Petrak, M. L. [ed.]. 1982. Diseases of cage and aviary birds. Lea & Febiger, Philadelphia.

Pevzner, I., A. Nordskog, and M. L. Kaeberle. 1975. Immune response and the B blood group locus in chickens. Genetics 80:753–759.

Robinson, W. L., and E. G. Bolen. 1989. Wildlife ecology and management. 2nd ed. Macmillan, New York.

SAS Institute. 1985. SAS user's guide: statistics version 5th ed. SAS Institute, Inc., Cary, NC.

Sheldon, B. C. 1993. Sexually transmitted disease in birds: occurrence and evolutionary significance. Phil. Trans. R. Soc. Lond. B 339:491–497.

Stern, N. J., R. J. Meinersmann, N. A. Cox, J. S. Bailey, and L. C. Blankenship. 1990. Influence of host lineage on cecal colonization by *Campylobacter jejuni* in chickens. Avian Diseases 34:602–606.

Yogasundram, K., S. M. Shane, and K. S. Harrington. 1989. Prevalence of *Campylobacter jejuni* in selected domestic and wild birds in Louisiana. Avian Diseases 33:664–667.

Zuk, M. 1991. The role of parasites in sexual selection: current evidence and future directions. Adv. Study Behav. 21:39–68.

The Condor 98:172–175

THE EFFECT OF MALE PRESENCE ON NESTLING GROWTH AND FLUCTUATING ASYMMETRY IN THE BLUE TIT[1]

Mats Björklund
Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

Key words: Blue tit; growth; fluctuating asymmetry; brood reduction; paternal care.

Generally, lack of paternal effort in temperate passerine bird species manifests itself in terms of either fewer fledged young, and/or lighter young (Björklund and Westman 1986, Sasvári 1986, Kempenaers 1994). However, the effect of male absence on the growth of young is poorly known (Sasvári 1986). Recent interests in fluctuating asymmetry (defined as random fluctuations from perfect symmetry of bilateral traits) have suggested that developmental stress caused by inadequate nutrition, for example caused by limited paternal care, can lead to an increased level of asymmetry (Palmer and Strobeck 1986, Watson and Thornhill 1994). A high level of asymmetry can be an indicator of poor feeding conditions during growth or the inability of certain individuals to cope with poor growing conditions, and thus serve as a cue for genetically-based mate choice (Møller and Pomiankowski 1993, Watson and Thornhill 1994). This suggests that chicks without paternal care might suffer not only in terms of being lighter at fledging but also by a higher degree of asymmetry, leading to reduced reproductive success.

In this paper I will analyse the effect of male absence on a number of breeding parameters in the Blue Tit (*Parus caeruleus*). In this species male paternal effort is extensive and normally at the same rate as female effort (Perrins 1979). In particular I concentrate on clutch size and number of fledged young, as well as growth of individual chicks in biparentally attended as opposed to uniparentally attended nests. Furthermore, I examine the degree of fluctuating asymmetry in chicks in the two classes of nests with the expectation that asymmetry will be higher in broods without male attendance.

METHODS

The field work was carried out in the surroundings of Uppsala, central Sweden, during May and June 1994. All the Blue Tit pairs were found breeding in luxuriant deciduous forests. Nest boxes were checked regularly and the date of first egg, clutch size and the day of hatching were recorded. At two days of age, one young in each nest was randomly picked and marked. This chick was then measured at 2, 5, 8, 11 and 14 days of age. At age 14 days, all young in the nest were counted and weighed. I measured wing length, tarsus length, tail length, bill length, skull length and body mass. However, since all these traits are heavily intercorrelated (Björklund, unpubl.) only tarsus, wing and mass measures will be used in the present analysis. Tarsus length was measured to the nearest 0.1 mm, wing length to the nearest 1.0 mm, and mass to the nearest 0.5 g. To estimate fluctuating asymmetry (FA) wing length was measured on both sides from day 8 and after (i.e., when feathers start to grow), since it is known that growth of feathers is condition dependent (e.g., Grubb 1989). To be able to separate measurement error from estimates of FA each chick was measured twice (see below). When chicks were eight days or older, adults were captured.

Normally, when nest boxes were opened, the male behaved very aggressively especially when young approached fledging (14 days). However, at some boxes

---

[1] Received 26 June 1995. Accepted 30 August 1995.

TABLE 1. Breeding parameters for Blue Tit broods with and without a male. Date of first egg and hatching date with April 1 as day 1. Figures in the table are means (SD), unless otherwise stated. The *P*-values refer to a one-way ANOVA except in the case of clutch size, first egg and hatching date, where a Mann-Whitney U-test was used. Wilks' Lambda refers to a MANOVA where the three traits were tested simultaneously for the two groups. *n*-values are 8 or 9 in the without male group, and between 43 and 55 in the with male group.

Trait and age	With male	Without male	*P*
Clutch size (median)	11	10	0.32
Fledglings	9.9 (2.55)	5.7 (2.42)	0.0004
First egg (median)	31	33	0.10
Hatching date (median)	55	58	0.10
Tarsus: 2 days (mm)	7.8 (1.03)	7.6 (0.56)	0.64
Wing (mm)	6.6 (0.73)	6.4 (0.52)	0.48
Mass (g)	2.2 (0.56)	2.2 (0.56)	0.25
		Wilks' lambda	0.39
Tarsus: 5 days (mm)	12.2 (1.35)	10.9 (1.00)	0.013
Wing (mm)	11.6 (2.06)	9.7 (1.00)	0.006
Mass (g)	5.0 (0.92)	4.0 (0.78)	0.004
		Wilks' lambda	0.034
Tarsus: 8 days (mm)	16.3 (1.01)	14.7 (1.08)	0.00005
Wing (mm)	22.6 (3.22)	18.1 (3.37)	0.0003
Mass (g)	8.1 (1.13)	6.8 (1.15)	0.002
		Wilks' lambda	0.001
Tarsus: 11 days (mm)	18.0 (1.27)	17.8 (0.68)	0.70
Wing (mm)	32.4 (4.12)	28.9 (2.52)	0.030
Mass (g)	10.2 (1.41)	9.7 (1.07)	0.41
		Wilks' lambda	0.14
Tarsus: 14 days (mm)	18.8 (0.70)	18.4 (0.48)	0.22
Wing (mm)	42.3 (4.01)	39.1 (2.54)	0.055
Mass (g)	11.0 (1.11)	10.8 (1.15)	0.64
		Wilks' lambda	0.18
Mean nestling mass (g)	11.0 (0.93)	10.3 (1.22)	0.10

no males were ever seen, nor trapped in the boxes. Since males were so conspicuous at most boxes, the absence of a male at the frequent measuring and capturing visits will be regarded as evidence for a complete absence of the male. Since males were *always* seen at the other boxes, but *never* at these boxes, the likelihood of a false scoring seems very low. The reason for this absence was not known.

All body-trait measurements were ln-transformed before analysis to decouple possible relations between means and variances. Traits were normally distributed at all ages (Shapiro-Wilks test). Analysis of differences between groups was made by a one-way ANOVA. However, since all traits were strongly intercorrelated, a MANOVA was also performed and the corresponding multivariate Wilks' Lambda values will be given (Morrison 1990). Other variables, like day of hatching, were analyzed by Mann-Whitney *U*-test, since they were not possible to transform to normality.

To analyze FA I used a mixed model two-way ANOVA, where individuals are treated as the random factor and the sides (left and right) as the fixed factor (Palmer and Strobeck 1986, Merilä and Björklund 1995). This procedure makes the error variance equal to the measurement error. The variance component corresponding to the interaction mean square equals the level of fluctuating asymmetry and can be estimated as s^2_{IxS} = FA = $(MS_{interaction} - MS_{error})/2$. This approach has the advantage of providing a measure of FA that is unbiased with regard to measurement error, and also gives the proportion of total variance that is accounted for by differences between individuals (estimated as $s^2_{IND} = (MS_{individuals} - MS_{error})/4$) and by FA. To test differences in FA between groups I used the different values of s^2_{IxS} for each group in an ordinary *F*-test using the approximate degrees of freedom given by Palmer (1994).

RESULTS

In nine cases (11%) of a total of 82 breeding pairs, the female was raising her brood with no apparent male contribution. There were no differences in time of first egg, time hatching, nor in clutch size (Table 1) between male-attended and uniparental nests. At age 2 days there were no differences in size of the chicks in the two groups of broods. However, at age 5 days and age 8 days, considerable differences were recorded between chicks in the two groups in all traits, whereas at ages 11 days and 14 days there were only differences in wing length. There was a significant difference in the number of fledged young between nests with and those without a recorded male presence. The mean nestling weight did not differ between the groups.

Significant FA was found at all age stages in the group with male attendance, but only at age 14 days in the

TABLE 2. Fluctuating asymmetry in nestling Blue Tits as estimated by a two-way mixed model ANOVA for each category (with or without male) at three age stages (8, 11, and 14 days). Columns represent mean squares (MS) for each effect, F-values, degrees of freedom, P-value, and percentage of total variation (%) that is accounted for by each effect.

	With male					Without male				
	MS	F	df	P	%	MS	F	df	P	%
8 days										
Individuals	40.75	354.32	50	<0.001	98.1	40.92	294.7	8	<0.001	98.3
sides	0.04	0.15	1	0.70	0.0	0.03	0.13	1	0.73	0.0
FA	0.29	2.56	50	<0.001	0.9	0.22	1.55	8	0.21	0.4
error	0.16		100		1.0	0.14		18		1.3
11 days										
Individuals	54.56	222.78	49	<0.001	97.4	27.64	126.35	7	<0.001	95.5
Sides	1.59	3.51	1	0.07	0.1	0.28	0.66	1	0.44	0.0
FA	0.45	1.85	49	0.005	0.7	0.42	1.94	7	0.13	1.4
error	0.24		98		1.8	0.22		16		3.1
14 days										
Individuals	54.38	141.72	43	<0.001	95.0	25.37	355.17	6	<0.001	96.3
Sides	0.56	0.53	1	0.47	0.0	0.000	0.0000	1	1.000	0.0
FA	1.04	2.71	43	<0.001	2.3	0.42	5.83	6	0.0032	2.6
error	0.38		86		2.7	0.071		14		1.1

group without male attendance (Table 2). Partitioning of variance components can thus, strictly speaking, only be made at this age for this group, but for comparison approximate values are given at all age stages. There was no significant difference in FA between the groups at age 14 days (the only age stage possible to test statistically; Table 2). If anything the amount of FA was higher in the group with male attendance than in the group without attendance ($F_{17,5} = 1.90$, $P = 0.25$). This could be a result of the low number of broods without males, thus reducing the power of the test. However, the ANOVA approach has been shown to be a highly powerful test even for relatively small sample sizes (Björklund and Merilä, unpubl.) which strengthens the conclusion that the differences between the groups are real.

There was no relation between growth rate and FA. In both groups at all periods, the correlation between growth in one time period (for example 8–11 days) and asymmetry (the unsigned difference between the sides) at the end of the period (11 days), was not significantly different from a zero expectation (correlations ranging from −0.21 to +0.21, $P > 0.1$ in both groups). The amount of FA at age 11 was not correlated with the amount of FA at age 14 days in either group.

DISCUSSION

The results show that the absence of a feeding male has the most pronounced effect on the chicks during the time of maximum growth between 5 and 8 days. Since the number of eggs in the brood did not differ between the groups, whereas the number of fledged young did, it is likely that the main period of brood reduction occurred between 5 and 8 days. This happened gradually over time such that at the early ages most young were still present, while during growth young were found dead in the nest box and broods became successively smaller. Unfortunately, no exact data were collected on the rate of brood reduction. After the number of young were reduced in the brood, the remaining chicks apparently grew faster than chicks in broods with male presence since there were no differences in mass at ages 11 and 14 days.

The uniparentally raised chicks did not have a higher degree of FA than the chicks with male attendance. Moreover, the proportion of total variation in wing length accounted for by FA was very low in all groups at all ages, in particular in relation to variation in absolute size among individuals. This suggests that the increased stress imposed on the chicks in the nests without a male did not manifest itself in terms of higher levels of FA but rather in terms of differences on size, at least up to age 14 days. The wings are about two-thirds of their adult length at age 14 days (Björklund, in press), but even if asymmetry will increase up to adult size, it is unlikely that the variance in wing length between left and right sides (= FA) will be even close to the variance in overall size among individuals. Since chicks without male parental efforts grew faster at the end of the period (see above) it may expected that this could manifest itself in terms of a correlation between growth rate and asymmetry, and that individuals having a certain asymmetry at one age will continue to have this asymmetry provided that individuals differ in their abilities to cope with stress. However, no such relationships were found. Growth rate and asymmetry were uncorrelated and the asymmetry at one age stage was not carried over to the next age stage. This suggests that differences in the size of the sides were merely accidents, or part of a natural growing scheme, rather than an indicator of differences in the abilities of individuals to cope with stress. Unequal growth rates of the sides in the tail have been demonstrated in the Paradise Whydah (Barnard 1994).

As this study exclusively deals with a single trait, overall effects on asymmetry including other unmeasured traits cannot be excluded (Watson and Thornhill 1994). However, as asymmetry in wing length has been shown to correlate to asymmetry in other characters (Møller 1994), there is no *a priori* reason to believe that while it is absent in wing length in Blue Tit nestlings it is prevalent in other characters.

I thank Juha Merilä and Staffan Ulfstrand for valuable comments. This work was funded by grants from the Swedish Natural Science Research Council.

LITERATURE CITED

BARNARD, P. 1994. Ornament and body size variation in some African passerine birds. Ph.D.diss., Department of Zoology, Uppsala University, Sweden.

BJÖRKLUND, M. 1995. Similarity of growth among Great Tits (*Parus major*) and Blue Tits (*P. caeruleus*). Biol. J. Linn. Soc. In press.

BJÖRKLUND, M., AND B. WESTMAN. 1986. Adaptive advantages of monogamy in the Great Tit (*Parus major*): an experimental test of the polygyny threshold model. Anim. Behav. 34:1436–1440.

GRUBB, J. C. JR. 1989. Ptilochronology: feather growth bars as indicators of nutritional stress. Auk 106: 314–320.

KEMPENAERS, B. 1994. Polygyny in the Blue Tit: unbalanced sex ratios and female aggression restrict mate choice. Anim. Behav. 47:943–957.

MERILÄ, J., AND M. BJÖRKLUND. 1995. Fluctuating asymmetry and measurement error. Syst. Biol. 44: 97–101.

MORRISON, D. F. 1990. Multivariate statistical methods. MacGraw-Hill, New York.

MØLLER, A. P. 1994. Sexual selection in the Barn Swallow (*Hirundo rustica*). IV. Patterns of fluctuating asymmetry and selection against asymmetry. Evolution 48:658–670.

MØLLER, A. P., AND A. POMIANKOWSKI. 1993. Fluctuating asymmetry and sexual selection. Genetics 89:267–279.

PALMER, A. R. 1994. Fluctuating asymmetry analyses: a primer, p. 335–364. *In* T. A. Markow [ed.], Developmental instability: its origins and evolutionary implications. Kluwer Academic Publisher, Netherlands.

PALMER, A. R., AND C. STROBECK. 1986. Fluctuating asymmetry: measurement, analysis, pattern. Ann. Rev. Ecol. Syst. 17:391–421.

PERRINS, C. 1979. British Tits. Collins, London.

SASVÁRI, L. 1986. Reproductive effort of widowed birds. J. Anim. Ecol. 55:553–564.

WATSON, P. J., AND R. THORNHILL. 1994. Fluctuating asymmetry and sexual selection. Trends Ecol. Evol. 9:21–25.