Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation

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Individuals of many species differ consistently in their behavioral reaction to mild novel challenges. Suites of these behaviors are referred to as behavioral syndromes or personalities. Personality traits are often phenotypically and genetically correlated. Therefore, animal personalities are generally considered as broad characteristics, with underlying genetical and physiological mechanisms that are expressed across situations and contexts. Because there are carryover effects between situations, animals are not entirely flexible in their behavior in each situation. This may cause behaviors to seem nonadaptive in isolated situations. To test whether individuals with different personalities could react differently to changes in their environment, we studied context dependence of personalities in the great tit (Parus major). We tested birds categorized as either fast or slow explorers for their latency to come back to a feeding table after a mild startle (risk-taking behavior) in a nonsocial followed by a social context. We found that the relation between exploratory behavior and risk-taking behavior depended on the social context. Females in general returned later in the social test, while male reaction to the presence of a conspecific was dependent on their behavioral type. Slow males thereby reacted to the behavior of the companion and fast males did not. These results show that although personalities have a rigid structure the relation between personality traits is context dependent. These results are discussed in the perspective of the adaptive significance and maintenance of personalities. Key words: Behavioral syndromes, boldness, exploration, Parus major, personality, risk taking.

Individuals of many species differ consistently in their behavioral and physiological reaction towards mild challenges (Gosling and John, 1999; Koolhaas et al., 1999; Wilson et al., 1994). Suites of consistent and correlated behaviors across situations or contexts have been labeled as temperament, coping styles, or coping strategies (Boissy, 1995; Koolhaas et al., 1999; Wechsler, 1995) comparable with human personalities (Bouchard and Loehlin, 2001; Zuckerman, 1991). A situation is thereby defined as a given set of conditions at one point in time and a context as a functional behavioral category like, for example, feeding, mating, or parental care (Sih et al., 2004a). In behavioral ecology we mostly refer to these suites as behavioral syndromes (Sih et al., 2004a) or “animal personalities” (Dall et al., 2004; Groothuis and Carere, 2005).

Animal personalities are often considered as general characteristics, with underlying genetical and physiological mechanisms, that are expressed across situations and contexts (Koolhaas et al., 1999; Van Oers et al., 2004a). Thereby, animals are not entirely flexible in their behavior in each situation because there are carryover effects between situations, which may cause behaviors to seem nonadaptive in isolated situations (e.g., Sih et al., 2004b). However, Wilson et al. (1994) suggested that to be adaptive, individual differences may well have to be context dependent. They thereby state that each context that influences survival and reproduction potentially requires a different adaptive response, at least if these traits are adaptive. This idea was confirmed in several studies that describe the context dependence of the relation between personality traits (Coleman and Wilson, 1998; Dingemanse and De Goede, 2004; Réale et al., 2000). Hence, it may be adaptive to have individual differences in some contexts but not in others. This apparent contradiction that variation in personality is either a constraint (“constraint hypothesis”) or adaptive (“adaptivity hypothesis”) is based on the idea that the independent evolution of personality traits is hindered by a common genetical and physiological background (Bell, 2005). Here, we propose that differences in the way genotypes react to environmental variation (i.e., reaction norms) might be an alternative in explaining the adaptive significance of animal personalities.

The present study investigates whether the relation between two personality traits that have been shown to be phenotypically and genetically correlated in great tits (Parus major) can vary over contexts. We thereby focus on two traits that have ecological significance for this species: exploration and risk-taking behavior. Exploratory behavior is defined as any behavior that provides the animal with information about its environment (Birke and Archer, 1983). Verbeek et al. (1994) showed that individual great tits consistently differed in exploratory behavior, measured as the reaction to a novel environment, comparable to an open-field test (Walsh and Cummins, 1976). Exploratory behavior is heritable in great tits (Dingemanse et al., 2002; Drent et al., 2003) and phenotypically correlated with aggressive behavior in pairwise confrontations (Verbeek et al., 1996), recovery time and behavior after a contest (Verbeek et al., 1999), reaction to stress (Carere and Van Oers, 2004; Carere et al., 2001), and foraging behavior (Drent and Marchetti, 1999; Marchetti and Drent, 2000).
The second trait, risk-taking behavior, is based on the trade-off individuals have between foraging and the risk of being predated. Therefore, animals often must balance the benefits of approaching a food source with the benefits of avoiding predators, particularly if resources and predators coexist (Lima, 1998; Lima and Dill, 1990). Many factors influence the trade-off between predation risk and feeding, such as hunger level (Damsgard and Dill, 1998), food availability (Dill and Fraser, 1997; Martin et al., 2003), food properties (Cooper, 2000), and the absolute and relative predation risk (Martin and Lopez, 1999). The predictability of predation risk (Sih, 1992), the quality of hiding places (Martin and Lopez, 2000), and the distance to a possible hiding place or shelter (Walther and Gosler, 2001) also alter the balance between foraging and risk avoidance. Because individual differences in risk-taking behavior are related to other behaviors (e.g., Blaszczyk et al., 2000; Culshaw and Broom, 1980) and approach and avoidance motivation have been identified as an important factor in studies on consistent individual differences in behavioral traits (Budavari and Zhiukov, 1998; Elliot and Thrash, 2002; Van Oers et al., 2004b), covariation with other behavioral traits may also have an important impact on the trade-off between risk taking and foraging. In the great tit, individuals of the line selected for fast exploratory behavior (FE) return more quickly to a feeding table with mealworms after being startled than do individuals from the slow line (SE) (Van Oers et al., 2004b). In this startle test birds were tested in a nonsocial context. Great tits, however, live in social groups during an important part of their life (Drent, 1984), and several studies have shown that this social lifestyle can affect the behavior of the animal (for a review see Gallet and Giraldeau, 2001). The presence of conspecifics has well-known effects on the decisions to forage as opposed to avoid predators (for a review see Lima and Dill, 1990). This can be because individuals within groups may be more willing to take risks than solitary individuals because living in groups decreases the individual predation risk (Elgar, 1989). However because group living also increases competition for food (Goss-Custard, 1980), certain individuals might be more willing to take risks than others to be able get their share of the available resources (Grand and Dill, 1999). The composition of a group might therefore influence individual risk-taking behavior (Candolin, 1998; Kavaliers and Choleris, 2001). Individuals may also benefit from gaining information from others within the group or from copying their behavior (Krebs and Inman, 1992; Marchetti and Drent, 2000; but see Giraldeau et al., 2002). Hence, the relation between behaviors may vary according to the presence and the behavior of other group members.

Here, we investigate whether the relation between exploratory behavior and risk-taking behavior in hand-reared juvenile great tits is different in a social compared to a nonsocial context. We thereby concentrate on differences in the reaction to a mild startle, first between two tests of single individuals followed by a test with a male adult conspecific (companion). This approach will allow us to test if the relationship between exploratory behavior and risk-taking behavior in great tits depends on the presence and the behavior of a companion and to distinguish between these effects and habituation effects. Context dependence in these traits would indicate that, despite rigid differences appearing early in life, individuals are nevertheless able to exhibit some, potentially adaptive, plasticity in personality.

METHODS

Subjects and housing

We removed 90, 10-day-old nestling great tits from 15 nests of two natural populations (Westerheide, near Arnhem; and Oosterhout, near Nijmegen, The Netherlands). This group of 90 birds was initially collected for a selection study (see Van Oers et al., 2004b). After collection from the field, nestlings were divided into family groups of four to five siblings. These sibling groups were placed in natural nests in wooden boxes. Each box contained three compartments, and within each compartment there was one sibling group. The young were hand-reared on a mixed diet of wax moth larvae; crickets; and a mixture of ground beef heart, wheat, curd, calcium, and vitamins. On fledging (17–20 days after hatching), sibling groups were housed in small wire cages of 0.5 × 0.4 × 0.4 m, each with two perches. At day 20, small cups with beef-heart mixture supplemented with insect food and water were placed in the cages. Within a few days after the first young started to exploit this food, hand-feeding was gradually stopped. Hand-feeding has no obvious influence on the behaviors of interest (Drent et al., 2003). At the age when wild juveniles become independent of their parents (day 35), we housed our subjects individually in cages of 0.9 × 0.4 × 0.5 m with solid bottom, top, side, and rear walls; a wire mesh front; and three perches. Birds were kept under natural light conditions with acoustical and visual contact with one another. Juveniles of parents with different scores were housed in the same room. Each cage was connected to a light-tight observation room of 4.2 × 2.5 × 2.3 m via a sliding door of 20 × 20 cm in the rear wall.

At an age of about 10 weeks we took a blood sample of 10 μl from the brachial vein in the wing. Birds were sexed using the method of Griffiths et al. (1998). About 4 weeks later birds were housed in semiopen outdoor aviaries (2.0 × 4.0 × 2.5 m) in unisex flocks of 6–8 individuals, for a period of 6–8 weeks. After this, they were placed back into their home cage. During all stages, we provided the birds with ad libitum water, commercial seed mixture, and calcium. This was supplemented daily with mealworms and a mixture containing sour milk, ground beef heart, a multivitamin and calcium solution, and commercial egg mixture. Birds were kept under natural light conditions, with visual and vocal contact with other birds. Birds had no access to food 2 h prior to the tests and were deprived of mealworms 2 days before testing to increase their tendency to take mealworms during the test. We knew the sex and exploratory score of 54 juveniles of the pool of 90 at the start of the experiment, and so they were used as focal animals for the social and nonsocial startle tests using the half of the observation room (nonstandard startle tests). We weighed all birds and measured their tarsus before the experiments.

Behavioral tests

Exploratory behavior

We recorded exploration of a novel environment (for a schematic overview of the room see Dingemans et al., 2002) 1 day after birds had been housed individually at an age of 30–35 days. Observations were made between 0815 and 1230 h. The test was conducted in a light-tight observation room of 4.2 × 2.5 × 2.3 m containing five artificial trees (for details see Drent et al., 2003; Verbeek et al., 1994). Eight sliding doors along each 4.2-m wall connected the birds’ living cages with the observation room. To let birds enter the room, we darkened their cages with a towel, and we opened the sliding doors along each 4.2-m wall. The birds’ living cages were connected to the observation room via a sliding door of 20 × 20 cm in the rear wall.
were classified as FE, all others were classified as SE (16 FE males, 13 SE males, 9 FE females, and 11 SE females).

Original startle test
The original startle test, as described in detail by Van Oers et al. (2004b), took place in the same experimental room. Sixteen individual cages were connected with the room by sliding doors of 20 × 20 cm. Three artificial trees and a feeding table with a dish with mealworms were present. The feeding table was equipped with a hinged steel plate. A cord that was connected to this plate was led through the keyhole of the door so that the observer could handle it from outside the observation room; releasing the pressure on the cord caused the plate to immediately spring up in front of the bird, and pulling the cord back brought the plate to its original position, invisible for the bird.

The startle test consisted of three phases. After entering the room, a focal bird flew around for a short time (1–10 s) before landing on a tree. We measured the time from when the bird landed on a tree until it took the first worm from the feeding bowl (first-worm latency). In all cases focal birds took the worm to an artificial tree and ate it there. Because the experimental setup was new to the birds, they had to adjust to the novel situation. We therefore expected that differences in the first-worm latency reflect differences in exploratory behavior. Hence, we predicted that FE birds would approach the feeding table earlier than would SE birds. During the second phase, we measured the time from when a bird had eaten the first worm until it returned to the feeding table to get another worm. We refer to this period as the “second-worm latency.” We assumed after this phase birds were accustomed to the situation and knew where the food source was. Thus, we predict that FE birds would be similar to SE birds in the latency to the second worm. In the third phase the birds were startled just as they tried to get the second worm. We then measured the time it took them to return to the table and actually take the second worm. The startle latency was assumed to measure the level of risk a bird was willing to take after a potentially dangerous event.

Experimental startle tests
The experimental startle tests (i.e., nonsocial and social startle test) took place in the same experimental rooms as the original startle test, except that these rooms were divided in two equal parts by a transparent foil (Figure 1). All focal birds were first tested in a nonsocial context (i.e., without companion; nonsocial startle test) and then with a companion (social startle test).

The nonsocial startle test was conducted in the same way as the original startle test and took place in the left part of the observation room. In the social startle test the 28 FE and 26 SE focal birds were randomly paired with one of 8 FE companions and 8 SE companions. These companions were birds of the fifth generation of the lines selected for “fast” (FE companions) and “slow” (SE companions) exploratory behavior (Drent et al., 2003). Each companion was used once to four times. At the beginning of the test we let a companion enter in the right part of the room. In this phase of the test the companions were allowed to become familiar with the observation room and the feeding table. Once the companion had either eaten a worm or had been present for 5 min (four cases), we switched off the light after which the juvenile test bird would enter the left part of the observation room. In the social startle test the same measurements as in the nonsocial test were taken. In addition we counted the number of table visits by the companion. As a measure of the activity of the companions, we used the mean number of table visits per minute over the whole test period of the focal bird (companion activity rate).

We stopped the nonsocial startle tests when a bird did not take the first worm within 30 min (one case). We also stopped the test when the second-worm latency exceeded 10 min (1 case). These data points were excluded from the analysis. When a focal bird did not go back to the feeding table within 15 min (nonsocial startle test: five cases; social startle test: eight cases), the birds were assigned a latency of 15 min.

Learning effects
Because we always conducted the nonsocial startle test before the social startle test, learning effects could affect the results of the latter. To be able to distinguish between learning effects and effects caused by the experimental change from a social to a nonsocial context, we compared the nonsocial startle test with the original startle test. For 45 out of the 54 focal animals we checked what changes in behavior could be assigned to learning effects to be able to compare these effects with the results of the comparison of the social startle test with the nonsocial startle test.

Statistical analyses
We log transformed all latencies as they showed an increased variability with increasing values (Zar, 1999). The residuals of
the regression of weight against tarsus were used as a measure of the physical condition of the bird (Horak et al., 1998). In five cases we missed either an individual’s value for the nonsocial startle test or for the social startle test. These individuals were omitted, leaving 49 out of 54 focal animals for the analysis.

We used Generalized Linear Modeling (GLM) to test the influence of exploratory type, sex, and the interaction between these factors on the first-worm latency, second-worm latency, and startle latency. Companion properties in relation to behavioral type were analyzed using t tests. A repeated-measures GLM was used to analyze the changes in these variables between the two nonsocial tests and from a nonsocial to a social context. Repeated-measures ANOVAs thereby use the relative change in latency from the nonsocial startle test to the social startle test as a dummy variable (context). In these models we included behavioral type (type; FE or SE) and sex as factors and companions’ activity rate (companion) as a covariate. All analyses on context dependence are therefore using context as the main factor and the interactions of context with the variables of interest. General context dependence was tested with only context in the model. All other variables were then added to the model (full model) and with a backward procedure removed when least significant, until only significant variables were present in the model (minimal adequate model). Variables were tested in this minimal adequate model. We used SPSS 12.0.1 software to analyze all data. Two adult birds seem to have high activity rates. When these points were removed from the analyses, none of the conclusions drawn from the following results would have changed. All analyses were done on individual basis, but because not all birds originated from different nests, nest of origin (nest) was taken as a factor into the analysis.

Ethical note
All birds used were hand-reared individuals that were taken from natural nests at day 10 after hatching. Survival was 95% during hand-rearing and 99% in their first year after fledging. In general, birds were reintroduced to the wild when they were not needed for breeding or other experiments. This was done in times of stable weather conditions and when enough natural food sources were available. Birds were kept in large outdoor aviaries, which were opened after a week. Birds were still fed in and outside the aviary. In the course of about 3 weeks they got used to feeding for themselves. A capture-recapture experiment was conducted to evaluate this method in 1994. A group of local birds was captured in mist nets, ringed, and released again. A year later the recapture probability of these local birds was 19% compared to 18% for the reintroduced birds (Drent P and Verholt W, unpublished data). Permission for bird collection, breeding, testing, and blood sampling was granted to K.O. and P.D. by the legal comity “KNAW Dier Experimenten Commissie (DEC).”

RESULTS
We could find no evidence for observer (one-way ANOVA: $F_{1,49} = 0.002, p = .96$), condition (linear regression: $R^2 = .012$, $F_{1,49} = 0.59, p = .45$), or time of the day (linear regression: $R^2 = .009, F_{1,49} = 0.45, p = .51$) effects on the startle latency or effects of any of the interactions between these variables in the startle tests.

Nonsocial startle test
As expected if the exploratory behavior that distinguished SE from FE represents a general difference in personality, the two groups differed in the latency to take the first worm after entering the observation room (GLM: $F_{1,47} = 7.48, p < .01$) and the latency to return to the feeding table after being startled (GLM: $F_{1,47} = 9.88, p < .005$). FE birds were faster in both instances. However, there was no difference between these two groups in the latency to return to the table after eating the first worm (GLM: $F_{1,47} = 0.14, p = .71$), which means that in this phase birds had become accustomed to the situation. We also found no effects of sex or the interaction between sex and exploratory type on any of the three measured behaviors (GLM: first-worm latency, sex: $F_{1,46} = 0.18, p = .67$; sex × type: $F_{1,45} = 1.16, p = .31$; second-worm latency, sex: $F_{1,47} = 0.74, p = .40$; startle latency, sex: $F_{1,46} = 0.42, p = .52$; sex × type: $F_{1,45} = 1.33, p = .26$).

Learning effects
We compared the behavior of the birds in response to the nonsocial experiment to their behavior in the original startle test. We did this to detect learning effects caused by the repetition of the test and to be able to separate these effects from context effects in the comparison between the nonsocial and the social startle test later on. Learning effects could possibly interfere with our results, when these are different for FE and SE birds. We thereby found significant differences in behavior. Birds took less time to take the first worm in the nonsocial test compared to the original startle test (repeated measures GLM: context; $F_{1,44} = 5.85, p < .05$). Although in both tests FE birds used less time to take the first worm than SE birds, there was no difference in the decrease of this latency time between the behavioral types (repeated measures GLM: context × type; $F_{1,45} = 1.45, p = .24$) or between the sexes (repeated measures GLM: context × sex; $F_{1,43} = 3.00, p = .09$). From this we conclude that both types learn from the repetition of the test and that they do not differ in the way they learn.

No learning effects were found for the second-worm latency. There was no increase or decrease in this behavior when comparing the two tests (repeated measures GLM: context; $F_{1,44} = 1.07, p = .31$). As expected from the results within trials, neither sex (repeated measures GLM: context × sex; $F_{1,45} = 0.12, p = .73$) nor type (repeated measures GLM: context × type; $F_{1,45} = 0.23, p = .63$) affected the difference in second-worm latency between trials.

For the startle latency we found a significant difference in the way the sexes reacted to the repetition of the nonsocial test (repeated measures GLM: context × sex; $F_{1,43} = 4.29, p < .05$). Females did not differ between the two tests (repeated measures GLM: context; $F_{1,12} = 0.04, p = .85$), while males returned to the feeding table sooner after the startle in the nonsocial startle test (repeated measures GLM: context; $F_{1,26} = 22.04, p < .0001$), independent of their behavioral type (repeated measures GLM: context; $F_{1,25} = 0.21, p = .89$).

Companion activity
In the social startle test, we used the companion’s activity rate as a measure of its behavioral phenotype. We found that FE companions differed from SE companions in their behavior in the phase where they were allowed to familiarize with the test setup (without focal birds). FE companions needed less time to take the first worm from the feeding table than SE companions ($t$ test; $t_{42} = 2.74$ and $p < .01$), which is a confirmation of the difference in exploratory behavior. The analysis of the companions’ activity rate showed that FE birds visited the feeding table more often per minute than did SE birds (GLM: $F_{1,47} = 7.48, p < .01$).
Nonsocial versus social context

To test whether birds were influenced by the presence and behavior of the companion, we used the social and the nonsocial startle test of one individual in a repeated measures analysis. We first analyzed if first-worm latency depends on context and how it is affected by a companion. In general, focal birds took less time to take their first worm when a companion was present (repeated measures GLM: context; F_{1,49} = 28.27, p < .0001), independent of the focal birds’ exploratory type (repeated measures GLM: context × type; F_{1,48} = 0.02, p = .90), sex (repeated measures GLM: context × sex; F_{1,48} = 0.21, p = .65), or nest (repeated measures GLM: context × nest; F_{1,43} = 0.63, p = .82, Figure 2). The effect of context was influenced by the companion’s behavioral type: the higher the companion’s activity, the larger this time difference (repeated measures GLM: context × companion; F_{1,47} = 4.37, p < .05).

In the second part of the experiment, we analyzed the difference in second-worm latency between the nonsocial and the social test situation and whether this difference in latency depended on the companion activity. Neither the presence of a companion (repeated measures GLM: context; F_{1,48} = 2.68, p = .11) nor the companion’s behavior (repeated measures GLM: context × companion; F_{1,47} = 0.39, p = .53) affected a focal bird’s latency to second worm (Figure 3), and there were no differences related to sexes (repeated measures GLM: context × sex; F_{1,47} = 1.52, p = .22) and types (repeated measures GLM: context × type; F_{1,49} = 1.0, p = .32).

We also tested if a companion influenced the response in the startle test. We found a significant interaction effect between the sex of the subject and the presence of a companion on startle latency (repeated measures GLM: context × sex; F_{1,47} = 7.13, p < .01). We therefore analyzed the difference in startle latency between the social and nonsocial startle test separately for females and males. In contrast to our expectation, females had longer startle latencies in the presence of a companion than alone (repeated measures GLM: context; F_{1,19} = 4.93, p < .05; Figure 4), independent of exploratory type (repeated measures GLM: context × type; F_{1,18} = 0.07, p = .79) or companion’s activity (repeated measures GLM: context × companion; F_{1,18} = 0.58, p = .46).

By contrast, males tended to have shorter startle latencies in the presence of a companion (repeated measures GLM: context; F_{1,28} = 3.54, p = .07; Figure 4). Furthermore, male type interacted and the companion’s behavior interacted to affect the change in behavior between contexts (repeated measures GLM: context × type × companion; F_{1,25} = 5.99, p = .02; Figure 4). Thereby, SE males had shorter startle latencies when the activity of the companion increased (repeated measures GLM: context × companion; F_{1,14} = 8.79, p < .01), while FE males did not react to companion activity (repeated measures GLM: context × companion; F_{1,10} = 0.74, p = .41).

DISCUSSION

In this study we tested the relation between two personality traits in different contexts. We showed that the correlation between exploratory behavior and risk-taking behavior is dependent on the presence and behavior of a companion that was foraging in an adjacent compartment. Companions had a complex effect on subjects’ response to a startle. Slow explorers of both sexes became more bold in the presence of a companion, whereas the response of fast explorers depended on sex, with females becoming less bold in the presence of a companion. With these results we show that despite a strong genetic correlation (Van Oers et al., 2004b), and a possibly rigid underlying physiological mechanism (Koolhaas et al., 1999), phenotypic correlations between personality traits depend on the context in which they are measured.

One aspect of our experimental design complicates our interpretation of these results. All birds experienced the nonsocial context before the social one, so differences in responses could be due to learning effects, independent of the presence of a companion (Dingemanse et al., 2002, Drent and Marchetti, 1999). However, we found that repetition of the startle test without a companion actually increased first-worm latency and had no effect on the second phase of the test. The response to a startle differed by sex, with males returning sooner in the second trial, whereas females did not
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It would have expected an interaction between context and did not. If copying were occurring in our experiments, we would have expected an interaction between context and behavioral type on first-worm latency. We did not find this, and so conclude that copying is unlikely to have occurred.

From our previous study we know that the second phase of the test, the second-worm latency, reflects the hunger state of the animal. No habituation effects were present in the second phase of the test. In the comparison between the social and the nonsocial test, the second-worm latency was affected neither by the presence nor by the activity rate of the companion. We found no type or sex effects. This indicates that when novelty effects are still present in this phase, the approach motivation for feeding is relatively stronger.

In the last phase of the test, males and females reacted differently to the repetition of the nonsocial test and to the change in context. Females did not change their behavior in the repetition of the nonsocial test but were less prone to take risks in the social compared to the nonsocial test. This was most likely caused by the fact that all companions were males. Females could then be more vigilant in the social context either because they are attracted to the males or because males dominate females (Benus et al., 1990; Drent and Marchetti, 1996; Verbeek et al., 1994). First, females could have recognized the companion as a possible partner and therefore waited longer to return to the feeding table. In this case they could have lost time by social interaction. Second, because males are dominant over females, the females could have associated the startle with an aggressive act of the neighboring male companion. They thereby might have increased their vigilance regarding foraging by waiting to decrease the chance of behavioral interference while foraging.

However, for the males the change in startle latency between the nonsocial and the social context differed between the behavioral types. We found that only SE males reacted to the activity rate of the neighboring bird. Thereby, a combination of habituation effects and fear reduction or safety effect due to the companion’s foraging activity can explain the reaction of SE males. These effects are more likely due to fear reduction because we found a difference in context effects between the behavioral types when comparing the social and the nonsocial after controlling for the activity of the companion and not in the comparison between the two nonsocial tests. From our data it seems most likely that the FE birds only show a habituation effect and are not affected by the companion. This result confirms earlier studies of individual differences where aggressive, fast explorers are more routine-like and behave more autonomously than nonaggressive slow explorers (Drent and Marchetti, 1999; Marchetti and Drent, 2000). The absence of an effect of the companion’s activity on the decrease in startle latency can be explained by the fact that FE males develop routine behavior more quickly in which they become less sensitive for external signals. The lack of an effect for FE birds could also arise when FE males were inhibited by the companions, like the females were. The focal birds were all juveniles, who have a subordinate role towards adult birds. However, the difference between SE and FE birds cannot be explained by this.

Our results are comparable to those of Coleman and Wilson (1998), who found context specificity of shyness and boldness in a natural population of juvenile pumpkinseed sunfish. These results were also confirmed in other studies (Bell and Stamps, 2004; Réale et al., 2000; Sih et al., 2003; Van der Kooij et al., 2002). However, in these studies, context dependence was linked to the absence of phenotypic correlations of a single trait measured in multiple contexts, without knowledge of the genetic structure. As shown in several studies, different personality traits in great tits are not only phenotypically (Van Oers et al., 2004b; Verbeek et al., 1996) but also genetically (Van Oers et al., 2004a) correlated within the same context. Because the behavioral traits studied...
are measurements of reactions to an external stimulus, context-dependent variation in behavior is most likely being caused by several factors. Besides the effect of the context itself, learning effects, variation in the stimulus, or measurement variation can be responsible for the lack of phenotypic correlation between traits in multiple contexts. We have therefore shown that the “constrained hypothesis,” which states that variation in personality exists because of limiting possibilities for traits to evolve separately, and the “adaptation hypothesis,” which assumes variation in personality have arisen because of an adaptive advantage of certain combinations of alleles, are not mutually exclusive.

Our results support the hypothesis that personalities do not match the traditional concept of a one-dimensional behavioral continuum. This idea was already established in studies on animal personalities that make use of factorial analysis like in human personality studies (for a review see Gosling and John, 1999). So, personalities consist of multiple genetically correlated traits and not one general dimension. Therefore, phenotypic correlations between these traits over contexts can be low. This shows that comparing phenotypic correlations over contexts can be misleading and emphasizes the importance of estimating genetic correlations in studies of closely linked traits (Cheverud, 1988; Houle, 1991; Roff, 1995).

In conclusion, this study shows that consistent individual differences in one context may produce predictable outcomes in other environments, provided one knows the reaction norms and one has determined the changes in the environmental conditions. Context dependence of behavioral traits may be caused by more factors than a different phenotypic expression of a genotype in a certain environment alone and is therefore no proof for the adaptiveness of variation in behavioral traits over several environments. Reaction norms are not determined by the adaptiveness of the variation in each context separately; but as a consequence of varying context, a compromise to optimize fitness over the whole range of contexts has evolved (De Jong, 1999). It is therefore to be expected that not just one strategy but several strategies may reach the same optimal solution for the combination of situations. Because phenotypic correlations between personality traits are not consistent over context, fitness differences between personalities are also expected to be context dependent. Hence, although every environmental condition could favor its own phenotype, changing environments in space and/or time, and therefore changing selection pressures, could be a plausible mechanism for the existence and maintenance of consistent behavioral variation in several traits.

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