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Variation in offspring quality with cavity orientation in the great tit

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In birds, the quality of offspring immediately prior to fledging is an important determinant of survival and fecundity. Factors that alter offspring quality at fledging may thus be expected to become strong nest-site selection pressures. However, this fitness component is often overlooked when parental nest-site selection and breeding success are considered. Previous research has found that the frequency of nestbox occupations by great tits *Parus major* is lower for boxes facing south-southwest than for boxes facing other directions although, curiously, there is no corresponding difference in breeding success (mean number of young to fledge). In this study, we used measures of offspring quality to determine whether there was any association with nestbox orientation that might explain the apparent avoidance of boxes facing south-southwest. Offspring quality correlated with orientation using several condition-related biometrics: (1) weight, (2) wing length, and (3) tarsus length. Fluctuating asymmetry of a bilateral trait (tarsus length) also correlated with orientation. Further analysis using Generalised Linear Mixed Modelling revealed that chicks from boxes facing south-southwest were of significantly lower quality (lighter, smaller and more asymmetrical) than chicks from boxes facing other directions. Crucially, the orientation of nestbox-avoidance and the orientation associated with lowest offspring quality were the same (south-southwest). The correlation between nestbox avoidance patterns and offspring quality provides a potential evolutionary ecological explanation for the behavioural aversion of adults to nesting in boxes facing south-southwest. This highlights the importance of quantifying offspring quality, in addition to quantity, in studies of parental productivity and nest-site selection across taxa.

Running title
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Introduction

Materials and methods

Avian nest-site selection and reproductive success can be influenced by many interacting environmental variables (STAUFFER & BEST 1982). One variable that has been shown to be important in secondary cavity-nesting species (species that use natural or previously-excavated cavities) is cavity entrance orientation. This can influence reproductive behaviour in one of four different ways. Firstly, orientation may affect neither cavity selection nor breeding success, as in the case of the black-capped chickadee *Poecile atricapillus* (MENNILL & RATCLIFFE 2004). Secondly, orientation can influence both nest-site selection and breeding success. This has not been well-studied for secondary cavity-nesting birds, but has been observed for species such as cactus wrens *Camplylorhynchus brunneicapillus* that build domed nests with a side entrance hole (AUSTIN 1974). Thirdly, some species apparently select nest cavities independently of orientation, even though orientation subsequently affects their breeding success. For example, while eastern bluebirds *Sialia sialis* do not choose nest cavities according to the direction they face (PINKOWSKI 1976), individuals nesting in northeast-facing cavities fledge significantly more young than those using cavities facing west (DHONDT & PHILLIPS 2001). This may occur when nest-site selection is constrained by the availability of natural or previously-excavated cavities. In terms of evolutionary ecology, the most intriguing situation is the fourth: the counter-intuitive possibility that a species exhibits an orientation preference that is not, apparently, converted into increased reproductive success.

Previous research has revealed that the frequency of nestbox occupation by great tits *Parus major* L. correlates with orientation such that nestboxes facing south-southwest (the direction of prevailing wind and rain at the study site in the southwest region of the UK) are used less frequently than boxes facing other directions (GOODENOUGH et al. 2008; Fig 2a). The avoidance of these nestboxes is intriguing given that the same study found that the standard measures of breeding success (whether absolute: clutch size, number of young to hatch, number of young to fledge; or relative: proportion of eggs to hatch per clutch or young to fledge per brood) are no lower for boxes facing south-southwest than for those facing any other direction. Why should great tits exhibit an apparent directional avoidance in their nest-site selection when the use of boxes facing south-southwest does not appear to be detrimental to their breeding success?

We suggest that nesting in boxes facing south-southwest reduces offspring quality in a manner that is not detectable using the standard measures of breeding success described above (number of young to fledge etc.). The condition of offspring at fledging is an extremely important determinant of immediate post-fledging and first-winter survival (NAEF-DAENZER et al. 2001, MONRÓS et al. 2002), as well as reproductive success (PERRINS & MCCLEERY 2001). However, although offspring quality is intrinsically linked to the direct fitness of the parent birds, it is an often overlooked fitness component in studies of parental productivity and nest-site

selection, which tend to focus on number of offspring produced. This is despite the known trade-off between offspring quantity and offspring quality in several species, including the great tit (SMITH et al. 1989). If nesting in boxes facing south-southwest reduces offspring quality, this could explain the directional avoidance

84   exhibited by great tits during nestbox selection in a similar way to nest-site selection being influenced by offspring predation risk (FONTAINE & MARTIN 2006, SCHMIDT et al. 2006).

In this study, we examine the possibility that there is an association between offspring quality and nestbox orientation that might explain the apparent avoidance of boxes facing south-southwest by quantifying

88   offspring quality immediately prior to fledging and relating this to nestbox orientation. Unlike simply recording the number of young to fledge, measurements of offspring quality allow differentiation between the fledging of fit and healthy young (that have a relatively good chance of survival) and unfit young (that have a relatively poor chance of long-term post-fledging survival). This approach has been used previously in avian studies to

92   quantify the effect of ectoparasites on breeding success (e.g. RICHNER et al. 1993) and to determine the influence of habitat on breeding success (SÁNCHEZ et al. 2007).

96 *Study area*

This study was undertaken at Nagshead Nature Reserve (Gloucestershire, UK): the same site where the relationship between nestbox orientation and occupation was quantified for great tits using data from 1990-2004 (GOODENOUGH et al. 2008). In 2006, the Reserve managed 347 equally-sized nestboxes as part of the

100 longest-running nestbox scheme in the UK (CAMPBELL 1968). All nestboxes occupied by great tits in 2006 ($n = 49$) were included in the study.

Orientation of nestboxes

104 To determine the nestbox orientation, a line-of-sight compass (Silva Voyager 8040) was used to record the bearing (to the nearest 1º) of an imaginary line passing perpendicularly through the entrance hole from directly in front of the nestbox. The reading was then transformed to give the angle faced by that nestbox in degrees from magnetic north (RENDELL & ROBERTSON 1994). Measurements were taken at 10 m from the

108 nestbox to ensure an accuracy of ± 1º (verified trigonometrically and by pilot experimentation). During fieldwork, the nestbox was identified by a unique number, not by its orientation, to avoid experimental bias. Nestbox orientation followed a von Mises distribution (the circular equivalent of a normal distribution).

112 *Chick biometrics*

Biometrics of chicks ($n = 232$) from each nest ($n = 49$) were taken 15 days after hatching. This was as near to fledging as possible while mitigating the risk of disturbance-induced premature fledging. Usually, all chicks from a nestbox were removed to a holding bag for measurement (on two occasions, a weak runt was not

116 removed as the risk to the bird was considered too great). In about 10% of cases, it was not possible to measure all the birds within 15 min (the maximum time set by the recorder to reduce the risk of desertion). In these cases, unmeasured chicks were returned to the nestbox with their measured siblings to ensure the welfare of the birds (GAUNT & ORING 1999). Chicks were taken from the holding bag blindly to eliminate any

120 unintentional bias towards selecting bigger chicks for measurement. To reduce measurement error due to inter-recorder variation (NISBET et al. 1970), all biometrics were taken by the same trained recorder. Several biometrics (right wing length and the length of both tarsi) were taken together with weight (RISING & SOMERS 1989, GOSLER et al. 1998). Wing length was measured to the nearest 1 mm with a stopped ruler

124 using the flattened-straightened wing method: the distance from the carpel joint to the tip of the longest primary wing feather (SVENSSON 1992). Tarsus length was measured to the nearest 0.1 mm with dial calipers (DialMax D-2921/B/KWB) using the maximum tarsus method (GOSLER 2004). Weight was taken to 0.1 g

using a spring balance (Pesola, Switzerland), the bird being restrained in a clear polythene cone clipped to

128   the balance. Calibration of the balance was checked periodically.

As the growth and development of bilateral traits (e.g. wing or tarsus lengths) is controlled by the same gene, the lengths of such pairs of traits in an individual bird should theoretically be identical. However, perfect symmetry is rare and is reduced by environmental stress which adversely affects the precision with which

132   developmental homeostasis can be maintained (HOFFMANN & PARSONS 1991, ANDERSSON 1994, BJÖRKLUND 1996, MØLLER 1997). Thus the asymmetry of a bilateral trait provides an indication of the condition of that bird during the development of that trait, as asymmetry and condition are negatively related (PARSONS 1992). Here, the lengths of the left and right tarsi were taken as a measure of asymmetry. Tarsus length was

136   chosen rather than wing length as the trait could be measured on both sides of each bird using the same hand – in this case the right hand of the recorder (this is not possible if wing length is measured, since the right wing of the bird is measured with the right hand and the left wing with the left hand). In this way, the possibility that human handedness causes asymmetric measurement in biologically symmetrical individuals (HELM &

140   ALBRECHT 2000) was avoided. Tarsus asymmetry was appropriate for altricial chicks and is one of the few bilateral traits which is fully developed at 15-day post-hatching in the study species (GRIECO 2003). It is sensitive to small changes in condition (LENS et al. 1999) and is a strong predictor of asymmetry in other traits (LENS & VAN DONGEN 1999). The ability of nesting environment to affect tarsus growth (not asymmetry)

144   has previously been shown by ALATALO & LUNDBERG (1986). The length of both tarsi was recorded for all chicks measured in 47 of the 49 nests analysed (224 out of 232 chicks) (in two nests, the young were very small and handling time precluded the recording of this measurement).

148   *Determining offspring quality*

Offspring quality is often best determined using residuals created by regressing weight against a measure of size (RISING & SOMERS 1989, JAKOB et al. 1996) or against the first principal component resulting from principal components analysis of several measures of size (GOSLER et al. 1998). However, as chicks lose weight

152   immediately prior to fledging (GOSLER 1993) it was not considered appropriate to use residuals in this study of growing chicks as slight differences in age (for example due to hatching asynchrony) could bias the results, with older chicks being quantified as being in relatively poorer condition than younger ones. Instead, the actual biometrics were used, with birds in better condition expected to be larger and heavier than those in poorer

156   condition (GOSLER et al. 1998). All biometrics used in this study have been used previously to predict juvenile survival or recruitment (GARNETT 1981, TINBERGEN & BOERLIJST 1990, MONRÓS et al. 2002).

To consider offspring quality using asymmetry in tarsus length, the right tarsus length was subtracted from the left to give the difference for each representative chick (LENS & VAN DONGEN 1999). The sign of an index

160 value gave the direction of the difference (positive values were derived for birds with a longer left tarsus, negative ones for birds with a longer right tarsus). The absolute value of the difference was used in analyses. Tarsus asymmetry is known to be independent of tarsus length in studies of chicks of the same age and same species (TEATHER 1996).

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Repeatability of tarsus asymmetry measurements

The difference between tarsus length measurements of the same bird does not distinguish between true asymmetry and measurement error (SWADDLE et al. 1994, BJÖRKLUND 1996, HARPER 1999) and thus it was

168 important to quantify measurement error statistically. Repeat measurements (each tarsus measured twice) were taken for a small sub-sample of birds at the beginning of the study. Replicates were then analysed using a two-way mixed model ANOVA according to the method of BECHSHØFT et al. (2008) whereby the absolute difference between the lengths of the right and left tarsi were entered as the dependent variable,

172 with the side of bird (1 = right, 2 = left) entered as a fixed factor and individual entered as a random factor. The repeatability of measurements among individuals was calculated as the relationship between MS_{SI} (mean squares of the sides x individual interaction) and MS_{error} (mean squares of the variance of the repeated measurements [error]) according to the equation: repeatability = $(MS_{SI} - MS_{error}) / (MS_{SI} + MS_{error})$

176 (after BECHSHØFT et al. 2008). Once the repeatability of measurements had been established (see Results), asymmetry data were entered into analyses of nestbox orientation.

Statistical analysis

180 In most biometric studies, each bird can be considered independent of other birds in the sample. However, in this study, the chicks from one nestbox were not independent of one another, being close kin and sharing the same box. It was not, therefore, appropriate to enter the measurements from all individuals directly into an analysis, without first accounting for this replication. Two types of analysis were undertaken to determine

184 any associations between offspring quality and orientation, each accounting for replication in a different way. In the first analysis, mean within-brood offspring quality was calculated for each measure of condition (weight, wing length, tarsus length and absolute tarsus asymmetry) to give four estimates of average offspring within each brood. Use of the mean within-brood value for each parameter controlled for replication

188 since only one value was entered per nest. Each per-brood measure of offspring quality was correlated with orientation using circular-linear correlation (BATSCHELET 1981) using Oriana Circular Statistics for Windows

version 2.0 (Kovach Computing Services, Pentraeth, Wales). This circular statistical approach had the advantage of analysing data on a continuous scale that allowed for 0° and 360° being equivalent (MARDIA

192 and JUPP 2000). However, use of mean within-brood values (necessitated because of the difficulties of including random factors in circular analyses) did result in some data loss. In the second analysis, Generalised Linear Mixed Models (GLMMs) were used to analyse offspring quality in relation to orientation when the latter variable was entered categorically with four classes corresponding to the four compass

196 quarters. In these analyses, measurements for all 232 chicks were included and within-brood replication was accounted for by entering nestbox as a random factor. Four models were constructed using SPSS for Windows version 16, each using a different measure of offspring quality (see above). When models returned a significant result, Tukey honestly significant difference post-hoc testing was used to determine where

200 (i.e. between which categories) the difference lay. Bonferroni adjusted *P* values were used in both circular-linear correlations and GLMM models that used biometric data (size and weight) to allow for repeated tests being undertaken (RICE 1989). These values were reported in addition to the standard *P* values. Offspring quality in great tits can be related to brood size (PERRINS 1979, GOSLER 1993). Although analysis

204 by GOODENOUGH et al (2008) showed that there was no difference in brood size with orientation at the study site during the years 1990-2004 – indeed it was this fact that prompted the current study – it was necessary to verify that there was no correlation between brood size in the current dataset since this would have meant that ascribing any difference in offspring quality to orientation might have been compromised. This was

208 achieved using circular-linear correlation after brood size was log transformed (*ln* + 1). Lay date, an important predictor of fitness in birds (GARNETT 1981, CICHON & LINDÉN 1995), was also correlated with orientation, again using circular-linear correlation, after lay date was converted to an interval index whereby 1 = 1st April.

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Repeatability of tarsus asymmetry measurements

The repeatability of the tarsus measurements (*r*) was tested using a two-way mixed modal ANOVA as detailed

216 above. This gave a very high repeatability statistic of 0.90 (MS_{SI} = 2.13, MS_{error} = 0.11), suggesting that the

asymmetry measurements are highly reliable (BECHSHØFT et al. 2008) and that the results of subsequent

analyses can be used with confidence.

220 *Orientation, lay date and brood size*

There was no significant relationship between orientation and lay date (circular-linear correlation

r = 0.096, *n* = 49, *P* = 0.652) or between orientation and brood size (*r* = 0.166, *n* = 49, *P* = 0.283; calculation

performed on *ln* + 1 transformed count data).

224

Nestbox orientation and offspring quality

Nestbox orientation was found to influence offspring quality when the latter was determined by weight, size

(wing length and tarsus length) and bilateral asymmetry (the difference between the left and right tarsi). The

228 influence of orientation on offspring quality as determined by these four measures was calculated using

parametric circular-linear correlation on mean within-brood values (Fig. 1a-d), and using a GLMM with

orientation category (0-89°, 90-179°, 180-269° and 270-359°) as the dependent variable on the full dataset

with nest as a random factor (Table 1; Fig. 2b-e). The only non-significant result was the circular-linear

232 correlation between orientation and tarsus length (Fig. 1c), which became just non-significant (*P* = 0.051)

when Bonferroni adjustment was made to the *P* value.

In all GLMM analyses, post-hoc testing confirmed that the significant result in the overall model was caused

by differences between offspring quality from young in boxes facing south-southwest (category 3) compared

236 with each of the other three categories (categories 1, 2 and 4), which did not differ significantly amongst

themselves. As an example, Tukey honestly significant difference tests on the GLMM created when tarsus

asymmetry was used as the measure of offspring quality showed a significant difference between category

3 and the other categories (*P* < 0.001), but not between any other categories (*P* values ranged between

240 0.909 and 0.999).

Nestbox orientation and offspring quality

244 Offspring quality in great tits correlates with nestbox orientation: specifically, condition is significantly lower in chicks from boxes facing the south-west compass quarter compared with those from boxes facing any other direction. This reduction in offspring quality is a robust difference, having been quantified using several biometrics (two measures of size and weight) and tarsus asymmetry data, in both circular and GLMM analyses

248 with all results being significant with the exception of one at $P = 0.051$ following Bonferroni correction. Crucially, the directedness of the reduction in offspring quality is the same as the directedness of nestbox avoidance by adult birds during nestbox selection (Fig. 2; GOODENOUGH et al. 2008).

252 *Importance of offspring quality*

The condition of offspring at fledging is an extremely important determinant of immediate and first-winter survival (MOSS 1972, GARNETT 1981, TINBERGEN & BOERLIJST 1990, NAEF-DAENZER et al. 2001, MONRÓS et al. 2002), longevity (LINDSTRÖM 1999), and lifetime mass (PERRINS & MCCLEERY 2001). It is also linked to

256 recruitment into the breeding population (BOTH et al. 1999), mate-attractiveness for males (MØLLER 1992) and clutch size for females (HAYWOOD & PERRINS 1992). Birds that are in better condition at fledging (male or female) are also likely to have a higher dominance rank (RICHNER et al. 1989) which may enable them to obtain a high-quality mate or territory with associated implications on survival and breeding success

260 (VERHULST et al. 1997). Although poor-quality offspring are sometimes able to employ compensatory responses (e.g. rapid post-fledging growth), these usually have fitness or longevity-related costs themselves (BIRKHEAD et al. 1999, METCALFE & MONAGHAN 2001).

264 *Correlation between nestbox avoidance patterns and offspring quality: parental responsiveness?*

Given the importance of offspring quality, factors that reduce the condition of young should become strong nest-site selection pressures because the fitness of parent birds increases not with the number of offspring to fledge, but with the number of offspring who survive, enter the breeding population, and successfully raise

268 their own offspring, all of which are linked to offspring quality. The correlation between patterns of nestbox avoidance (reduced occupation of boxes facing south-southwest) and offspring quality (lowest in boxes facing south-southwest) suggests the responsiveness of parent birds to these selection pressures. It is still possible that nestboxes facing south-southwest are occupied by adult birds of lower quality such that there is a genetic

272 component to the relationship between offspring quality and orientation (GOSLER & HARPER 2000). This is less likely than the alternative explanation of adaptive nestbox choice because it does not explain why nestboxes

facing south-southwest are occupied less frequently than those facing other orientations when there is a surplus of nestboxes (about 28% of Nagshead nestboxes remain unoccupied each year). Moreover, there is

276   no relationship between lay date and orientation as might be expected if better quality females have a directional bias as females in better condition tend to lay earlier (PERRINS & MCCLEERY 2001). However, this possibility cannot be discounted on the basis of the current correlative study. There are several possible future experiments that could be undertaken to resolve the causality question and further advance understanding. It

280   would be useful to alter the orientation of certain nestboxes during incubation and then measure of offspring quality at day 15 post hatching to disassociate parental nestbox selection and offspring quality. More information could also be gained from undertaking a partial cross-fostering experiment whereby some chicks from each brood are swapped soon after hatching with those of another brood from a nestbox facing a

284   different direction (e.g. LUCAS & HEEB, 2005). Quantification of condition prior to fledging could then be used to determine the relative contribution of genetics and environment (including nestbox orientation) on offspring quality. If an experimental approach were not possible, it would be useful to quantify parental (or certainly maternal) quality and include this in a fully factorial GLMM with offspring quality as the dependant variable. If

288   there were an interaction between orientation and parental quality in the prediction of offspring quality, this would be good evidence that the influence of parental quality on offspring quality is modified by orientation. If adult great tits are responding to factors that decrease offspring quality by avoiding specific nest sites, this would be empirical evidence that nest-site selection can be an adaptive mechanism to enhance offspring

292   quality. This situation has been documented previously for the keelback snake *Tropidonophis mairii* in Australia (BROWN & SHINE 2004) and would also parallel the "preference-performance" or "mother knows best" hypothesis of ecological entomology which predicts that there is a strong selection pressure on maternal oviposition behaviour in insect herbivores, particularly for those whose offspring have a limited

296   dispersal capacity (JAENIKE 1978, DOAK et al. 2006, JOHNSON et al. 2006).

Possible reasons for reduced offspring quality in boxes facing south-southwest

Assuming that reduced offspring quality is the result of environment rather than genetics, there are several

300   possible hypotheses to explain why this might have occurred. Firstly, the microclimate in boxes facing south-southwest might be less favourable. Temperature measurements inside nestboxes (A. Goodenough unpublished data) indicate that boxes facing south-southwest have higher peak internal temperatures (c. 1 °C) than other boxes. This could cause thermal stress in chicks (VAN BALEN & CAVÉ 1970, DAWSON & WHITTOW

304   2000), particularly in warm springs. Nestboxes facing south-southwest could also be more exposed to prevailing wind and rain (previously found to influence nesting success in bird species: NILSSON 1975) given

that the prevailing winds in the study site are southwesterly. Secondly, parasite loads might be higher in nestboxes facing south-southwest, possibly as a result of nestbox microclimatic differences. As parasitism

308   can have a significant impact on nesting success (NEWTON 1998), chick behaviour (SIMON et al. 2005) and survival (CHAPMAN & GEORGE 1991), high parasite load could negatively impact upon chick condition. Thirdly, nestbox bacterial and/or fungal loading might be higher for boxes facing south-southwest, again possibly because of the warmer and moister environment. The influence of microbial species on nesting is poorly

312   understood (LUCAS & HEEB 2005), but high levels of pathogenic species could have a significant influence on condition (NUTTALL 1997). Future research to establish the reasons for the non-uniformity in offspring quality nestbox orientation would be useful to expand the findings of this study.

Table 1 – GLMM analyses of offspring quality as determined by several condition-related biometrics and bilateral asymmetry against orientation category (0-89°, 90-179°, 180-269° and 270-359°). Bonferroni adjusted P values were calculated for GLMMs on biometrics to allow for family-wise error.

| Source	df	SS	MS	F	P	$Adj.\ P$
Weight						
Orientation category	3	69.35	23.12	8.947	< 0.001	< 0.001
Error	228	589.08	2.484			
Corrected total ($r^2 = 0.105$)	231	658.407				
Wing length						
Orientation category	3	563.41	187.80	8.13	0.007	0.021
Error	228	6296.19	27.62	4.18		
Corrected total ($r^2 = 0.052$)	231	6642.41				
Tarsus length						
Orientation category	3	14.01	4.67	5.52	0.001	0.003
Error	228	5082.43	23.10			
Corrected total ($r^2 = 0.100$)	231	564.84				
Tarsus asymmetry						
Orientation category	3	3.41	1.34	3.30	< 0.001	N/A
Error	220	7.51	0.03			
Corrected total ($r^2 = 0.312$)	223	10.92				
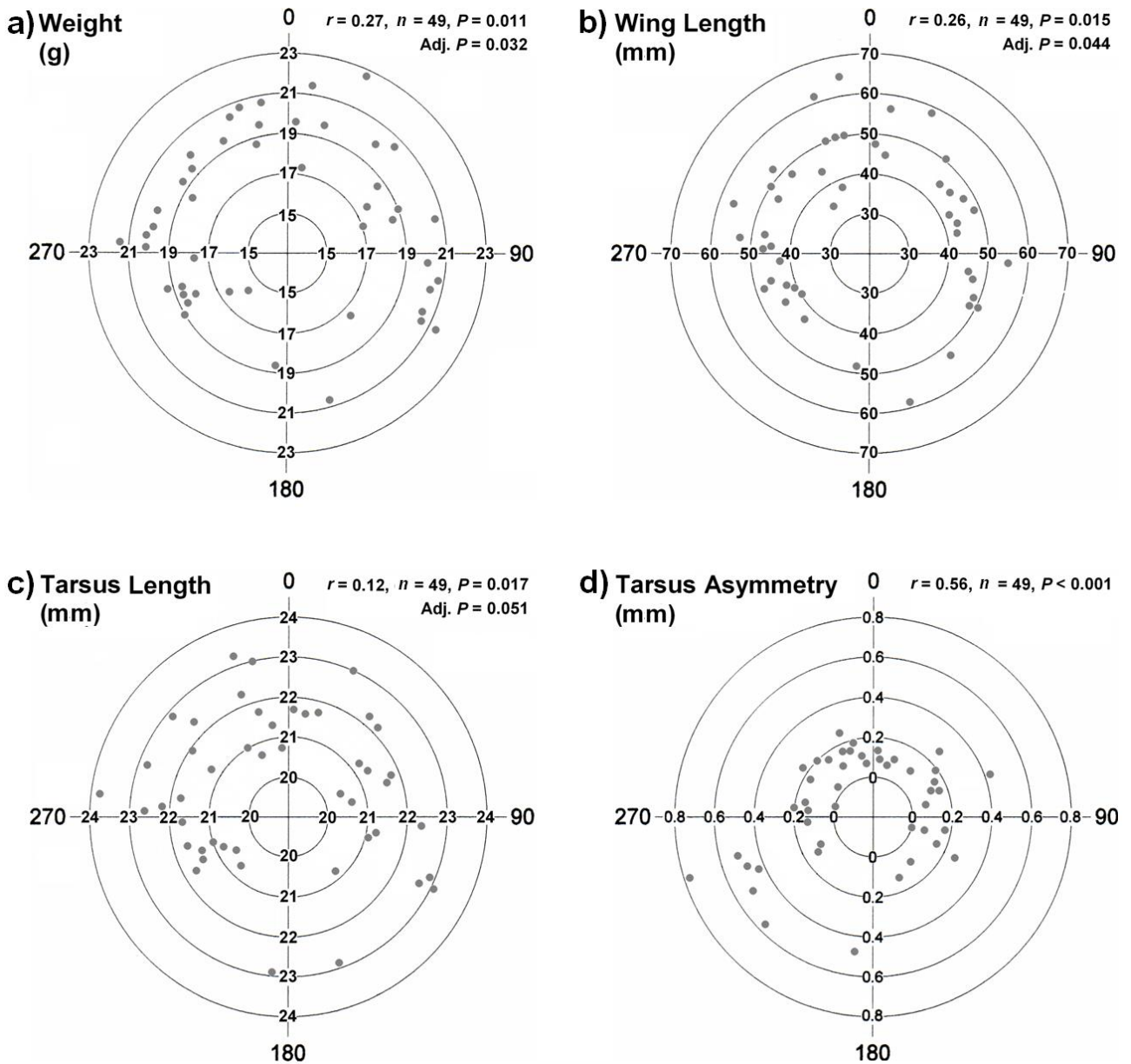
Fig 1 – Circular linear correlation between mean within-brood offspring quality and orientation according to the condition-related traits of (a) weight (heavier being better), (b) wing length and (c) tarsus length (bigger being better), and tarsus asymmetry (low values being better). Each datapoint equals one brood ($n = 49$ except for tarsus asymmetry where $n = 47$ – see text for details). Bonferroni adjusted P values were calculated for correlations on biometric data (a-c) to allow for family-wise error.
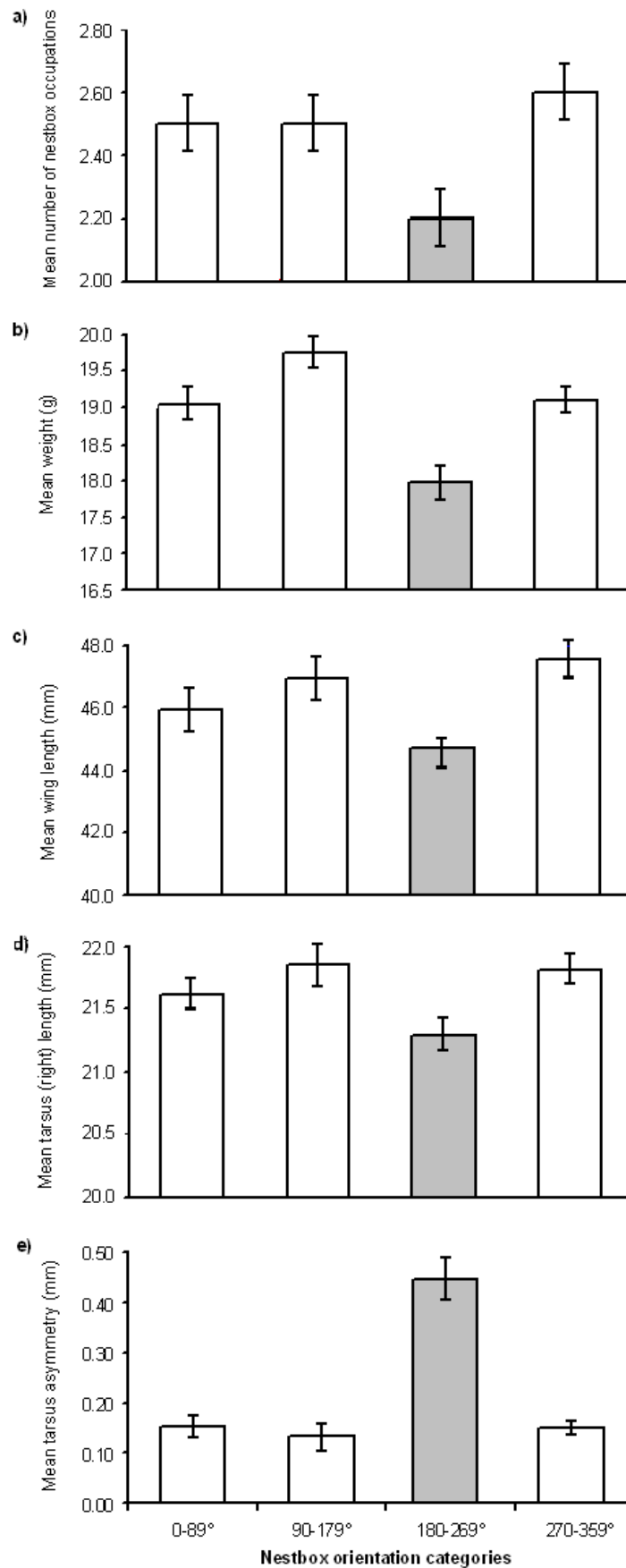
14

Fig. 2 – The association (means ± SEM) between nestbox orientation category, occupation and offspring quality in the great tit showing: (a) the mean number of occasions during the period 1990-2004 that boxes at the study site were occupied ($n = 584$ nests) showing reduced occupation of boxes facing south-southwest and (b-e) offspring quality in 2006 shown using condition-related traits of (b) weight (heavier being better; $n = 232$ chicks), (c-d) size (bigger being better; $n = 232$ chicks) and (e) the difference between the left and right tarsi (low values being better; $n = 224$ chicks). The grey shading indicates the direction that is statistically less-preferred (a – two-tailed t-test comparing occupations of boxes facing south-southwest with those facing other directions $t = 1.980$, df = 226, $P = 0.049$ (data from GOODENOUGH et al. 2008)) or less-successful (b-e – see text).

<center>REFERENCES</center>

- ALATALO R.V. & LUNDBERG A.1986. Heritability and selection on tarsus length in the pied flycatcher (*Ficedula hypoleuca*). *Evolution* 40: 574-583.

- ANDERSSON M. 1994. Sexual selection. *New Jersey: Princeton University Press*.

- AUSTIN G.T. 1974. Nesting success of the cactus wren in relation to nest orientation. *Condor* 76: 216-217.

- BATSCHELET E. 1981. Circular statistics in biology. *London: Academic Press*.

- BECHSHØFT T.Ø., RIGÉT, F.F., WIIG Ø. & SONNE C. 2008. Fluctuating asymmetry in metric traits; a practical example of calculating asymmetry, measurement error and repeatability. *Annales Zoologici Fennici* 45: 32-38.

- BIRKHEAD T.R., FLETCHER F. & PELLATT E.J. 1999. Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society (B)* 266: 385-390.

- BJÖRKLUND M. 1996. The effect of male presence on nestling growth and fluctuating asymmetry in the blue tit. *Condor* 98: 172-175.

- BOTH C., VISSER M.E. & VERBOVEN N. 1999. Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society (B)* 266: 465-469.

- BROWN G.P. & SHINE R. 2004. Maternal nest-site choice and offspring fitness in a tropical snake (*Tropidonophis mairii*, Colubridae). *Ecology* 85: 1627-1634.

- CAMPBELL B. 1968. The Dean nest box study, 1942-1964. *Forestry* 41: 27-46.

- CHAPMAN B. & GEORGE J. 1991. The effects of ectoparasites on cliff swallow growth and survival, pp. 69-92. In: Loye J.E, & Zuk M., Edits. Bird-parasite interactions: ecology, evolution and behaviour. *Oxford: Oxford University Press*.

- CICHON M. & LINDÉN M. 1995. The timing of breeding and offspring size in great tits (*Parus major*). *Ibis* 137: 364-370.

- DAWSON W.R. & WHITTOW G.C. 2000. Regulation of body temperature, pp. 344-390. In: Whittow G.C., Edit. Sturkie's avian physiology, 5th ed. *London: Academic Press*.

- DHONDT A.A. & PHILLIPS T. 2001. A question of preference – does the orientation of a nest box affect the breeding success of cavity-nesting birds? *Birdscope* 15: 1-3.

- DOAK P., KAREIVA P. & KINGSOLVER J. 2006. Fitness consequences for choosy oviposition for a time-limited butterfly. *Ecology* 87: 395-408.

- FONTAINE J.J. & MARTIN T.E. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. *The American Naturalist* 168: 811-818

- GARNETT M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major. Ibis* 123: 31-41

- GAUNT A.S. & ORING L.W. (edits) 1999. Guidelines to the use of wild birds in research, 2nd ed. *Washington, D.C.: The Ornithological Council.*

- GOODENOUGH A.E., MAITLAND D.P., HART A.G. & ELLIOT S.L. 2008. Nestbox orientation: a species-specific influence on occupation and breeding success in woodland passerines. *Bird Study.* 55: 222-232.

- GOSLER AG. 1993. The great tit. *London: Hamlyn Limited.*

- GOSLER A.G. 2004. Birds in the hand, pp. 85-118. In: Sutherland W.J. et al., Edits. Bird ecology and conservation: a handbook of techniques. *Oxford: Oxford University Press.*

- GOSLER A.G. & HARPER D.G.C. 2000. Assessing the heritability of body condition in birds: a challenge exemplified by the great tit *Parus major* L. (Aves). *Biological Journal of the Linnean Society* 71: 103-117.

- GOSLER A.G., GREENWOOD J.J.D., BAKER J.K. & DAVIDSON N.C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. *Bird Study* 45: 92-103.

- GRIECO F. 2003. Greater food availability reduces tarsus asymmetry in nestling blue tits. *Condor* 105: 599-603.

- HARPER D.G.C. 1999. Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Animal Behaviour* 58: 553-562.

- HAYWOOD S. & PERRINS C.M. 1992. Is clutch size in birds affected by environmental conditions during growth? *Proceedings of the Royal Society (B)* 249: 195-197.

- HELM B. & ALBRECHT H. 2000. Human handedness causes directional asymmetry in avian wing length measurements. *Animal Behaviour* 60: 899-902.

- HOFFMANN A.A. & PARSONS P.A. 1991. Evolutionary genetics and environmental stress. *Oxford: Oxford University Press.*

- JAENIKE J. 1978. On optimal oviposition behaviour in phytophagous insects. *Theoretical Population Biology* 14: 350-356.

- JAKOB E.M., Marshall S.D. & Uetz G.W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77: 61-67.

- JOHNSON S.N., Birch A.N.E., Gregory P.J. & Murray PJ. 2006. The 'mother knows best' principle: should soil insects be included in the preference-performance debate? *Ecological Entomology* 31: 395-401.

- LENS L. & VAN DONGEN S. 1999. Evidence for organism-wide asymmetry in five bird species of a fragmented afrotropical forest. *Proceedings of the Royal Society (B)* 266: 1055-1060.

- LENS L., VAN DONGEN S., WILDER C.M., BROOKS T.M. & MATTHYSEN E. 1999. Fluctuating asymmetry increases with habitat disturbance in seven bird species of a fragmented afrotropical forest. *Proceedings of the Royal Society (B)* 266: 1241-1246.

- LINDSTRÖM J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* 14: 343-348.

- LUCAS F.S. & HEEB P. 2005. Environmental factors shape cloacal bacterial assemblages in great tit *Parus major* and blue tit *P. caeruleus* nestlings. *Journal of Avian Biology* 36: 510-516.

- MARDIA K.V. & JUPP P. 2000. Directional statistics. *Chichester: John Wiley & Sons.*

- MENNILL D.J. & RATCLIFFE L.M. 2004. Nest cavity orientation in black-capped chickadees *Poecile atricapillus*: do the acoustic properties of cavities influence sound reception in the nest and extra-pair mating? *Journal of Avian Biology* 35: 477-482.

- METCALFE N.B. & MONAGHAN P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution* 16: 254-260.

- MØLLER A.P. 1992. Female swallow preference for symmetrical male sexual ornaments. *Nature* 357: 238-240.

- MØLLER A.P. 1997. Developmental stability and fitness: a review. *The American Naturalist* 149: 916-932.

- MONRÓS J.S., BELDA E.J. & BARBA E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* 99: 481-488.

- MOSS D. 1972. A statistical analysis of clutch size in the great tit *Parus major* L. [MSc Thesis]. *Oxford: University of Oxford.*

- NAEF-DAENZER B., WIDMER F. & NUBER M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70: 730-738.

- NEWTON I. 1998. Population limitation in birds. *London: Academic Press.*

- NILSSON S.G. 1975. Kullstorlek och häckningsframgång i holkar och naturliga hål (Clutch size and breeding success of birds in nest boxes and natural cavities). *Vår Fågelvärld* 34: 207-211 (in Swedish).

- NISBET I.C., BAIRD J., HOWARD D.V. & ANDERSON K.S. 1970. Statistical comparison of wing-length measured by four observers. *Bird-Banding* 41: 307-308.

- NUTTALL P. 1997. Viruses, bacteria and fungi of birds, pp. 271-302. In: Clayton D. & Moore J., Edits. Host-parasite evolution: general principles and avian models. *Oxford: Oxford University Press.*

- PARSONS P.A. 1992. Fluctuating asymmetry: a biological monitor of environmental and genomic stress. *Heredity* 68: 361-364.

- PERRINS C.M. 1979. British tits. *London: Collins.*

- PERRINS C.M. & McCLEERY R.H. 2001. The effect of fledging mass on the lives of great tits *Parus major*. *Ardea* 89: 135-142.

- PINKOWSKI B.C. 1976. Use of tree cavities by nesting eastern bluebirds. *Journal of Wildlife Management* 40: 556-563.

- RENDELL W.B. & ROBERTSON R.J. 1994. Cavity-entrance orientation and nest-site use by secondary hole-nesting birds. *Journal of Field Ornithology* 65: 27-35.

- RICE W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.

- RICHNER H., SCHNEITER P. & STIRNIMANN H. 1989. Life-history consequence of growth rate depression: an experimental study on carrion crows (*Corvus corone corone* L.). *Functional Ecology* 3: 617-624.

- RICHNER H., OPPLIGER A. & CHRISTE, P. 1993. Effect of an ectoparasite on reproduction in great tits. *Journal of Animal Ecology* 62: 703-710.

- RISING J.D. & SOMERS K.M. 1989. The measurement of overall body size in birds. *The Auk* 106: 666-674.

- SÁNCHEZ S., CUERVO, J.J. & MORENO, E. 2007. Does habitat structure affect body condition of nestlings? A case study with woodland great tits *Parus major*. *Acta Ornithologica* 42: 200-204.

- SCHMIDT K.A., OSTFELD R.S. & SMYTH K.N. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* 148: 22-29.

- SIMON A., THOMAS D.W., SPEAKMAN J.R., BLONDEL J., PERRET P. & LAMBRECHTS M.M. 2005. Impact of ectoparasitic blowfly larvae (*Protocalliphora* spp.) on the behavior and energetics of nestling blue tits. *Journal of Field Ornithology* 76: 402-410.

- SMITH H.G., ALLANDER H.K & NILSSON J.-A. 1989. The trade-off between offspring number and quality in the great tit *Parus major. Journal of Animal Ecology* 58: 383-401.

- STAUFFER D.F. & BEST L.B. 1982. Nest-site selection by cavity-nesting birds of riparian habitats in Iowa. *Wilson Bulletin* 94: 329-337.

- SVENSSON L. 1992. Identification guide to European passerines, 4th ed. *Stockholm: Svensson.*

- SWADDLE J.P., WITTER M.S. & CUTHILL I.C. 1994. The analysis of fluctuating asymmetry. *Animal Behaviour* 48: 986-989.

- TEATHER K. 1996. Patterns of growth and asymmetry in nestling tree swallows. *Journal of Avian Biology* 27: 302-310.

- TINBERGEN J.M. & BOERLIJST M.C. 1990. Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology* 59: 1113-1127.

- VAN BALEN J.H. & CAVÉ A.J. 1970. Survival and weight loss of nestling great tits, *Parus major*, in relation to brood-size and air temperature. *Netherlands Journal of Zoology* 20: 464-474.

- VERHULST S., PERRINS C.M. & RIDDINGTON R. 1997. Natal dispersal of great tits in a patchy environment. *Ecology* 78: 864-872.