Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings

Maria I. Sandell

Department of Animal Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden (maria.sandell@zooekol.lu.se)

Any reduction in the fitness of a breeding female induced by the settlement of additional females with her mate creates a conflict between the sexes over mating system. In birds, females are often aggressive towards other females but few studies have been able to quantify the importance of female–female aggression for the maintenance of monogamy. This study of the European starling, *Sturnus vulgaris*, quantifies male and female behaviour towards a potential prospecting female, presented in a cage during the pre-laying period, and relates it to the subsequent mating status of the male. A solitary breeding male was given the opportunity to attract an additional mate, which almost half of the males did. No biometric characters of the male or female were related to the subsequent mating status. Males demonstrated mate-attraction behaviour towards the caged female but the behaviour of the male did not predict the likelihood to attract an additional female. However, the proportion of time that the female spent near the potential settler was related to mating status, indicating that females that reacted more strongly towards a potential female competitor maintained their monogamous status. These results suggest that female behaviour may play an important role in shaping the mating system of facultatively polygynous species.

Keywords: polygyny; female aggression; monogamy; *Sturnus vulgaris*; sexual conflict; intrasexual conflicts

1. INTRODUCTION

Male investment in nestling feeding has been shown to increase the survival or quality of young (Bart & Tornes 1989; Wolf *et al.* 1988). When males mate with more than one female, there may be a conflict between the sexes over the allocation of male parental care between broods (Slagsvold & Lifjeld 1994). Females should try to maximize the investment by their mates into their own brood (Trivers 1972), and the ultimate female strategy to secure full male assistance is to prevent other females from settling with the same male (Davies 1989). Female–female interactions that interfere with the settlement of additional females have been suggested to be important for the maintenance of monogamy in several species (Yasukawa & Searcy 1982; Hannon 1984; Breichagen & Slagsvold 1988; Dunn & Hannon 1991; Veiga 1992; Kempenaers 1994; Sandell & Smith 1997), but the extent to which female–female aggression can determine male mating status is largely unknown.

The European starling is a facultatively polygynous species where females suffer a cost of polygyny due to reduced male investment in their brood (Sandell *et al.* 1996). The cost is related to the length of the breeding interval (Smith *et al.* 1994; Sandell *et al.* 1996; but see Pinxten & Eens 1994) and secondary females obtain more male assistance the closer in time they settle in relation to the primary female (Sandell *et al.* 1996). A previous study has shown that female starlings are aggressive towards other females and that the pattern of

aggression is consistent with the defence of male parental care hypotheses (Slagsvold & Lifjeld 1994; Sandell & Smith 1997). This study measures the level of female–female aggression in starlings during the pre-laying period and relates it to the subsequent mating status of the observed birds.

2. METHODS

The study was performed in the Revinge area in southern Sweden during 1994–97 (see Smith *et al.* (1994) for further details). Males arrive at the breeding grounds in February–March and defend one or several nest sites; females arrive shortly after. Egg laying starts in late April–early May and the starling is single-brooded in this area.

The study was made in nestboxes that were placed separately in trees with a minimum distance of 100 m in between each nestbox. Each male defending a solitary nestbox was provided with an additional nestbox at a distance of 2–10 m *ca.* two weeks before egg laying, which gave the male an opportunity to attract a secondary female. Most secondary females settle and start breeding within a week after the start of breeding by the primary female (Smith & Sandell 1998). Before the additional nestbox was provided, the resident birds were marked with acrylic paint which enabled identification of the birds at capture later in the season.

Nests were inspected from the middle of April until laying had commenced, and any nest building activities were noted. Nests may contain green nest material with or without a partly built nest. The green nest material, e.g. leaves, lichen and

flowers, is presumably used in mate attraction (Fauth *et al.* 1991; Eens *et al.* 1993; Gwinner 1997; but see Clark & Mason 1988). Laying date, clutch size and number of fledglings were monitored by regular nest inspections. The start of the laying period varied between years and a relative laying date was calculated by subtracting the earliest known laying date that year from each breeding attempt.

Females were only caught during the nestling period, whereas males were captured during all phases of the breeding cycle. Adult birds were ringed with an aluminium ring and a unique combination of colour rings. Tarsus length (cf. Alatalo *et al.* 1990), wing length, body mass and length of throat feathers were measured on all birds.

Mating status was determined by observations of male nest building, incubation and nestling feeding. Polygynously mated females were assigned mating status in relation to the order in which they started egg laying, as laying order generally reflects mating order (Smith & Sandell 1998; this study). Furthermore, some secondary females were assigned mating status on the basis that no male was seen feeding at their nest over a 1 h interval during the nestling period. I considered the nest to belong to the male that bred in the adjacent nestbox as a monogamous male feeds at the same rate as the female (Sandell *et al.* 1996).

Three trials were excluded from the analyses because the nest of the resident female was predated during laying or early incubating. Another three trials, performed at nests where I was unable to confirm that the male present at the pre-laying observation still had access to the nestboxes during breeding, were also excluded from all analyses.

(a) *Cage experiment*

In 1994–97, the behaviour of males and females towards a potential intruding female starling was examined during the pre-laying period of the already mated female by presenting a caged female to the breeding pair. The nestbox, which contained nest material (e.g. a partly built nest), was considered as the nest of the resident female and the cage (30 cm × 15 cm × 20 cm) was placed on the adjacent nestbox. If none of the nestboxes contained nest material, the cage was placed on the new nestbox. The behaviour of the resident pair was observed from a car 50–100 m away using a fixed-interval sampling method for 15 min (Martin & Bateson 1986; see Sandell & Smith (1997) for further details). Two or three different females were presented each year. The observation started when one of the breeding individuals arrived at the nest site. If none of the breeding birds had arrived after 30 min, the presentation was terminated.

The intensity of female aggression towards the potential intruder was measured as the proportion of time that a breeding female spent near the cage (i.e. on the cage or within 1 m from the cage) after arrival at the nest site (Sandell & Smith 1997). The proportion of time near the cage was also used as an indication of male behaviour towards a potential female intruder. In addition, I calculated the proportion of time that the resident male or female spent at the nest site after their first arrival there (i.e. within 10 m of the nestboxes and consequently also including time spent near the cage). Male song was analysed both as the number of song bouts that were initiated and as the proportion of fixed-interval sampling occasions in which males sang. Only the number of song bouts initiated was calculated for females. All interactions between the male and female were noted. This included copulations and aggressive interactions such as physical attacks, chases and supplanting attacks (see van

der Mueren (1980) for further description of these behaviours). I also noted if a breeding bird tried to attack the caged bird when sitting on the cage.

The male and the female of a breeding pair arrived simultaneously at the nest site in many trials (49%). There were only six trials where the time interval between the arrival of the male and that of the female exceeded 2 min (2.5–7.5 min), and females were the first to arrive at the nest site as often as the male (binomial test: $n = 20$, $p = 0.42$).

(b) *Time budget studies*

Time budget studies were performed at the nests of 26 pairs during the pre-laying period of 1995 and 1997. Time budget studies were always performed before the cage experiment; seven of the trials were conducted on the same day and the remaining were observed 1–7 days before the cage experiment. I used a fixed-interval sampling method (Martin & Bateson 1986), where I recorded every minute the location and activity of the breeding birds for 30 min and used the same categories when analysing behaviour as in the cage experiments.

(c) *Statistics*

Statistics were analysed with SYSTAT (Wilkinson 1992) and SAS Institute Inc. (1993). Data that could not be normalized were analysed with non-parametric tests.

3. RESULTS

The relevance of the results relies on the assumption that the individuals that were present at the observations in the pre-laying period also bred in the nestboxes. Over 80% of the females were identified during the pre-laying period by observations of colour rings or acrylic paint on wings and heads. All identified females bred in the nestboxes, indicating that this assumption is correct. The remaining females were unmarked during both pre-laying observations and at the time of capture during nestling feeding. All females that were identified and present during the pre-laying period obtained monogamous or primary mating status. All males were identified as present during both the pre-laying period and breeding.

Expect for short visits by other birds, only a single female appeared at the nest site during all pre-laying observations, both during cage experiments and during time budget studies. Secondary females start egg laying within a few days after settlement (Pinxten *et al.* 1989; Sandell & Diemer 1998) and because the cage experiments were conducted 3–28 days before the start of laying of secondary females (mean 11.6 days, $n = 15$), and time budget studies were conducted 2–19 days before (mean 8.7, $n = 9$), it is likely that the male was only mated to one female at the time of observation.

(a) *Cage experiments*

The behaviour of 39 breeding pairs towards a potential intruder was analysed; 61% of the males remained monogamous despite the opportunity to mate polygynously. The potential intruder was presented from 11 days before the original female started egg laying until the morning before the original female laid her first egg. Relative time until laying began had no effect on the behaviour of the breeding birds (Spearman rank correlations: male

Figure 1. The proportion of time (mean $\pm$ s.e.) spent near the caged female during the pre-laying period by monogamous females and by females whose mate attracted an additional female.

proportion of time near cage, $r_s = -0.27$, $n = 39$, $p > 0.1$; male time at nest site, $r_s = 0.15$, $n = 39$, $p > 0.2$; female time near cage, $r_s = -0.10$, $n = 39$, $p > 0.5$; female time at nest site, $r_s = 0.12$, $n = 39$, $p > 0.4$). There was no difference in relative laying date between females of monogamous and primary mating status (range 0–5 days; Mann–Whitney U -test: $U = 215$, $n_1 = 24$, $n_2 = 15$, $p = 0.29$).

There was a significant positive correlation between the time females and males spent at the nest site ($r_s = 0.59$, $n = 39$, $p < 0.001$). However, although females spent just as much time at the nest site as males (75.6% versus 71.9%, respectively; Wilcoxon sign rank test: $z = 1.31$, $n = 39$, $p = 0.19$), females spent more time near the cage (43.0% versus 23.4%; $z = 3.46$, $n = 39$, $p = 0.001$).

Fifteen of the 39 males produced song when sitting near the cage and these males were more likely to interact with their own female (73% versus 21% of the males also made supplanting attacks towards their mate; chi-squared test: $\chi^2 = 10.52$, d.f. 1, $n = 39$, $p = 0.001$). However, there was no difference in the proportion of time spent at the nest site between singing and non-singing males ($U = 135$, $n_1 = 24$, $n_2 = 15$, $p = 0.19$).

Logistic regression showed that the subsequent mating status of the pairs was predicted by female behaviour towards the potential intruder, whereas male behaviour had no effect on mating status. In a backward stepwise exclusion (at $p > 0.1$), with the predictors year, days until start of laying, male and female proportion of time at nest site, male and female proportion of time near the potential intruder, proportion of time males spent singing and number of song bouts per minute by the male and the female, only the proportion of time females spent near the intruder had a significant effect on mating status (logistic regression, $\chi^2 = 7.34$, d.f. 1, $n = 39$, $p = 0.007$; figure 1).

The presence or absence of her own mate did not affect female behaviour towards the caged female. Females spent as much time near the cage if the male was at the

Table 1. *Biometric measurements of males and females that remained monogamously mated compared with pairs that became polygamously mated*

(Measurements are mean $\pm$ s.d. (n). Data tested with logistic regression.)

	monogamous	polygynous	p values
male tarsus (mm)	34.8 $\pm$ 0.7 (22)	34.5 $\pm$ 0.6 (14)	0.18
male wing (mm)	135.5 $\pm$ 2.2 (18)	135.1 $\pm$ 3.2 (8)	0.72
male throat feather (mm)	23.6 $\pm$ 1.0 (15)	25.2 $\pm$ 2.2 (6)	0.36
female tarsus (mm)	34.0 $\pm$ 0.6 (19)	33.9 $\pm$ 0.8 (15)	0.60
female wing (mm)	132.3 $\pm$ 2.0 (12)	131.3 $\pm$ 2.5 (11)	0.28

nest site as if he was absent ($z = 1.10$, $n = 18$, $p = 0.27$). However, female behaviour was affected by the activity of the male when he was present. Females spent more time near the cage if their mate sang towards the caged female (61.8% versus 31.3%; $U = 109.5$, $n_1 = 24$, $n_2 = 15$, $p = 0.04$). Female song and female attacks directed towards the potential intruder were related to proportion of time near the cage. Females that sang spent more time at the cage (70.8% versus 27.5%; $U = 56.5$, $n_1 = 14$, $n_2 = 25$, $p < 0.001$) and so did females that tried to peck the caged female (70.1% versus 36.1%; $U = 63$, $n_1 = 8$, $n_2 = 31$, $p = 0.03$).

Body size or age of the breeding birds did not affect mating status (table 1). Males that put green nest material in the nestbox where the resident female did not breed were no more likely to attract an additional mate, regardless of whether the male did it before the start of laying of the first-mated female, or if it occurred after the female had started egg laying (before laying, $\chi^2 = 0.57$, d.f. 1, $n = 37$, $p = 0.45$; after laying, $\chi^2 = 1.50$, d.f. 1, $n = 37$, $p = 0.22$). Birds other than the resident pair were present in 12 trials but they stayed for only short periods (less than 2 min). Nine of the visiting birds were females and they were chased away by the resident female.

(b) Time budget studies

Time budget studies were performed from 15 days before laying until the day before laying. Females spent more time at the nest site the closer to the start of egg laying ($r_s = 0.47$, $n = 27$, $p < 0.05$), whereas the proportion of time spent at the nest site by males was unrelated to breeding phase ($r_s = 0.26$, $n = 25$, $p > 0.5$). However, there was still a significant correlation between the time spent at the nest site for the female and male of a breeding pair ($r_s = 0.78$, $n = 27$, $p < 0.001$).

There were no significant effects of female or male behaviour that could explain mating status, but there was a tendency for males that attracted an additional female to spend more time singing (logistic regression: $\chi^2 = 2.89$, d.f. 1, $n = 26$, $p = 0.09$, with stepwise backward exclusion with the variables year, relative date, male and female time near cage and at nest site, and proportion and frequency of male song). There was no correlation between the behaviour of males or females towards a

caged intruder and the behaviour at the nest site during observations in nests where both the time budget studies and the cage experiment were performed ($n=13$). The proportion of time at nest site was not correlated between the two studies in either sex ($p>0.2$ for both males and females), neither was the singing intensity of males ($p>0.2$).

4. DISCUSSION

This study suggests that females vary in their response towards potential secondary females and that this variation can be used to predict the subsequent mating status of the male. Females that remained monogamous despite the male's opportunity to attract a secondary female reacted more strongly towards a potential female settler, and the proportion of time females spent near the cage was also associated with song and physical attacks by the females. Female song is primarily associated with territorial defence or aggressive interactions (Catchpole & Slater 1995; Eens 1997). Aggressive behaviour in birds involves a complex of visual and vocal displays (van der Mueren 1980; Svare 1983) and it may be difficult to adequately measure a bird's reaction towards another individual. The time females spent near the caged female was, in a previous study, related to both the reproductive phase of the resident female, i.e. the temporal variation in costs of polygyny, and the opportunity for males to attract additional mates, indicating that it may be used as an index of female reaction towards a potential secondary female (Sandell & Smith 1997). However, females may limit a male's ability to attract other females by other means than aggressive interactions, e.g. by soliciting copulations when the mate is courting other females (Eens & Pinxten 1995). In this study, it was not possible to examine the effect of such behaviour as there were few females soliciting during both the cage experiment ($n=4$) and the time budget studies ($n=4$).

(a) *Constraints on female aggression*

There may be both ecological and physiological mechanisms that produce a trade-off between aggressive behaviour and reproduction in females (Rose 1983; Stearns 1989). During the pre-laying period, females spend much time foraging and this may be important for female condition during breeding (Haywood & Perrins 1992). This suggests that females are time-limited during this period and that the time that females can allocate towards guarding their mating status is constrained.

In birds, aggressive behaviour appears to be under hormonal control (Harding 1983); in many species, androgens are involved in mediating aggression, territorial defence and singing in female birds (Harding 1983; Monaghan & Glickman 1993; Wingfield 1994). However, increased levels of androgens may interfere with female reproductive behaviour (Packer *et al.* 1995; Searcy 1988). Gonadal hormones such as oestrogen and progesterone may also have an opposite effect on aggressive behaviour (Monaghan & Glickman 1993). If ovarian hormones inhibit the expression of aggression or if androgens interfere with the start of reproduction, females face a situation where they must trade potential

benefits of aggressive behaviour with the costs of delayed breeding.

(b) *Intersexual interactions and the maintenance of monogamy*

Maintenance of monogamy in spite of male opportunity to attract secondary females by already mated females is in strong contrast to optimal mating behaviours of the male. Consequently, several behavioural strategies for males to counteract female behaviour have been suggested in the starling, e.g. defending nest sites far apart (Sandell & Smith 1996), interfering with the aggressive behaviour of primary females (Merkel 1980; Pinxten *et al.* 1989) or refusing to copulate with their primary mate when she solicits (Eens & Pinxten 1995). In this study, males frequently attacked their mate and this behaviour was related to the intensity of male mate-attraction behaviour.

In the European starling, there is a potential for a sexual conflict over the number of breeding partners (Smith *et al.* 1994; Pinxten *et al.* 1989; Smith & Sandell 1998). Males benefit from mating with several females as their reproductive success increases (Smith & Sandell 1998), whereas mated females suffer from the settlement of additional females. Secondary females produce both fewer young and young of lower quality than both monogamous and primary females (Smith & Sandell 1998; Pinxten & Eens 1990). However, there are no unmated males defending nestboxes present at the start of the synchronized laying period (M. I. Sandell, unpublished data), indicating that secondary status may be the best option for unmated females. Hence, in the starling, females may have different optimal mating systems depending on their situation and future mating opportunities.

Studies on the origin of polygyny usually focus on costs and consequences of females settling with already mated males (Orians 1969; Searcy & Yasukawa 1989). However, such studies must incorporate the extent to which resident females can affect their mate's mating status, as this will interact with the optimal choice that prospecting females make and may lower the level of polygyny. Hence, female-female aggression may be important in explaining the maintenance of monogamy in many of the predominantly monogamous species with a low degree of polygyny (Arcese 1989; Veiga 1992; Slagsvold 1993; Kempenaers 1994; Slagsvold & Lifjeld 1994; Sandell & Smith 1997).

I thank Måns Bruun, Michael Diemer, Ulf Ottosson and Henrik Smith for help in the field. Henrik Smith also provided valuable comments on the manuscript. The study was supported by grants from the Swedish Royal Academy of Science.

REFERENCES

- Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1990 Phenotypic selection on heritable size traits, environmental variance and genetic response. *Am. Nat.* **135**, 464–471.
- Arcese, P. 1989 Intrasexual competition and the mating system in primarily monogamous birds: the case of the song sparrow. *Anim. Behav.* **38**, 96–111.
- Bart, J. & Tornes, A. 1989 Importance of monogamous male birds in determining reproductive success: evidence for house wrens and a review of male-removal studies. *Behav. Ecol. Sociobiol.* **24**, 109–116.

- Breichagen, T. & Slagsvold, T. 1988 Male polyterritoriality and female–female aggression in pied flycatchers *Ficedula hypoleuca*. *Anim. Behav.* **36**, 604–606.
- Catchpole, C. K. & Slater, P. J. B. 1995 *Bird songs: biological themes and variations*. Cambridge University Press.
- Clark, L. & Mason, J. R. 1988 Effect of biologically active plants used as nest material and the derived benefit to starling nestlings. *Oecologia* **77**, 174–180.
- Davies, N. B. 1989 Sexual conflict and the polygamy threshold. *Anim. Behav.* **38**, 226–234.
- Dunn, P. O. & Hannon, S. J. 1991 Intraspecific competition and the maintenance of monogamy in tree swallows. *Behav. Ecol.* **2**, 258–266.
- Eens, M. 1997 Understanding the complex song of the European starling: an integrated ethological approach. In *Advances in the study of behaviour*, vol. 26 (ed. P. J. B. Slater), pp. 355–434. London: Academic Press.
- Eens, M. & Pinxten, R. 1995 Inter-sexual conflicts over copulations in the European starling: evidence of the female mate-guarding hypothesis. *Behav. Ecol. Sociobiol.* **36**, 71–81.
- Eens, M., Pinxten, R. & Verheyen, R. F. 1993 Function of the song and song repertoire in the European starling (*Sturnus vulgaris*): an aviary experiment. *Behaviour* **125**, 51–66.
- Fauth, P. T., Krementz, D. G. & Hines, J. E. 1991 Ectoparasitism and the role of green nest material in the European starling. *Oecologia* **88**, 22–29.
- Gwinner, H. 1997 The function of green plants in nests of European starlings (*Sturnus vulgaris*). *Behaviour* **134**, 337–351.
- Hannon, S. J. 1984 Factors limiting polygyny in the willow ptarmigan. *Anim. Behav.* **32**, 153–161.
- Harding, C. F. 1983 Hormonal influences on avian aggressive behaviour. In *Hormones and aggressive behavior* (ed. B. B. Svare), pp. 223–247. New York: Plenum Press.
- Haywood, S. & Perrins, C. M. 1992 Is clutch size in birds affected by environmental conditions during growth? *Proc. R. Soc. Lond. B* **249**, 195–197.
- Kempnaers, B. 1994 Polygyny in the blue tit: unbalanced sex ratio and female aggression restrict mate choice. *Anim. Behav.* **47**, 943–957.
- Martin, R. & Bateson, P. 1986 *Measuring behaviour*. Cambridge University Press.
- Merkel, F. W. 1980 Sozialverhalten von individuell markierten Staren, *Sturnus vulgaris*, in einer kleinen Nistkastenkolonie. III. Die Rolle der Polygynie. *Luscinia* **44**, 133–158.
- Monaghan, E. P. & Glickman, S. E. 1993 Hormones and aggressive behaviour. In *Behavioral endocrinology* (ed. J. B. Becker, S. M. Breedlove & D. Crews), pp. 261–285. Cambridge, MA: The MIT Press.
- Orians, G. H. 1969 On the evolution of mating systems in birds and mammals. *Am. Nat.* **103**, 589–603.
- Packer, C., Collins, D. A., Sindimvo, A. & Goodall, J. 1995 Reproductive constraints on aggressive competition in female baboons. *Nature* **373**, 60–63.
- Pinxten, R. & Eens, M. 1990 Polygyny in the European starling effect on female reproductive success. *Anim. Behav.* **40**, 1035–1047.
- Pinxten, R. & Eens, M. 1994 Male feeding of nestlings in the facultatively polygynous European starling: allocation patterns and effect on female reproductive success. *Behaviour* **129**, 113–140.
- Pinxten, R., Eens, M. & Verheyen, R. F. 1989 Polygyny in the European starling. *Behaviour* **111**, 234–256.
- Rose, M. J. 1983 Theories of life history evolution. *Am. Zool.* **23**, 15–23.
- Sandell, M. I. & Diemer, M. 1998 Intraspecific brood parasitism—a strategy for floating females in the European starling (*Sturnus vulgaris*). *Anim. Behav.* (In the press.)
- Sandell, M. I. & Smith, H. G. 1996 Already mated females constrain male mating success in the European starling. *Proc. R. Soc. Lond. B* **263**, 743–747.
- Sandell, M. I. & Smith, H. G. 1997 Female aggression in the European starling during the breeding season. *Anim. Behav.* **53**, 13–23.
- Sandell, M. I., Smith, H. G. & Bruun, M. 1996 Paternal care in European starling, *Sturnus vulgaris*: nestling feeding. *Behav. Ecol. Sociobiol.* **39**, 301–309.
- SAS Institute Inc. 1993 *SAS Technical Report P-243. SAS/STAT Software: GENMOD procedure, release 6.09*. Cary, NC: SAS Institute Inc.
- Searcy, W. A. 1988 Do female red-winged blackbirds limit their own breeding densities? *Ecology* **69**, 85–95.
- Searcy, W. A. & Yasukawa, K. 1989 Alternative models of territorial polygyny in birds. *Am. Nat.* **134**, 323–342.
- Slagsvold, T. 1993 Female–female aggression and monogamy in great tits, *Parus major*. *Ornis Scand.* **24**, 155–158.
- Slagsvold, T. & Lifjeld, J. T. 1994 Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* **143**, 59–94.
- Smith, H. G. & Sandell, M. I. 1998 Intersexual competition in a polygynous mating system. *Oikos*. (In the press.)
- Smith, H. G., Ottosson, U. & Sandell, M. 1994 Intrasexual competition among polygynously mated female starlings (*Sturnus vulgaris*). *Behav. Ecol.* **5**, 57–63.
- Stearns, S. C. 1989 Trade-offs in life history evolution. *Funct. Ecol.* **3**, 259–268.
- Svare, B. B. 1983 *Hormones and aggressive behaviour*. New York: Plenum Press.
- Trivers, R. L. 1972 Parental investment and sexual selection. In *Sexual selection and the descent of man 1871–1971* (ed. B. Campbell), pp. 136–179. Chicago, IL: Aldine Press.
- van der Mueren, E. 1980 Intraspecific aggression in a group of caged starlings (*Sturnus vulgaris*). *Le Gerfaut*. **70**, 455–470.
- Veiga, J. P. 1992 Why are house sparrows predominantly monogamous? A test of hypotheses. *Anim. Behav.* **43**, 361–370.
- Wilkinson, L. 1992 *SYSTAT for Windows*. Everston, IL: SYSTAT Inc.
- Wingfield, J. C. 1994 Hormone–behavior interactions and mating systems in male and female birds. In *The differences between the sexes* (ed. R. V. Short & E. Balaban), pp. 303–330. Cambridge University Press.
- Wolf, L., Ketterson, E. D. & Nolan, V. Jr 1988 Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit? *Anim. Behav.* **36**, 1601–1618.
- Yasukawa, K. & Searcy, W. A. 1982 Aggression in female red-winged blackbirds: a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* **11**, 13–17.