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Fitness consequences of avian personalities in a fluctuating environment

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Individual animals differ in the way they cope with challenges in their environment, comparable with variation in human personalities. The proximate basis of variation in personality traits has received considerable attention, and one general finding is that personality traits have a substantial genetic basis. This poses the question of how variation in personality is maintained in natural populations. We show that selection on a personality trait with high heritability fluctuates across years within a natural bird population. Annual adult survival was related to this personality trait (behaviour in novel environments) but the effects were always opposite for males and females, and reversed between years. The number of offspring surviving to breeding was also related to their parents' personalities, and again selection changed between years. The observed annual changes in selection pressures coincided with changes in environmental conditions (masting of beeches) that affect the competitive regimes of the birds. We expect that the observed fluctuations in environmental factors lead to fluctuations in competition for space and food, and these, in association with variations in population density, lead to a variation in selection pressure, which maintains genetic variation in personalities.

Keywords: fitness; genetic variation; personality; exploration; boldness

1. INTRODUCTION

In a wide range of vertebrates, individuals differ in their propensity to take risks, particularly in novel or challenging situations (Wilson *et al.* 1994; Boissy 1995; Koolhaas *et al.* 1999; Gosling 2001). These individual differences in behaviour often arise early in life (Kagan *et al.* 1988; Verbeek *et al.* 1994), have substantial additive (Boissy 1995; Koolhaas *et al.* 1999; Dingemans *et al.* 2002; Drent *et al.* 2003) and non-additive genetic components (Bouchard & Loehlin 2001; Van Oers *et al.* 2004) and are regarded as personality differences (Wilson *et al.* 1994; Gosling 2001; Gosling & Vazire 2002) because they are expressed in many different situations (Kagan *et al.* 1988; Wilson *et al.* 1994; Boissy 1995; Koolhaas *et al.* 1999; Gosling 2001). The processes responsible for the maintenance of variation in personality in natural populations are largely unknown but probably involve fluctuating selection pressures caused by environmental variability (e.g. ecological cycles) and frequency-dependent selection (Wilson *et al.* 1994; Wilson 1998). Spatiotemporal variation in selection on personality has not yet been studied in natural populations, and only a few studies have measured selection on personality traits (Armitage 1986; Eaves *et al.* 1990; Réale *et al.* 2000; Armitage & Van Vuren 2003; Réale & Festa-Bianchet 2003). By measuring the fitness consequences of an avian personality trait in the wild during three successive years, we show that strong alternating selection acted on this personality trait. The direction of selection differed between sexes and between years.

We have examined how natural selection acts on personalities in a natural population of a passerine bird, the great tit, *Parus major*. Great tits are non-migratory territorial songbirds that live in forests in Europe and Asia. Individual great tits differ in the way they explore novel environments ('fast' versus 'slow') (Verbeek *et al.* 1994; Dingemans *et al.* 2002). Individuals at the extremes of the trait distribution use different strategies to cope with novel or challenging situations (Verbeek *et al.* 1994; Koolhaas *et al.* 1999). Fast explorers have an active coping strategy: they are aggressive, bold in exploration, insensitive to external stimuli and rely on routines, whereas slow explorers use a passive coping strategy: they are relatively non-aggressive, shy in exploration, sensitive to external stimuli and readily adjust their behaviour to changes in their environment (Verbeek *et al.* 1996, 1999; Marchetti & Drent 2000). Exploratory behaviour is highly repeatable and has a substantial additive genetic component ($h^2 = 0.3\text{--}0.6$) in both wild-caught (Dingemans *et al.* 2002) and captive-bred (Drent *et al.* 2003; Van Oers *et al.* 2004) great tits. We measured the phenotypic variation in exploratory behaviour in a natural population by taking individual great tits to the laboratory for a single day, where an exploration test was performed in a novel environment, and releasing them afterwards (Dingemans *et al.* 2002). We assessed the survival between breeding seasons of these individuals and the recruitment of their offspring in their natural habitat, and we examined correlations between these fitness components and the bird's behavioural phenotype, using exploratory behaviour as a predictor of an individual's personality.

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Table 1. Model selection of adult survival rate (ϕ) and recapture rate (P) between breeding seasons (years) of great tits as a function of individual exploratory behaviour b , sex s and year t ($t_1 = 1999-2000$, $t_2 = 2000-2001$, $t_3 = 2001-2002$) or $t_{1\&3}$ vs t_2 (combined estimate for t_1 and t_3 versus t_2).

($P(\cdot)$) denotes an equal capture probability for all individuals. Models are sorted in ascending order by their QAICc values after correcting for overdispersion ($\hat{c} = 1.7559$). Note that not all models are shown.)

model	QAICc	number of parameters	Qdeviance
1. $\phi(b, t_{1\&3} \text{ vs } t_2, b \times s, b \times t_{1\&3} \text{ vs } t_2, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	260.98	7	246.616
2. $\phi(b, s, t_{1\&3} \text{ vs } t_2, b \times s, b \times t_{1\&3} \text{ vs } t_2, s \times t_{1\&3} \text{ vs } t_2, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	263.58	9	245.000
3. $\phi(b, s, t, b \times s, b \times t_{1\&3} \text{ vs } t_2, s \times t, b \times s \times t_{1\&3} \text{ vs } t_2)P(\cdot)$	267.03	11	244.173
4. $\phi(b, s, t, b \times s, b \times t, s \times t, b \times s \times t)P(\cdot)$	271.32	13	244.126
5. $\phi(b, s, t, b \times s, b \times t, s \times t)P(\cdot)$	276.37	11	253.512
6. $\phi(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)P(\cdot)$	280.88	19	240.334
7. $\phi(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)P(b, b^2, s, t, b \times s, b^2 \times s, b \times t, b^2 \times t, s \times t, b \times s \times t, b^2 \times s \times t)$	304.86	36	223.416

2. METHODS

(a) Data collection

Data were collected from a nest-box population of great tits in the Westerheide area, central Netherlands, between 1998 and 2002. Outside the breeding season, we captured birds for behavioural scoring using standard methods (Dingemane *et al.* 2002). Birds of unknown behavioural score were transported to the laboratory (1–32 birds per day) and housed individually (Dingemane *et al.* 2002). The following morning, we measured the exploratory behaviour (Verbeek *et al.* 1994; Dingemane *et al.* 2002) of each bird individually in a sealed room (4.0 m \times 2.4 m \times 2.3 m) containing five artificial trees, before we released them near their individual place of capture within 14–24 h of capture (Dingemane *et al.* 2002). We used the total number of flights and hops within the first 2 min as an index of exploratory behaviour and corrected the scores for date of capture, based on within-individual changes in behaviour with capture date (Dingemane *et al.* 2002).

In the breeding season, we captured adults in the nest-box with spring traps when their offspring were 8–10 days old. Both adults and offspring were then given individually numbered rings to allow for later identification when their chicks were ringed in the nest. We use two fitness components that are together a good approximation of the number of genes that a bird contributes to the population in the next breeding season. The first is the annual number of offspring that survive to the next breeding season that a pair produces (i.e. offspring recruitment). The second is the survival of adults from one breeding season to the next. Breeding adults were included in the analysis only if they were tested before the breeding season, to prevent the results from being biased by the effects of differential mortality between breeding and testing. Juveniles could not be tested before they became independent of their parents; consequently, viability selection between hatching and testing could not be measured.

(b) Survival analyses

We estimated the annual survival of adults between breeding seasons for the years 1999–2002. Because some individuals escape detection while they are alive, capture probabilities have to be accounted for when estimating true survival. We used MARK v. 3.2 to estimate annual survival (ϕ) and capture probability (P) simultaneously (White & Burnham 1999). Our main goal was to test whether survival probabilities depended on individual exploratory behaviour (linear term, b ; quadratic term, b^2),

sex (s), year (t) or their interactions. The initial model (model 7 in table 1) estimated the relationship between ϕ and a three-way interaction between exploratory behaviour (both linear and quadratic terms), sex and year, including all lower-term interactions and main effects on both ϕ and P . We then fitted simpler models and used the Akaike's Information Criterion (AIC) to select the most parsimonious model (White & Burnham 1999), i.e. the model that fits the data best with the fewest parameters, resulting in the lowest QAICc value (AIC adjusted for overdispersion; see table 1).

Parameter estimates of the best models were examined to evaluate whether the model could be further simplified, for instance by grouping factor levels with similar parameter estimates (Crawley 1993). We tested the significances of explanatory variables by comparing nested models using likelihood ratio tests (LRTs). We corrected for overdispersion by adjusting the quasi-likelihood parameter (\hat{c}). Although these estimates of adult survival do not account for dispersal, they are unlikely to be biased because in this species dispersal is restricted to juveniles (Greenwood & Harvey 1982).

(c) Analysis of offspring number

The number of offspring a pair produced that survived to breeding was determined by catching most breeding adults in each breeding season (capture probability = 0.727 ± 0.098 , estimate based on the survival analyses in MARK) and counting the number of recaptured young per pair in the next breeding season that bred in our study area. We analysed the number of surviving offspring using general linear models (GLM) with Poisson errors (Crawley 1993). Exploration scores as linear and quadratic terms were included in the models, because we did not have *a priori* expectations of the shape of the effects. We did not always test both male and female parents before the breeding season, and therefore we give separate analyses for the effects of male and female parent's exploratory behaviours as well as for the simultaneous effect of both sexes. Sample sizes depend on the number of parents tested. In the analysis of the effect of male exploration score on the number of surviving offspring, inclusion of the year 1999 resulted in a non-converging model (owing to the distribution of the data in this year; see Crawley 1993), and this model is based on 2000 and 2001 only; for the same reason the analysis of the simultaneous effect of both parents was restricted to 2000. The estimates are based on local recruits and do not include dispersal. We have no means of controlling for dispersal patterns quantitatively.

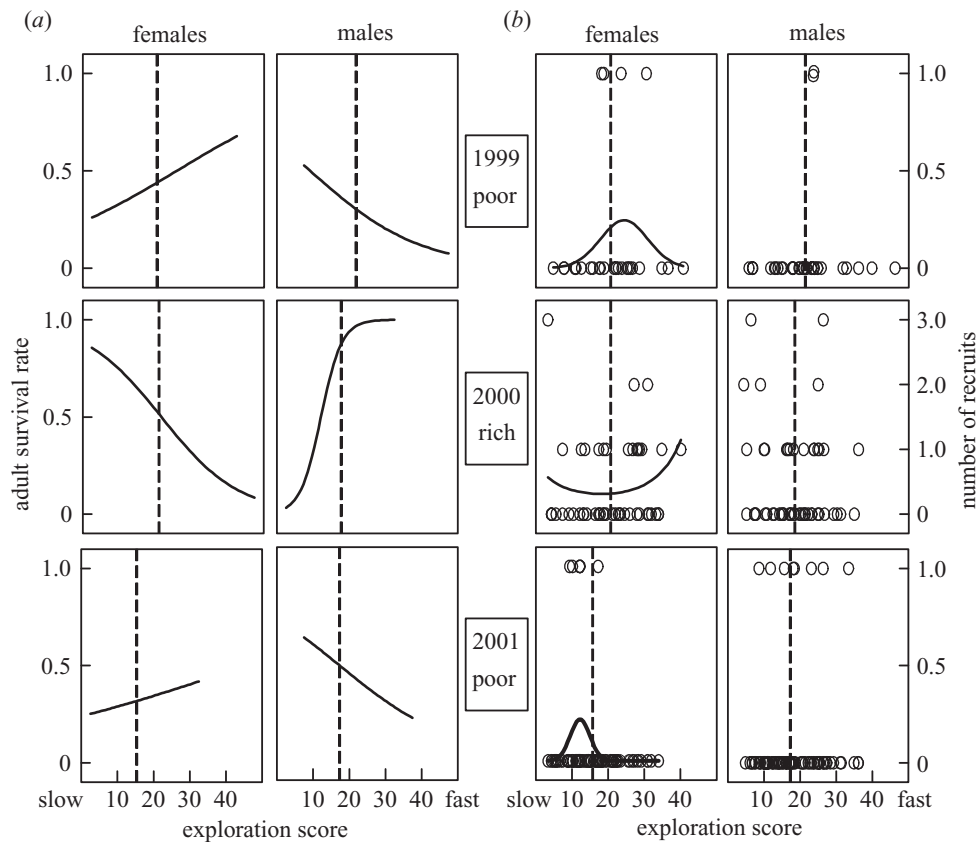


Figure 1. The relationship between two fitness components and individual personality for three successive years (1999–2001) in male and female great tits. (a) Annual adult survival as a function of individual exploratory behaviour. Lines represent the slopes of the relationship between adult survival and exploration score, calculated from the model $\phi(b, s, t, b \times s, b \times t, s \times t, b \times s \times t)P(\cdot)$. Number of live encounters per year, females: 1999, 37; 2000, 58; 2001, 78; and males: 1999, 36; 2000, 46; 2001, 64; effective sample size = 319. (b) Number of offspring surviving to breeding (recruits) as functions of the exploratory behaviours of their parents. The solid lines give the significant regression line from a Poisson regression. Sample sizes per year are females: 1999, 29; 2000, 50; 2001, 82 and males: 1999, 32; 2000, 51; 2001, 81. The dashed lines give the arithmetic mean exploration score for each sex and year combination.

3. RESULTS AND DISCUSSION

Selection on avian personality measured by adult survival between breeding seasons fluctuated strongly between the years and was in each year opposite for males and females, and changes over the years in selection on personality differed between males and females (figure 1a; table 1, LRT model 4 versus 5, $\chi^2 = 9.386$, d.f. = 2, $p = 0.0092$). In 1999 and 2001 slow-exploring males and fast-exploring females tended to survive better, whereas in 2000 the reverse was observed (the effects of individual behaviour were linear within each combination of sex and year; LRT model 4 versus 6: $\chi^2 = 3.792$, d.f. = 6, $p = 0.7048$). In each sex, the slopes and intercepts were similar for the first and third years (LRT model 2 versus 4: $\chi^2 = 0.837$, d.f. = 4, $p = 0.9284$), and the most parsimonious model included a common intercept for the first and third years as well as a three-way interaction between individual behaviour, sex and year (table 1, model 1), indicating that within sexes the selective regimes were similar in 1999 and 2001 but different in 2000. Capture probabilities did not differ between categories of birds (see table 1; LRT model 6 versus 7: $\chi^2 = 16.922$, d.f. = 17, $p = 0.4596$).

The number of offspring that survived and bred in the local study area was related to the personality of the

mother, and again fluctuated between years (figure 1b; Poisson regression; females: year \times exploratory behaviour (both linear and quadratic terms included) $\chi^2 = 11.7$, d.f. = 4, $p = 0.03$; males (only 2000 and 2001): $\chi^2 = 1.32$, d.f. = 2, $p = 0.52$). In the two years with low winter food (1999 and 2001), few young recruited as breeders in the local population, and selection tended to be stabilizing. By contrast, in the one year with high recruitment (2000) selection tended to be disruptive, with females at both ends of the distribution producing more recruits. For fathers there was no significant effect of personality on the number of recruits produced, although the trends in fathers were similar to those in mothers and did not differ significantly in analyses including both fathers and mothers (year \times sex \times exploration score: $\chi^2 = 3.753$, d.f. = 2, $p = 0.153$; sex \times exploration score: $\chi^2 = 0.002$, d.f. = 1, $p = 0.964$). For the middle year (2000) we had enough data to analyse the combined effect of fathers' and mothers' personalities on the numbers of recruits produced. In this year the number of recruits depended on the phenotypes of the parents: pairs consisting of two fast-exploring partners or two slow-exploring partners had the highest numbers of recruits, whereas other combinations had lower numbers of recruits (figure 2; interaction of male \times female exploratory behaviour: $\chi^2 = 4.162$, d.f. = 1,

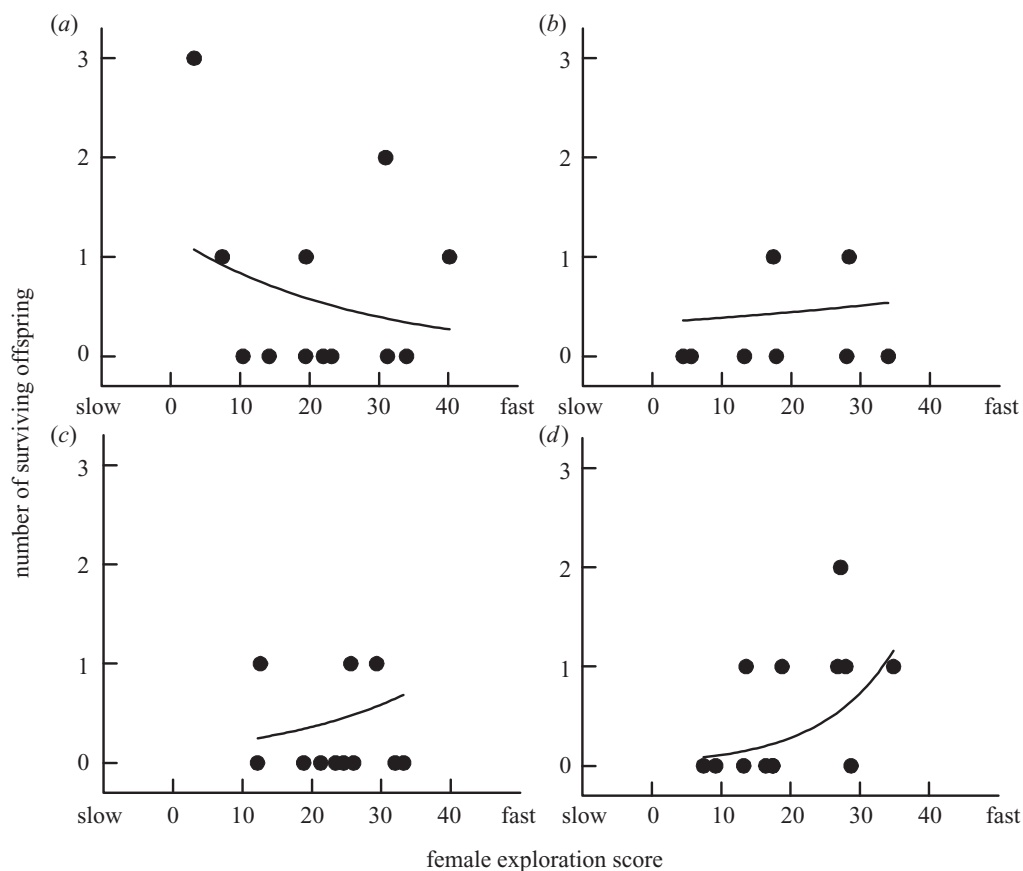


Figure 2. The effect of the exploratory behaviour of both parents on the number of offspring surviving to breeding in the year 2000 ($n = 44$ pairs). On the x -axis we give the exploratory behaviour of the females. Male exploratory scores are divided into four groups of approximately equal numbers, and the different graphs show: (a) the lower 25% ('slowest'); (b) the 25–50% ('slow-medium'); (c) the 50–75% ('medium-fast'); and (d) the highest 25% ('fastest') of the distribution of male scores. The regression lines are from a GLM with Poisson errors, and for each graph separately the average score of the male is entered in the equation to produce the regression line.

$p = 0.046$). The disruptive selection in 2000 (figure 1*b*) is thus the result not only of the personalities of the mothers, but also of the personalities of their mates (figure 2).

Fastest-exploring parents have offspring that disperse furthest (Dingemanse *et al.* 2003). As a consequence we have probably underestimated the real number of surviving offspring of those parents, and pairs of two fast-exploring parents are thus expected to perform even better than suggested in figure 2. We are aware that this bias in the estimated offspring survival can affect our estimates of selection, but it cannot explain the annual variation in selective pressures for this fitness component, because patterns of dispersal did not differ between years (Dingemanse *et al.* 2003). Recently we have collected additional support for the finding that the interaction between the parents' exploratory behaviours indeed affects the number of recruits. We found that assortative pairs of extreme phenotypes also produced offspring with the highest fledgling condition (Both *et al.* 2004).

Because assortative pairs produce more viable offspring per breeding season, we expected the birds to pair assortatively with respect to exploratory behaviour. Contrary to this expectation, the birds mated disassortatively, although this pattern occurred only when the male partner was older than 1 year (figure 3; ANCOVA with male phenotype as a dependent variable: female phenotype \times male age: $F_{1,191} = 5.67$, $p = 0.018$). Three hypotheses can

explain these intriguing findings. First, mates adjust their own behaviour after pair formation to contrast their partner's exploratory behaviour, but because most individuals were tested as juveniles before they mated we reject this possibility. Second, disassortative pairing is a by-product of the strong—but opposite—directional selection on adult males and females. Third, if intermediate phenotypes have the highest fitness, disassortative mating may be an adaptive mate choice because parents at the extremes of the trait distribution can produce intermediate offspring only by pairing disassortatively. Support for the latter explanation is found in the lower variance in adult survival for intermediate phenotypes (figure 1*a*), resulting in a higher overall life expectancy. Because exploratory behaviour is heritable (Dingemanse *et al.* 2002) (h^2 estimates based on mid-parent–mid-offspring regressions for the years 1999–2001 are on average 0.340 ± 0.138 (GLM controlling for year: $F_{1,60} = 6.049$, $p = 0.017$)), disassortative mating may thus allow adults to produce offspring with the highest life expectancy and hence increase their lifetime fitness.

Selection on a personality trait in this wild bird population changes from year to year, but what is the ecological background of these differences? The observed annual changes in selection pressures coincided with annual changes in environmental conditions: the presence of mast seeding of beeches, *Fagus sylvaticus*. The winters of 1999–

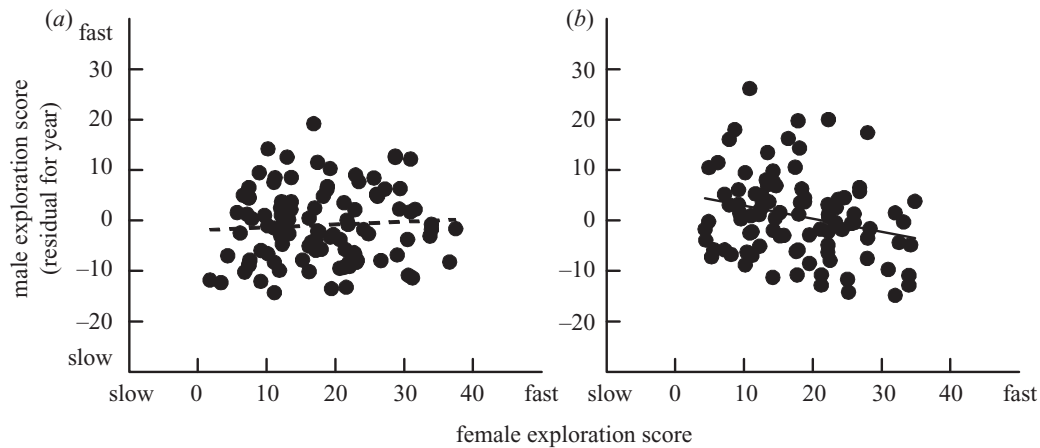


Figure 3. The observed correlation between male and female exploratory behaviour for pairs of great tits: (a) 1-year-old males, and (b) older males. Data are analysed with ANCOVA with male exploratory behaviour as the dependent variable (year: $F_{3,191} = 3.80$, $p = 0.01$; male age \times female exploratory behaviour: $F_{1,191} = 5.67$, $p = 0.02$). Female age was not significantly correlated with male exploratory behaviour or with any of the other interaction terms (all $p > 0.14$).

2000 and 2001–2002 were without beech mast ('poor' winters), whereas in 2000–2001 there was a good beech crop ('rich' winter), and we found similar selection patterns in the two poor winters but an opposite pattern in the rich winter for both fitness components (figure 1). We therefore suggest that the observed annual changes in selection pressures may have their origin in this environmental cycle. Beech masting results both in more relaxed competition for food during winter and in increased competition for territory space in the following spring because both juvenile and adult survivals are higher in years with beech masting (Van Balen 1980; Perdeck *et al.* 2000). The consequences of beech masting are likely to differ between classes of individuals, and this may explain why selection on personality in adults differed between the sexes. Because females are subordinate to males, we expect them to be more affected by competition for winter food, while we expect males to be more affected by competition for territorial space. Fast-exploring females may benefit from their aggressiveness when competing for clumped resources in poor years, while slow-exploring females may survive better than fast-exploring females in rich years because in those years overt aggressiveness may be maladaptive and result in increased mortality (Sih *et al.* 2003). Similarly, we suggest that fast-exploring territorial males may benefit from their aggressiveness in rich years, when competition for territorial space is increased, because their aggressiveness may make them more successful in excluding the large numbers of competitors (i.e. non-territorial juveniles) from their territories. Hence, they may survive better because they are less likely to lose their territory. Again, when competition is relaxed, overt aggressiveness may result in net costs rather than net benefits, and in those years selection may favour slow-exploring territorial males. Earlier work on this species showed that selection on juveniles acts on their physical characteristics (i.e. body condition at fledging) (Tinbergen & Boerlijst 1990) especially during years with high densities (Both *et al.* 1999). The large number of recruits produced by the assortative fast and slow pairs in the rich year may indeed be explained by a higher fledgling condition of their offspring (Both *et al.* 2004). Interestingly, while these pair

combinations also produced relatively heavy offspring in the poor years (Both *et al.* 2004), they nevertheless did not produce more recruits. Hence, the extent to which selection favoured certain physical and behavioural characteristics of juveniles may have differed between poor and rich years.

Although we do not yet fully understand the processes maintaining genetic variation in personality traits, the fluctuating selection pressures reported in this paper are likely to help maintain higher levels of additive genetic variation in avian personality than expected from mutation alone (Burger & Gimelfarb 2002). In humans, children at the extremes of the shy–bold continuum are less flexible in their behaviour than children in the middle (Kagan *et al.* 1988). Therefore, an interesting possibility is that fluctuating selection reflected in offspring recruitment (figure 1b) in part resulted from selection favouring individuals with more flexible behaviour (Wilson *et al.* 1994). Interestingly, the higher variance in adult survival for the more extreme phenotypes (figure 1a) suggests that adults of intermediate phenotype have a higher life expectancy. Quantitative genetics analyses suggest that the genetic variation in great tit personality is caused by various loci with small effect (Drent *et al.* 2003). Hence, the degree of heterozygosity on all loci may enable individuals of intermediate phenotype to react more flexibly to the challenges of their fluctuating environment. If intermediate phenotypes are indeed more viable under certain selective regimes (Wilson *et al.* 1994) because they have a heterozygous advantage, this may be an additional and strong mechanism that can help to explain the maintenance of genetic variation in personality traits, comparable with frequency-dependent selection on the level of individual loci. Interestingly, intermediate personalities did not have the highest survival within any of the six classes of sex and year (figure 1a), suggesting that this phenotype is a jack of all trades and master of none.

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