



Male plumage, paternal care and reproductive success in yellow warblers, *Dendroica petechia*

G. A. LOZANO & R. E. LEMON
Department of Biology, McGill University

(Received 4 August 1994; initial acceptance 2 November 1994;
final acceptance 30 May 1995; MS. number: A6876R)

Abstract. Using morphological or behavioural features correlated with paternal care, females can, prior to mating, assess the potential parental contribution of males. As a first step in a study of female mate choice in yellow warblers, this study was designed to examine the importance of paternal care by males of differing chest striping. Contrary to a previous report, paternal care was not negatively correlated with male chest striping. Paternal care was highly variable between individuals. Females did not compensate for experimentally induced reductions of paternal care, which resulted in significantly reduced nestling growth. Therefore, in the absence of alternative mating opportunities, males must maintain their contributions of paternal care or pay the cost of reduced fitness.

© 1996 The Association for the Study of Animal Behaviour

In species with biparental care, females may benefit by choosing mates who provide suitable paternal care. Searcy (1979) stated that if female mate choice is to be considered adaptive, the traits selected in males must (1) affect the females' fitness, (2) have enough variation for selection to be possible and (3) be reliably indicated by some cue that females can observe at the time of choice. Searcy's third criterion is especially important for females trying to choose males on the basis of paternal care. Behavioural or morphological male traits correlated with paternal care could be used by females for these purposes.

There are several instances in which paternal care is correlated with behavioural traits that females can assess before mating. The singing rate of stonechats, *Saxicola torquata*, correlates with paternal care, but not with greater fledging success (Greig-Smith 1982). Male courtship rate in damselfish, *Stegastes partitus*, correlates with the number of eggs received from females and the survival of the eggs (Knapp & Kovach 1991). The frequency of courtship feeding correlates with the amount of paternal care provided in herring gulls, *Larus argentatus* (Niebuhr 1981), as well as

with the total weight of the clutch and brood and the number of nestlings fledged in common and arctic terns, *Sterna paradisaea* (Nisbet 1973). In red-winged blackbirds, *Agelaius phoeniceus*, courtship time correlates with the amount of paternal care provided (Searcy & Yasukawa 1981; Eckert & Weatherhead 1987).

Morphological traits correlated with paternal care could also affect female mate preferences. Among biparental fish, females sometimes prefer larger males, presumably because these males take a more active role in guarding the eggs or brood (Downhower & Brown 1980; Grant & Colgan 1983; Keenleyside et al. 1985; Bisazza & Marconato 1988; Côte & Hunte 1989). In great tits, *Parus major*, female choice is partially based on the size of the male black chest stripe (Norris 1990a); Norris (1990b) argued that this preference occurs because the size of the stripe correlates with male nest attentiveness and nestling fledging weight.

Studd & Robertson (1985a) compared yellow warbler males with different amounts of brown streaking on their chests and found that lightly streaked males visited their nests more often than did heavily streaked males. They also showed that heavily streaked males elicit more intense responses from territorial males, react more intensively while defending their territories, spend more time on their territories (Studd & Robertson

Correspondence: G. A. Lozano, Department of Biology, McGill University, 1205 Dr Penfield Ave., Montreal, Quebec H3A 1B1, Canada (email: lozano@bio1.lan.mcgill.ca).

1985b), and spend more effort on territorial defence (Studd & Robertson 1988). Hence, the importance of paternal care appears to differ between females depending on the male they have mated: heavily striped males defend more vigorously their presumably better territories but do not feed their nestlings as much as lightly striped males do.

In this study we used yellow warblers to examine the importance of male help to females mated to males with differing amounts of brown breast striping. We predicted that if male help is experimentally reduced, females mated with lightly streaked males would suffer greater reproductive losses than females mated with heavily streaked males. For this test to be meaningful, we needed to confirm that the correlation found by Studd & Robertson (1985a) also occurred in our population. However, we did not find this correlation. We consequently used the data to test whether paternal care, irrespective of chest streaking, was important to female fitness. We estimated female fitness by measuring nestling survival and growth, and parental care by quantifying nestling feeding and nest visiting rates.

METHODS

We carried out the field work at Pointe à Fourneau (45°22'N, 73°51'W), on Île Perrot, Quebec, Canada from May to July 1992. We used mist nets to catch the birds. We banded each captured bird with a numbered aluminium USFWS band and a unique combination of three coloured plastic bands. The colour of leg bands affects mate choice preferences in zebra finches, *Phoebastria guttata* (Burley et al. 1982). We do not know if this is true for yellow warblers, nor what colours, if any, are preferred, but to avoid this possibility we did not use any colours naturally found on yellow warblers. We also recorded the tarsus, wing chord, rectrix, ninth primary feather lengths and weight of each bird captured.

We decreased paternal care by males in the experimental group by glueing a small weight near the base of the tail (Wright & Cuthill 1989). The weight in this case was 0.5 g, which was approximately 4.9% of the body mass of these birds. We captured 75 adult yellow warbler males at our study site in 1992; these had an average (\pm SE) mass of 10.21 ± 0.03 g. We used males from a

second group of nests as controls; these males were captured, handled, and released without any added weight. We used 34 males: 16 controls and 18 experimentals.

When we assigned nests to a treatment, we mixed nestlings between broods. To do this we took all nestlings from the population at approximately the same stage of development. From this pool, we assigned four nestlings to each nest. Each nest ended up with four young of relatively uniform size, some of which had been originally at that nest. This procedure removed any potential correlations between the quality of the parents and their young. These manipulations took place on the day of hatch or the next day.

Every day beginning 2 days after hatch we carried out 30-min watches at each nest. During these watches we recorded the number of nestling feedings and nest visits, and time spent brooding by the parents. Nest visits include nestling feedings. The two variables were noted because parents sometimes visit the nest with food in their beaks but fail to deliver it, visit without any food, or visit only to remove faecal sacs. We measured nestling masses after the first and second nest watches, and masses, ninth primary feather and tarsus lengths after the third nest watch. Fledging normally occurs around day 10, but any attempts to approach a nest when nestlings are older than 6 days may result in all or some nestlings prematurely leaving the nest. Therefore we did not disturb nestlings after the fourth and fifth watches. To minimize other potential sources of variance we carried out nest watches only during the mornings.

We used one-tailed Spearman's correlations to test the negative correlation between plumage striping and paternal care reported by Studd & Robertson (1985a). The predicted differences in feeding and visiting rates, brood sizes and mean nestling weights were tested using type III sums of squares, mixed effects, unbalanced, univariate, repeated-measures ANCOVAs, with treatment as a class variable, nest within treatment, nestling age as a covariate, and treatment*age interaction effects. We removed the interaction and nestling age effects if they were not significant. We used the nest within-treatment effect to remove any variance owing to differences between nests within a treatment. We analysed the predicted effects of the reduced male help on nestling mass and size using one-tailed *t*-tests.

Table I. Spearman's correlation coefficients testing the expected negative relation between paternal care and male brown breast streaking

Nestling age	Nestling feeding	Nest visiting
Day 2 <i>N</i> =16*	-0.2153 (0.2116)	-0.2006 (0.2282)
Day 4 <i>N</i> =16	-0.0182 (0.4734)	-0.1602 (0.2768)
Day 6 <i>N</i> =15	0.1085 (0.6498)	0.2968 (0.8587)
Day 8 <i>N</i> =12	-0.1647 (0.3045)	-0.1961 (0.2707)
Day 10 <i>N</i> =6	0.0147 (0.5111)	0.0147 (0.5111)

One-tailed *P*-values in parentheses.

*Sample sizes vary because nests were lost to predators, inclement weather, and, by day 10, fledging.

We quantified male breast striping in the following manner. We took at least two photographs of the ventral surface of each male. Four volunteers independently and subjectively placed each photograph in one of five categories according to the area of brown breast streaking. We obtained a value for each male from each scorer by averaging the scores (1–5) of his representative photographs. We obtained each male's final score by averaging the four independent scores.

Studd & Robertson (1985b) quantified male plumage by 'centring a clear plastic grid (2 × 2 cm), consisting of 25 smaller squares, on the breast. A standardized method of grid placement was used on each bird. The percentage of brown plumage was then estimated within each square and averaged over all 25 to obtain the overall estimate' (page 1104).

To compare the two methods of quantifying male plumage, we used 23 museum yellow warbler skins. Each specimen was photographed at least twice and the photographs were scored as previously described. We also quantified the plumage of these specimens using Studd & Robertson's (1985a, b, 1988) method, with the following clarifications: (1) the grid was held curved around the bird's body and placed on the chest with the upper edge aligned with the forward-most edge of the striping, (2) the area of brown plumage within each of the 25 squares was estimated to the nearest tenth, (3) if two estimates of one specimen were obtained, they were averaged, and (4) all

measurements were carried out by only one individual (G.A.L.).

To evaluate the repeatability of the two methods, we took two estimates from 16 museum specimens using the plastic grid method, and we scored photographs from 35 museum specimens twice, as already described. To avoid potential biases, we did not take the two plastic grid estimates from each skin consecutively, and we recorded all estimates on a tape-recorder and later transcribed them. Similarly, the same group of four people scored the photographs of the museum specimens the second time but after an interval of several weeks. We quantified the repeatability by estimating the % measurement errors using a model II ANOVA (Bailey & Byrnes 1990), and by means of a correlation analysis.

RESULTS

Comparisons of Grid and Photograph Methods of Plumage Scoring

The measures obtained with the two methods were significantly but not strongly correlated ($r=0.53511$, $N=23$, $P=0.0085$). The two plumage scores obtained by ranking the photographs were significantly correlated ($r=0.9796$, $N=35$, $P=0.0001$). Using a model II ANOVA, measurement error of the photograph method was estimated at 2.086%. The two measurements obtained with the plastic grid method were also significantly correlated ($r=0.7587$, $N=16$, $P=0.0007$). Measurement error of the plastic grid method was estimated at 49.23%.

Importance of Paternal Care

We used males in the control group to test the negative correlation between paternal care and chest striping reported by Studd & Robertson (1985a). However, we did not find this correlation (one-tailed r_s , $P_s > 0.05$; Table I), whether paternal care was estimated by nestling feeding or nest visiting rates. Using averages of each male over all nest watches, as did Studd & Robertson (1985a), again, there were no significant correlations between male plumage and either nestling feeding ($r_s=0.01259$, $N=16$, $P=0.9631$) or nest visiting rates ($r_s=0.08278$, $N=16$, $P=0.7605$). Therefore, we could not test the original prediction.

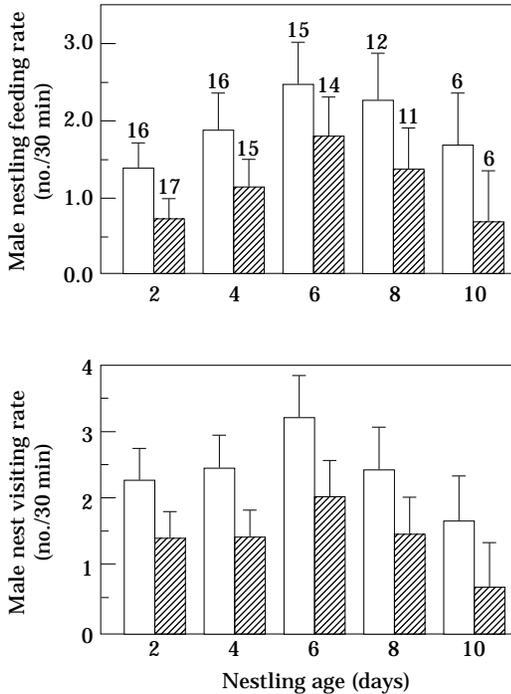


Figure 1. Effectiveness of experimental manipulations at reducing paternal care. Above the bars are the number of nests, which are the same for all graphs and decrease with nestling age because nests were lost to predators, inclement weather, and, by day 10, fledging. Results of statistical tests (see Methods) are as follows. Nestling feeding: treatment, $P=0.0449$; nest within treatment, $P=0.0003$. Nest visiting: treatment, $P=0.0167$; nest within treatment, $P=0.0001$. □: Control, ▨: experimental birds.

Male size is another male trait that females may attempt to use to predict paternal care, but in the control group neither mean male nestling feeding nor mean male nest visiting rate was correlated with male size (PC1 resulting from a PCA on the correlation matrix of all morphological variables measured: $r = -0.35845$, $P=0.1895$; $r = -0.30657$, $P=0.2664$, respectively; $N=15$) or male body mass ($r = -0.12932$, $P=0.6460$; $r = -0.06767$, $P=0.8106$, respectively; $N=15$).

The added weights were effective at reducing paternal care, both in terms of nestling feeding and nest visiting rates (Fig. 1). These reductions in male help had no effect on nestling survival (Fig. 2), or on mean size (tarsus and ninth primary feather lengths at day 6, one-tailed t -tests: $N=29$, $P=0.1738$ and 0.0657 , respectively), but significantly decreased mean nestling masses (Fig. 3).

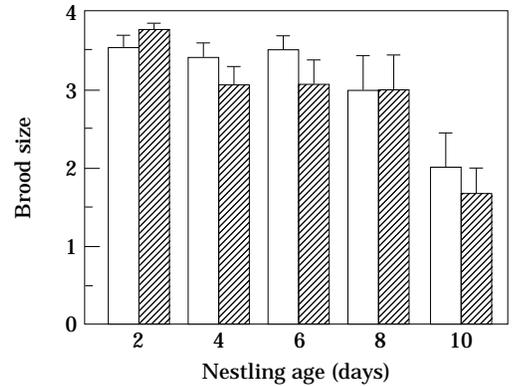


Figure 2. Effect of reduced male help on nestling survival. Results of statistical tests (see Methods) are as follows. Treatment, $P=0.21$; nestling age, $P=0.0001$. □: Control, ▨: experimental birds.

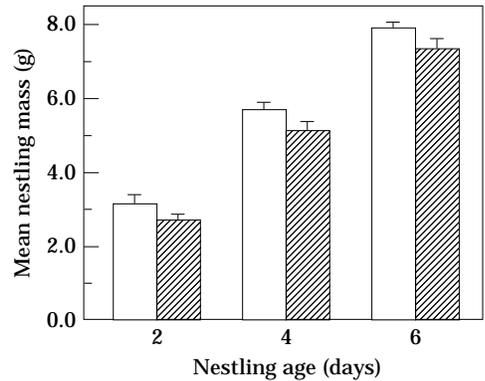


Figure 3. Effect of reduced male help on nestling mass. Results of statistical tests (see Methods) are as follows. Treatment, $P=0.0001$; nestling age, $P=0.0001$. □: Control, ▨: experimental birds.

Females did not compensate for the reduction in male help (Fig. 4). Total nestling feeding and nest visiting rates were not significantly lower in the experimental group, although the differences were in the expected direction (Fig. 5). There were no significant differences in time spent brooding. Statistically similar results were obtained if female nestling feeding and nest visiting rates were calculated based only on the time not spent brooding.

DISCUSSION

Male Chest Striping and Paternal Care

We designed this study to compare the importance of male help to females mated with males

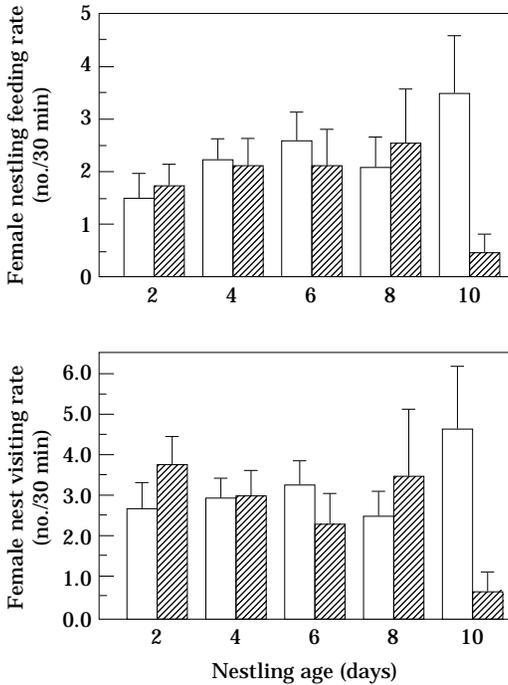


Figure 4. Female response to reduced paternal care. Results of statistical tests (see Methods) are as follows. Nestling feeding: treatment, $P=0.8882$. Nest visiting: treatment, $P=0.9004$. □: Control; ▨: experimental birds.

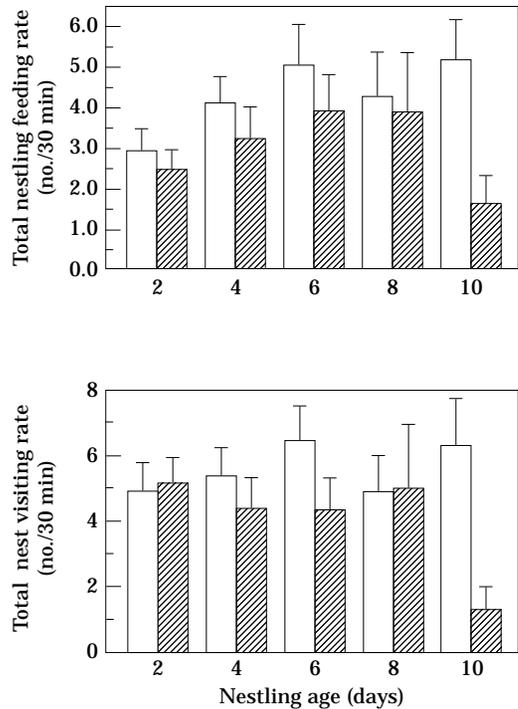


Figure 5. Effect of reduced paternal care contribution on total nestling feeding and nest visiting rates. Results of statistical tests (see Methods) are as follows. Nestling feeding: treatment, $P=0.241$. Nest visiting: treatment, $P=0.2835$. □: Control, ▨: experimental birds.

with different amounts of breast streaking. This study was based on the results of Studd & Robertson (1985a), who found a negative correlation between male chest striping and paternal care. Unlike Studd & Robertson (1985a), we did not find this correlation. There are several possible explanations for the discrepancy.

First, the two methods used to quantify breast striping may have differed. However, plumage estimates obtained with the grid method were significantly and positively correlated with plumage estimates obtained with the photograph method. Furthermore, comparisons using museum specimens showed that the photograph method was more reliable than the plastic grid method. The estimates used to compare the two methods were taken from museum specimens, and therefore more care and time could be used to obtain each estimate than would be possible in the field.

Second, the relationship between male plumage and paternal care may be so weak that sometimes

it will not be found. Studd & Robertson (1985a) found significant negative correlations between paternal care and plumage in both 1982 and 1983. The 1982 correlation was obtained using 13 birds from two localities, and was particularly influenced by one point: a bird with the lowest plumage score and the highest feeding rate. Without this point the correlation is not significant ($r_S = -0.467$, $N=12$, $P=0.126$). The 1983 correlation is based on 27 birds from three areas. Separate analyses for each area yield non-significant correlations ($r_S = -0.617$, $N=9$, $P=0.077$; $r_S = -0.401$, $N=13$, $P=0.174$; $r_S = -0.800$, $N=5$, $P=0.104$, respectively). These analyses show that the reported negative correlation between plumage and paternal care is variable and not very robust.

Third, intraspecific variation in behaviour occurs in many species, and separate populations can show different qualities (Lott 1991). It is possible that the Quebec population that we

studied is distinct from Studd & Robertson's (1985a). This explanation is not satisfactory, however, without explicit reasons as to why these differences should exist.

Regardless of which, if any, of the proposed explanations is correct, these results indicate that male chest striping is not a reliable indicator of paternal care in the population that we studied. Until we find other male features that, at the time of mating, females can use to predict paternal care, it will be difficult to test whether female yellow warblers choose mates based on paternal care.

The Importance, Variability and Predictability of Paternal Care

In most studies testing whether paternal care is important to female fitness, paternal care is reduced by simply removing the males. Results from these studies vary from failing to detect any effects of male removal on female fitness (Gowaty 1983; Hannon 1984; Greenlaw & Post 1985; Martin et al. 1985; Martin & Cooke 1987; Sasvári 1990; Wolf et al. 1991; Hipes & Hepp 1993), to finding effects only if the male is removed when nestlings are very young (Sasvári 1986) or only in some years (Bart & Tornes 1989; Duckworth 1992), to finding the expected decreases in survival (Smith et al. 1982; Sasvári 1986; Lyon et al. 1987; Wolf et al. 1988; Johnson et al. 1992) or growth (Weatherhead 1979; Smith et al. 1982; Lyon et al. 1987; Whillans & Falls 1990; Johnson et al. 1992). Comparisons between aided and unaided females may reveal that females have higher reproductive outputs when males are present, but they say little as to why a certain level of parental care is maintained.

Experimental studies in which paternal care is reduced without actually removing the males are of a more subtle nature. Like Wright & Cuthill's (1989, 1990) work with starlings, *Sturnus vulgaris*, our results show that even partial reductions of paternal care significantly affect nestling growth. Higher post-fledging survival of heavier nestlings has been observed in many species (e.g. Perrins 1965, 1988; Patterson et al. 1988; Tinbergen & Boerlijst 1990; Hochachka & Smith 1991; Husby & Slagsvold 1992). Therefore, this study shows that in yellow warblers paternal care is likely to be important to female fitness.

Another prerequisite of female mate choice based on paternal care is that paternal care must

be variable between males. The male within-treatment effects on paternal care were highly significant (Fig. 1), which indicates that a large amount of the variance in paternal care is due to differences between males.

Finally, even if paternal care is variable and important to females, female mate choice based on paternal care cannot occur unless females can predict the level of parental care that any given male is going to provide. Studd & Robertson (1985a) suggested that male plumage can be used as an indicator of future paternal care. We failed to find this relationship in our population. Other features could potentially be used by females to predict paternal care, but in our control group neither mean male nestling feeding nor mean male nest visiting rate was correlated with male size. Our subsequent work will be aimed at determining whether paternal care is correlated with aspects of singing behaviour, and whether females choose males themselves, and not simply their territories.

Female Responses to Decreases in Paternal Care

Interestingly, females did not compensate for the decrease in male help. Were they unable or unwilling to do so? Parental care studies on a variety of birds have repeatedly shown that females increase their nestling feeding rates after the removal of their mates (e.g. Weatherhead 1979; Smith et al. 1982; Greenlaw & Post 1985; Sasvári 1986; Lyon et al. 1987; Hatchwell & Davies 1990; Sasvári 1990; Whillans & Falls 1990; Duckworth 1992). Brood manipulation experiments also show that birds can increase their parental effort in an attempt to meet the requirements of their brood (e.g. Gori 1988; Smith et al. 1988; Whittingham 1989). It seems, then, that generally birds are able to increase their food delivery rates.

Although in male removal or clutch manipulation studies females are obviously aware that their situation has changed, it is possible that females in our experiment were unable to judge accurately how much males were contributing to the rearing of their nestlings. Alternatively, maternal care may vary independently of paternal care. In either case, the fact that females did not compensate for decreases in male help means that females cannot be exploited by males into doing more than their 'fair share' of parental care.

If females were to compensate, either partially or completely, for reductions in male help, males

could not only reduce their costs of paternal care, but also have more time to attempt to obtain secondary mates and extra-pair copulations, or even completely desert their females. Male help is important to nestling growth, so males would not be expected to decrease their paternal contribution. If the costs of reduced male help are low, however, such as in conditions of high food abundance, or if the likelihood of obtaining extra-pair copulations and/or secondary females is high, males should be expected to reduce their paternal effort. Unfortunately, although food abundance and parental care can be fairly easily manipulated and quantified, yellow warbler copulations are seldom observed, so it will be difficult to determine the incidence of extra-pair copulations using standard field techniques.

ACKNOWLEDGMENTS

We thank C. Daniel for helping with the field work, the Quebec Provincial Police for assisting with some transportation problems, J. Mountjoy for identifying the local avifauna, the Royal Ontario Museum for allowing us to use their collection, NSERC and FCAR for financial support, and W. Blanckenhorn, M. Bryant, L.-A. Giraldeau, J. Grant, K. Johnson, J. Mountjoy, S. Perreault and K. Yasukawa for their comments on the manuscript.

REFERENCES

- Bailey, R. C. & Byrnes, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst. Zool.*, **39**, 124–130.
- Bart, J. & Tornes, A. 1989. Importance of monogamous male birds in determining reproductive success. *Behav. Ecol. Sociobiol.*, **24**, 109–116.
- Bisazza, A. & Marconato, A. 1988. Female mate choice, male–male competition and parental care in the river bullhead, *Cottus gobio* L. (Pisces, Cottidae). *Anim. Behav.*, **36**, 1352–1360.
- Burley, N., Krantzberg, G. & Radman, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. *Anim. Behav.*, **30**, 444–455.
- Côte, I. M. & Hunte, W. 1989. Male and female mate choice in the redlip blenny: why bigger is better. *Anim. Behav.*, **38**, 78–88.
- Downhower, J. F. & Brown, L. 1980. Mate preferences of female mottled sculpins, *Cottus bairdi*. *Anim. Behav.*, **28**, 728–734.
- Duckworth, J. W. 1992. Effects of mate removal on the behaviour and reproductive success of reed warblers *Acrocephalus scirpaceus*. *Ibis*, **134**, 164–170.
- Eckert, C. G. & Weatherhead, P. J. 1987. Male characteristics, parental quality and the study of mate choice in the red-winged blackbird (*Agelaius phoeniceus*). *Behav. Ecol. Sociobiol.*, **20**, 35–42.
- Gori, D. F. 1988. Adjustment of parental investment with mate quality by male yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). *Auk*, **105**, 672–680.
- Gowaty, P. A. 1983. Male parental care and apparent monogamy among eastern bluebirds (*Sialia sialis*). *Am. Nat.*, **121**, 149–157.
- Grant, J. W. A. & Colgan, P. W. 1983. Reproductive success and mate choice in the johnny darter. *Can. J. Zool.*, **61**, 437–446.
- Greenlaw, J. S. & Post, W. 1985. Evolution of monogamy in seaside sparrows, *Ammodramus maritimus*: test of hypotheses. *Anim. Behav.*, **33**, 373–383.
- Greig-Smith, P. W. 1982. Song-rates and parental care by individual male stonechats (*Saxicola torquata*). *Anim. Behav.*, **30**, 245–252.
- Hannon, S. J. 1984. Factors limiting polygyny in the willow ptarmigan. *Anim. Behav.*, **32**, 153–161.
- Hatchwell, B. J. & Davies, N. B. 1990. Provisioning of nestlings by dunlocks, *Prunella modularis*, in pairs and trios: compensation reactions by males and females. *Behav. Ecol. Sociobiol.*, **27**, 199–209.
- Hipes, D. L. & Hepp, G. R. 1993. Effect of mate removal on nest success of female wood ducks. *Condor*, **95**, 220–222.
- Hochachka, W. & Smith, J. N. M. 1991. Determinants and consequences of nestling condition in song sparrows. *J. Anim. Ecol.*, **60**, 995–1008.
- Husby, M. & Slagsvold, T. 1992. Post-fledging behaviour and survival in male and female magpies *Pica pica*. *Ornis Scand.*, **23**, 483–490.
- Johnson, L. S., Merkle, M. S. & Kermott, L. H. 1992. Experimental evidence for importance of male parental care in monogamous house wrens. *Auk*, **109**, 662–664.
- Keenleyside, M. H. A., Rangle, R. W. & Koppers, B. U. 1985. Female mate choice and male parental defense behaviour in the cichlid fish *Cichlasoma nigrofasciatum*. *Can. J. Zool.*, **63**, 2489–2493.
- Knapp, R. A. & Kovach, J. T. 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behav. Ecol.*, **2**, 295–300.
- Lott, D. F. 1991. *Intraspecific Variation in the Social Systems of Wild Vertebrates*. Cambridge: Cambridge University Press.
- Lyon, B. E., Montgomerie, R. D. & Hamilton, L. D. 1987. Male parental care and monogamy in snow buntings. *Behav. Ecol. Sociobiol.*, **20**, 377–382.
- Martin, K. & Cooke, F. 1987. Bi-parental care in willow ptarmigan: a luxury? *Anim. Behav.*, **35**, 369–379.
- Martin, K., Chooch, F. G., Rockwell, R. F. & Cooke, F. 1985. Reproductive performance in lesser snow geese: are two parents essential? *Behav. Ecol. Sociobiol.*, **17**, 257–263.
- Niebuhr, V. 1981. An investigation of courtship feeding in herring gulls *Larus argentatus*. *Ibis*, **123**, 218–223.

- Nisbet, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in common terns. *Nature, Lond.*, **241**, 141-142.
- Norris, K. J. 1990a. Female choice and the evolution of conspicuous coloration of monogamous great tits. *Behav. Ecol. Sociobiol.*, **26**, 129-138.
- Norris, K. J. 1990b. Female choice and the quality of parental care in the great tit *Parus major*. *Behav. Ecol. Sociobiol.*, **27**, 275-281.
- Patterson, I. J., Dunnet, G. M. & Goodbody, S. R. 1988. Body weight and juvenile mortality in rooks *Corvus frugilegus*. *J. Anim. Ecol.*, **57**, 1041-1052.
- Perrins, C. M. 1965. Population fluctuations and clutch size in the great tit, *Parus major* L. *J. Anim. Ecol.*, **34**, 601-647.
- Perrins, C. M. 1988. Survival of young great tits: relationships with weight. *Acta Int. ornithol. Congr.*, **XIX**, 892-899.
- Sasvári, L. 1986. Reproductive effort of widowed birds. *J. Anim. Ecol.*, **55**, 553-564.
- Sasvári, L. 1990. Feeding response of mated and widowed bird parents to fledglings: an experimental study. *Ornis Scand.*, **21**, 287-292.
- Searcy, W. A. 1979. Female choice of mates: a general model for birds and its application to red-winged blackbirds (*Agelaius phoeniceus*). *Am. Nat.*, **114**, 77-100.
- Searcy, W. A. & Yasukawa, K. 1981. Does the 'sexy son' hypothesis apply to mate choice in red-winged blackbirds? *Am. Nat.*, **117**, 343-348.
- Smith, H. G., Källander, H., Fontell, K. & Ljungström, M. 1988. Feeding frequency and parental division of labour in the double-brooded great tit *Parus major*. *Behav. Ecol. Sociobiol.*, **22**, 447-453.
- Smith, J. N. M., Yom-Tov, Y. & Moses, R. 1982. Polygyny, male parental care, and sex ratio in song sparrows: an experimental study. *Auk*, **99**, 555-564.
- Studd, M. V. & Robertson, R. J. 1985a. Sexual selection and variation in reproductive strategy in yellow warblers (*Dendroica petechia*). *Behav. Ecol. Sociobiol.*, **17**, 101-109.
- Studd, M. V. & Robertson, R. J. 1985b. Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). *Anim. Behav.*, **33**, 1102-1113.
- Studd, M. V. & Robertson, R. J. 1988. Differential allocation of reproductive effort to territorial establishment and maintenance by male yellow warblers (*Dendroica petechia*). *Behav. Ecol. Sociobiol.*, **23**, 199-210.
- Tinbergen, J. M. & Boerlijst, C. M. 1990. Nestling weight and survival in individual great tits (*Parus major*). *J. Anim. Ecol.*, **59**, 1113-1127.
- Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding savannah sparrows. *Auk*, **96**, 391-401.
- Whillans, K. V. & Falls, J. B. 1990. Effects of male removal on parental care of female white-throated sparrows, *Zonotrichia albicollis*. *Anim. Behav.*, **39**, 869-878.
- Whittingham, L. A. 1989. An experimental study of paternal behavior in red-winged blackbirds. *Behav. Ecol. Sociobiol.*, **25**, 73-80.
- 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.
- Wolf, L., Ketterson, E. D. & Nolan, V., Jr. 1991. Female condition and delayed benefits to males that provide parental care: a removal study. *Auk*, **108**, 371-380.
- Wright, J. & Cuthill, I. 1989. Manipulation of sex differences in parental care. *Behav. Ecol. Sociobiol.*, **25**, 171-181.
- Wright, J. & Cuthill, I. 1990. Biparental care: short-term manipulation of partner contribution and brood size in the starling, *Sturnus vulgaris*. *Behav. Ecol.*, **1**, 116-124.