



Personalities in great tits, *Parus major*: stability and consistency

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We carried out a longitudinal study on great tits from two lines bidirectionally selected for fast or slow exploratory performance during the juvenile phase, a trait thought to reflect different personalities. We analysed temporal stability and consistency of responses within and between situations involving exploratory and sociosexual behaviour. Exploratory behaviour was assessed both in the juvenile phase and in adulthood (2–3-year interval) by means of a novel object test and an open field test. We assessed agonistic behaviour twice in adulthood with a 7-month interval by confronting males with either a caged or a free-moving intruder. We assessed sexual behaviour in adulthood by presenting two caged conspecifics of the opposite sex. Exploratory scores still differed between the lines at both ages; however, slow birds became faster with age and were less stable than fast birds. Slow explorers spent more time in agonistic displays and took longer to attack than fast birds. Slow birds also took longer than fast birds to approach a member of the opposite sex. We conclude that, at the level of line, behavioural differences were stable over time and extended to other situations. At the individual level, consistency across time and situations was less evident overall, but fast birds tended to be more consistent than slow birds. Slow explorers could be described as reactive copers, showing a relatively high degree of behavioural plasticity, and fast explorers as proactive, in line with similar studies in rodents.

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Individuals differ nonrandomly in how they deal with stressors and novelties and appear to vary along a behavioural continuum from shy to bold (Wilson et al. 1993, 1994; Verbeek et al. 1994; Schwabl 1995). In the past decade, it has become clear that these differences covary with other behavioural traits, such as aggression, exploration, risk taking, fearfulness and reactivity. For example, bold and less fearful individuals are more aggressive than shy and fearful ones (e.g. Verbeek et al. 1996; Malmkvist & Hansen 2002). Several lines of evidence, including selection line experiments, suggest that these differences are

aspects of a coherent and heritable behavioural organization maintained by natural selection (Koolhaas et al. 1999; Drent et al. 2003; Dingemanse et al. 2004; Sih et al. 2004; Groothuis & Carere 2005). Such individual behavioural organizations have been observed in a wide range of taxa, including invertebrates. They are referred to as behavioural syndromes, predispositions, profiles, coping styles, strategies and axes (Sih et al. 2004; Groothuis & Carere 2005), comparable to human personalities (Gosling 2001).

The study of animal personalities has critical implications for evolution, because when different behaviours are correlated they evolve not in isolation, but as a package owing to pleiotropy, gene linkage or common proximate mechanisms (Price & Langen 1992; Sih et al. 2004). These correlations are not always adaptive and can generate trade-offs across situations that may be important in evolution. Why correlated suites of behaviour are favoured rather than single traits is not known, but an important implication is that behaviours that are part of such sets of traits should not be studied in isolation, since the evolution of one behaviour can be constrained by its linkage to other behaviours. It is therefore of interest to demonstrate the

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consistency and stability of such behavioural organizations with longitudinal studies (Sih et al. 2004).

Several studies have investigated the consistency of behavioural responses over time and across different tests or situations. Some approach the problem at the individual level, while others make use of genetic lines selected on parameters thought to reflect personality traits. These latter studies tend to define the behavioural phenotypes in discrete categories, such as styles or strategies, emphasizing a primacy of genetic factors underlying personality traits (e.g. Benus et al. 1991; Malmkvist & Hansen 2002; Drent et al. 2003). So far, the results have given conflicting evidence and whether individual differences in behavioural strategies are context specific or domain general is controversial (e.g. Spoolder et al. 1996; D'Eath & Burn 2002; but see Dickson et al. 1970; Hessing et al. 1993; Réale et al. 2000; Visser et al. 2001). At the group level generalization seems more evident (Benus et al. 1987, 1990, 1991; reviewed in Steimer et al. 1997; Koolhaas et al. 1999, 2001; Malmkvist & Hansen 2002; Groothuis & Carere 2005). However, to our knowledge, few studies have tested life-long stability of group differences (Koolhaas et al. 1999; Garipey et al. 2001; Cavigelli & McClintock 2003).

In the great tit, a small passerine bird, many individuals within a given population show extreme phenotypes, being 'fast' (or bold) or 'slow' (or shy) in exploration tasks including novelty responses (Verbeek et al. 1994). There is a considerable amount of both additive genetic variation and dominance genetic variation of such personality traits in wild great tit populations (van Oers et al. 2004a), and selection line experiments have shown high heritability ($54 \pm 5\%$) for early exploratory behaviour based on four generations of artificial selection (Drent et al. 2003). These trait characteristics correlate both phenotypically and genetically with differences in aggression (Verbeek et al. 1996; van Oers et al. 2004b), foraging behaviour (Verbeek et al. 1994; Marchetti & Drent 2000), response to stress and risk-taking behaviour (Verbeek et al. 1999; Carere et al. 2001, 2003; Carere & van Oers 2004; van Oers et al. 2004c). The lines seem to resemble selection lines established from wild house mouse, *Mus domesticus*, populations that differ in aggression ('proactive' and 'reactive' copers, Koolhaas et al. 1999; Groothuis & Carere 2005). They are thought to be relatively stable with age. The differences in exploration and novelty response have predictive value for differences in aggression and dominance 12–16 weeks later (Verbeek et al. 1994, 1996, 1999; Verbeek 1998). However, no studies specifically designed to follow the same individuals of the selection lines in different situations and over a long time span have directly assessed the consistency and stability of such correlated suites of traits.

We studied temporal stability and consistency within a situation and consistency across different situations. We differentiate between consistency and stability because, while stable traits are also consistent over time, consistent traits are not necessarily stable over time. An example of the latter is that individuals may become more aggressive with age, whereas the rank order of their aggression scores within each age class can remain the same (e.g. Roberts &

DelVecchio 2000). We followed longitudinally a single cohort of two great tit lines of fast and slow explorers, assessing exploratory behaviour (two independent tests), agonistic behaviour and sexual behaviour (Table 1).

Our first aim was to characterize the lines at the behavioural level across different situations and analyse their temporal stability. Therefore, we compared the behaviour of the two lines over two ages and across different situations. Based on previous studies on birds phenotypically characterized as fast or slow explorers (Verbeek et al. 1994, 1996), we expected to find line differences in other situations, in particular agonistic behaviour. Our second aim was to analyse consistency over time and across different situations at the level of the individual. Therefore, we computed correlations of the behaviours over two age classes and across different situations separately in the two lines.

METHODS

Subjects

The great tit is a territorial, nonmigratory passerine bird (body mass: 16–20 g) inhabiting woods and parks. At our latitude the breeding season is relatively short (April–June), with most chicks hatching in the first half of May. Males are territorial throughout the annual cycle, but during autumn and winter, particularly when food is scarce, individuals may form flocks with a clear social rank order (Drent 1983). Male–male competition is common, and the species has an elaborate repertoire of agonistic behaviour (Blurton-Jones 1968; Wilson 1992). In The Netherlands the estimated survival rate in the first year is around 0.25, and for older birds around 0.50 (Tinbergen & Daan 1990). Maximal life span is 9 years. In captivity, survival is much higher (0.80–0.95) and maximal life span is 10 years (P. J. Drent, unpublished data).

In 1993, an artificial bidirectional selection programme was started on the basis of the outcome of exploration tests carried out at the age of 35–50 days (Drent et al. 2003). We used 20 fast (10 males, 10 females) and 14 slow birds (8 males, 6 females) of the third and fourth generation originating from this programme. No full or half-siblings were present. All birds were experienced breeders and were naïve with respect to experiments other than the exploration tests. Most of the birds (23) hatched in 1996; the remaining hatched in 1995 (5), in 1994 (4) and in 1997 (2). Hereafter we categorize birds as juvenile or adult, since there was no evidence for an effect of age. Neither body mass nor tarsus length differed between the two lines at any age and these variables did not correlate significantly with any behavioural measure analysed in this study.

Housing During the Juvenile Phase

Table 1 gives an overview of the tests, the time schedule and the housing conditions. The experimental birds hatched at the Centre for Terrestrial Ecology, Heteren, The Netherlands where they were reared and tested for early exploratory behaviour (Drent et al. 2003). They were

Table 1. Summary of the tests used to evaluate consistency of behavioural traits in male and female great tits of the two selection lines

Test	Stimuli	Duration	Timing	Housing	Comment
Novel environment	Novel environment with artificial trees	10 min	Juvenile phase (35–40 days, June 1996) and adulthood (September 1999)	Individual cage indoor	Criteria for bidirectional selection, score 0–10*
Novel object	Novel object in home cage	Two tests 2 min each	Juvenile phase (45 days, June 1996) and adulthood (September 1999)	Individual cage indoor	Criteria for bidirectional selection, score 0–10*
Agonistic behaviour I	Male intruder	Three sessions 10 min each	Adulthood, August 1998	Outdoor aviary with pair mate	Caged intruder
Agonistic behaviour II	Male intruder	10 min	Adulthood, February 1999	Individual cage indoor	Free intruder
Sexual behaviour	Live, opposite sex, caged	30 min	Adulthood, March 1999	Outdoor aviary	Two caged stimuli

Agonistic behaviour was tested only in males. See [Methods](#) for details.

*The combination of these tests (exploration score 0–20) is the selection trait ([Drent et al. 2003](#)).

the offspring of pairs kept in aviaries. Eggs of these pairs were incubated and chicks reared by wild foster parents until day 10 after hatching and hand reared in standard conditions from day 10 until independence (for details see [Verbeek et al. 1994](#); [Drent et al. 2003](#)). Thereafter (days 25–30 after hatching), they were housed individually in standard cages (0.9 × 0.4 m and 0.5 m high) with a wooden bottom, top, sides and rear walls, a wire-mesh front and three perches. They were kept under natural light conditions and had auditory and visual contact with other individuals housed in the same room. Food (commercial seed mixture, sunflowers and a protein-rich mixture supplemented daily with mealworms) and water were provided ad libitum. During autumn and early winter birds were housed in outdoor aviaries (2.0 × 4.0 m and 2.5 m high) in unisex flocks of six to eight individuals, whereas from late winter to early summer they were kept in similar aviaries, but in male–female pairs for breeding and the selection experiment ([Drent et al. 2003](#)).

Housing During Adulthood

The birds were moved when about 2 years old (March 1998) to the facilities of the Biological Centre of the University of Groningen, Haren, The Netherlands, about 170 km north of the original location. Upon arrival they were housed in male–female pairs of the same line in outdoor aviaries for breeding. The aviaries (1.5 × 3.0 m and 2.0 m high) had solid walls and ceiling, and wire mesh at the front. They contained a nestbox, perches on the left and right walls and a feeding table in the centre (40 × 40 cm). The bottom was covered with sand. Food was similar to that in the individual standard cages. During the first test of agonistic behaviour, carried out after the breeding season immediately after moult (August 1998), birds were still housed in this way ([Table 1](#)).

One month later (September 1998), all birds were individually housed in standard cages (0.8 × 0.4 m and 0.4 m high) with a sawdust-covered solid bottom, top, side and rear wooden walls, a wire-mesh front and three perches. Cages were kept indoors in a room (4.6 × 2.8 m

and 2.6 m high) under artificial light conditions (10:14 h light:dark regime), each bird having auditory and visual contact with other conspecifics. Food and water were as in the aviaries. Under these housing conditions the males underwent the second test of agonistic behaviour (February 1999). Thereafter, birds were rehoused in the outdoor aviaries individually and, after 3–5 days of habituation, underwent the sexual behaviour tests (March 1999). After that, the same pairs of the previous year (when possible) were formed for breeding. In late summer (September 1999), all birds were again moved indoors and housed individually in standard cages as described before for the final exploration tests.

Exploration Tests

Details of the tests are provided elsewhere ([Drent et al. 2003](#)). Briefly, for the novel environment test birds were allowed to explore a room with five artificial wooden trees for 10 min. The time needed to visit four of the five trees was converted linearly to a 0–10 scale. A score of 10 meant that the bird reached the fourth tree within 1 min and a score of 0 that it did not reach the fourth tree within 10 min. For the novel object test, two sessions were carried out with a novel object on one of the outer perches. We used a penlight battery on the first day and an 8-cm pink rubber toy on the third day. We recorded the latency to approach the object and the shortest distance to it within 120 s and converted the results for each session linearly to a 0–5 scale. A score of five was given when the bird pecked the object and a score of zero when the bird did not land on the perch with the object. The sum of the three test scores (0–20) is the selected trait, where 0 is the extreme 'slow' and 20 is the extreme 'fast' bird ([Drent et al. 2003](#)).

During the juvenile phase, the tests were performed at days 35–40 (novel environment) and days 45–50 (novel object) after hatching. During adulthood (3 years) they were performed in the same sequence and at an interval of 3–5 days between tests.

Agonistic Behaviour Tests

A live adult great tit male of unknown exploration score confined in a wire cage (20 × 20 × 20 cm) was used as a stimulus and put in the centre of the feeding table of the aviary for 10 min. We recorded the latency to approach it and the behaviour of the experimental male. The test started when we put the cage with the stimulus bird into the aviary and stopped after 10 min. We repeated it for 3 consecutive days at the same time of day (between 1000 and 1400 hours). Each session was recorded on videotape with a Camcorder (Canovision EX1 Hi) focused on the table. Tapes were scored afterwards at normal speed by a person unaware of the selection line of the animals, using a keyboard event recorder (Observer version 3.0, Noldus Information Technology b.v. Wageningen, The Netherlands). We focused on the male's behaviour, since the female pair mate did not show active involvement in the agonistic interactions. We observed the latency (s) to land on the table with the cage (approach to the stimulus) and the total duration (s) of two display postures (wings-out and tail fanning, [Blurton-Jones 1968](#)).

Seven months later (February 1999, [Table 1](#)), each male, housed in an indoor cage, was individually confronted in his resident cage with one of three full-grown males acting as intruders (age: 7 months) for 10 min. The three intruders had the same parents and age, similar weight and were experimentally naïve. Each resident was tested once between 1000 and 1400 hours. We did maximum of three tests per day, each test with a different intruder–resident dyad. Each intruder was used once per day. Observations were made from behind a wooden panel, which was put in the room 2 days before the first confrontation. Tests were recorded on videotape and two independent persons scored tapes at slow motion. We considered the following parameters: latency to attack, frequency of attack episodes and time spent displaying (mainly the horizontal posture, sometimes combined with wings-out and tail fanning, [Blurton-Jones 1968](#)). No main effect of the intruder or its interaction with line emerged in any of the three parameters measured (e.g. ANOVA with line and intruder as fixed variables for log-transformed attack latency: $F_{2,16} = 0.43$, $P = 0.66$). One slow and one fast male did not land on the table during the first test and one slow male did not attack during the second test. They were assigned a latency of 600 s.

We acknowledge that in the first test using only one individual as a stimulus is not ideal because the two lines might respond differently to that particular bird. To limit and standardize its behavioural performance we confined it in a small cage (see also [Ethical Note](#) for additional information). The results of this test were, however, very similar to that in which we used more stimuli (the second test, see [Results](#)), while in the latter there was no effect of the stimulus bird (see above).

Sexual Behaviour

Both males and females were tested independently in early spring in outdoor aviaries in the framework of a parallel study on partner preference in relation to coping

strategy ([Groothuis & Carere 2005](#)). Each subject was exposed in a single 30-min session simultaneously to two stimulus birds. Each stimulus bird was confined in a cage (30 × 40 cm and 25 cm, provided with a perch, water and food), each of a different line and of opposite sex to the experimental bird. Tests were carried out between 0700 and 1000 hours and behaviour was observed from behind a one-way screen. After 15 min, we exchanged the positions of the two cages to control for any side preference. Stimulus birds were used not more than twice and always in different combinations. For the purposes of this study we scored for both experimental males and females the latency to approach the first of the two stimuli. All individuals approached the stimulus bird within the cutoff time.

Analysis

Behavioural parameters were not normally distributed. To test the performance in the exploration tests over time (temporal stability) we used parametric factorial analysis of variance considering line and sex as grouping factors and age (juvenile phase and adulthood) as the repeated measure factor. The exploration score and the novel environment test needed a square-root transformation to meet the assumptions of the parametric analysis. Multiple comparisons for the variable line in adulthood were performed by Tukey–Kramer LSD (least significant difference) test. Within-line comparisons were performed by paired *t* test. Since transformation did not normalize the data, we used Mann–Whitney *U* test to test line differences in the remaining behavioural parameters, including the first agonistic behaviour test in which the three consecutive sessions were pooled. Consistency over time and across situations at the individual level was assessed first by partial correlation after MANOVA with line as the between-subjects factor, and then by Spearman rank order correlation computed separately in the two lines. We considered five different situations in adulthood: novel object (one variable); novel environment (one variable); agonistic behaviour with caged intruder (two variables); agonistic behaviour with free intruder (three variables); and sexual behaviour (one variable). Since agonistic behaviour was tested only in males, we calculated correlations for this sex only. We predicted negative correlations between exploration scores and the latencies measured in the other situations, since the former increase while the latter decrease with increasing boldness. All statistical tests are two tailed.

Owing to the long time course of the study, not all results include observations of the 34 birds originally assigned to the experiment. Two females of the fast line died from natural causes and a few other birds were not used for other reasons, such as imperfect feather condition or unexpected environmental disturbance during the tests. Sample size is therefore slightly reduced in some tests. Exact sample sizes are reported in the figures.

Ethical Note

Individual housing is a common procedure in research using this resident and highly territorial species

(e.g. Verbeek et al. 1994; Dingemanse et al. 2002). Birds were individually housed, but had visual and acoustic contact with other conspecifics of both sexes in the same room. When facing a social challenge, great tits may show temporary changes in some behavioural and physiological parameters, but well within the range of the adaptive stress response (Carere et al. 2001, 2003). Furthermore body mass was not affected in our studies, no bird became sick or died after the agonistic tests and all individuals could be used for breeding later on. In the first test of agonistic behaviour (see above) the caged intruder was confined in a small wire cage. During the trials no physical contact occurred. In all instances, the resident male landed on the table and hopped around the cage containing the intruder bird displaying agonistic postures. The bird used as a stimulus was an adult captive male previously habituated to the small cage. During the tests it never showed any sign of stress. In a few instances it reacted to the approaching resident by displaying agonistic postures, freezing or attempting to escape, but mostly it remained quiet. It was used for a maximum of 30 min per day (three 10-min sessions with an interval of 30 min in which it received mealworms) and then released back in its home cage, where its behaviour did not show any sign of abnormality. As for the freely moving intruders (three males), in most cases attacks were ‘supplanting’ attacks (Blurton-Jones 1968) without physical contact. Physical fights occurred in only two of 16 confrontations. These two interactions were immediately stopped and we ascertained that the birds involved did not show any sign of injury. Each intruder had in total only five to six confrontations and only one per day. After each confrontation it was always put back in its home cage, where its behaviour did not show any sign of abnormality.

The birds used as stimuli during the sexual behaviour tests were confined in a cage bigger than the one used for the aggression tests and provided with a perch. During the tests the stimulus birds behaved normally, sometimes trying to interact with the experimental bird when the latter showed interest towards them.

The procedure to breed the selection lines fostering eggs laid in captivity to wild parents is reported in detail elsewhere (Drent et al. 2003). The original clutches of the wild foster parents were successfully reallocated to other nests with eggs of similar laying date.

The study was approved by the University of Groningen Animal Experimentation Committee.

RESULTS

Temporal Stability of Line Differences

Overall, slow birds had lower exploratory scores than fast birds, while a significant interaction of age with line was also evident in both tests (Fig. 1a, b, see legend for statistics). Within-line comparisons (paired *t* test) revealed that for the novel environment test no significant changes with age were found in the fast line ($t_{18} = 1.5, P = 0.14$), while the increase in the slow line was not quite significant ($t_{13} = -1.9, P = 0.08$). For the novel object

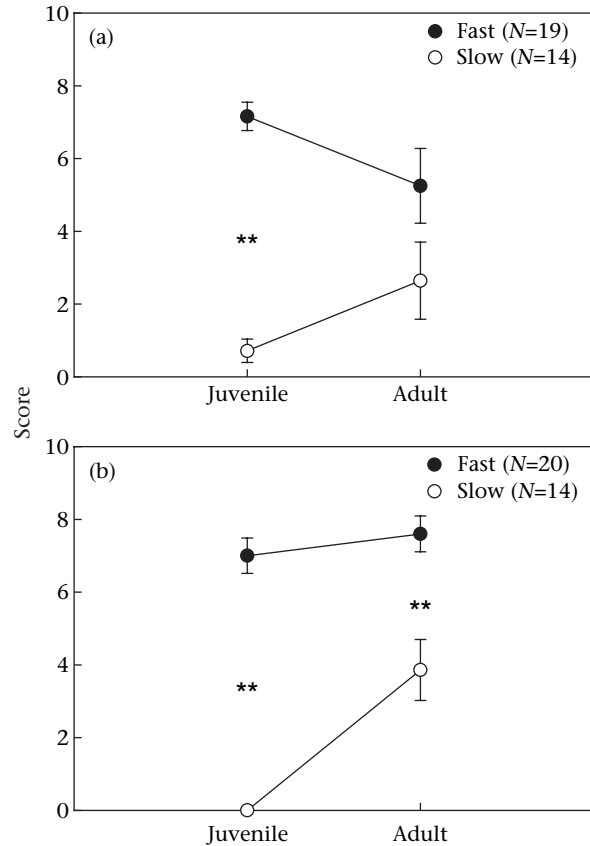


Figure 1. Exploration scores of great tits (males and females pooled) of the two selection lines across age. (a) Novel environment test: ANOVA: line: $F_{1,29} = 31.2, P < 0.001$; age \times line: $F_{1,29} = 6.3, P < 0.02$. (b) Novel object test: line: $F_{1,30} = 79.5, P < 0.001$; age: $F_{1,30} = 19.8, P < 0.001$; age \times line: $F_{1,30} = 10.3, P < 0.001$. Values are means \pm SE. ****** $P < 0.01$. All other main factors and interactions are not significant.

score the slow line showed a significant increase with age ($t_{13} = -4.6, P < 0.001$), but not the fast line ($t_{19} = -1.1, P = 0.29$). Post hoc comparisons for the variable line in adulthood produced significant differences in the novel object ($P < 0.01$), but not in the novel environment score.

No main effect of sex or its interaction with age was detected, but the interaction of sex with line was significant for the novel environment test. In the slow line, females showed higher scores than males in both the juvenile and adult phase (line \times sex: $F_{1,29} = 4.8, P < 0.04$, data not shown).

Thus, lines differed markedly in the exploration traits for which they were selected during the juvenile phase. The line difference was still present in adulthood for the novel object test. The fast line was more stable than the slow line in the novel object score.

Consistency Across Situations

Fast males were quicker to approach live conspecifics than slow males: this was significant in the second test of agonistic behaviour (Mann–Whitney *U* test: first test: $U = 19, N_1 = 7, N_2 = 8, P = 0.30$; second test: $U = 12,$

$N_1 = N_2 = 8$, $P < 0.04$; Fig. 2a, c). In both tests fast males spent significantly less time displaying than slow males (fast: $U = 11$, $N_1 = 7$, $N_2 = 8$, $P < 0.05$; slow: $U = 1$, $N_1 = N_2 = 8$, $P < 0.001$; Fig. 2b, d). The fast males also attacked the free intruder more frequently than the slow males ($U = 9$, $N_1 = N_2 = 8$, $P < 0.015$; Fig. 2e).

In the presence of caged conspecifics of the opposite sex, fast males took less time than slow males to approach the stimulus ($U = 11$, $N_1 = 10$, $N_2 = 8$, $P = 0.01$; Fig. 3a). Females showed a nonsignificant trend of a similar difference ($U = 11$, $N_1 = 8$, $N_2 = 6$, $P = 0.09$; Fig. 3b).

So, in the same birds the line difference in behaviour extended to situations other than those used in the selection experiment.

Within-lines Temporal Consistency

The juvenile and adult scores within the novel object and within the novel environment test did not correlate significantly with each other in the fast line, although the latter approached significance (novel object: $r_s = 0.31$,

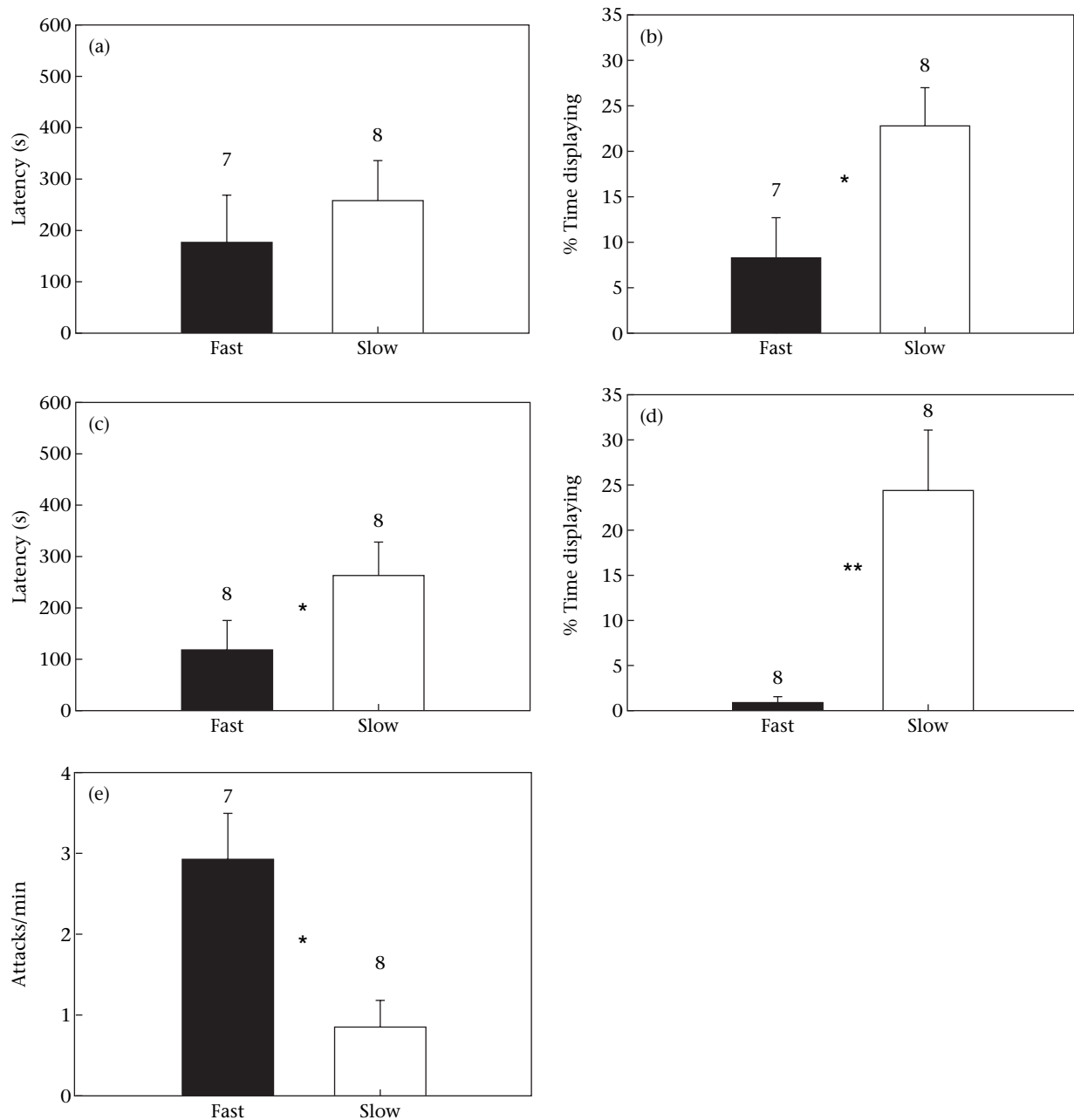


Figure 2. Agonistic behaviour of male great tits of the two selection lines in response to a caged male and to a freely moving male. (a) Latency to approach a caged male. (b) Time spent in agonistic displays towards a caged male. (c) Latency to attack a free male intruder. (d) Time spent in agonistic displays towards a free intruder. (e) Frequency of attacks towards a free intruder: sample sizes are indicated above the bars. Values are means \pm SE. * $P < 0.05$; ** $P < 0.01$.

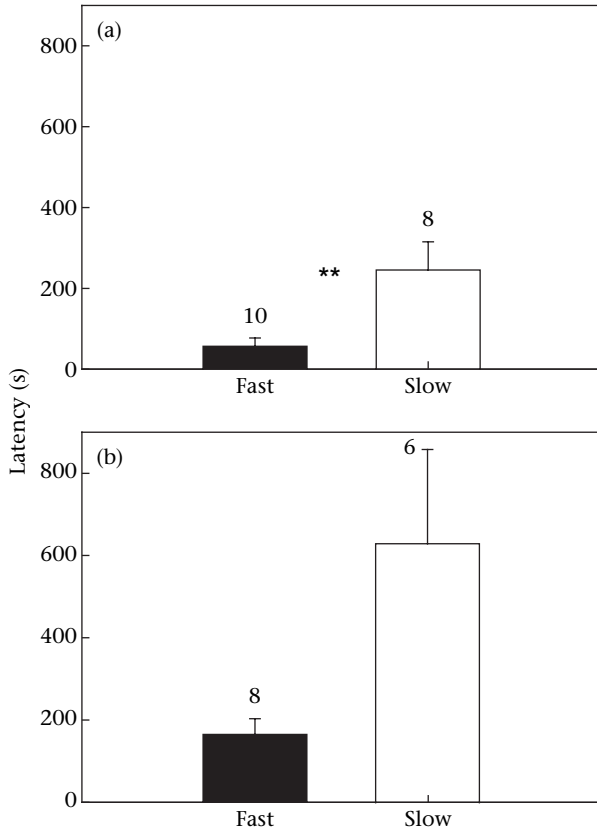


Figure 3. Latency to approach a conspecific of the opposite sex in (a) male and (b) female great tits of the two selection lines. Sample sizes are indicated above the bars. Values are means \pm SE. ****** $P < 0.01$.

$N = 19$, $P = 0.18$; novel environment: $r_s = 0.76$, $N = 20$, $P = 0.07$). For the slow line, the lack of sufficient variation in the novel object score in the juvenile phase (caused by a ‘floor effect’ given by the cutoff time of 2 min) precluded the computation. The novel environment score did not correlate significantly over time ($r_s = 0.26$, $N = 14$, $P = 0.37$).

Thus, at the individual level in both lines we did not find any clear consistency over time.

Within-lines Situation Consistency

The partial correlation matrix did not show any significant consistency across the different situations, except for the display rate in the two agonistic tests (Table 2). Since the two tests were conducted 7 months apart, this indicates a high degree of individual consistency over time too. Latency to attack was negatively correlated with attack rate.

The Spearman correlation coefficients between all variables across the five situations computed separately in the two lines were in general higher in the fast than in the slow birds (Table 3). In the fast males there was consistency between the novel object test and both agonistic tests, especially the first one. In the slow males, the only significant consistencies were again between exploration and aggression. Thus, there was some consistency across situations in behaviour, which was more evident in the fast than in the slow line.

DISCUSSION

Temporal Stability of Line Differences

The two selection lines still differed in exploratory behaviour 2–3 years after the first tests. However, over this time interval birds of the slow line became faster in exploration, and the line difference persisted in adulthood only for the novel object test. Previous studies on juvenile male great tits phenotypically characterized as fast or slow explorers also indicated trends in the same direction, since slow birds tend to become faster over time (Verbeek et al. 1994; Drent & Marchetti 1999). Age-dependent changes in the distribution of attack latencies in the direction of a reduction in differences have been reported for adult male wild rats, *Rattus norvegicus* (Koolhaas et al. 1999). In

Table 2. Partial correlation matrix (MANOVA, adjusted for line) for the five different situations (novel object, one variable; novel environment, one variable; agonistic behaviour with caged intruder, two variables; agonistic behaviour with free intruder, three variables; sexual behaviour, one variable) in adult males of the two lines pooled

Test	Novel object	Novel environment	Caged intruder		Free intruder		
			Latency to approach	Time spent displaying	Latency to approach	Time spent displaying	Attack rate
Novel environment	0.39						
Caged intruder							
Latency to approach	-0.22	-0.27					
Time spent displaying	-0.19	-0.04	-0.59				
Free intruder							
Latency to approach	-0.09	-0.04	0.43	0.03			
Time spent displaying	-0.35	0.11	-0.34	0.60*	0.02		
Attack rate	-0.01	-0.01	-0.45	-0.08	-0.91**	-0.09	
Sexual behaviour							
Latency to approach female	0.51	0.24	0.07	-0.26	0.19	-0.29	-0.22

$N = 15-18$.
* $P < 0.05$; ** $P < 0.01$.

Table 3. Correlation coefficients (Spearman) for the five different situations in adult males of the fast line (above the diagonal, bold) and slow line (below the diagonal)

Test	Caged intruder					Free intruder				
	Novel object	Novel environment	Latency to approach	Time spent displaying	Latency to approach	Latency to approach	Time spent displaying	Attack rate	Latency to approach female	Novel object
Novel environment	0.73*		-0.11	-0.06	-0.11	-0.09	0.19		-0.41	0.26
Caged intruder										
Latency to approach	0.05	-0.32	0.71	-0.67	0.71	-0.67	-0.64		0.68	-0.92**
Time spent displaying	-0.43	-0.08	-0.33	0.78*	-0.33	0.78*	0.15		-0.55	0.80*
Free intruder										
Latency to approach	0.19	0.17	0.12	0.09	-0.07	-0.14	-0.88**		0.59	-0.45
Time spent displaying	-0.55	-0.03	-0.31	0.86**	-0.07	-0.10	0.19		-0.63	0.62
Attack rate	-0.24	-0.26	-0.25	-0.17	-0.92**	-0.10			-0.67	0.36
Sexual behaviour										
Latency to approach female	0.67*	0.59	0.00	-0.05	0.19	-0.36	-0.17			-0.27

N slow line = 8, N fast line = 7-10.

* $P < 0.05$; ** $P < 0.01$.

mice of two lines selected for high and low aggression, longitudinal evaluations showed that repeated exposure to the test situation (days 42, 72 and 235) reduced latencies to and increased frequencies of attack and that these effects were more pronounced in the low-aggressive line (Garipey et al. 2001). These developmental changes from juvenile to adulthood are similar to ours and indicate a more marked propensity to change-over time in animals that respond initially less to the challenges.

Consistency Across Situations

In accordance with the prediction, the line difference extended to agonistic behaviour. Birds that were slow in exploration took longer to attack the intruder and spent significantly more time displaying than fast animals. Since agonistic display behaviour can be considered a component of social exploration, serving to gain information about the opponent and communicate information about aggressive motivation (Wilson 1992; Hurd & Enquist 2001), we conclude that animals adopting different exploratory strategies in a nonsocial setting generalize these to social situations. Differences in aggression have been reported for confrontations in groups of juvenile great tits (10-15 weeks old) phenotypically characterized as fast or slow, as well as in pair-wise confrontations between a fast and a slow male: fast explorers initiated the interaction sooner than slow explorers and birds that started more fights also won more fights (Verbeek et al. 1996; Drent & Marchetti 1999). The line difference was also generalized in a sexual context, at least for latencies. When the birds were exposed to stimuli of the opposite sex they again differed in the latency to approach it: fast males immediately approached one of the females, whereas slow individuals took much longer. This suggests that the selection lines differ in social exploration, including contexts of intersexual interactions.

At the group level, generalization has been reported in several cases. Benus and co-workers found significant correlations between responses to a changing environment, attack latency and routine formation in mice, identifying 'active' and 'passive', or 'proactive' and 'reactive' copers, both strategies aiming at successful environmental control (Benus et al. 1987, 1990, 1991, reviewed in Koolhaas et al. 1999, 2001). Similar evidence has been found for rats (Steimer et al. 1997; Koolhaas et al. 1999), while more recent work showed that farm minks *Mustela vison*, selected for confident and fearful behaviour towards humans generalize their fear responses across several social and nonsocial situations over a 6-weeks' period of tests (Malmkvist & Hansen 2002).

Within-line Consistency

We did not find clear evidence of consistency over time, whereas across situations this was to some extent the case for the fast birds, in which exploration predicted socio-sexual behaviour in some variables. In the slow birds, few

or no significant correlations across situations were found. The fact that the MANOVA partial correlation matrix adjusted for line did not show any significant result (except for display rate), despite the doubling of the sample size, suggests that lines do differ in consistency. Lower consistency among slow individuals may indicate that they show a greater potential to achieve multiple or alternative phenotypes than fast individuals, and this is in line with the more marked propensity to change over time observed in the slow line. These results would suggest that phenotypic behavioural plasticity is a character in its own right (Stearns 1989; Komers 1997; Lowe & Bradshaw 2001), an idea supported by differences in the gene expression of structures underlying neuronal plasticity in mice adopting different coping strategies (Feldker et al. 2003). Paradoxically, the slow individuals could be described as showing a personality profile composed of traits that are not consistent across time and situation. The presence of intrinsically 'unstable' and 'inconsistent' individuals in populations may partly explain the highly controversial results on whether behavioural strategies are context specific or domain general (see below).

However, we acknowledge that our results, including the lack of consistency, have to be treated with caution, since they may depend on the lack of statistical power. With $N = 19$ the minimum detectable correlation with a power of 0.9 is 0.6, assuming a perfect reliability of the measurements, which is rarely the case for behavioural observations. This argument may also in part explain the controversial results in the literature on domain specificity and domain generality. For example, no correlation was found between responses to social and nonsocial challenges in pigs, *Sus scrofa* (e.g. Spooler et al. 1996; D'Eath & Burn 2002; but see Hessing et al. 1993). In juvenile pumpkinseed sunfish, *Lepomis gibbosus*, individual differences in shyness and boldness did not correlate across contexts (Coleman & Wilson 1998), and a similar conclusion was reached for bighorn ewes (Réale et al. 2000) and young horses, *Equus caballus* (Visser et al. 2001). Studies in passerine birds (great tits and zebra finches, *Taeniopygia guttata*) indicate consistency across contexts (maximum of 6–18 weeks, Verbeek et al. 1994, 1996, 1999; Drent & Marchetti 1999; Beauchamp 2000). In pigs aggression has been predicted by previous outcomes of the back test (e.g. Hessing et al. 1993), but these results could not be replicated and have been criticized (e.g. Jensen 1995; D'Eath & Burn 2002). Consistency across two test domains involving novelty and conspecifics was also found in guppies, *Poecilia reticulata* (Budaev 1997).

Instead, consistency and stability over time have been found more often, but mainly over a limited timescale of days or weeks (e.g. fish: Coleman & Wilson 1998; great tits Drent & Marchetti 1999; in guinea pigs, *Cavia aperea*: Albers et al. 1999; bighorn ewes, *Ovis canadensis*: Réale et al. 2000; monkeys, *Macaca mulatta*: Maestripieri 2000; but see Ruis et al. 2000 for intratest inconsistencies in young pigs. In fish, aggression was stable and consistent over a period spanning an early juvenile phase through sexual maturity (Francis 1990). In young horses, long-term consistency in the same situation could not be demonstrated convincingly (Visser et al. 2001).

Proactive and Reactive Strategies or Fearfulness?

We gave the birds an array of challenges that measure aspects of initiative or proactivity. The behavioural patterns observed in the two lines in response to these challenges make the fast and slow great tits resemble the short and long attack latency mouse selection lines (SAL and LAL, Benus et al. 1991; Koolhaas et al. 1999). Selection on this trait in mice also resulted in differences in exploratory behaviour (van Oortmerssen & Bakker 1981; Benus et al. 1991; Koolhaas et al. 1999). The differences in aggression in mice were subsequently shown to correlate with other physiological and behavioural aspects such as routine formation and hypothalamus–pituitary–adrenal axis (re)activity (Benus et al. 1991; Koolhaas et al. 1999; Veenema et al. 2003) and it was concluded that they reflected proactive and reactive strategies (Koolhaas et al. 1999). Similar line differences in routine formation and stress physiology have now been found in fast and slow great tits as well (Verbeek et al. 1994; Drent & Marchetti 1999; Carere et al. 2003; Carere & van Oers 2004). Thus, the characteristics of the fast great tits would correspond to those of aggressive mice (SAL line), adopting a proactive coping style to obtain control over the social and physical environment; the characteristics of the slow great tits would correspond to those of nonaggressive mice (LAL line), adopting a reactive coping style. The similar effect of selection in different domains may be caused by a common basal mechanism underlying the two strategies, holding up across species and groups. Experiments using aggression as a selection trait in great tits and exploration as a selection trait in mice should be carried out to clarify this issue.

The two types of birds may differ in general fearfulness. The extent to which exploration towards a novel stimulus occurs depends in part on how much it is inhibited by fear (Hughes 1997). This in turn would affect the risk assessment behaviour and the speed of decision making, which are expressed in the time spent in agonistic displays and in the propensity to approach both social and nonsocial objects. Fearfulness may be a basic feature of personality, predisposing animals to consistent responses and at the same time making them highly sensitive to experiential factors (Boissy 1995; Greenberg & Mettke-Hofmann 2001; Malmkvist & Hansen 2002; Cavigelli & McClintock 2003). Components of fearfulness may therefore contribute to the personality differences. Indeed, a recent experiment conducted in a different cohort of the same selection lines showed that fast birds return more quickly than slow birds to a feeder where they had experienced a frightening stimulus (van Oers et al. 2004c). Thus, fast and slow birds differ in fearfulness, and thereby risk-taking behaviour, and this is part of the avian personality construct.

In conclusion, at the level of line, behavioural differences were stable over time and extended to other situations. At the individual level consistency across time and situations was less evident, especially in the birds of the slow line. Slow explorers could be described as reactive copers, showing a relatively high degree of behavioural plasticity, and fast explorers as proactive, in line with similar studies in rodents.

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References

- Albers, P. C. H., Timmermans, P. J. A. & Vossen, J. M. H. 1999. Evidence for the existence of mothering styles in guinea pigs (*Cavia aperea* F. Porcelles). *Behaviour*, **136**, 469–479.
- Beauchamp, G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour*, **137**, 301–314.
- 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., den Daas, S., Koolhaas, J. M. & van Oortmerssen, G. A. 1990. Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive mice. *Behaviour*, **112**, 176–193.
- Benus, R. F., Bohus, B., Koolhaas, J. M. & van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47**, 1008–1019.
- Blurton-Jones, N. G. 1968. Observations and experiments on causation of threat displays of the great tit (*Parus major*). *Animal Behaviour Monographs*, **1**, 75–158.
- Boissy, A. 1995. Fear and fearfulness in animals. *Quarterly Reviews of Biology*, **70**, 165–191.
- Budaev, S. V. 1997. 'Personality' in the guppy (*Poecilia reticulata*): a correlational study of exploratory behavior and social tendency. *Journal of Comparative Psychology*, **111**, 399–411.
- Carere, C. & van Oers, K. 2004. Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiology and Behavior*, **82**, 905–912.
- 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. *Physiology and Behavior*, **73**, 427–433.
- Carere, C., Groothuis, T. G. G., Möstl, E., Daan, S. & Koolhaas, J. M. 2003. Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Hormones and Behavior*, **43**, 540–548.
- Cavigelli, S. A. & McClintock, M. K. 2003. Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *Proceedings of the National Academy of Sciences U.S.A.*, **100**, 16131–16136.
- Coleman, K. & Wilson, D. S. 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Animal Behaviour*, **56**, 927–936.
- D'Eath, R. B. & Burn, C. C. 2002. Individual differences in behaviour: a test of 'coping style' does not predict resident-intruder aggressiveness in pigs. *Behaviour*, **139**, 1175–1194.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–937. doi:10.1006/anbe.2002.2006.
- Dingemans, N. J., Both, C., Drent, P. J. & Tinbergen, J. M. 2004. Fitness consequences of avian personalities. *Proceedings of the Royal Society of London, Series B*, **271**, 847–852.
- Dickson, D. P., Barr, G. R., Jahnson, C. P. & Wieckert, P. A. 1970. Social dominance and temperament of Holstein cons. *Journal of Dairy Science*, **53**, 904–907.
- Drent, P. J. 1983. The functional ethology of territoriality in the great tit (*Parus major* L.). Ph.D. thesis University of Groningen.
- Drent, P. J. & Marchetti, C. 1999. Individuality, exploration and foraging in hand raised juvenile great tits. In: *Proceedings of the 22nd International Ornithological Congress, Durban* (Ed. by N. J. Adams & R. H. Slotow), pp. 896–914. Johannesburg: Birdlife South Africa.
- Drent, P. J., van Oers, K. & van Noordwijk, A. J. 2003. Realised heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **270**, 45–51. doi:10.1098/rspb.2002.2168.
- Feldker, D. E., Datson, N. A., Veenema, A. H., Meulmeester, E., de Kloet, E. R. & Vreugdenhil, E. 2003. Serial analysis of gene expression predicts structural differences in hippocampus of long attack latency and short attack latency mice. *European Journal of Neuroscience*, **17**, 379–387.
- Francis, R. C. 1990. Temperament in a fish. A longitudinal-study of the development of individual-differences in aggression and social rank in the midas cichlid. *Ethology*, **86**, 311–325.
- Gariepy, J.-L., Bauer, D. J. & Cairns, R. B. 2001. Selective breeding for differential aggression in mice provides evidence for heterochrony in social behaviour. *Animal Behaviour*, **61**, 933–947.
- Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, **127**, 45–86.
- Greenberg, R. & Mettke-Hofmann. 2001. Ecological aspects of neophobia and neophilia in birds. In: *Current Ornithology*. Vol. 16 (Ed. by V. Nolan Jr & C. F. Thompson), pp. 119–178. New York: Kluwer Academic/Plenum.
- Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioural Reviews*, **29**, 137–150.
- Hessing, M. J. C., Hagelsø, A. M., van Beek, J. A. M., Wiepkema, P. R., Schouten, W. G. P. & Krukow, R. 1993. Individual behavioural characteristics in pigs. *Applied Animal Behaviour Science*, **37**, 285–295.
- Hughes, R. N. 1997. Intrinsic exploration in animals: motives and measurement. *Behavioural Processes*, **41**, 213–226.
- Hurd, P. L. & Enquist, M. 2001. Threat displays in birds. *Canadian Journal of Zoology*, **79**, 931–942.
- Jensen, P. 1995. Individual variation in the behaviour of pigs: noise or functional coping strategies? *Applied Animal Behaviour Science*, **44**, 245–255.
- Komers, P. E. 1997. Behavioural plasticity in variable environments. *Canadian Journal of Zoology*, **75**, 161–169.
- 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. *Neuroscience and Biobehavioural Reviews*, **23**, 925–935.
- Koolhaas, J. M., de Boer, S. F., Buwalda, B., van der Vegt, B. J., Carere, C. & Groothuis, A. G. G. 2001. How and why coping systems vary among individuals. In: *Coping with Challenge: Welfare in Animals including Humans* (Ed. by D. M. Broom), pp. 197–209. Dahlem: Dahlem University Press.

- Lowe, S. E. & Bradshaw, J. W. S. 2001. Ontogeny of individuality in the domestic cat in the home environment. *Animal Behaviour*, **61**, 231–237.
- Maestripietri, D. 2000. Measuring temperament in rhesus macaques: consistency and change in emotionality over time. *Behavioural Processes*, **49**, 167–171.
- Malmkvist, J. & Hansen, S. W. 2002. Generalization of fear in farm mink, *Mustela vison*, genetically selected for behaviour towards humans. *Animal Behaviour*, **64**, 487–501. doi:10.1006/anbe.2002.3058.
- Marchetti, C. & Drent, P. J. 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, **60**, 131–140.
- van Oers, K., Drent, P. J., De Jong, G. & Van Noordwijk, A. J. 2004a. Additive and nonadditive genetic variation in avian personality traits. *Heredity*, **93**, 496–503.
- van Oers, K., de Jong, J., Drent, P. J. & van Noordwijk, A. J. 2004b. Genetic correlations of avian personality traits. *Behavior Genetics*, **34**, 611–619.
- van Oers, K., Drent, P. J. & Van Noordwijk, A. J. 2004c. Realized heritability and repeatability of risk taking behaviour in relation to avian personalities. *Proceedings of the Royal Society of London, Series B*, **271**, 65–73.
- van Oortmerssen, G. A. & Bakker, T. C. M. 1981. Artificial selection for short and long attack latencies in wild *Mus musculus domesticus*. *Behavior Genetics*, **11**, 115–126.
- Price, T. & Langen, T. 1992. Evolution of correlated characters. *Trends in Ecology and Evolution*, **7**, 307–310.
- Réale, D., Gallant, B. Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597. doi:10.1006/anbe.2000.1530.
- Roberts, B. W. & DelVecchio, W. F. 2000. The rank-order consistency of personality traits from childhood to old age: a quantitative review of longitudinal studies. *Psychological Bulletin*, **126**, 3–25.
- Ruis, M. A. W., te Brake, J. H. A., van de Burgwal, J. A., de Jong, I. C., Blokhuis, H. J. & Koolhaas, J. M. 2000. Personalities in female domesticated pigs: behavioural and physiological indications. *Applied Animal Behaviour Science*, **66**, 31–47.
- Schwabl, H. 1995. Individual variation of the acute adrenocortical response to stress in the white-throated sparrow. *Zoology*, **99**, 113–120.
- Sih, A., Bell, A. M., Chadwick Johnson, J. & Ziemba, R. E. 2004. Behavioral syndromes: an integrative overview. *Quarterly Reviews of Biology*, **79**, 241–277.
- Spoolder, H. A. M., Burbidge, J. A., Lawrence, A. B., Simmins, P. H. & Edwards, S. A. 1996. Individual behavioural differences in pigs: intra- and inter-test consistency. *Applied Animal Behaviour Science*, **49**, 185–198.
- Stearns, S. 1989. The evolutionary significance of phenotypic plasticity. *BioScience*, **39**, 436–445.
- Steimer, T., La-Fleur, S. & Schulz, P. E. 1997. Neuroendocrine correlates of emotional reactivity and coping in male rats from the Roman high (RHA/Verh)- and low (RHA/Verh)- avoidance lines. *Behavior Genetics*, **27**, 503–512.
- Tinbergen, J. & Daan, S. 1990. Family planning in the great tit (*Parus major*). Optimal clutch size as integration of parent and offspring fitness. *Behaviour*, **114**, 161–190.
- Veenema, A. H., Meijer, O. C., de Kloet, R. E., Koolhaas, J. M. & Bohus, B. G. 2003. Differences in basal and stress-induced HPA regulation of wild house mice selected for high and low aggression. *Hormones and Behavior*, **43**, 197–204. doi:10.1016/S0018-506X(02)00013-2.
- Verbeek, M. E. M. 1998. Bold or cautious. Behavioural characteristics and dominance in great tits. Ph.D thesis, University of Wageningen.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, **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.
- Visser, E. K., van Reenen, C. G., Hopster, H., Schilder, M. B. H., Knaap, J. H., Barneveld, A. & Blokhuis, H. J. 2001. Quantifying aspects of young horses' temperament: consistency of behavioural variables. *Applied Animal Behaviour Science*, **74**, 241–258.
- Wilson, J. D. 1992. Correlates of agonistic displays by great tits *Parus major*. *Behaviour*, **121**, 168–213.
- Wilson, D. S., Coloman, K., Clark, A. B. & Biedeman, L. 1993. Shy–bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.
- Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994. Shyness and boldness in humans and other animals. *Trends in Ecology and Evolution*, **9**, 442–445.