several unpaired males in the population, it is very

surprising at all that some males succeeded in attracting two females. Therefore, the fact that the polygynous males tended to be small badged whereas unpaired males tended to be large badged is highly suggestive of a female mating preference for small-badged males (although this interpretation is potentially confounded by correlates between male phenotype and other direct benefits; see, for example, Alatalo *et al.* (1986)). To our knowledge, the only previous example of a female preference for the least showy males is that of sympatrically breeding flycatchers, where females of one species preferred the least ornamented conspecific males to minimize the risk of hybridization (Sætre *et al.* 1997).

Our finding of a female preference for the least showy males is of greater interest when put into the context of other studies of sexual selection in the house sparrow. Our result completes a continuum from a Danish population in which there is a strong female preference for large-badged males (Møller 1987, 1988, 1989, 1990), through several other populations in which there seems to be no specific preference with regard to male ornament size (Veiga 1993, 1995, 1996; Kimball 1996; Cordero *et al.* 1998), to the Lundy population in which there is an apparent preference for small-badged males (see table 3).

The fact that different populations of the same species exhibit such profound differences in the female preference for male phenotype can be most easily reconciled by the idea that the female preference is extremely plastic, i.e. the same females will express different preferences under different circumstances. The alternative of selection for females exhibiting different fixed preferences in separate populations seems unlikely, although it has occurred under strong natural selection in the Trinidadian guppy, *Poecilia reticulata* (Endler & Houde 1995).

Although latently assuming that female preference will consistently favour males with the largest or most ornamental trait, most theories of sexual selection (reviewed in Andersson (1994) and Jennions & Petrie (1997)) do not implicitly exclude the possibility of a flexible female

preference. Moreover, the idea of flexible female mate choice might be particularly relevant to resource-based mating systems, such as that of the house sparrow, in which females might potentially gain many different kinds of resources from a male. In birds, such benefits might include breeding territories, nest sites or paternal care through either chick-provisioning or nest defence. Under this sort of breeding system it is possible that any particular male faces a trade-off in the resources that he can acquire so that no male can offer the 'best of all benefits'. It is more likely that some males can provide, for example, good nest sites, whereas different males can provide other resources. Now, if female requirements for either good nest sites, or other resources, vary over time or between locations, it would pay females to show flexible mate choice. In situations in which good nest sites are in short supply, females should prefer males with signals that suggest that they can provide such sites. Conversely, where good nest sites are plentiful, females should select males with signals that suggest that they can provide other scarce resources.

We suggest that such differences in female requirements occur between house sparrow populations, and might be responsible for the observed differences in female preferences between populations (table 3). In the Danish population, good nest sites were at a premium, with 19 out of 77 nests built in unsuitable open sites (unsuitable as demonstrated by the high level of mortality caused by chicks falling from these nests (Møller 1988)). Indeed, the quality of nest site within the Danish population was reported to be the largest component of the variation in reproductive success (Møller 1988). In contrast, in the Lundy population, nest site quality had very little effect on reproductive success: 40 males had 85 identical nest-boxes to choose from, all of which were suitable for house sparrows (79 out of 85 boxes were used by a breeding pair at least once between 1994 and 1997 and only one nest was ever constructed in an unsuitable open site). Although on Lundy the overabundance of nest-boxes was provided by ourselves, the variation in the availability of good nest sites between these two populations might simply reflect two ends of a natural continuum, with different house sparrow populations experiencing very different levels of nest site availability. In this situation, as was outlined in the informal model above, it might be adaptive for the Danish females to base mate choice on sexual ornaments that indicate the acquisition of a good nest site. In the Lundy population, in contrast, it might be adaptive to base mate choice on ornaments that indicate the acquisition of the most locally important trait. For instance, because nest predators are absent from Lundy and chicks could not fall out of nest-boxes, it is likely that starvation is the most common cause of chick mortality. Male chick-feeding effort might therefore be the most important trait to a female in the Lundy population.

There is even a potential mechanism to explain why individual males might face a trade-off between being able to acquire a good nest site and being able to provide paternal care. By experimentally increasing the level of circulating testosterone in certain males, Hegner & Wingfield (1987) showed that in house sparrows testosterone level was positively associated with the frequency of sexual displays and success in intrasexual

competition, but was negatively associated with paternal care. Indeed, the ability of the testosterone-implanted males to provide care was so impaired that the offspring of these males suffered a significant decrease in survival. It therefore seems very likely that gonadal steroids such as testosterone might force a trade-off between male competitive ability and male paternal ability. What has not yet been fully revealed is the relationship between hormone production and plumage-based sexual ornaments. As discussed by Folstad & Karter (1992), the development of many male-specific sexual ornaments is testosterone dependent, so the size of the ornament is likely to signal whether the male will provide a good nest site (high testosterone) or good parental care (low testosterone). However, for plumage-based ornaments the mode of development is far less clear, with the overall development of the trait not being dependent on testosterone (Owens & Short 1995). It remains to be discovered whether other factors, such as corticosteroids or body condition, are responsible for limiting ornament size (Møller 1995) or whether testosterone is indeed responsible for the relatively subtle differences in badge size between individual males in house sparrows (M. Evans, A. Goldsmith and S. Norris, personal communication).

In summary, we feel that differences between populations in mate choice criteria could be real and suggest that the idea of highly flexible female preference can sit comfortably with most other theories of sexual selection, even though they generally assume a constant positive directionality of female preference (Andersson 1994). Similarly, the interdependence of ornament size, hormone levels and characteristics such as aggressiveness and the provisioning of parental care is consistent with condition-dependent based models of sexual selection (see, for example, Williams 1966; Hoelzer 1989; Heywood 1989; Hamilton & Zuk 1982). Indeed, we suggest further that the existence of trade-offs between several male traits that are reliably signalled by the same sexual ornament, far from hindering female choice for that ornament, will actually promote more adaptive decision-making. This would result in a highly flexible female preference, as seems to be occurring across different populations of the house sparrow.

We thank the Landmark Trust and the residents of Lundy for permission to perform this study, Ian Hartley, Dave Richardson, Douglas Ross, Ben Sheldon and Ian Stewart for support in the field and useful discussion, and also Kate Buchanan, Jacob Höglund, Marion Petrie, Ben Sheldon, José Veiga and two anonymous reviewers for their constructive comments on earlier drafts of this manuscript. This work was supported by the UK Natural Environment Research Council.

REFERENCES

- Alatalo, R. V., Lundberg, A. & Glynn, C. 1986 Female pied flycatchers choose territory quality and not male characteristics. *Nature* **323**, 152–153.
- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1990 Phenotypic selection on heritable size traits: environmental variance and genetic response. *Am. Nat.* **135**, 464–471.
- Andersson, M. 1994 *Sexual selection*. Princeton University Press.
- Burley, N. 1986 Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**, 415–445.

- Cordero, P. H., Wetton, J. H. & Parkin, D. T. 1998 Extra-pair paternity and male badge size in the house sparrow. *J. Avian Biol.* (In the press.)
- Endler, J. A. & Houde, A. E. 1995 Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* **10**, 22–29.
- Falconer, D. S. 1960 *Introduction to quantitative genetics*. London: Longman.
- Fisher, R. A. 1930 *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Folstad, I. & Karter, A. J. 1992 Parasites, bright males, and the immunocompetence handicap. *Am. Nat.* **139**, 603–622.
- Griffith, S. C., Stewart, I. R. K., Dawson, D. A., Owens, I. P. F. & Burke, T. 1999 Extra-pair paternity in mainland and island populations of a socially monogamous bird, the house sparrow (*Passer domesticus*): is there an 'island effect'? *Biol. J. Linn. Soc.* (In the press.)
- Hamilton, W. D. & Zuk, M. 1982 Heritable true fitness and bright birds: a role for parasites? *Science* **218**, 384–387.
- Hegner, R. E. & Wingfield, J. C. 1987 Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male house sparrows. *Auk* **104**, 462–469.
- Heywood, J. S. 1989 Sexual selection by the handicap mechanism. *Evolution* **43**, 1387–1397.
- Hoelzer, G. A. 1989 The good parent process of sexual selection. *Anim. Behav.* **38**, 1067–1078.
- Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.* **72**, 283–327.
- Johnstone, R. A. 1995 Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol. Rev.* **70**, 1–65.
- Kimball, R. T. 1995 Sexual selection in the house sparrow. PhD thesis, University of New Mexico.
- Kimball, R. T. 1996 Female choice for morphological traits in house sparrows, *Passer domesticus*. *Ethology* **102**, 639–648.
- Kimball, R. T. 1997 Male morphology and nest-site quality in house sparrows. *Wilson Bull.* **109**, 711–719.
- Kirkpatrick, M. & Ryan, M. J. 1991 The evolution of mating preferences and the paradox of the lek. *Nature* **350**, 33–38.
- Møller, A. P. 1987 Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Anim. Behav.* **35**, 1637–1644.
- Møller, A. P. 1988 Badge size in the house sparrow *Passer domesticus*: effects of intra- and intersexual selection. *Behav. Ecol. Sociobiol.* **22**, 373–378.
- Møller, A. P. 1989 Natural and sexual selection on a plumage signal of status and on morphology in house sparrows, *Passer domesticus*. *J. Evol. Biol.* **2**, 125–140.
- Møller, A. P. 1990 Sexual behaviour is related to badge size in the house sparrow *Passer domesticus*. *Behav. Ecol. Sociobiol.* **27**, 23–29.
- Møller, A. P. 1995 Hormones, handicaps and bright birds. *Trends Ecol. Evol.* **10**, 121.
- Owens, I. P. F. & Short, R. V. 1995 Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. *Trends Ecol. Evol.* **10**, 44–47.
- Qvarnström, A. & Forsgren, E. 1998. Should females prefer dominant males? *Trends Ecol. Evol.* **13**, 498–501.
- Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. 1998 Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* **67**, 518–536.
- Sætre, G., Moum, T., Bures, S., Král, M., Adamjan, M. & Moreno, J. 1997 A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature* **387**, 589–592.
- Solberg, E. J. & Ringsby, T. H. 1997 Does badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology* **103**, 177–186.
- Svensson, L. 1984 *Identification guide to European passerines*. Stockholm: British Trust for Ornithology.
- Tinbergen, J. M. & Boerlijst, M. C. 1990 Nestling weight and survival in individual great tits. *J. Anim. Ecol.* **59**, 1113–1127.
- Veiga, J. P. 1990 Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. *Behav. Ecol. Sociobiol.* **27**, 345–350.
- Veiga, J. P. 1993 Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution* **47**, 1161–1170.
- Veiga, J. P. 1995 Honest signalling and the survival cost of badges in the house sparrow. *Evolution* **49**, 570–572.
- Veiga, J. P. 1996 Permanent exposure versus facultative concealment of sexual traits: an experimental study in the house sparrow. *Behav. Ecol. Sociobiol.* **39**, 345–352.
- Veiga, J. P. & Puerta, P. 1996 Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc. R. Soc. Lond. B* **263**, 229–234.
- Williams, G. C. 1966 *Adaptation and natural selection*. Princeton University Press.