

Intensity of nest defence is related to offspring sex ratio in the great tit *Parus major*

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Nest-defence behaviour of passerines is a form of parental investment. Parents are selected, therefore, to vary the intensity of their nest defence with respect to the value of their offspring. Great tit, *Parus major*, males were tested for their defence response to both a nest predator and playback of a great tit chick distress call. The results from the two trials were similar; males gave more alarm calls and made more perch changes if they had larger broods and if they had a greater proportion of sons in their brood. This is the first evidence for a relationship between nest-defence intensity and offspring sex ratio. Paternal quality, size, age and condition, lay date and chick condition did not significantly influence any of the measured nest-defence parameters.

Keywords: nest defence; sex ratio; great tit, *Parus major*

1. INTRODUCTION

Nest predation is the single most important variable affecting reproductive success in many passerine species (Ricklefs 1969; Martin & Roper 1988; McCleery & Perrins 1991). The reproductive success of an individual parent depends on it producing offspring and protecting them until independence, as well as surviving to reproduce during the rest of its lifetime (Wiklund 1995, 1996). An individual must, therefore, choose the appropriate responses to predators posing a threat to its offspring, itself or both.

The most consistent pattern found in studies of avian nest defence has been an increase in the level of the parental response to predators from clutch initiation to fledging (e.g. Biermann & Robertson 1981; Regelman & Curio 1983; Montgomerie & Weatherhead 1988; Wiklund 1990a). This supports the prediction from parental investment theory (Trivers 1972) that parents should risk more in defence of young that are more valuable to them. The intensity of nest defence is also expected to be positively correlated with brood size because the benefits of deterring a predator will increase with offspring number (Williams 1966; Wiklund 1990b). Parents are also selected to vary their level of investment between sons and daughters, depending on the fitness costs and benefits accruing through each of the offspring sexes. In sexually dimorphic species, such as the great tit, *Parus major* (Perrins 1963), the larger sex (males in this case) may cost more to produce than the smaller sex. Fisher (1958) suggested that under such conditions the sex ratio should be biased towards individuals of the smaller sex. Hence, at the time of fledging, offspring of the more expensive sex represent a greater individual reproductive value to the parents than offspring of the cheaper sex. Male-biased broods might, therefore, be defended more vigorously than broods containing more females.

Our study aimed to examine the effects of sex ratio and brood size on the nest-defence behaviour of male great

tits. Defence behaviour of the great tit is exhibited for offspring protection, not only self-preservation. Adult great tits defend only at their own nest and not at the nests of their neighbours, where they remain silent (Shalter 1979).

2. METHODS

(a) *Sampling*

We studied a nest-box-breeding population of great tits in Marley Wood, Oxfordshire. All nest-boxes were monitored regularly throughout the 1998 breeding season to determine clutch size and lay date of each egg. Breeding males were trapped at the nest, using automatic spring-powered traps, on day 7 (day 1 was the day of hatching) or later. The age of each male was determined from plumage (Svensson 1992) and in the analysis birds were classified as one year old or older. The following biometrics were determined for all captured males: (i) tarsus length (from the nuchal notch to the furthest extension of the leg, with the foot held at a right angle, in millimetres); (ii) mass (to 0.1 g on a Pesola balance); and (iii) breast-stripe width across the sternum (in millimetres).

Nests were inspected every three days following hatching of the first egg. All chicks were weighed, measured and ringed on day 15, when a blood sample was also obtained by brachial venipuncture (under licence from English Nature and the Home Office). Blood samples were kept cool in the field and then stored in the laboratory at -20°C until DNA extraction.

(b) *Molecular sexing*

Since the sex of great tit nestlings cannot reliably be determined from morphological characteristics, a DNA test for sex was used (see Radford & Blakey (2000) for details of protocol).

(c) *Nest-defence trials*

We examined the response of 23 male great tits to a model great spotted woodpecker, *Dendrocopos major*, which is a natural predator of great tit nests but not of adults (Perrins 1979). The stuffed specimen was attached to the front of the nest-box, in an upright posture with the bill horizontal and the wings folded over the tail, and a taped recording of a great spotted woodpecker call was started below the nest-box. The observer retreated 5 m to avoid being perceived as a threat to the nest

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Table 1. *Effect of brood size, offspring sex ratio and male breast-stripe size on male great tit nest-defence behaviour*

(*F*-values from a general linear model, using adjusted sums-of-squares. Trial 1: results from GSW trial on day 16 of the nestling period; trial 2: results from CDC trial on day 17 of nestling period. Superscripts: n.s., not significant; * < 0.05, ** < 0.01, *** < 0.005.)

predictor variable	trial	defence measure				
		latency (s)	no. alarm calls	no. perch changes	mean distance (m)	closest distance (m)
brood size	1	5.04*	6.17*	7.32*	1.15 ^{n.s.}	0.33 ^{n.s.}
	2	5.18*	15.27***	25.20***	2.01 ^{n.s.}	0.80 ^{n.s.}
sex ratio	1	3.17 ^{n.s.}	10.65***	8.79**	0.16 ^{n.s.}	0.06 ^{n.s.}
	2	1.98 ^{n.s.}	9.33**	9.50**	0.06 ^{n.s.}	0.00 ^{n.s.}
male stripe	1	1.15 ^{n.s.}	0.20 ^{n.s.}	1.97 ^{n.s.}	0.01 ^{n.s.}	0.23 ^{n.s.}
	2	0.05 ^{n.s.}	0.09 ^{n.s.}	0.03 ^{n.s.}	0.25 ^{n.s.}	0.38 ^{n.s.}

and the attending adults. After 30 s the response of the defending male was recorded for a 3-min trial; data collected included latency of response, number of alarm calls, number of perch changes, and a continuous visual determination of distance from the nest. Each nest was tested once, between 09.00 and 11.00 on day 16 of the nestling period. Trials took place only when the weather was not inclement.

A great tit chick distress call was recorded on day 17 of the nestling period. We examined the defence response of the same 23 male great tits to this recorded call and to the presence of an observer (who might be regarded as a threat to both nestlings and adults). We assumed that the intensity of the response would reflect the response to any potential predator. Previous studies have shown a significant correlation between the response of parent birds to a human intruder and model predators (Eckert & Weatherhead 1987), and that parent birds which respond more vigorously to humans suffer lower nest predation (Andersson *et al.* 1980; Greig-Smith 1980). The observer sat beneath the nest-box with the tape recorder. As in the model predator experiment described above, 30 s were allowed to elapse before the 3-min trial was begun. The same nest-defence parameters were collected as before. Each nest was tested once, between 09.00 and 11.00 on day 17.

One of us (J.K.B.) measured and ringed the chicks and the other (A.N.R.) completed all the observations in both sets of field trials. Since the nestlings were only sexed following the completion of the field experiments, nest-defence responses were recorded blind to knowledge of brood size and sex ratio.

(d) *Statistical analysis*

All analyses of nest-defence parameters were performed using MINITAB v.12 (Minitab Inc. 1998). The number of alarm calls and perch changes were Poisson distributed, and were therefore square-root transformed. If a male returned during the trial, the actual number of alarm calls and perch changes recorded was increased proportionally, to ensure a standard measure between males. Sex-ratio data were proportional and were therefore arcsine square-root transformed before inclusion in parametric models. Both chick and adult condition were the residuals from regression of body weight on tarsus length. Brood condition was taken as the average condition of all chicks in the brood. For each measure of nest defence, a general linear model was performed, which initially included each of the tested parameters. Non-significant variables were sequentially removed to create a minimal adequate model. The remaining variables were then tested in a sequential sum-of-squares model.

Analyses of brood sex ratios were performed using GLIM v.4 (NAG 1993). The null model was specified with the number of males in a brood as the dependent variable and brood size as the binomial denominator, using binomial error distribution and a logit link. The backward-deletion procedure for model simplification was followed (Crawley 1993).

3. RESULTS

There were strong positive relationships between the number of alarm calls and the number of perch changes ($n = 23$, $r > 0.72$, $p < 0.01$), and between the mean and closest approach distances ($n = 23$, $r > 0.68$, $p < 0.01$). None of the other correlation coefficients differed significantly from zero ($n = 23$, $r < 0.25$, n.s.).

Both the number of alarm calls (table 1, figure 1a) and the number of perch changes (table 1) made by the defending male were significantly positively correlated with offspring sex ratio in both the great spotted woodpecker (GSW) trial and the chick distress call (CDC) trial. Brood size significantly positively predicted the number of alarm calls given by the defending male in both trials (table 1, figure 1b) and the number of perch changes made in both trials (table 1). The latency of response of the returning male was also significantly predicted by brood size in both trials (table 1). In both trials, the interaction term between brood size and sex ratio was found to significantly predict both the number of alarm calls (table 2) and perch changes (GSW trial: $F_{1,22} = 14.96$, $p < 0.005$; CDC trial: $F_{1,22} = 9.74$, $p < 0.01$). There was no significant relationship between brood size and offspring sex ratio ($F_{1,22} = 2.08$, $p = 0.164$).

Male breast-stripe width did not significantly influence any nest-defence parameter in either trial (table 1). Likewise, there was no significant effect of male age, condition or tarsus length, lay date or chick condition on any of the five defence measures in the GSW trial ($F_{1,22}$ range: 0.02–2.42, n.s.) or the CDC trial ($F_{1,22}$ range: 0.01–4.22, n.s.).

Within our study sample, 94 out of 185 hatched chicks were male. The cohort sex ratio did not differ significantly from unity (goodness-of-fit against the Mendelian expectation of equal numbers of both sexes: $G_1 = 0.049$, $p > 0.80$). The proportion of sons did not vary with lay date ($\Delta D_1 = 2.002$, $p > 0.10$), male breast-stripe width ($\Delta D_1 = 1.567$, $p > 0.60$), male condition ($\Delta D_1 = 0.101$, $p > 0.70$), or male tarsus length ($\Delta D_1 = 0.115$, $p > 0.70$).

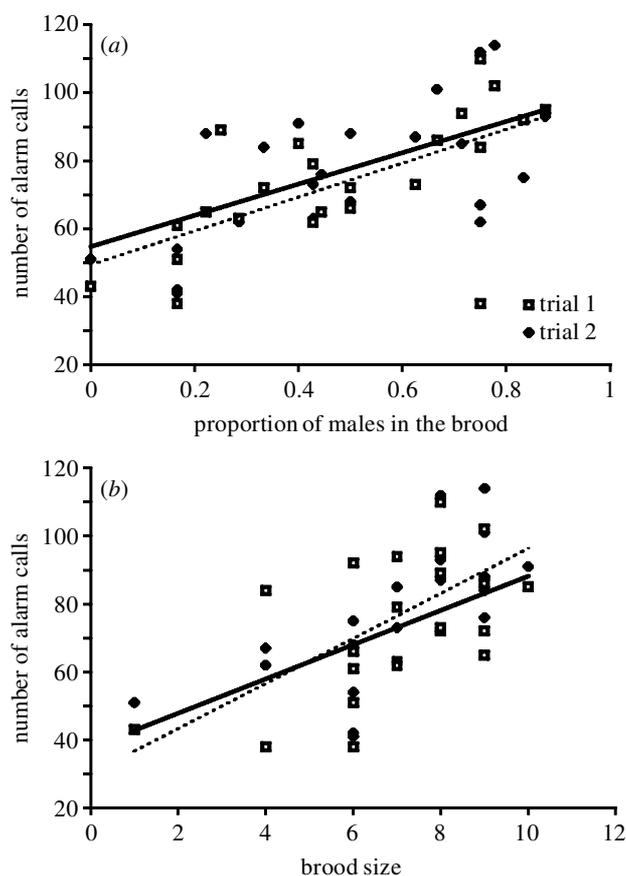


Figure 1. The number of alarm calls given by the defending male great tit in relation to (a) offspring sex ratio, and (b) brood size, in response to a GSW (trial 1) and a great tit CDC (trial 2). Best-fit lines are shown for trial 1 (dashed) and trial 2 (solid).

Table 2. Minimal adequate general linear model, using sequential sums-of-squares, for the number of alarm calls given by defending male great tits in (a) GSW trial and (b) CDC trial

(d.f. = 1, for all terms.)

source	F-ratio	coefficient	<i>p</i>
(a)			
brood size	14.97	-0.0073	0.001
sex ratio	12.09	-0.179	0.003
interaction	4.70	0.4076	0.049
(b)			
brood size	37.43	0.0119	0.001
sex ratio	13.64	-1.193	0.002
interaction	10.26	0.5224	0.005

4. DISCUSSION

The results show a significant influence of offspring sex ratio and brood size on the nest-defence behaviour of male great tits. Both the number of alarm calls and the number of perch changes (which are strongly correlated) increased significantly with the proportion of males in the brood as well as with brood size. As brood size was not correlated with sex ratio, broods with a greater proportion of male chicks were defended more vigorously than those of the same size containing more females. The

significant interaction term suggests that the effect of these two variables is additive.

Since the population sex ratio did not differ significantly from unity, the sexual size dimorphism of nestling great tits is unlikely to be sufficiently large to have a direct influence on defence intensity. There are two other potential explanations for the relationship between offspring sex ratio and nest-defence intensity. The first is that pairs are able to adjust their brood sex ratios (Gowaty 1991). For example, females mated to 'good-quality' males, who are more vigorous nest defenders, might lay male-biased clutches if their male offspring benefit in some way. Possible benefits, from inherited 'good' genes, include an increased likelihood of sons obtaining extra-pair copulations or of obtaining and defending a good territory. This explanation may be unlikely since there was no evidence of a skewed sex ratio within broods in relation to male condition, breast-stripe width, tarsus length, or lay date. Also, male breast-stripe size, which is considered an indicator of male quality (Norris 1993), did not significantly predict any measures of nest-defence intensity in this study. However, there may be another indicator of male quality used by females in mate choice.

As an alternative to the above, fathers may assess the proportion of males in a brood. Little is known about the proximate cues used by parents to discriminate between offspring sex, but the differential allocation of parental care towards offspring of different sexes does occur (e.g. Stamps *et al.* 1987; Gowaty & Droge 1991; Nishiumi *et al.* 1996). Adults may assess the amount of provisioning given relative to the brood size, and thus derive an idea of brood sex ratio. Other possibilities are that young males and females start begging at different ages or beg at different rates (Teather 1992), or that the begging calls of the sexes differ acoustically, as occurs in young zebra finches, *Taeniopygia guttata* (Balda, cited in Stamps *et al.* 1987). A recent study by Lessells *et al.* (1998) found no significant effect of experimentally manipulated offspring sex ratio on the nest-defence intensity of male great tits. However, that study only analysed the closest approach distance of the defending male. Similarly, our study also found no significant effect of this measure. This is not unexpected, because the closest approach distances of defending adults in a woodland-nesting species depend on the topography surrounding the nest site.

An increase in nest-defence intensity with increased brood size has been found in a number of other studies (Robertson & Biermann 1979; Greig-Smith 1980; East 1981; Knight & Temple 1986; Wiklund 1990b), although previous work on great tits has produced equivocal results (Regelmann & Curio 1983; Curio & Regelmann 1987). In theory, the larger the brood, the greater the proportion of genes contributed to the lifetime reproductive output of the parent. This assumes that birds know their average clutch size, and hence value a current brood with reference to it. There is evidence that clutch size is, to some degree, inherited (Noordwijk *et al.* 1980) and that short-term modifications of clutch size induced by environmental conditions are also heritable (Perrins & Birkhead 1983). Brood defence should, therefore, be geared to brood size relative to deviations from individual expected values, not to the population average. The best test of the effect

of brood size on defence intensity would be to examine the parent's ability to adapt the defence level to experimentally manipulated brood size (e.g. Wiklund 1990b).

In this study we have assumed that risk-taking behaviour, such as defence against nest predators, may be explained in terms of the reproductive value of offspring. Dale *et al.* (1996), however, point out that there are two alternative explanations: the parent's own vulnerability to predation, and the harm that offspring would suffer if they were left alone. Most likely, all three explanations are relevant to any species, but their relative importance will vary according to a number of variables, including breeding condition, type of predator and relative value of current versus future reproduction. The experimental design may also influence which benefit is detected. Future work should, therefore, take this into account as well as using experimental manipulations in an effort to distinguish between the potential competing hypotheses suggested by our results.

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REFERENCES

- Andersson, M., Wiklund, C. G. & Rungren, H. 1980 Parental defence of offspring: a model and an example. *Anim. Behav.* **28**, 536–542.
- Biermann, G. C. & Robertson, R. J. 1981 An increase in parental investment during the breeding season. *Anim. Behav.* **29**, 487–489.
- Crawley, M. J. 1993 *GLIM for ecologists*. Oxford, UK: Blackwell Scientific Publications.
- Curio, E. & Regelmann, K. 1987 Brood defence in the great tit: the influence of age, number and quality of young. *Ardea* **75**, 35–42.
- Dale, S., Gustavsen, R. & Slagsvold, T. 1996 Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behav. Ecol. Sociobiol.* **39**, 31–42.
- East, M. 1981 Alarm calling and parental investment in the robin *Erithacus rubecula*. *Ibis* **123**, 222–230.
- 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.
- Fisher, R. A. 1958 *The genetical theory of natural selection*. New York: Dover Publications.
- Gowaty, P. A. 1991 Facultative manipulation of sex ratios in birds. In *Current ornithology*, vol. 8 (ed. D. M. Power), pp. 141–171. New York: Plenum Press.
- Gowaty, P. A. & Droge, D. L. 1991 Sex ratio conflict and the evolution of sex-biased provisioning in birds. In *Acta XX Congress on International Ornithology* (ed. B. D. Bell), pp. 932–945. Wellington, NZ: New Zealand Ornithological Congress Trust Board.
- Greig-Smith, P. W. 1980 Parental investment in nest defence by stonechats (*Saxicola torquata*). *Anim. Behav.* **28**, 604–619.
- Knight, R. L. & Temple, S. A. 1986 Nest defence in the American goldfinch. *Anim. Behav.* **34**, 887–897.
- Lessells, C. M., Oddie, K. R. & Mateman, A. C. 1998 Parental behaviour is unrelated to experimentally manipulated great tit brood sex ratio. *Anim. Behav.* **56**, 385–393.
- McCleery, R. H. & Perrins, C. M. 1991 Effects of predation on the numbers of great tits *Parus major*. In *Bird population studies, relevance to conservation and management* (ed. C. M. Perrins, J. D. Lebreton & G. J. M. Hirons), pp. 129–147. Oxford University Press.
- Martin, T. E. & Roper, J. J. 1988 Nest predation and nest site selection of a western population of the hermit thrush. *Condor* **90**, 51–57.
- Minitab, Inc. 1998 *MINITAB reference manual for Windows*. Release 12. Pennsylvania: State College.
- Montgomerie, R. D. & Weatherhead, P. J. 1988 Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**, 167–187.
- NAG 1993 *Generalised linear interactive modelling*. Oxford, UK: The Numerical Algorithms Group Ltd.
- Nishiumi, I., Yamagishi, S., Maekawa, H. & Shimoda, C. 1996 Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. *Behav. Ecol. Sociobiol.* **39**, 211–217.
- Noordwijk, A. J. van, Balen, J. H. van & Scharloo, W. 1980 Heritability of ecologically important traits in the great tit. *Ardea* **68**, 193–203.
- Norris, K. 1993 Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* **362**, 537–539.
- Perrins, C. M. 1963 Some factors influencing brood size and populations in great tits. DPhil thesis, University of Oxford, UK.
- Perrins, C. M. 1979 *British tits*. London: Collins.
- Perrins, C. M. & Birkhead, T. R. 1983 *Avian ecology*. New York: Chapman & Hall.
- Radford, A. N. & Blakey, J. K. 2000 Is variation in brood sex ratios adaptive in the great tit (*Parus major*)? *Behav. Ecol.* (In the press.)
- Regelmann, K. & Curio, E. 1983 Determinants of brood defence in the great tit *Parus major*. *Behav. Ecol. Sociobiol.* **13**, 131–145.
- Ricklefs, R. E. 1969 An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* **9**, 1–48.
- Robertson, R. J. & Biermann, G. C. 1979 Parental investment strategies determined by expected benefits. *Z. Tierpsychol.* **50**, 124–128.
- Shalter, M. D. 1979 Responses of nestling passerines to alarm calls. *Ibis* **121**, 362–368.
- Stamps, J. A., Clark, A., Kus, B. & Arrowood, P. 1987 The effects of parent and offspring gender on food allocation in budgerigars. *Behaviour* **101**, 177–199.
- Svensson, L. 1992 *Identification guide to European passerines*. Stockholm, Sweden: Bonnier.
- Teather, K. L. 1992 An experimental study of competition for food between male and female nestlings of the red-winged blackbird. *Behav. Ecol. Sociobiol.* **31**, 81–87.
- 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.
- Wiklund, C. G. 1990a The adaptive significance of nest defence by merlin, *Falco columbarius*, males. *Anim. Behav.* **40**, 244–253.
- Wiklund, C. G. 1990b Offspring protection by merlin *Falco columbarius* females; the importance of brood size and expected offspring survival for defense of young. *Behav. Ecol. Sociobiol.* **26**, 217–223.
- Wiklund, C. G. 1995 Nest predation and life-span: components of variance in LRS among merlin females. *Ecology* **76**, 1994–1996.
- Wiklund, C. G. 1996 Breeding lifespan and nest predation determine lifetime production of fledglings by male merlins *Falco columbarius*. *Proc. R. Soc. Lond.* **B263**, 723–728.
- Williams, G. C. 1966 Natural selection, costs of reproduction and a refinement of Lack's principle. *Am. Nat.* **100**, 687–690.