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Review

Avian personalities: characterization and epigenesis

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Abstract

The work presented here aims at understanding the nature, epigenesis and function of personality types (here called behavioral profiles) in birds, focusing on a wild bird species, the great tit (*Parus major*). Lines bidirectionally selected for exploration show a wide array of social and non-social behavioral differences, and also some differences in physiological parameters. Line differences in these characteristics and their relationships show significant temporal consistency. The results show a surprising similarity between the great tit and a rodent model, suggesting a fundamental principle in the organization of behavioral profiles. The nature of this principle and whether or not it is multi-dimensional is discussed. However, the similarity with a chicken model is less clear, which points to some caution for generalization. The epigenesis of great tit behavioral profiles is discussed. Selection experiments with replication and backcrosses reveal a strong genetic basis, and suggest an influence of maternal effects. Ontogenetic manipulations indicate strong developmental plasticity, suggesting adaptive adjustment to prevailing environmental circumstances. They also show that behavioral characteristics belonging to the same profile can become uncoupled. Finally, field data on several fitness parameters of the different personalities in wild great tits are summarized. These data suggest that variation in selection pressure in time and space and assortative mating are plausible mechanisms accounting for the maintenance of different behavioral profiles within the same population.

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Keywords: Personality; Behavioral profiles; Behavioral syndromes; Coping styles; Birds; Epigenesis; Ontogeny; Fitness; Assortative mating

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1. Introduction

1.1. Why and how to study personalities

Behavioral and physiological differences between individuals of the same species are extremely common, even within the same age, sex and in standardized conditions. These differences have for a long time been neglected as biologically meaningful variation, being interpreted as either the consequence of inaccurate measurements or non-adaptive variation around an adaptive mean. In contrast, such variation in human behavior is often interpreted as reflecting consistent individual variation, indicative of differences in personality or temperament. In addition, humans who work intensively with, or take care for a small number of individuals of the same animal species often attribute different personalities to their animals, anecdotally suggesting the existence of consistent inter-individual differences in behavior of animals other than humans. Nevertheless, scientific research of animal personalities is only a relatively new field, to our opinion for two main reasons. First, behavioral and physiological research on animals tends to focus on differences between populations or treatments, without following individuals for a longer time span. Second, behavioral biologists are reluctant to use psychological labels and approaches that are common in research on humans, but difficult or even impossible to use in research on species where communication by language and introspection is impossible. The question whether animals have similar personalities as humans is difficult to answer as long as both fields use essentially different methodologies. It has been tried to translate behavioral observations in a wide array of animal species to the classification of personalities used in psychology, based on the five axis model [1,2]. Although this approach is seemingly successful, the translation of species-specific behaviors to these axes is a difficult enterprise that can at the most suggest, but never be

an independent objective test for possible similarities between our and other animal species.

The question whether animals show differences in personalities is open for biological research when the concept of personality is translated to an entity that can be studied with the adequate research tools of the biological sciences, based on objective quantification. A basic attribute of personalities is that it reflects differences in behavior and its underlying machinery, that are consistent across situations or contexts and stable over time [3]. Behavioral ecologists have long been recognizing consistent and stable inter-individual differences in behavior or even suites of traits, such as the occurrence of different or alternative behavioral strategies like territorial ‘holders’ versus ‘sneakers’ [4], or ‘scrounger’ versus ‘producers’ [5]. More recently, researchers in the field of stress physiology have advocated the importance of so-called coping styles, different strategies to deal with environmental challenges [6–8]. Both fields tend to dichotomize individual differences into opposite strategies, partly because of working with selection lines. However, complex and continuous variation is probably more characteristic for the natural situation. For example, wild individuals of the same sex and species differ in a more continuous way in exploration or boldness, which is often either generalized to different contexts or related to differences in other behavioral traits [9–12]. Clearly, evidence is accumulating that individuals differ consistently in whole suites of traits or behavioral profiles.

The study of these individual differences in suites of traits is highly relevant for the following reasons. First, it can shed light on fundamental aspects of the causation and function of behavior, and also demonstrate the value of a more holistic approach over studying certain behaviors in isolation from others [3]. Second, it is important for the interpretation and design of many animal experiments, since individuals with different behavioral profiles may react differently to the same treatments. Third, different animal

personalities may show differences in vulnerability to stress and artificial housing conditions, leading to differences in welfare in, for example, commercial housing conditions. Forth, a better understanding of animal personalities may help to provide a better understanding of the context and evolution of human personalities.

Studying animal personalities requires all of the following approaches [13]: (i) Descriptive studies revealing information about the nature of behavioral profiles, including the links among several behaviors, and how specific they are for different situations; (ii) Physiological and genetic studies revealing information about the causal mechanisms underlying the relation among several behaviors of the same profile, such as pleiotropy or gonadal hormones; (iii) Ontogenetic studies to shed light on the degree of phenotypic plasticity in the behavioral profiles and whether they can be adjusted to the environment; (iv) Field studies on survival and reproduction to understand how the co-existence of different behavioral profiles in the same species is maintained despite the fact that directional selection to the best strategy would eliminate behavioral variation in the natural situation.

In this paper, we will review the data on personality types of the great tit (*Parus major*), which have been obtained on the basis of all of these four approaches over the past six years. Most attention will be given to the characterization of the behavioral profiles. These will be compared with those of another avian species, the domestic chicken, and of another well-studied model, the house mouse.

1.2. On terminology

Consistent differences between individuals have been labeled as differences in personality, temperament, coping styles or strategies, behavioral syndromes, boldness and neophobia [1,3,7,9,14]. The first two have a connotation that is related to the classification of human personalities in terms of psychological labels, difficult to validate for other animal species and so we will not use them here. Coping styles have mainly been used in the context of stress physiology, and refer to the capacity and strategy of animals when dealing with challenging situations. Although the advantage of this term is its functional context, its pre-assumption about the primary function of the strategies and the confusion in the literature about the meaning of the word stress led us to avoid this label on this occasion. The two last labels specify the individual differences in terms of their underlying mechanisms and will be discussed after presenting our data. Behavioral syndromes [3] is a nicely descriptive term emphasizing the ‘package’ character of personalities. However, the term is often used in the context of disease-related abnormal variation, whereas we are explicitly confined within the boundaries of normal variation. We shall therefore use here the term ‘behavioral profiles’ including both behavior and its underlying machinery, the physiology. We define these partly based

on the definition of behavioral syndromes by Sih and co-workers [3]. Animals should show: (1) differences between individuals in behavior or physiology that are consistent over time. This does not exclude that these consistent differences can change over time, for example due to aging. However, inter-individual differences should not be due to temporal motivational changes; (2) these individual differences should consist of more than one feature. When considering behavior for example, it may be one type of behavior, expressed in different situations, such as aggression to a conspecific and to a predator, or as a territory owner and in a group of conspecifics, or to males and to females. Or it might be different behaviors, such as aggression and exploration. Both cases refer to one of the most intriguing parts of the profiles: a link between different features that limits the organism’s freedom to adjust its behavior to each situation without modifying other components of the package. However, these are two different types of profiles: the first one is behavior specific (assuming the animal uses the same motor patterns in different contexts, since aggression to conspecifics may actually consist of different behaviors than anti-predatory aggression), while the second one is not. In the latter case we assume that differences in exploration are not due to differences in aggression. So care has to be taken that the tests for different behaviors are really independent tests (for example, exploration should not be tested in a social context where social dominance can directly influence the exploration performance); (3) the relation between traits should be stable. That is, aggressive animals showing more exploration should do so in different situations or ages; (4) all traits should be measurable in an objective way, and preferably in a quantitative manner. The latter is important since categorical measurements or the use of cut-off time in experiments can suggest larger differences between profiles than is justified.

1.3. Why study birds

Many neuroendocrine mechanisms related to behavior and other complex processes are rather similar among vertebrates, and birds have always been an important source of information for behavioral biologists [15–17]. Thanks to the work of field ethologists and ecologists, there is a much more extensive knowledge of all aspects of behavior under natural conditions in birds than in many other vertebrate taxa, including mammals. Therefore, the study of personalities traits in birds can be translated into a natural context more easily than in other taxa allowing to take into account ecological and evolutionary aspects. For example, traits like neophobia and exploration have been extensively studied in relation to ecological plasticity, opportunism, or innovative behavior, which are all potential driving forces in evolution [14,18]. Further, from the applied perspective, avian species are very relevant because of their extensive use in commercial farming and being a key target in conservation

biology. For example, the degree of behavioral flexibility may determine how species or populations cope with anthropogenic influences on their habitat and food sources.

1.4. *The great tit as a model*

We will mostly focus on the great tit (*Parus major*), a small, non-migratory songbird of forest areas and a key species for ecological research in Europe [19] for the following reasons: (i) its behavioral ecology is well known in many respects; (ii) the individual variation in behavioral profiles appears to match well the patterns described in other species [20]; (iii) selection lines have been established for some aspect of this individual differentiation [21]; (iv) the species can be bred in captivity and nestling can be reared by hand. This allows further genetic experimentation, the manipulation of rearing conditions to study developmental plasticity, and testing behavior under controlled conditions. These advantages created the possibility for a large research program, studying the nature, ontogeny, genetic background and functional significance of the different strategies, in four linked programs, under the coordination of TG. This review summarizes part of these projects.

2. Characterization of great tit behavioral profiles

2.1. *The selection lines*

Most of the characterization of the behavioral profiles in the great tit has been conducted on selection lines for fast and slow exploration originating from wild populations [21]. To some extent these have been validated by studies on unselected birds from the field [22], and by an additional selection line [23]. We will discuss the results in this order, and therefore start with a short description of the selection experiment. To avoid confusion we will label birds from the fast or slow selection lines with capitals, in contrast to those from unselected populations.

Selection was started with birds collected as nestlings in the field (81 nestlings from 11 pairs), brought to the laboratory and hand-reared until independence [21]. Soon after independence two behavioral tests were carried out that had previously shown a significant positive correlation [24]. The *Novel Environment* test consisted of releasing individual birds for 10 min in a novel room containing five artificial trees. The time needed to visit four of these trees was converted linearly to a scale from zero (birds did not reach the criterion within the 10 min, SLOW birds) to 10 (birds visited all four trees within the first minute, FAST birds). The *Novel Object* tests consisted of testing in the home cage during 120 s the response to a penlight battery (first day) and a rubber toy (pink panther) respectively, on two subsequent days. Also the response to the two consecutive trials with the different objects had previously shown significant positive correlation [24]. The latency to

approach the object and the shortest distance reached to this object were scored. In each test a score of 0 was given when the bird did not land on the perch with the novel object (SLOW), and a score of five when the bird pecked the object (FAST). The sum of the three tests scores ranging from 0 to 20 was used as selection criterion. Eggs of both SLOW and FAST pairs, breeding in captivity, were combined to form mixed broods consisting of a similar number of fast and slow nestlings and fostered to nests of wild birds in the field. About 10 days after hatching, birds were taken into the laboratory and hand-reared. This procedure ensured that neither parental nor sibling effects contributed to the outcome of selection, except for the possibility of maternal effects, contributing to egg quality (see below). Both lines were started and maintained with nine pairs. For the parental generation birds that showed the highest and lowest summed scores were selected from two wild populations. For later generations pairs were formed from the offspring by selecting the individuals with the highest scores for the fast line and the lowest scores for the slow line, avoiding full-sib and first-cousin mating. Selection rapidly led within four generation to a divergence in the exploration score, which was evident already after two generations, with a change in mean score from 1.78 to -1.31 units per generation (up- and down-selection respectively). Realized heritability was estimated to be relatively high (0.54) [21].

We will first discuss all available studies that looked at behavioral and physiological differences between birds of the selection lines belonging to different cohorts of the third and fourth generation. These are summarized in Table 1. Next, we will validate the results on the basis of studies on unselected birds and another selection experiment. Thereafter, we will discuss the nature of the behavioral profiles. All differences we refer to are statistically significant, unless stated otherwise.

2.2. *Exploratory behavior*

Not only the combined scores of the Novel Object tests and the Novel Environment test differed between the lines as a results of selection already after two generations [21], but also the scores of each of the two types of tests separately after 3–4 generations (N FAST = 19; N SLOW = 14) [25]. It has been claimed that in the Novel Environment test SLOW birds are slower to reach all four trees, since they search more thoroughly than FAST birds [24]. SLOW birds tend to hop within trees from branch to branch, while FAST birds tend to fly between trees [26]. Whether this reflects a difference in activity or really a difference in exploration is not yet totally clear. FAST birds tended to be more active when housed individually [27]. However, the activity in the home cage was unrelated to the Novel Object test, although the relation with the Novel Environment test was not analyzed [24]. One study claimed that in the first 2 min of the test more SLOW than FAST birds performed pecking at branches and more looking at corners between branches

and the stem of the tree [26]. To interpret the Novel Environment test it is important to test whether SLOW birds really find more hidden food than FAST birds during exploratory performance.

In addition, other behaviors that may be related to exploration differed between the lines. In an experiment in which great tits of the first generation of the selection lines had to learn to find hidden food in a bowl of a particular color, birds of the FAST line decreased their visits to other bowls more quickly than SLOW birds, although they reached similar levels after three days [26]. In addition, when the food of the rewarded bowl was removed in subsequent tests, birds of the SLOW line increased the frequency of visiting other bowls more than FAST birds while the latter continued to visit the previously rewarded bowl relatively often. The authors conclude that both results indicate that FAST birds more quickly form behavioral routines than SLOW birds. Although the first results may be due to differences in speed of learning (no data on obtaining the food rewards are given), this seems unlikely based on the lack of evidence for this in other tests [28].

Exploration of a novel environment as well as routine formation might be strongly related to risk taking behavior. Indeed, in an experiment in which birds were startled at the feeding bowl, birds from the FAST line returned to the same bowl with a shorter latency than birds from the SLOW line [23].

To analyze whether differences in exploration strategy are related to differences in cognitive abilities, birds of both lines were subjected to two learning tasks: finding food based on visual cues, and on spatial cues respectively. No evidence was found that the selection lines differ in learning abilities. However, in a retention task 65 h after the learning task with visual cues FAST birds out performed SLOW birds [28]. This may relate to the apparent higher tendency of FAST birds to form routines.

Birds from the two lines also differed in exploration and foraging behaviors that have a social component. First, in individually housed birds the percentage of time spent near a conspecific in a small cage attached to the home cage was higher in SLOW than in FAST birds [27]. Second, when birds had to search for hidden food in bowls of different color and form, FAST birds more often copied the choice for a particular bowl by a conspecific tutor. This tutor bird was trained to find food in a particular bowl and housed in an identical room, separated by a transparent partition from the one of the experimental bird [29]. The authors suggest that FAST birds tend to follow a scrounger strategy and SLOW birds a producer strategy [5]. This would make sense since the former are more aggressive than the latter and therefore probably relatively successful in stealing food while the latter would be better explorers. However, all tutor birds were females of the FAST type and all experimental birds were males. Since FAST males have more interest in FAST females than SLOW males (see below) this may have confounded the results and the experiment should perhaps

Table 1
Overview of the behavioral and physiological differences between the FAST and SLOW great tits

Feature	Fast vs slow	References
Approach latency to novel object	S > F	[21,24,25]
Exploration speed novel room	F > S	[21,24,25]
Routine formation in foraging	F > S	[24,26]
Risk taking	F > S	[23]
Retention of information	F > S	[28]
Social exploration	S > F	[27]
Tutor copying in foraging	F > S	[29]
Begging	F > S	[30]
Attack latency to intruder	S > F	[10,25]
Attack frequency	F > S	[25]
Frequency of agonistic displays	S > F	[25]
Latency to approach female	S > F	[25]
Impact social challenge	F > S	[11,27]
HPA reactivity to social challenge	S > F	[32]
Recovery body T after handling	F > S	[33]
Timing of reproduction	S > F	[57]
Stability over time	F > S	[25]

See text for details (section 2.1 to 2.4).

be repeated with other combinations of experimental and tutor birds.

In conclusion, the selection lines differ in the reaction to a novel object and in the way they move through a novel room, evidencing the genetic component of the fast/slow trait. Additional data suggest that the latter reflects a difference in exploration strategy. Fast birds may perhaps explore less thoroughly and are less risk sensitive. Furthermore, FAST birds seem to be more prone to form routines and, consistent with that, to remember earlier acquired information. Finally, FAST birds may be more likely to adopt the scrounger strategy during foraging than the SLOW birds (Table 1).

2.3. Social behavior

Birds of the third and fourth generation of the selection lines were used for further characterization of the behavioral profiles. To study how early in ontogeny the selection lines differ in behavior, offspring solicitation behavior (called ‘begging behavior’ by ornithologists) was tested in standard stimulus tests both before and after fledging in nestlings hatched from 7 pairs of each line. FAST nestlings begged more persistently and more intensively than SLOW nestlings, but only around fledging and not at earlier ages [30]. This may have important consequences for obtaining food from the parents during sibling competition.

Male aggressive behavior was evaluated in two tests: by means of a caged male intruder, offered in the center of the aviary where the experimental male was housed with its mate; and by releasing a live male intruder in its home cage when housed individually (N FAST = 7; N SLOW = 8) [25]. Latency to attack was shorter for FAST males compared

with SLOW males in both tests, but only significantly so in the second test, probably because a caged intruder is perceived as less risky than a free-moving one. Attack rate was only scored in the second test and significantly higher for FAST males. In contrast, in both tests the duration of threat displays was significantly longer in SLOW males. The results indicate that FAST birds attack earlier and more vigorously, while SLOW birds first tend to obtain information by means of social displays. This would fit with the above mentioned line difference in risk taking behavior.

Sexual behavior to birds of the opposite sex and of both lines has been tested in both males and females [25,31]. Latency to approach the member of the opposite sex was shorter in both males (highly significant, N FAST=10; N SLOW=8) and females ($p=0.09$, N FAST=8; N SLOW=6) of the FAST line compared to those of the slow line. The frequency of sexual displays did not differ.

In conclusion, line differences clearly extend to social contexts. Latency to approach the stimulus is relatively shorter in FAST birds, both in non-social, aggressive and sexual contexts. In addition, FAST birds seem to be more competitive, both in early competition for food (begging behavior) and in later aggression tests (Table 1).

2.4. Coping with stress

In an experiment with caged males of both selection lines of the third and fourth generation, birds were given a social defeat by confronting them with aggressive unselected males that had been given prior access to half of the home cage of the experimental resident male. As a consequence of the set up the latter often lost the fight. Specifically, six out of six SLOW and six out of 10 FAST males were defeated, although this did not differ between the lines ($p=0.11$). Based on behavioral observations before and after the fight the impact of this social defeat was established [27]. FAST birds showed a stronger reduction in activity than SLOW birds immediately after the social defeat. This suggests that they are more sensitive to this kind of social stress. Other parameters (body temperature, breathing rate and social exploration) showed changes over time similar to what has been found in mammalian species, but these did not differ between the lines [27].

Corticosteroid metabolites in fecal samples collected between 30 and 45 min after the social defeat and on the subsequent day showed an increase in the SLOW but not in the FAST birds. [32]. Thus, stress of social origin has a differential impact on the two types of birds, with potentially important consequences at the population levels. Great tits very frequently engage in agonistic interactions, both in flocks and during territorial defense, while population density, and thereby the number of interactions, shows marked seasonal fluctuations in the wild.

The response to predation was measured in birds with unknown genetic background but phenotypically characterized as Fast or Slow by a standard catching and handling

protocol at the end of the dark period and during daytime [27,33]. The procedure increased both body temperature and breathing rate. The decrease in body temperature in the period after catching was more marked in the Fast than in the Slow birds during the diurnal phase. Breathing rate decreased strongly in the course of 4 blocks of 15 s, the last one probably reflecting basal levels more closely. Breath rate in the last block was almost significantly lower in Fast than in Slow birds (N FAST=10; N SLOW=6, $p=0.06$).

In conclusion, these data suggest that FAST birds are more sensitive to a social defeat. However, the physiological data suggest that they cope with challenges more easily in the course of time after the challenge than SLOW birds. No differences in body mass or tarsus length between the two types of birds were found in any of the published studies (Table 1).

2.5. Validation from other sources

The results presented above are all collected on birds from the same selection experiment. No replicas of these lines have been made and it could be argued that the results need validation from other experiments. The results so far may not reflect the linkage between traits in natural populations, but may be an accidental byproduct of the selection, due to genetic drift and the characteristics of the birds from which the selection started. However, information from two other sources strongly support the data presented so far: (i) Data from unselected birds, both juveniles and adults collected from the field; (ii): Data from another selection experiment.

2.5.1. Data from unselected birds

In several experiments birds were taken as nestlings from unselected populations in the field, hand-reared until independence, and tested on various behaviors. Part of these experiments provided in fact the inspiration for the selection experiment and its characterization discussed above.

In several independent experiments it was found that the individual scores for the two Novel Object tests and the Novel Environment test correlate among each other [24]. Further, like in the selection lines, relatively slow explorers performed more branch hops than fast explorers. The slower birds also more persistently visited a particular empty food bowl on which they previously were trained to find food, supporting the relation between exploration and routine formation [24]. Finally, the return latency after being startled at a feeding bowl was lower for birds with faster scores in the Novel Environment test, although it did not correlate with the behavior in the Novel Object test [23].

Aggressive behavior of hand-reared juveniles from the field also correlated with the combined score for the Novel Object test and the Novel Environment test that characterizes exploratory behavior [10]. In an intruder test with a randomly chosen male intruder, male Fast birds more often

initiated fights than Slow males and won more interactions. In a confrontation between a Fast and a Slow male the latter won significantly more often. These data support the data from the selection lines. However, in the unselected juveniles Fast birds performed the horizontal display (see below) more often, while in the birds from the selection lines FAST birds performed less display than the slow explorers. This discrepancy may be due to the fact that in the latter study other displays were measured that seem to reflect defensive aggression (such as wings-out and tail-fanning) while the horizontal display is an offensive display [34]. See also [11] for a similar result in wild juveniles.

The relation between exploration and the impact of social stress was validated by aviary experiments with unselected hand-reared birds. Fast birds took longer to initiate a new fight after having lost a couple of fights in a row than Slow birds [11]. This differential effect of social defeat is probably responsible for the finding that there is not a clear coherent relation between social dominance and exploration. Relatively fast birds initially win more fights in new groups, but may end up at the lower end of the dominance rank order due to their vulnerability to losing fights. Some data on social dominance support this interpretation [11] but many more experiments with independent groups of birds are needed here.

2.5.2. Data from additional genetic analyses

An analysis of the relation between mid-offspring and mid-parent values for the combined exploration scores (Novel Object and Novel Room tests) from wild hand-reared birds revealed heritability between 0.25 and 0.33 [21]. Similar data have been obtained on birds that were caught in the wild and had been reared by their parents [22]. Although these heritability estimates (broad sense) may be confounded by the sharing of environmental factors between parents and offspring, the results are consistent with the data from the selection line experiment (realized heritability, based on actual genetic improvement across several generations).

Moreover, based on the finding that risk taking behavior (latency to return after a startle response on the feeding bowl) differed between the original selection lines for exploration, a bi-directional selection experiment for this response was conducted [23]. This was successful, showing heritability of 0.19. This value is much lower than that for exploratory behavior (0.54, see above), and the authors suggest two possible explanations for this: first, risk taking behavior was tested almost two months later than exploratory behavior, which may have created more opportunity for experience to modify the response. Second, selection on risk taking behavior might be more severe, leading to less additive genetic variation. In any case, we consider this additional selection experiment as very promising, and further analysis evidenced that risk taking behavior and exploratory behavior show high genetic correlations [35]. Since each selection experiment may be seen as a sample

size of one, it is of great relevance to study the effect of the second selection experiment on the other behaviors of the great tit profiles.

2.6. Consistency and stability

So far the data of the great tits fulfill most of the criteria mentioned above for behavioral profiles, except for those related to consistency and stability. Are the differences between FAST and SLOW birds consistent over time, and are the profiles as a package stable over time? Several lines of evidence indicate that this is the case.

Carere and co-workers [25] tested exploration in an independent cohort of the original selection lines (third and fourth generation N FAST = 19; N SLOW = 14, both sexes) both in the juvenile and the adult phase, over a two to three years time interval. The scores in the Novel Object tests, the Novel Room test and their combined scores (the selection criterion) differed between the lines not only in the juvenile phase, but also in adulthood, except for the Novel Object score for adult females. Despite this temporal consistency between the lines, the line differences became smaller in adulthood, because SLOW birds became significantly faster while FAST birds did not change with age.

Temporal consistency at the individual levels was less evident. Within lines, the juvenile and adult scores for the combined exploration data correlated significantly for the FAST birds but not for the SLOW birds. For the separate exploration scores for the Novel Object and the Novel Environment test, only the latter approached significance, and only for the FAST birds. The lack of consistency within the SLOW birds is mainly due to the lack of variation in the juvenile scores that consisted mainly of zero scores and therefore precluded any meaningful analyses.

Similar results have been found for wild hand-reared tits, showing a high correlation between the Novel Object tests between 9 and 18 weeks old birds, while birds became faster with age [24]. In addition, Dingemanse and co-workers [22] found significant repeatability scores (ranging between 0.27 and 0.48) for the number of movements in the Novel Environment test in birds caught twice in the wild and released in between the tests. This parameter highly correlated with the latency to reach the fourth tree in the same test, used in the other studies. Finally, over about one year interval a significant repeatability of 0.26 was found for risk taking behavior in hand-reared captive birds taken from the wild [23]. Overall, the data indicate that individuals show some temporal consistency in exploration, with slow birds showing greater plasticity (or instability) than fast birds.

As far as social behavior is concerned, its consistency over time can be analyzed for aggressive behavior, since an intruder test has been conducted twice on the same birds of the selection lines with a seven months interval (N FAST = 7; N SLOW = 8) [25]. The time spent on agonistic displays was consistent over time both at the level of selection line and at the individual level. The first results indicate that also

the package of behaviors is stable over time. Indeed, in the lines selected for exploration the difference in both exploration and display performance between FAST and SLOW explorers was apparent both in one year old and one and a half year old birds [25]. Correlations between several other parameters of tests conducted at different ages showed high coefficients (between 0.6 and 0.7), but did not reach significance ($0.05 < p < 0.1$) due to very small sample sizes ($N_{\text{FAST}} = 7$, $N_{\text{SLOW}} = 8$).

In conclusion, line differences in exploration and social behavior show temporal consistency over a time period that is substantial given the short life span of the species. Evidence indicates that the relation between exploration and social behavior is also consistent over time. In addition, the SLOW individuals may entail a larger potential to achieve multiple or alternative phenotypes than fast individuals, showing a high degree of plasticity. The presence of intrinsically ‘unstable’ individuals in populations may partly explain the highly controversial results on the issue whether behavioral strategies are context-specific or domain general. These results highlight the idea that phenotypic behavioral plasticity is a character in its own right [36–38].

3. The nature of the behavioral profiles

Consistent behavioral differences between individuals have been labeled in several ways (see introduction). To what extent can we attribute the different behavioral profiles in the great tit to one or several axis, and what might be the nature of these axes?

The different profiles have been labeled as fast and slow explorers, based on the difference in latency time in the exploration tests [10,11,21–24,27]. These labels, although nicely descriptive, do not cover the wide array of behaviors that differ between the profiles. The profiles have also been labeled as bold and cautious [20], in line with a similar, but not the same, classification for other animals including humans: the boldness versus shyness classification [9,12]. Such a classification would cover the differences in latency in aggression and the sexual test, as well as the difference in risk taking behavior [9]. It may also be in line with the high frequency of display behavior in the SLOW birds, since these cautious or shy animals would use these displays to gain more information from the opponent while the fast and bold animals almost immediately decide to attack. The line difference in begging could also be explained in this framework. This difference in begging emerged around fledging, at an age the birds became more fearful. SLOW birds, being more shy or cautious, would then be more suppressed in their begging behavior.

Differences in boldness, cautiousness or fearfulness may even account for other aspects of the profiles [39,40]. Fast explorers, being bolder towards conspecifics, may more easily forage in the proximity of conspecifics and therefore

more easily copy their foraging habits. Further, a lower tendency for routine formation in the slow explorers may be due to the fact that these more cautious birds have a higher tendency to scan the environment, being therefore more alert to changes in food distribution. Such a higher sensitivity to external stimuli may also explain why slow or cautious birds show less stability over time in some behavioral characteristics, because they are more prone to change on the basis of experience. It may also explain why slow birds are more sensitive to challenges such as handling in HPA reactivity and body temperature and why slow birds take longer to begin reproducing in captivity. Finally, a difference in sensitivity to details of the environment may more adequately account for the difference in exploration in the Novel Environment test than boldness, if slow birds indeed spent more time actively exploring details of the artificial trees [26].

Such a difference in the sensitivity to external cues is a key aspect of a classification of coping styles: ‘proactive’ versus ‘reactive’ control of behavior [7,8]. Proactive animals would be controlled primarily by feed-forward mechanisms, relying on internal cues, based on their experience. Reactive animals would rely on feedback information provided by the environment. In mice, experiments in mazes that were slightly modified or were turned in the horizontal plane so that external cues changed after the animals reached a certain learning criterion indeed showed that less aggressive (or reactive) mice reacted more adequately to these modifications than aggressive (or proactive) mice [41]. Blocking one of two entrances to a food compartment also led to fewer errors in less aggressive mice [42]. Also, less aggressive mice adjusted their circadian activity more rapidly to a change in light-dark scheme than aggressive mice [43]. Whether the openness to environmental stimuli causes the difference in boldness or vice versa is as yet unclear.

In conclusion, we think that the great tit behavioral profiles may at the moment best be described in terms of to what extent they rely on, or are open for, details of their environment. However, whether this would be the only axis that can explain all the differences between the profiles is as yet unclear. Surely, it may not account for the higher vulnerability to losing a social defeat. However, it may well be that the impact of such a defeat is higher in the fast explorers since they fight more vigorously and the degree of the defeat is stronger in such interactions. If so, the lines do not differ in vulnerability but in experience as a consequence of their own behavior. This should be investigated in more detail and points to an important consideration in the classification of behavioral profiles: Most of the interpretations presented above are post-hoc explanations. It is extremely important for further progress to test specific a priori expectations based on well-conceived hypotheses about the nature of the profiles that are open for falsification.

4. Comparison with a mammalian model

The classification of behavioral profiles in terms of their sensitivity to the environment is to a large degree based on work with selection lines for aggression of wild house mice, originally called SAL (Short attack latency) and LAL (Long attack latency). This raises the question to what extent line differences in the great tit are similar to those of the mice. For 7 out of the 17 variables mentioned in Table 1 similar data have been collected for the selection lines of the mice (Table 2). Tests for aggression [6,44] and social defeat [45,46] were conducted in a similar way as with the great tit, by confronting the animal with an intruder in its home cage. The experiments testing routine formation in the mice have been described above and show some similarity in design with the one used for the tits. To enable comparison, we now will label the FAST tits as proactive and the SLOW tits as reactive, based on the discussion above. Surprisingly, in all seven cases the difference between the selection lines is in the same direction (Table 2), despite the fact that the tits were selected on exploration and the mice on aggression. This similarity between different taxa suggests a fundamental

Table 2
Comparison between the FAST and SLOW Great tit lines and the proactive and reactive (or short and long attack latency) mouse lines

Feature	Great tit	House mouse	References
	Proactive (FAST) vs reactive (SLOW)	Proactive (SAL) vs reactive (LAL)	
Approach latency to novel object	S>F		
Exploration speed novel room	F>S		
Routine formation in foraging	F>S	SAL>LAL	[42]
Risk taking	F>S		
Retention of information	F>S		
Social exploration	S>F		
Tutor copying in foraging	F>S		
Begging	F>S		
Attack latency to intruder	S>F	LAL>SAL	[6]
Attack frequency	F>S	SAL>LAL	[44]
Frequency of agonistic displays	S>F	LAL>SAL	[44]
Latency to approach female	S>F	LAL>SAL	[42]
Impact social challenge	F>S	SAL>LAL	[46]
HPA reactivity to social challenge	S>F	LAL>SAL	[45]
Recovery body T after handling	F>S		
Timing of reproduction	S>F		
Stability over time	F>S		

principle in the organization of animal personalities. It is now time to design experiments that specifically test the similarity between both species in the other aspects of the behavioral profiles. At the same time experiments using aggression as a selection trait in great tits and exploration as a selection trait in mice should be carried out to reach a clear conclusion on this issue.

5. Comparison with a chicken model

It has been argued that two lines of the leghorns, selected for productivity traits, reflect the proactive and reactive styles too [8,47]. The so called HP line (High Feather pecking frequency) and LP line (Low Feather pecking frequency) differ in HPA (re)activity in a similar way as in proactive and reactive mice [47,48]. The chicken lines also show differences in other physiological parameters (noradrenalin levels, resistance in manual restraint [47], heart rate variability [49], and dopamine en serotonin turnover [48]). These have also been studied in alternative models to the mouse model: the wild rat and the domestic pig. These larger species facilitate physiological research, and based on both behavioral and physiological studies it has been argued that in these two species similar coping strategies exist as in the house mice [7,8,47,48]. In all cases the physiological parameters show great similarity between the chicken and the mammalian species, in such a way that it suggests that HP birds are proactive and LP birds are reactive copers.

Unfortunately, most physiological data are not available for the great tit. In order to facilitate comparison between the great tit, the chicken and the mice models, behavioral differences between the chickens lines were studied. These data do not support the classification of the chicken lines as proactive and reactive copers. HP or proactive birds were less active in a novel room than LP or reactive birds, and showed a longer duration of tonic immobility in the classical back test [50,51]. This indicates a higher instead of a lower level of fearfulness in proactive than in reactive chickens [51]. Their latency to approach a novel food item was also longer instead of shorter than LP birds [51]. This discrepancy between the similarity in physiology and dissimilarity in behavior between the chicken and the mammalian species may be caused by a different selection regime on the highly domesticated strain of the chicken. However, it warrants further research and some caution with the interpretation of behavioral profiles as being similar in different taxa.

6. Gene–environment interactions

The selection lines in the great tit provide evidence for a strong genetic effect on behavioral profiles, in line with similar data on the house mice (see above). In addition, a quantitative genetic study was carried out of the behavior in

the Novel Environment and the Novel Object tests, based on the selection lines for exploration, reciprocal F1 and reciprocal first backcross generations. This revealed evidence for both additive and dominance genetic effects, pleiotropic effects, but no effect of sex dependent expression [52]. In particular, a significant additive maternal component was found for the response to a novel object suggesting a role for maternal effects [52]. Although a larger sample size is needed here, the results open the possibility for environmental influences on the development of behavioral profiles.

Since the selection lines have been established with cross-fostered eggs, maternal effects may have influenced the behavioral differences between the lines via maternal release in the egg. Avian eggs contain substantial levels of maternal androgens in the yolk [53]. Early exposure to androgens are well known to influence a wide array of behaviors, including aggression, risk taking and boldness, and may therefore profoundly affect behavioral profiles. Maternal androgens have been shown to influence growth and various behaviors in both young [54,55] and almost adult [56] birds. Recent findings indicate that the selection lines for exploration differ in androgen levels in their eggs [57]. Interestingly, differential androgen exposure during embryonic life has also been implicated in the development of the coping styles in the mouse [58,59].

Rearing conditions seem to interact with genetic factors and play a prominent role in the development of behavior. In a year with poor food availability during the reproductive period, the proportion of fast birds increased in a wild population [20]. Inspired by this, two experiments were carried out in which chicks of the selection lines were food rationed [60]. First, in a within-nest design, food rationed and control chicks of the same line were in the same nest. SLOW offspring ($N=7$ nests), regardless of treatment, became much faster in their exploration than their parents. FAST offspring ($N=7$ nests), regardless of treatment, became more aggressive. This suggested that (1): an increase in sibling competition due to food rationing of some of the chicks might affect the behavioral profile of all chicks; (2): the link between different traits can be uncoupled in the course of ontogeny.

The first suggestion was tested in the second experiment with chicks from the SLOW line only. In this case a between-nest design was used, so that food rationed chicks ($N=5$ nests) could not influence the control chicks ($N=6$ nests) that were in other nests. In line with the expectation, now only the chicks from the experimental group became faster in their exploration score. Further support for the effect of sibling competition on the behavioral profile was found in the begging frequency of the control chicks: this was higher in the within-nest design where the experimental chicks could influence the control chicks, than in the between-nest design where this could not occur. Furthermore, this difference between the experiments mirrored the difference between the experiments in exploration (Fig. 1).

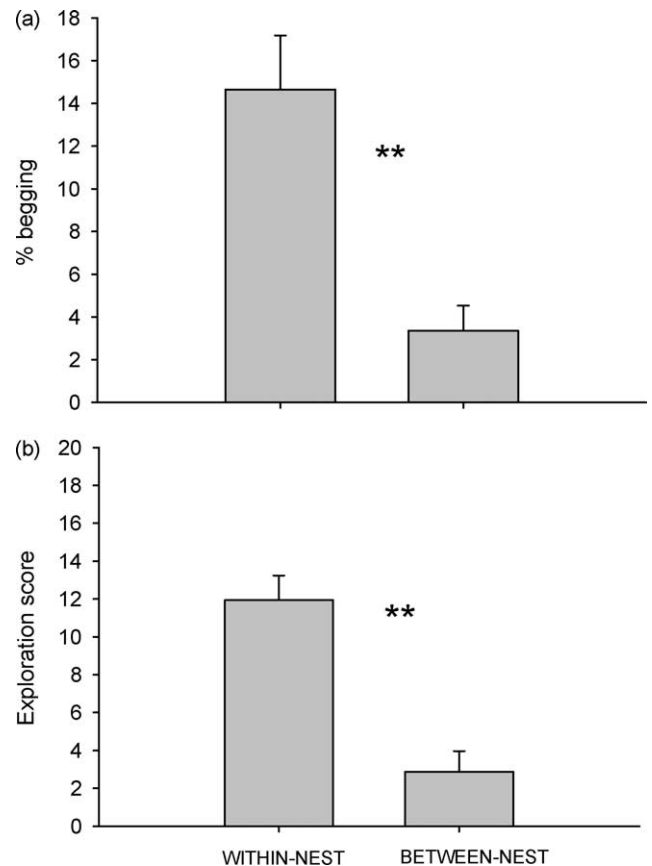


Fig. 1. Results of the within vs between-nests design. Begging behavior (a): percentage of time devoted to begging in a standard test) and the combined exploration score (b) used as selection criterion (Novel Environment and Novel Object) in control chicks of the SLOW line housed together with a food rationed sibling (exp 1, $n=15$) or with another control sibling (exp 2, $n=6$). Values are means with standard errors. $**p<0.01$ (Student t test on normalized data).

In conclusion, the results indicate that even in the case of pleiotropic effects or genetic linkage, each behavior of the package requires its own gene–environment interaction. An effect on only part of the package by manipulation of the early environment, in this case the sex ratio of the litter, was also found for the selection lines of wild house mice [61]. The results also open the possibility that experience, perhaps influenced by the parents via food provisioning and transfer of maternal hormones, can adjust the behavioral profile to the prevailing circumstances. Given the fact that all genes come to expression in interaction with other factors within and outside the animal, the strong effect of genes on behavioral profiles should not hamper ontogenetic research in the field, as seems currently to be the case in avian research.

7. Ecological and evolutionary aspects

One great advantage of using the great tit model is its possibility to study fitness consequences of the behavioral

profiles under natural conditions. Such an approach is extremely rare but indispensable to understand the selection pressures leading to maintenance of different behavioral profiles in the same population. The maintenance could come about by frequency or habitat dependent selection, and/or by selection regimes that fluctuate in time. This requires long-term studies in multiple populations in order to obtain under different selection pressures several estimates of Darwinian fitness that would best approximate the level of gene propagation of a given individual into the next generations. These complex requirements seriously hamper progress. It has been suggested that in the house mice proactive animals are favored during crowded but stable situations, while reactive animals would do better in an unstable situation, during migration and establishment of new colonies [8]. There is some evidence that the proportion of aggressive animals fluctuate in the course of time after establishment of the colony, but convincing evidence is unfortunately lacking [62]. A few studies with other species analyzed one or two fitness parameters in relation to boldness. Several fitness parameters were found to correlate with boldness (trappability) in bighorn sheep. The fitness effects partly depended on predation pressure, creating the possibility for fluctuating selection to maintain coexistence of phenotypes [12,63].

A whole series of studies on fitness consequences of the behavioral profiles have been recently conducted in the great tit. Wild birds were characterized by catching them in the field and taking them for one day to the laboratory for testing them in the Novel Environment test, after they were released in the original population. Based on the studies presented in the section on characterization, it was likely that the scores in the test would sufficiently characterize the profiles. A wide array of fitness parameters were measured in these birds, in different age classes and during three different years, one with extremely good food availability and two with poor food availability. An overview of the most important results published so far, is listed in Table 3.

Clearly, the score in the Novel Environment test, and thereby most likely the whole behavioral profile, correlated significantly with various parameters. Several lines of evidence indicated that dispersal was greater in Fast birds compared to Slow birds, perhaps as a result of their larger vulnerability to social defeat [64]. Fast territorial males had also higher dominance ranks than slow territorial males, whereas fast non-territorial juveniles had lower dominance ranks than slow non-territorial juveniles [65]. It has been therefore suggested that the relation between dominance and personality is context-dependent in the natural situation.

Recruitment of offspring was better for assortative pairs with either extreme fast or extreme slow scores, but only so in the year with high food availability. Offspring of disassortative pairs recruited more frequently in the two years with lesser food availability. Adult survival was related to the exploratory score reflecting the behavioral

Table 3
Overview of the fitness correlates of personality types in wild great tits

Fitness parameter	Fast vs slow	References
Dispersal	F>S	[64]
Dominance in territorial males	F>S	[65]
Dominance in non-territorial males	S>F	[65]
Recruitment offspring in poor years	FS=SF>FF=SS	[66]
Recruitment offspring in a good year	FF=SS>SF=FS	[66]
Female adult survival in poor years	F>S	[66]
Female adult survival in a good year	S>F	[66]
Male adult survival in poor years	S>F	[66]
Male adult survival in a good year	F>S	[66]

F, fast; S, slow. FF and SS, assortative pairs with respect to behavioral profile; FS and SF, disassortative pairs.

profile, but depending on both sex and food availability of that year [66].

In addition it was found with birds from the selection lines that FAST birds started egg laying earlier in the season than SLOW birds [57] (see Table 1). This might have strong fitness implications since reproductive success declines over the course of the breeding season in many bird species. Birds laying earlier in the season tend to produce better quality offspring and are able to produce second clutches as well [67,68].

An important way by which individual behavior can affect the genetic variance of a population is non-random mate choice [69]. Positive assortative mating is expected in all situations in which habitat dependent selection predominates, which can lead to parallel divergence in the traits of interest. Populations are then divided in subgroups homogeneous with respect to different behavioral phenotypes and allocated according to the optimal habitat condition. Positive assortative mating could also occur in situations of frequency dependent selection, assuming that the fitness of assortative pairs is higher than the fitness of disassortative pairs. Negative assortative mating could occur when the partners complement each other (for example proactive males might obtain the best territories and reactive females the best food exploiters). Finally, one phenotype may be favored over others by all phenotypes in case it would perform better in important challenges such as antipredator behavior [70], while the other type stays in the population if it would do better in juvenile survival. We ran a series of experiments in captivity in order to test the partner preference in the two selection lines [31]. Adult males of the FAST line consistently preferred females of the same line both in autumn and spring, while birds of the SLOW line did not show any clear preference, perhaps

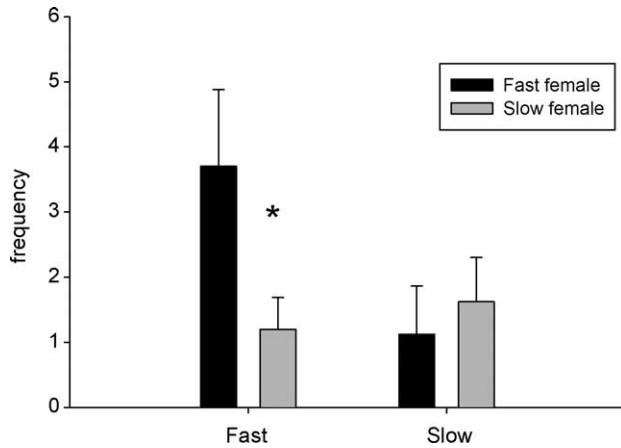


Fig. 2. Results of a double choice preference test carried out in spring in outdoor aviaries. Frequency of courtship displays which from males of the FAST ($n=10$) and the SLOW line ($n=8$) are directed towards a FAST and a SLOW stimulus female simultaneously exposed to the experimental subject. Test duration was 30 min, with inversion of the FAST and the SLOW stimulus after 15 min to control for side preference. Values are means with standard errors. $*p=0.02$ (Wilcoxon test).

because they need more time to form one (Fig. 2). Since the two lines do not differ in morphological characters, the results indicate a preference based on the behavioral profile of a partner, being able to display a fine-grained discrimination between conspecific individuals, which share most, but not all phenotypic traits.

In conclusion, the differential selection pressure on the behavioral profiles, fluctuates depending on food availability and this, as well as the indication for assortative mating, may help to explain the co-existence of the different profiles in the population. However, the results are complex and not yet fully understood on the basis of the nature of the different behavioral profiles. In addition, the sample size for poor food years was only two and for good years only one. Also, food condition during development may have affected to some extent the phenotype of the wild birds as measured in the Novel Environment test (see above), so that the test may not have been an adequate characterization of the heritable component of the profile. Further long-term studies, as well as studies on the fate of birds with known genetic background, hatched from selection lines egg and cross-fostered to wild nests in the field, are important challenges for the future.

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