

# Realized heritability of personalities in the great tit (*Parus major*)

Pieter J. Drent<sup>\*</sup>, Kees van Oers and Arie J. van Noordwijk

Netherlands Institute of Ecology, PO Box 40, 6666 ZG Heteren, The Netherlands

Behaviour under conditions of mild stress shows consistent patterns in all vertebrates: exploratory behaviour, boldness, aggressiveness covary in the same way. The existence of highly consistent individual variation in these behavioural strategies, also referred to as personalities or coping styles, allows us to measure the behaviour under standardized conditions on birds bred in captivity, link the standardized measurements to the behaviour under natural conditions and measure natural selection in the field. We have bred the great tit (*Parus major*), a classical model species for the study of behaviour under natural conditions, in captivity. Here, we report a realized heritability of  $54 \pm 5\%$  for early exploratory behaviour, based on four generations of bi-directional artificial selection. In addition to this, we measured hand-reared juveniles and their wild-caught parents in the laboratory. The heritability found in the mid-offspring–mid-parent regression was significantly different from zero. We have thus established the presence of considerable amounts of genetic variation for personality types in a wild bird.

**Keywords:** selection response; genetic variation; *Parus major*; behavioural strategies; personalities; exploration

## 1. INTRODUCTION

Individual animals often face an enormous temporal and spatial variation in their social and non-social environment. The ability to cope with this variation is an important determinant of fitness. Rapidly accumulating evidence for many vertebrates, including man, shows that individuals react to mildly stressful events in different ways. This behavioural variation is often highly consistent within individuals and independent of sex, age or social status. Different behavioural and physiological reactions are correlated (Mendl & Paul 1991), indicating that they are a fundamental aspect of behavioural organization comparable with variation in human personalities (Buss 1991). The reactions of individuals can be quantified on main axes such as ‘shyness–boldness’ (Wilson *et al.* 1994; Greenberg 1995), ‘exploration’ (Clark & Ehlinger 1987) or ‘aggressiveness’ (Benus *et al.* 1991; Sluyter *et al.* 1996). Individuals on the extremes of the main axes can be characterized as having different strategies or coping styles (review, Koolhaas *et al.* 1999).

At one end of the range we find an ‘active’ strategy, characterized by rapid decisions, manipulating stressful events, relatively insensitive to external stimuli, ready to form routines, a high level of aggressiveness, boldness, a high level of testosterone and a high reactivity of the sympathetic nervous system. At the other end of the range, we find a ‘passive’ strategy, characterized by caution in decisions, relatively highly sensitive and readily adjustable to the external situation, a relatively low level of aggressiveness, shyness and a high reactivity of the hypothalamic–pituitary–adrenal axis and the parasympathetic nervous system. These animals generally adapt themselves to the environment (Bohus *et al.* 1987; Benus *et al.* 1991; Hessing *et al.* 1994). This system can be captured in several terms: ‘coping styles’, ‘behavioural strategies’, ‘neophobia’

(review, Greenberg & Mettke-Hofmann 2001) and ‘A- or B-personalities’. Artificial selection in several domesticated mammalian species has shown that this behavioural variation has an important heritable component (e.g. Van Oortmerssen & Bakker 1981; Sluyter *et al.* 1995). In house mice, the existence of gene–environment interactions has been shown to some degree (Benus *et al.* 1987), indicating that early experiences can induce persistent behavioural changes in stress–response in adulthood (review, De Kloet *et al.* 1988). Many behavioural traits are potentially affected by many gene loci. However, only a subset of these loci is variable within populations. Among the key questions in describing different behavioural traits within natural populations is how this variation is caused and maintained, and what consequences this has for the individual fitness. For these questions, it is a prerequisite to assess the role and the structure of a genetic component in these behavioural traits in natural populations (Brodie & Russel 1999). A population is able to react in an adaptive way, only in the presence of genetic variation; at what rate this happens is dependent on the amount of genetic variation (Falconer & Mackay 1996).

In our model species, the great tit *Parus major*, hand-reared individuals of both sexes consistently differ in the way they explore a new environment (‘fast’ versus ‘slow’). This is strongly correlated with differences in behaviour towards novel objects (Verbeek *et al.* 1994; Drent & Marchetti 1999). There were significant differences among sib-groups in the outcomes of these tests (Verbeek *et al.* 1994; Drent & Marchetti 1999), indicating either a determination early in life or genetic effects. These individual differences in exploration and boldness have predictive value for differences in aggressiveness (Verbeek *et al.* 1996), recovery time and behaviour after lost contests (Verbeek *et al.* 1999), foraging behaviour (Marchetti & Drent 2000; Drent & Marchetti 1999) and reactions to stress (Carere *et al.* 2001). All of which are characters known to affect fitness.

<sup>\*</sup> Author for correspondence (drent@cto.nioo.knaw.nl).

A bi-directional selection experiment was started with wild-caught great tits hand reared in the laboratory. We used a combined score of the exploration of an unknown environment and the reaction to a novel object in the familiar environment. Both tests were performed approximately 40 days after hatching. Individuals with high and low scores were mated assortatively to become the parents of the  $F_1$  generation. We used a design with cross fostering and split broods to separate genetic effects from a possible parent-offspring resemblance caused by common environment effects. We report the results from the first four generations of selection on this score. Heritability estimates obtained in the laboratory do not automatically predict responses to selection in the wild. The expression of exploratory behaviour in birds raised in the laboratory could be context dependent (Lambrechts *et al.* 1999). Therefore, we assessed estimates of heritability of exploration of a novel environment in a natural population by collecting wild adult great tits and their nestlings from the field.

## 2. MATERIAL AND METHODS

### (a) *Study species*

The great tit is a common monogamous territorial passerine, which breeds in secondary holes and artificial nest-boxes in all types of wooded areas throughout Europe and parts of Asia and North Africa (Perrins 1965). Individuals frequently have to cope with temporal and spatial variation in their social and non-social environment. Areas differ in the presence and distribution of resources such as food, roosting and breeding holes in both time and space (Gibb 1954; Betts 1955; Van Balen 1973, 1980). Males are territorial throughout the annual cycle, when foraging conditions in and around the territory allow. However, during autumn and winter, the spatial intolerance is often replaced by hierarchical intolerance during flocking behaviour with other neighbouring territory owners and their mates and non-territorial birds, particularly when food is locally unpredictable, scarce or difficult to find (Drent 1984). Females compete for males with a strong preference for males with territorial status. The hierarchical organisation in flocks is similar to the classic study of jays by Brown (1963; De Laet 1976; Drent 1983) and resembled the scrounger-producer system as pointed out by Barnard & Sibly (1981). Low-ranking birds often disperse from flock to flock and thereby between areas. After independence of the parents, that is *ca.* 35 days after hatching, the young form flocks in which social hierarchies develop. In this period juveniles disperse between flocks and areas, first caused by the earlier experiences by the parents and, later, by density and food availability and distribution (Goodbody 1952; Dhondt 1979; Drent 1984). From September of the year of fledging onwards, young males start to claim a territory or individual dominance area on vacant ground between the still-existing territories of adult males or on less attractive parts of large territories. Early territory ownership strongly increases survival, dispersal and reproduction thus fitness (Drent 1983, 1984).

### (b) *Animal collection from the field*

We collected nestlings from two wild populations at an age of 10 days after hatching. In 1993, we collected 81 nestlings from 11 broods. In 1998, 15 pairs were caught in the breeding boxes with spring traps and transported to the laboratory together with their 102 nestlings. These birds were taken from the same popu-

lations as those from 1998. In the laboratory, the adults were housed individually in standard cages of 0.9 m × 0.4 m × 0.5 m with solid bottom, top and rear walls and a wire-mesh front and three perches. They were tested for exploration of a standard novel environment 10 days after capture. After testing, the parents were released at their capture site.

We only collected broods without nestling mortality and with a normal nestling growth (weight on day 10: 13.0 g or higher) (see Van Balen 1973). For the later generations the nestlings were weighed at the age of 5 and 10 days. The tarsus was measured at day 10. If at an age of 5 days the weight of the young stayed behind the expectation of well-grown broods (less than 7.0 g) artificial food (frozen mealworms and larvae of the wax moth) was offered daily in a small cup inside the respective nest-box. Almost all these parents used this food, which resulted in a mean brood weight greater than 13 g on day 10 after hatching.

### (c) *Rearing of the young*

Ten-day-old nestlings, collected from the field, were divided into groups of 4–5 siblings. These groups were placed in natural nests in cardboard boxes. The young were hand reared on a mixed diet (Verbeek *et al.* 1994). Survival during hand rearing was 95%, and 17–20 days after hatching, the normal fledging age, the young start to leave the nests. The fledglings were then housed in small wire cages (0.5 m × 0.4 m × 0.4 m) with two perches, maintaining the sibling groups from the nestling phase. At day 20, small cups containing a beef heart mixture, supplemented with insect food and water were placed in the cages. Within a few days after the first young started to exploit this food, hand feeding was gradually withdrawn. At day 35 after hatching birds were housed individually in standard cages. At this age, juveniles in the field also normally become independent of their parents. Birds were kept under natural light conditions with acoustic and visual contact with each other. Juveniles of parents with different scores were housed in the same room. Each cage was connected to a light-tight observation room (4.2 m × 2.5 m × 2.3 m) via a sliding door (20 cm × 20 cm) in the rear wall.

### (d) *Standard tests*

Two different tests were performed to all hand-reared juveniles. A novel environment test was conducted in a standard observation room (analogous to an open field test; for details see Verbeek *et al.* (1994)) two days after individual housing. The time needed to visit four of the five artificial wooden trees was converted linearly to a scale of 0–10. A score of 10 ('fast') means that the bird reached the fourth tree within 1 min and a score of 0 means that the bird did not reach the fourth tree within 10 min ('slow'). Respectively, 10 and 11 days later, this was followed by tests of the reaction to two different novel objects conducted in their individual cage (see also Verbeek *et al.* 1994). In these tests, a novel object was introduced on one of the outer perches. For this, a penlight battery was used on the first day and an 8 cm bendable pink rubber toy ('pink panther') on the second day. The latency to approach this object (in seconds) and the shortest distance to this object within 120 s were scored. The results for each test were converted linearly to a 0–5 scale. A score of 5 was given when the bird pecked the object, a score of zero when the bird did not land on the branch on which the object was situated. The sum of the test scores: 0–20 is the trait selected on, where 0 is the extreme 'slow' and 20 is the extreme 'fast' score.

### (e) *Bi-directional artificial selection of early exploratory behaviour*

For the parental generation, we selected those juveniles from the birds collected in 1993 that had the highest and lowest summed scores. Both fast and slow lines were started and maintained with nine pairs. Pairs were kept in aviaries (2.0 m × 4.0 m × 2.5 m) from December onwards. In spring, eggs were collected daily and exchanged with dummy eggs. Clutches of eight eggs from the same pair were brought to the field and incubated by foster females. One day after hatching, nestlings were exchanged to form mixed broods of, at most, eight young. As far as possible, each foster brood consisted of equal numbers of offspring from both selection lines. Nestlings were collected at an age of 10 days and then hand reared in mixed groups in the laboratory. For later generations we formed pairs from the offspring by selecting the individuals with the highest scores for the 'fast' line and lowest scores for the 'slow' line, avoiding full-sib and first-cousin mating. Hand rearing was identical to that carried out on the parental generation.

### (f) *Statistical analysis*

The narrow sense heritability ( $h^2$ ) measures the proportion of total variance that is attributed to the effect of genes and is defined as the ratio of additive genetic variance ( $V_A$ ) to total phenotypic variance ( $V_P$ ), with  $h^2 = V_A/V_P$  (Falconer & Mackay 1996; Lynch & Walsh 1998). We estimated the within-family in relation to between-family variance (also referred to as broad sense heritability) using a Kruskal–Wallis test with nest as a grouping variable. For this analysis, the data from both 1993 and 1998 were used. The resemblance of offspring to their wild-caught parents was calculated from weighted and non-weighted mid-offspring–mid-parent regression on the exploration of a novel room. For the analyses of the bi-directional selection lines, we used the mid-parent values and the mean of sib groups per guest pair. For the analysis of the foster parent effect in 1995 and 1996, we used a Poisson regression with juvenile exploration score, corrected for over-dispersion (for details see Crawley (1993)), as the dependent variable and foster parent and biological parent as factors in the full model. For this analysis, we used GLIM 4.0 for ecologists (Crawley 1993). For all other analyses, we used SPSS 10.1 software.

## 3. RESULTS

### (a) *Realized heritability of early exploratory behaviour*

In table 1 the population measures of the exploration score for the juvenile populations of 1993–1997 are given. Although there were fluctuations in the response to selection, the artificial selection experiment showed strong effects in four generations (figure 1a). In the up- and down-selection the mean score changed respectively from 1.78 to –1.31 units per generation. In figure 1b the cumulative response to selection (response compared with the starting population) has been plotted against the cumulative selection differential (the deviation of the individuals used as parents from the mean value in their generation). The realized heritability in the base population is the proportion of the total observed variance in the starting population that can be attributed to genetic factors, which in this case is calculated from the regression coefficient of the cumulative response to selection over the cumulative directional selection differential:  $0.545 \pm 0.046$  (linear regression;  $r^2 = 0.95$ ,  $F_{1,8} = 139.32$  and  $p < 0.0001$ ).

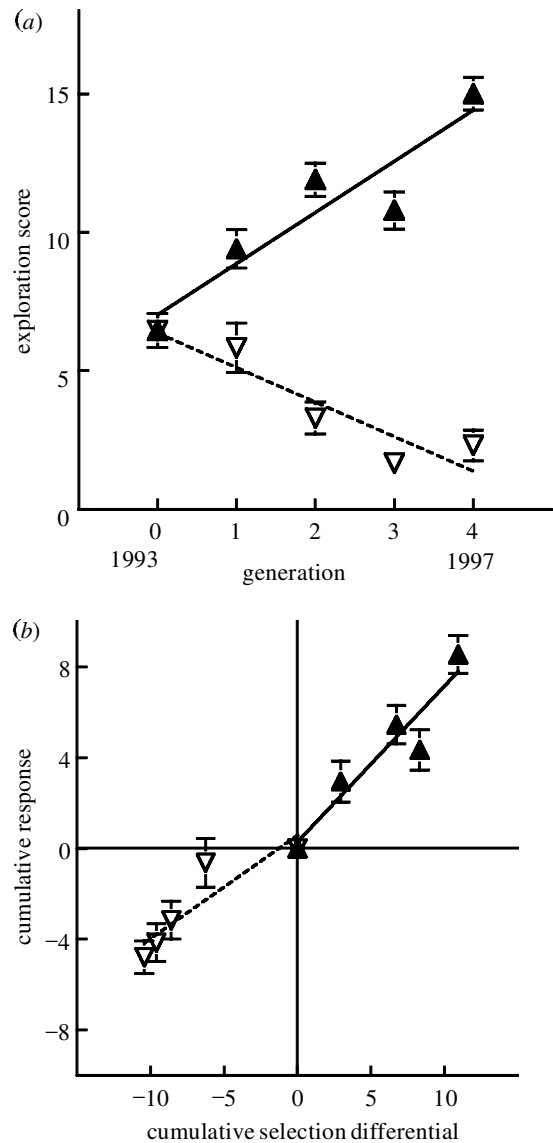


Figure 1. Response to artificial selection per generation (a) and relative to the cumulative selection differential (b) for both up-selection (filled triangle) and down-selection (inverted open triangle) with s.e.m. Lines represent regression lines for up- and down-selection. The slopes for up- and down-selection separately are 0.69 (linear regression;  $r^2 = 0.90$ ,  $F_{1,4} = 26.03$  and  $p = 0.015$ ) and 0.45 (linear regression;  $r^2 = 0.80$ ,  $F_{1,4} = 12.27$  and  $p = 0.039$ ), respectively.

Behavioural traits are usually quite sensitive to the environment in which individuals have grown up. A careful inspection of figure 1a shows that both lines have relatively low scores in the  $F_3$  and relatively high scores in the  $F_4$  generations. It is therefore necessary to investigate whether the effects of the microenvironment cause a parent–offspring resemblance. Our cross-fostering design, in which a large proportion of the offspring in the  $F_2$  (1995) and  $F_3$  (1996) generations from both selection directions were raised together in mixed broods by foster pairs in the field until 10 days after hatching, made it possible to analyse this in more detail. Maternal effects transmitted through egg characteristics however are, although unlikely, still possible. In figure 2, the mean exploration score of full sibs that were raised together in one foster

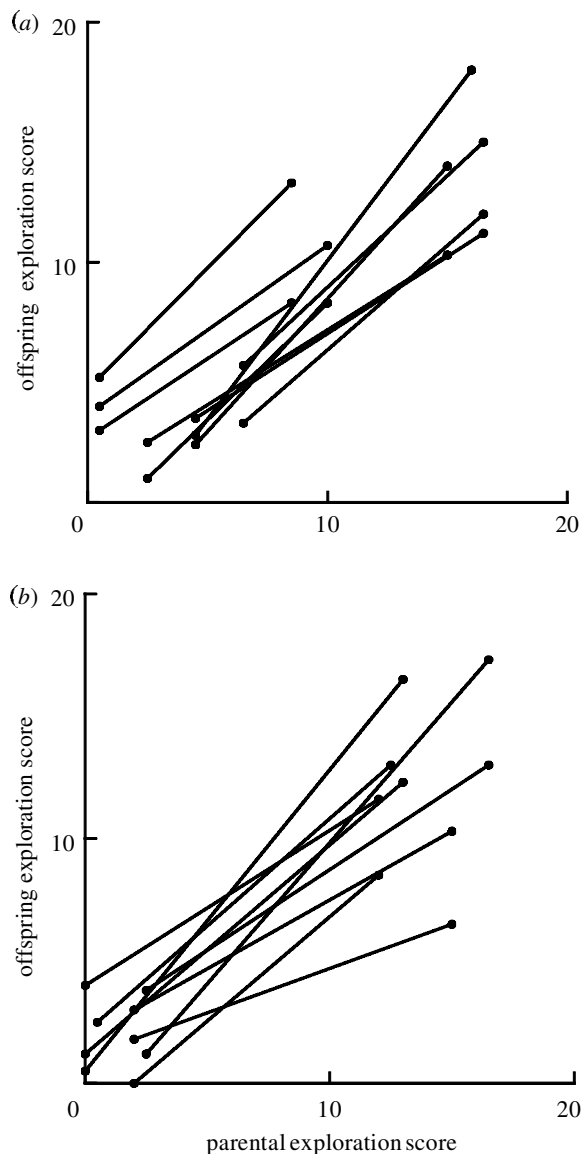


Figure 2. Effect of cross fostering for the  $F_2$  generation in 1995 (a) and the  $F_3$  generation in 1996 (b). Each line connects two dots, which represent one fast and one slow sib group, which were raised together in one foster group. Both graphs show data on nine foster groups.

nest are plotted against the mid-parent scores of their biological parents, for the  $F_2$  (figure 2a) and the  $F_3$  (figure 2b) generation. A line connects the two sib groups from the different selection lines that were raised together in one foster nest. In the absence of a genetic component, we would expect horizontal lines. In the case of solely genetic effects, the regression coefficient of the lines would approach one. Using the mean values of sib groups raised together in one foster nest, the regression coefficient of offspring values on parental values is 0.75 (range: 0.62–1.32; linear regression:  $R^2 = 0.70$ ,  $F_{1,18} = 42.99$  and  $p < 0.0001$ ; figure 2a) in the  $F_2$  generation and 0.73 (range 0.36–1.23; linear regression:  $R^2 = 0.68$ ,  $F_{1,21} = 45.14$  and  $p < 0.0001$ ; see figure 2b) for the  $F_3$  generation. Because eggs were brought to the field with minimum delay, and we maximized the number of chicks raised in mixed broods, combinations are often not symmetrical, which complicates statistical analysis. However, the results of a Poisson regression of juvenile exploration score with bio-

logical, and foster, parents as factors are clear. Both for the  $F_2$  and  $F_3$  data, there is a highly significant effect of biological parents (1995:  $\chi^2_8 = 56.48$  and  $p < 0.0001$ ; 1996:  $\chi^2_{10} = 72.11$  and  $p < 0.0001$ ) and no effect of foster parents (1995:  $\chi^2_{12} = 5.47$  and  $p = 0.94$ ; 1996:  $\chi^2_{17} = 8.33$  and  $p = 0.96$ ). Interactions were not significant (1995:  $\chi^2_2 = 0.12$  and  $p = 0.94$ ; 1996:  $\chi^2_3 = 1.94$  and  $p = 0.58$ ). Analysis of the data for both years combined confirms a significant effect of the biological parents, but no interaction and no effect of guest pairs. This implies that the effect of raising conditions within our set-up is small and that parent–offspring resemblance is not due to parental influences on the juvenile environment.

#### (b) *Heritability of wild-caught parents and their hand reared offspring*

To confirm whether the variation in our laboratory lines is related to the variation under natural conditions, we estimated the resemblance of exploration scores of adult great tits collected from the field and their laboratory-raised nestlings. We collected a second group of wild adult birds together with their 10-day-old offspring in 1998. There was no difference in mean exploration scores per nest between these juveniles and those collected in 1993 ( $t$ -test,  $t_{24} = 0.46$  and  $p = 0.65$ ). The within-nest variance was again smaller than the among-nest variance (Kruskal–Wallis test,  $\chi^2_{25} = 46.0$  and  $p = 0.006$ ). This demonstrates that young from the same brood show more resemblance to each other than to offspring of other broods. Exploration scores of the juveniles from this group were lower than those of their parents, which were measured as adults. This was probably due to a mixture of age and seasonal effects (Dingemanse *et al.* 2002).

We estimated the resemblance in this group as if it was heritability, although the measurements in parents and offspring were made at quite different ages. Both the weighted ( $h^2 = 0.247 \pm 0.101$  and  $p = 0.017$ ) and the non-weighted ( $h^2 = 0.331 \pm 0.114$  and  $p = 0.018$ ) mid-offspring–mid-parent regression were significantly different from zero, but not from each other ( $t$ -test,  $t_{107} = 0.181$  and  $p > 0.05$ ). Because these two methods produce the most extreme estimates of heritability, this indicates that family size had no major effect.

## 4. DISCUSSION

We have shown that variation in coping behaviour is heritable in a wild bird population by performing a bi-directional selection experiment in captivity. We found a strong response to selection after four generations of selection.

Laboratory conditions might overestimate natural heritabilities, owing to a reduction in environmental variability (Riska *et al.* 1989). Our heritability measures from the mid-offspring–mid-parent regression of wild-caught parents and their hand-reared offspring and the selection experiment in the great tit also show this. This result is also confirmed by a parallel study, where adults from a natural population were taken to the laboratory, tested and released within 24 h (Dingemanse *et al.* 2002). Using known family relationships, broad sense heritability estimates of ca. 30% for the behaviour in an unfamiliar room are similar to this resemblance of adult parents and juven-

Table 1. Population measures of the exploration score for the juvenile populations of 1993–1997.

(Abbreviations:  $S_{cum}$ , the cumulative selection differential;  $n$ , total number of offspring tested;  $m$ , mean; s.e.m., standard error of mean;  $h^2$ , heritability; s.e., standard error of heritability;  $V_P$ , phenotypic variance;  $V_A$ , additive genetic variance.)

type	year	$S_{cum}$	$n$	$m$	s.e.m.	$h^2$	s.e.	$V_P$	$V_A$
down-selection	1993		85	6.45	0.60			31.01	
	1994	-6.26	24	5.83	0.89	0.10	0.00	18.84	1.88
	1995	-8.59	37	3.30	0.57	0.37	0.21	12.10	4.45
	1996	-10.43	47	1.62	0.42	0.46	0.16	8.15	3.75
	1997	-9.61	35	2.31	0.56	0.43	0.13	10.93	4.71
up-selection	1994	2.94	52	9.40	0.68	1.00	0.00	24.29	24.29
	1995	6.74	43	11.91	0.60	0.81	0.10	15.28	12.35
	1996	8.33	60	10.80	0.67	0.52	0.18	26.81	13.97
	1997	10.95	31	15.00	0.59	0.78	0.13	10.80	8.43

ile offspring. This is in agreement with the result from several other comparative studies on the similarity between heritability estimates in the laboratory with those in the field (Riska *et al.* 1989; Weigensberg & Roff 1996). Laboratory estimates of heritability tend to be somewhat higher, but not significantly different.

Furthermore, we cannot completely exclude environmental maternal effects. In a model study Riska *et al.* (1985) pointed out that their influence will diminish after one generation of selection, which in our case would mean that the response to selection would have decreased or even been absent after the second generation of selection (for more details see Reznick & Bryga (1987)).

The question of the evolutionary origin and persistence of phenotypic variation in behavioural traits within populations is a central topic in biology. The genetics underlying individual variation in behaviour in natural populations is often not well known owing to the difficulties in distinguishing between environmental and genetic effects (Griffith *et al.* 1999). The extent to which environmental effects or genes determine individual variation in behaviour is essential for the explanation of coexistence of different phenotypes and thereby for the population dynamics and evolution of the system. The three key questions in understanding the presence of different behavioural traits within one natural population are: how the variation is caused, what the consequences are for the individual fitness and how the variation is maintained.

Behavioural strategies with restricted plasticity are suites of correlated behaviours that reflect within-individual consistency in reactions to cope with environmental challenges across context. In other words, an individual's reaction in one context is linked to its reaction in another context. The different traits of these strategies have not evolved in isolation but as a package (Price & Langen 1992; Lynch & Walsh 1998). The within-individual correlations between traits generate trade-offs in reaction norms across context, which can have a major role in evolution. In understanding the evolution towards behavioural strategies a useful analogy with consistent variation in life history could be made (Stearns 1997). Owing to the trade-offs generated by these correlations, depending on the selection regimes, individuals may not be able to maximize their effort in any given situation, so if we look to the result of one of these reactions in isolation, it often appears sub-optimal. Across contexts in the individual lifespan, the overall result could be more successful than to behave

optimally in one context and have to pay the cost in another context. Therefore, the combination of spatial- and temporal-social and non-social variation in the environment resulting in different selection regimes, and the trade-offs between different traits, can explain the maintenance of the different strategies (Mangel & Stamps 2001).

Genetic differences between behavioural strategies could have critical implications for ecology and evolution. Animals have to cope with an enormous spatial and temporal variation in their social and non-social environment. Under the non-social environment, man-caused changes and variability in the environment become increasingly important. The differences in ability to cope with challenges are an important determinant of differences in local survival, dispersal and reproduction (lifetime reproductive success, fitness). These in their turn determine differences in density and in the genetic structure of populations in time including the frequency distribution of behavioural strategies. Density and frequency distribution are a part of the social environment resulting in competition for resources and in frequency-dependent competition and/or cooperation in flocks and breeding couples, thereby influencing the fitness of their individual members.

Without knowledge of the context and the individual consistent behavioural strategies, it is not surprisingly that conflicting ecological results could arise. Different behaviours, which are part of the strategy, and different consistent behavioural strategies, should not be studied in isolation in one context, as is often done by behavioural ecologists. Understanding the outcome in any given context could require an understanding of the implications of their correlated behaviours over context. This implies that the relative success, in fitness terms, of individuals with different strategies often changes with the context, probably resulting in major consequences for differences in population size and structure (Drent & Marchetti 1999; Drent *et al.* 2002).

However, such knowledge is almost always lacking in studies on vertebrate species under natural conditions. Density-dependent selection could also be a mechanism for the cause of this variation (Chitty 1958). It was shown to be responsible for varying selection pressures, thereby accounting for maintenance of variation in throat colour in lizards (Sinervo *et al.* 2000). To our knowledge, only one other study in birds was able to couple genetic variation in behaviour to fitness consequences (Pulido *et al.*

2001). In respect of behaviour to cope with environmental challenges, only one vertebrate study in a population of wild house mice indicated that the relative frequency of coping strategies changes in the different population-dynamic phases, suggesting that differential selection on these heritable strategies occurs in the wild (Benus *et al.* 1987). Our results, and the extensive knowledge of the ethology and ecology of the great tit, indicate that this species is a suitable model to carry out such research in the wild, and our demonstration of considerable amounts of genetic variation is a major step forward.

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## REFERENCES

- Barnard, C. J. & Sibley, R. M. 1981 Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550.
- Benus, R. F., Koolhaas, J. M. & Van Oortmerssen, G. A. 1987 Individual differences in behavioural reaction to a changing environment in mice and rats. *Behaviour* **100**, 105–122.
- Benus, R. F., Bohus, B., Koolhaas, J. M. & Van Oortmerssen, G. A. 1991 Heritable variation in aggression as a reflection of individual coping strategies. *Experientia* **47**, 1008–1019.
- Betts, M. M. 1955 The food of titmice in oak woodland. *J. Anim. Ecol.* **24**, 282–323.
- Bohus, B., Benus, R. F., Fokkema, D. S., Koolhaas, J. M., Nyakas, C. A., Van Oortmerssen, G. A., Prins, A. J. A., De Ruiter, A. J. H., Scheurink, A. J. W. & Steffens, A. B. 1987 *Neuroendocrine states and behavioural and physiological stress responses*. Amsterdam, The Netherlands: Elsevier.
- Brodie, E. D. & Russel, N. H. 1999 The consistency of individual differences in behaviour: temperature effects of anti-predator behaviour in garter snakes. *Anim. Behav.* **57**, 445–451.
- Brown, J. L. 1963 Aggressiveness, dominance and social organization in the Stellar jay. *Condor* **65**, 460–484.
- Buss, D. M. 1991 Evolutionary personality psychology. *A. Rev. Psychol.* **42**, 459–491.
- Carere, C., Welink, D., Drent, P. J., Koolhaas, J. M. & Groothuis, T. G. G. 2001 Effect of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiol. Behav.* **73**, 427–433.
- Chitty, D. 1958 Regulation in numbers through changes in viability. *Can. J. Zool.* **38**, 99–113.
- Clark, A. B. & Ehlinger, T. J. 1987 Pattern and adaptation in individual behavioral differences. In *Perspectives in ethology*, vol. 7 (ed. Bateson, Klopfer), pp. 1–47. New York: Plenum Press.
- Crawley, M. J. 1993 *GLIM for ecologists*. Oxford: Blackwell Scientific.
- De Kloet, E. R., Rosenfeld, P., Van Eekelen, J. A., Sutanto, W. & Levine, S. 1988 Stress, glucocorticoids and development. *Prog. Brain Res.* **73**, 101–120.
- De Laet, J. 1976 *Gedrag en interacties van de Koolmees Parus major op de voertafel in de winter 1975–76*. Belgium: University of Gent.
- Dhondt, A. A. 1979 Summer dispersal and survival of juvenile great tits in southern Sweden. *Oecologia* **42**, 139–157.
- Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K. & Van Noordwijk, A. J. 2002 Repeatability and heritability of exploratory behaviour in wild great tits. *Anim. Behav.* (In the press.)
- Drent, P. J. 1983 The functional ethology of territoriality in the great tit (*Parus major* L.). University of Groningen.
- Drent, P. J. 1984 Mortality and dispersal in summer and its consequences for the density of great tits *Parus major* at the onset of autumn. *Ardea* **72**, 127–162.
- Drent, P. J. & Marchetti, C. 1999 Individuality, exploration and foraging in hand raised juvenile great tits. In *Proc. 22nd Int. Ornithol. Congr., Durban* (ed. N. J. Adams & R. H. Slotow), pp. 896–914. Johannesburg: Birdlife South Africa.
- Drent, P. J., Dingemanse, N. J. & Van Oers, C. H. J. 2002 Functional significance and heritability in coping strategies in a wild territorial passerine: the great tit. In *Bird research and breeding* (ed. C. Mettke-Hofmann & U. Ganslosser), pp. 25–46. Fürth, Germany: Filander.
- Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics*. New York: Longman.
- Gibb, J. 1954 Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96**, 513–543.
- Goodbody, I. M. 1952 The postfledging dispersal of juvenile titmice. *Br. Birds* **54**, 279–283.
- Greenberg, R. 1995 Novelty responses: the bridge between psychology, behavioral ecology and community ecology? *Trends Ecol. Evol.* **10**, 165–166.
- Greenberg, R. & Mettke-Hofmann, C. 2001 Ecological aspects of neophobia and neophilia in birds. In *Current ornithology*, vol. 16 (ed. V. Nolan & C. F. Thompson), pp. 119–178. New York: Plenum Press.
- Griffith, S. C., Owens, I. P. F. & Burke, T. 1999 Environmental determination of a sexually selected trait. *Nature* **400**, 358–360.
- Hessing, M. J. C., Hagelslo, A. M., Schouten, W. G. P., Wiepkema, P. R. & Van Beek, J. A. M. 1994 Individual behavioral and physiological strategies in pigs. *Physiol. Behav.* **55**, 39–46.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999 Coping styles in animals: current status in behavior and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935.
- Lambrechts, M. M., Perret, P., Maistre, M. & Blondel, J. 1999 Do experiments with captive non-domesticated animals make sense without population field studies? A case study with blue tits' breeding time. *Proc. R. Soc. Lond. B* **266**, 1311–1315. (DOI 10.1098/rspb.1999.0780.)
- Lynch, M. & Walsh, B. 1998 *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer.
- Mangel, M. & Stamps, J. 2001 Trade-offs between growth and mortality and the maintenance of individual variation in growth. *Evol. Ecol. Res.* **3**, 583–593.
- Marchetti, C. & Drent, P. J. 2000 Individual differences in the use of social information in foraging by captive great tits. *Anim. Behav.* **60**, 131–140.
- Mendl, M. & Paul, E. S. 1991 Parental care, sibling relationship and the development of aggressive behavior in 2 lines of wild house mice. *Behaviour* **116**, 11–41.
- Perrins, C. M. 1965 Population fluctuations and clutch-size in the great tit, *Parus major*. *J. Anim. Ecol.* **34**, 601–647.
- Price, T. & Langen, T. 1992 Evolution of correlated characters. *Trends Ecol. Evol.* **7**, 307–310.
- Pulido, F., Berthold, P., Mohr, G. & Querner, U. 2001 Heritability of the timing of autumn migration in a natural bird

- population. *Proc. R. Soc. Lond. B* **268**, 953–959. (DOI 10.1098/rspb.2001.1602.)
- Reznick, D. N. & Bryga, H. 1987 Life-history evolution in guppies (*Poecilia reticulata*): 1. Phenotypic and genetic changes in an introduction experiment. *Evolution* **41**, 1370–1385.
- Riska, B., Rutledge, J. J. & Atchley, W. R. 1985 Covariance between direct and maternal genetic effects in mice, with a model of persistent environmental influences. *Genet. Res.* **45**, 287–297.
- Riska, B., Prout, T. & Turelli, M. 1989 Laboratory estimates of heritabilities and genetic correlations in nature. *Genetics* **123**, 865–871.
- Sinervo, B., Svensson, E. & Comendant, T. 2000 Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* **406**, 985–988.
- Sluyter, F., Bult, A., Lynch, C. B., Van Oortmerssen, G. A. & Koolhaas, J. M. 1995 A comparison between house mouse lines selected for attack latency or nest building: evidence for a genetic basis for alternative behavioral strategies. *Behav. Genet.* **25**, 247–252.
- Sluyter, F., Van Oortmerssen, G. A. & Koolhaas, J. M. 1996 Genetic influences on coping behaviour in house mouse lines selected for aggression: effects of the y chromosome. *Behaviour* **133**, 117–128.
- Stearns, S. C. 1997 *The evolution of life histories*. Oxford University Press.
- Van Balen, J. H. 1973 A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. *Ardea* **61**, 1–93.
- Van Balen, J. H. 1980 Population fluctuations in the great tit and feeding conditions in winter. *Ardea* **68**, 143–164.
- Van Oortmerssen, G. A. & Bakker, T. C. M. 1981 Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behav. Genet.* **11**, 115–126.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994 Consistent individual differences in early exploratory behaviour of male great tits. *Anim. Behav.* **48**, 1113–1121.
- Verbeek, M. E. M., Boon, A. & Drent, P. J. 1996 Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* **133**, 945–963.
- Verbeek, M. E. M., De Goede, P., Drent, P. J. & Wiepkema, P. R. 1999 Individual behavioural characteristics and dominance in aviary groups of great tits. *Behaviour* **136**, 23–48.
- Weigensberg, I. & Roff, D. A. 1996 Natural heritabilities: can they be reliably estimated in the laboratory? *Evolution* **50**, 2149–2157.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994 Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.

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