Individualities in a flock of free-roaming greylag geese: Behavioral and physiological consistency over time and across situations

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Abstract

The concept of personality implies individual differences in behavior and physiology that show some degree of repeatability/consistency over time and across contexts. Most studies of animal personality, particularly studies of individuals' variation in physiological mechanisms, have been conducted on selected individuals in controlled conditions. We attempted to detect consistent behaviors as well as physiological patterns in greylag ganders (*Anser anser*) from a free-roaming flock living in semi-natural conditions. We tested 10 individuals repeatedly, in a handling trial, resembling tests for characterization of "temperaments" in captive animals. We recorded the behavior of the same 10 individuals during four situations in the socially intact flock: (1) a "low density feeding condition", (2) a "high density feeding condition", (3) a "low density post-feeding situation" and (4) while the geese rested. We collected fecal samples for determination of excreted immuno-reactive corticosterone (BM) and testosterone metabolites (TM) after handling trials, as well as the "low density feeding" and the "high density feeding" conditions. BM levels were very highly consistent over the repeats of handling trials, and the "low density feeding condition" and tended to be consistent over the first two repeats of the "high density feeding condition". Also, BM responses tended to be consistent across contexts. Despite seasonal variation, there tended to be inter-test consistency of TM, which pointed to some individual differences in TM as well. Aggressiveness turned out to be a highly repeatable trait, which was consistent across social situations, and tended to correlate with an individual's resistance during handling trials. Also, "proximity to the female partner" and "sociability" – the average number of neighboring geese in a close distance while resting – were consistent. We conclude that aggressiveness, "affiliative tendencies" and levels of excreted corticosterone and testosterone metabolites may be crucial factors of personality in geese.
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Introduction

Within a given species, individuals of the same sex and age commonly differ from one another in their behavior and physiology even under standardized conditions. Such variation has been shown for a wide variety of species (for reviews see Gosling and John, 1999; Koolhaas et al., 1999; Carere and Eens, 2005; Groothuis and Carere, 2005), and has been referred to as "coping styles" (Koolhaas et al., 1999), "temperaments" (Zuckerman, 1991), "behavioral profiles" (Groothuis and Carere, 2005), "behavioral syndromes" (Sih et al., 2004) or "personalities" (Zuckerman, 1991; for reviews see Gosling, 2001; Sih et al., 2004). All these concepts imply inter-individual differences, some degree of consistency in behavior and physiology over time and across situations/contexts, as well as heritability. Individual differences related to personality consist of at least two correlated features, which may be either

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different behaviors or one type of behavior expressed in different situations (Groothuis and Carere, 2005). Here, we will use the terms "personality traits" for behaviors that are repeatable and correlated, and "personality" for a suite of these traits.

Behavioral repeatability/consistency has been demonstrated in captive animals selected for extreme phenotypes, which were tested under standardized conditions (e.g. mice, *Mus musculus domesticus*, Benus et al., 1987, 1990, 1991; Koolhaas et al., 1999, 2001; Veenema et al., 2003; rats, *Rattus norvegicus*, Steimer et al., 1997; Koolhaas et al., 1999; great tits, *Parus major*, Verbeek et al., 1994; van Oers et al., 2004a; Groothuis and Carere, 2005; laying hens, *Gallus domesticus*, Korte et al., 1997, 1999; farm minks, *Mustela vison*, Malkvist and Hansen, 2002). These studies have provided evidence for proximate origins and mechanisms. Personality traits were shown to be moderately heritable (van Oortmerssen and Bakker, 1981; Benus et al., 1991; Koolhaas et al., 1999, Drent et al., 2003; van Oers et al., 2004a,b, 2005a) and to correlate with physiological mechanisms, e.g. the (re)activity of the hypothalamic–pituitary–adrenocortical (HPA) axis (Koolhaas et al., 1999; Carere et al., 2003; Cavigelli and McClintock, 2003; Veenema et al., 2003) and/or gonadal reactivity (for review see Koolhaas et al., 1997). Captive great tits tended to show repeatable corticosterone excretion (Cockrem and Silverin, 2002a). Populations in the wild showed lower repeatability and heritability estimates of behavioral traits, but there were no significant differences from values found in laboratory populations (for review see van Oers et al., 2005a; Dingemanse and Réale, 2005). Far less is known of variation or individual consistency in hormonal responses of wild or semi-wild populations.

However, many personality-related traits are not stable over time and across situations/contexts. Behavioral consistency may not persist over time due to experiences, environmental and seasonal variation, and developmental processes (Sih et al., 2004; Carere et al., 2005a). Long-term consistency of individual exploratory and socio-sexual behaviors was found to be distinct in one selection line of great tits ("fast line"), whereas birds from the other selection line ("slow line") showed more plasticity in their exploratory behavior (Carere et al., 2005b). Other studies revealed lower consistency over time (pigs, *Sus scrofa*, Mendl, 1993; horses, *Equus caballus*, Visser et al., 2001); yet other studies showed that consistency of a single trait as well as the relationship between different personality traits depended on the context/situation (e.g. pumpkinseed sunfish, *Lepomis gibbosus*, Coleman and Wilson, 1998; great tits, Dingemanse and de Goede, 2004). In particular, individual behavioral traits (e.g. great tits, van Oers et al., 2005b; cows, *Bos taurus*, Hopster, 1998), or the relations between different traits that are assumed to belong to the same component of personality, e.g. temperament, often differed when individuals were tested alone or in a group (bighorn sheep, *Ovis canadensis*, Réale et al., 2000; pig, Jensen, 1995; Spoodler et al., 1996; D'Eath and Burn, 2002; but see Hessing et al., 1993, 1994). Hence, social mechanisms may mask the expression of personality traits, both in individual's behavior and physiology (Mendl and Paul, 1991; Mendl and Deag, 1995; von Holst,

1998; DeVries, 2002; DeVries et al., 2003; Frigerio et al., 2003a; Scheiber et al., 2005a). Defining consistency of behavioral personality traits may be somewhat problematic also because some individuals are more stable in their behavior than others (Bem and Allen, 1974; Kagan et al., 1988; Wilson et al., 1994; Carere et al., 2005b). Individual trait stability may be a character in its own right (Stearns, 1989; Komers, 1997; Lowe and Bradshaw, 2001).

In this study, we searched for consistent individual behavioral and physiological patterns in ten male greylag geese (*Anser anser*), living in an intact social system, a free-roaming flock of about 170 individuals (Kotrschal et al., 2006). In particular, we were interested whether an individual's corticosterone and testosterone response was consistent. This may be of crucial importance, since this kind of hormonal data are lacking and findings may differ from studies performed under laboratory conditions even when exposing animals to the same stressor (e.g. Cockrem and Silverin, 2002b). In order to explore how different test situations, social embedding and season influence an individual's behavior and physiology, we tested the focal animals during three periods pertaining to three different seasonal phases. We performed handling tests, resembling tests for characterization of "temperament" in captivity/laboratories (e.g. Hessing et al., 1993; van Hierden et al., 2002; Carere and van Oers, 2004), as well as recorded their behavior in four different social flock situations: a low density feeding and a high density feeding condition, a low density post-feeding situation and while resting. After handling tests and two of the four social situations, we collected feces of the focal individuals for determination of excreted immuno-reactive corticosterone (BM) and testosterone (TM) metabolites. We asked (1) whether individuals responded equally to different tests and in different repeats/seasons; (2) which parameters were repeatable over time and (3) which parameters were consistent across different test situations on an individual basis. Assuming that active coping with challenge may be related to or be part of personality (e.g. Hessing et al., 1993, 1994; Koolhaas et al., 1999, 2001) not only when individuals are tested solitarily, but also when the individual is embedded in its intact social environment, we were interested in (4) whether personality traits were also found when focal individuals were within the flock, or whether traits were masked by the social embedding. We therefore compared resistance during handling tests to aggressive behavior while in the flock (e.g. Hessing et al., 1993, 1994). Finally, we explored (5) variability of an individual's aggression level in the social context.

Materials and methods

The flock

In 1973, a non-migratory flock of greylag geese was established in the valley of the river Alm in Upper Austria by the late Konrad Lorenz (Lorenz, 1988; Hemetsberger, 2001; Kotrschal et al., 2006). Life-history data of all flock individuals have been recorded ever since (Hemetsberger, 2001). The geese are free-ranging and roam the valley between the Konrad Lorenz Research Station (KLF) and a lake 10 km to the south, where they roost at night. Geese breed in the valley every year, either at natural nest sites or in breeding boxes provided by the KLF. Besides, hand-raising is carried out regularly in the area where goose

families raise their offspring. The flock is subject to natural selection factors. Up to 10% of the adult flock members per year are lost to predators (Kotrschal et al., 1992). They also experience full parasite loads and are usually not treated against disease. Geese are provided with supplemental food twice per day on the meadows in front of the research station. At the time of data collection, the flock consisted of approximately 170 individuals. The geese are marked by colored leg bands and are habituated to the close presence of humans which usually does not affect their levels of excreted immuno-reactive corticosterone metabolites or their heart rates (Frigerio and Wascher, unpublished).

All parts of the study meet the demands of Austrian animal welfare legislation.

Focal subjects

Ten greylag ganders of the same social category, i.e. paired without offspring, were chosen semi-randomly. The sex was clear from behavior (Lorenz, 1988) and life-history data. Paired males are generally intermediate in rank. During the course of this study, two of the focal individuals lost their partners. Consequently, their social status changed to lower ranking singletons (Lamprecht, 1986). The subjects' age ranged from two to ten years ($X\pm SD=4.7\pm2.5$).

Data collection

Behavioral protocols and fecal samples were collected during three periods between August 2003 and January 2004, which pertained to three different seasonal phases: (a) re-establishment of the flock in the late summer (August–September), (b) pre-migratory restlessness (October–November) and (c) stable winter flock (December–January). In every period, we tested each focal male in four test situations, with an additional test situation (see below) applied in phase (c). In every period, we first performed (i) a handling trial. Thereafter, each goose was subjected to the three social situations within 2 to 4 days. The order of the testing was as follows: (ii) "low density feeding condition", (iii) "low density post-feeding situation" and (iv) a "high density feeding condition". Which male was to be tested was chosen at random, but the order of tests remained the same. Geese were observed during (v) rest in phase (c) only. The measurements were repeated three times in test conditions (i) to (iv), or four times in test situation (v), respectively.

In (i), the "handling" trials, individual geese were caught by hand (i.e. picked up avoiding a chase) and held tightly for 5 min. We planned to perform handling trials during morning hours only. This, however, was not always possible. Each goose was caught twice in the morning, i.e. from 0800 to 0930 h, and once in the afternoon, i.e. from 1500 to 1630 h. During handling, we recorded the duration of struggling. Following the final handling trail, we took body weight and body size measurements of each individual, which increased handling time up to 7 min. During this time, behavior was not recorded. One of the focal animals could not be caught for the third handling trial.

The geese were then subjected to the four social flock situations. In (ii), the "low density feeding condition", food was spread widely over an area of approximately 160 m², compared to (iv), the "high density feeding condition", where the same amount of food was spread over an area of just 40 m². This prompted the 170 individuals to feed tightly together. Condition (ii) represents a standard feeding situation, whereas condition (iv) was shown to be a competitive feeding situation (Kotrschal et al., 1993; Weiß and Kotrschal, 2004), which modulates excretion of immuno-reactive corticosterone metabolites (Scheiber et al., 2005b). In both situations, behavioral observations started at the beginning of the morning feeding, i.e. from 0750 to 0820 h, and lasted until the focal goose left the feeding area. The standard morning feedings were followed by (iii), the "low density post-feeding situation", when geese spread over the meadows in front of the research station before they go to rest. During this time, geese usually seek contact with their social partners, engage in activities such as drinking, grazing, preening and settling for rest. Then the distance between sub-groups within the flock is at least 4 m. During (iii) each gander was observed for 25 min. In all three social flock situations, we recorded frequencies of agonistic interactions, i.e. aggressive behaviors (threat, peck, chase, beak up), retreats, being attacked (being threatened, being pecked, being chased), frequency of vigilance behaviors (head up, extreme head up) and percentage of time spent in locomotion. This description of behavioral patterns provided by Lorenz (1988) was the base of this ethogram.

In geese, dyadic relationships are manifested through distances between individuals during rest (Lorenz, 1988, Frigerio et al., 2003b). During condition (v), rest, which occurs usually from approximately 0930 to 1130 h or 1500 to 1600 h, we observed "proximity to the female partner" and "sociability" of focal males. We defined "sociability" as the average number of neighboring geese, excluding the female partner, resting in close distance. "Proximity to the female partner" was measured as the percentage of time spent with the female partner within a given distance. We scored three distance categories: up to 1 m, up to 2 and up to 3 m. To determine an individual's "sociability", we scored the number of neighboring individuals in the same distance categories. Data were recorded every 3 min. Each individual was observed twice in the morning and twice in the afternoon. Since it was not always possible to observe every focal individual for the entire period, data were expressed per unit of observation time (average number of geese at a certain distance).

Fecal samples

In geese, fecal samples represent an integrated, proportional record of the plasma glucocorticosterone and testosterone levels 30–180 min prior to defecation (Kotrschal et al., 1998; Kotrschal et al., 2000; Hirschenhauser et al., 2000; Scheiber et al., 2005b). We collected fecal samples after (i) handling trials and following the social situations (ii) and (iv). We started collecting samples as soon as behavioral observations were done, until 3 h from the beginning of the tests. Within that period, we attempted to collect each dropping of the focal individual. To avoid the effect of diurnal variation and the endogenous corticosterone early morning peak (Schütz et al., 1997), fecal samples in conditions (ii) and (iv) were collected only well after peak excretion occurs. Handling trials could only be performed opportunistically (see above). We therefore collected "matched control feces" on the following day, over the exact same time span as the previous day's handling trial. The change in corticosterone level in response to handling was determined by the difference between BM excreted after handling trials and BM collected during the matched control condition. We analyzed the change in corticosterone level in response to condition (iv), the same way, by matching it with condition (ii). Testosterone values were analyzed accordingly (see Data collection).

Fecal samples were frozen at −20°C within 1 h after their collection. 0.5 g of the sample was extracted in methanol as described by Kotrschal et al. (1998). BM and TM values were determined by enzyme immuno-assay (EIA) (Möstl et al., 1987; Palme and Möstl, 1993; Kotrschal et al., 2000) using group-specific antibodies as described elsewhere in detail (corticosterone assay: Kotrschal et al., 1998; testosterone assay: Hirschenhauser et al., 1999a,b). The sensitivity of the assay was less than 2 pg/well, and concentration limits for reliable measurement ranged from 0.1 to 288 ng/g feces for BM and from 0.14 to 88.71 ng/g feces for TM. The intra-assay coefficients of variation for corticosterone and testosterone metabolites were 12.5% and 13%, respectively. The inter-assay coefficients of variation for corticosterone and testosterone metabolites were 17% and 14.3%, respectively.

Statistical analyses

We used Shapiro–Wilk to test if data were normally distributed. If behavioral and hormonal data were not normally distributed, we log $(x+1)$ transformed them, rendering them suitable for parametric statistics.

We applied a Repeated Measures Design of a General Linear Model and type III sum of squares to assess the effect of different tests and repeats/season on the measured parameters. Within-subject factors were tests and repeats/season. The number of levels matched the number of tests and repeats in which a given parameter was recorded.

Intra-test consistency of three repeats in the same condition was quantified as repeatability, calculated following Lessells and Boag (1987). The degree of a trait's repeatability quantifies how the measurement of a particular trait is representative of an individual and gives an upper limit of its heritability (Falconer, 1996). To calculate context-generality/specificity, parameters between all possible pairs of different conditions were correlated. Where no significant differences between repeats were found, the data of all three repeats of the same test condition were directly included in the assessment of the inter-test correlation. Using this method, we cover all variances, which would otherwise be potentially violated, if we correlated a mean of a parameter over

repeats of one condition with a mean of that parameter over repeats of another condition (for discussion see Liu and Liang, 1992; Fleeson, 2004). Liu and Liang (1992) further argue that thereby a potential measurement error, possibly due to uncontrolled external/environmental factors, is avoided.

To avoid the effect of habituation due to repeated handling (see Results), we correlated aggression levels in the social conditions with the level of struggling of the first handling only. General aggression was calculated as the average rank across all social conditions. An individual's aggression level in any given social condition was expressed as the average rank over the repeats of the same condition.

An individual's BM and TM responses to any given condition were assessed by modeling linearly the cumulative amount of hormone excreted in all successive droppings, which we collected, i.e. from the end of the behavioral observations, until 3 h from the beginning of the tests. The overall excretion level of fecal BM and TM over time was estimated as the slope of the cumulative regression line (k). To compensate for the differences in the time of occurrence of the first sample and for potentially missed early samples, the cumulative lines were shifted to zero. Modulation of hormonal excretion in response to the challenging conditions (i) and (iv) was estimated as the difference between the slope of the regression line during challenge ($k1$) and that of the regression line in the appropriate matched control ($k2$) by dividing ($k1$) by ($k2$). We determined an individual's hormonal excretion using the "cumulative method" rather than calculating a mean as proposed by Scheiber et al. (2005b), because during challenges defecation is accelerated. As a result, a larger number of droppings per unit time are deposited, which may lead to an underestimate of hormonal levels. By applying the "cumulative method", time intervals between consecutive droppings as well as overall sampling time are integrated in the slope of the regression line, or in other words, the slope of the regression line describes the speed of hormone excretion (hormonal activity).

We were interested in the individual variability of aggressiveness. For this purpose, we calculated the average rank and standard deviation (SD) of aggressive behaviors across all social conditions for each individual. We used a general linear model to determine if the SD of the four extreme individuals, i.e. the two least and the two most aggressive ones, differed from the variability of aggressiveness of the intermediate ones.

Data were analyzed using the SPSS 12.0.1® statistical package. The results of all analyses are two-tailed and levels of significance are corrected using sequential Bonferroni post hoc tests whenever necessary (Rice, 1989).

Results

Main differences in behavioral and hormonal parameters between different tests and repeats/seasons (group level)

Differences in behavioral and hormonal parameters between different tests

The three tests in the social context differed in frequencies of aggressive behaviors ($F_{1.15,10.37}=13.282$, $P=0.003$; Fig. 1A), being attacked ($F_{2,18}=53.547$, $P<0.001$), vigilance ($F_{2,18}=38.208$, $P<0.001$; Fig. 1B) and retreat behaviors ($F_{2,18}=30.928$, $P<0.001$), as well as percentage of time spent in locomotion ($F_{1.25,11.24}=25.096$, $P<0.001$). We found no differences between the "high density feeding condition" and handling for BM ($F_{1,9}=0.179$, $P=0.682$), and TM responses ($F_{1,9}=1.839$, $P=0.208$).

Differences in behavioral and hormonal parameters between different repeats/seasons

In the "low density feeding condition", we found differences between seasons for percentage of time spent in locomotion ($F_{2,18}=5.996$, $P=0.010$) and TM ($F_{2,18}=4.307$, $P=0.030$). Also, after the first handling trial, males struggled significantly less ($F_{2,18}=13.724$, $P<0.001$).
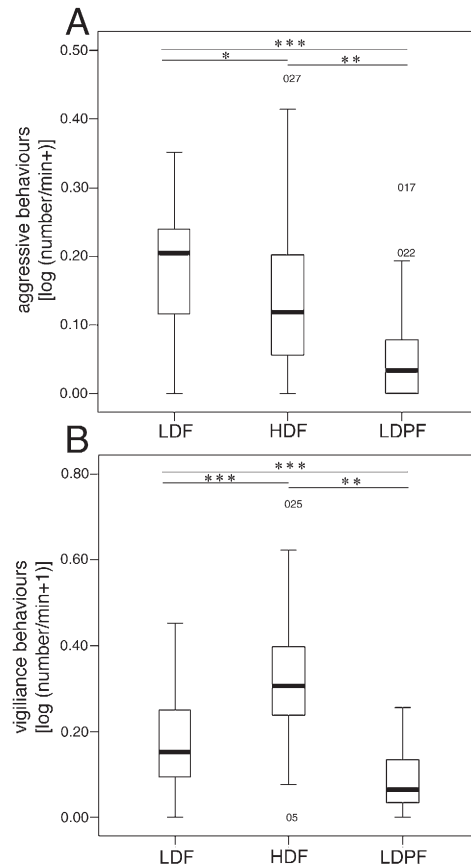

Fig. 1. Differences in the occurrence of behaviors during different test situations. (A) Frequency of aggressive behaviors in "low density feeding" (LDF), "high density feeding" (HDF) and "low density post-feeding situation" (LDPF); (B) frequency of vigilance behavior in "LDF", "HDF" and "LDPF". ***$P<0.001$, **$P<0.01$, *$P<0.05$.

Repeatability of behavioral and hormonal parameters

In the "low density feeding condition", males showed repeatability in their frequencies of aggressive behaviors (Table 1, Fig. 2A), retreat behavior and vigilance (Fig. 2D), but were inconsistent in the frequency of being attacked and in the percentage of time spent in locomotion (Table 1). Aggressiveness was repeatable also in the "high density feeding condition" (Table 1, Fig. 2B) and in the "low density post-feeding situation" (Table 1, Fig. 2C). During rest, proximity to the female partner was repeatable for the distances of up to 2 m (repeatability: $r=0.381$, $N=8$, $P=0.010$; Fig. 2E) and up to 3 m (repeatability: $r=0.352$, $N=8$, $P=0.016$). "Sociability" tended to be repeatable for the distance up to 1 (repeatability: $r=0.207$, $N=10$, $P=0.069$) and up to 2 m (repeatability: $r=0.198$, $N=10$, $P=0.077$; Fig. 2F). Struggling time during handling was inconsistent between the three repeats (repeatability: $r=-0.075$, $N=10$, $P=0.618$).

High repeatability for the excreted BM levels was detected in the "low density feeding condition" (Table 1, Fig. 2G) and in the first two handling trials (repeatability: $r=0.771$, $N=10$, $P=0.002$; Fig. 2H). BM in response to the third handling trial was excluded from this analysis, because geese were handled longer following this trial as body size measurements were

Table 1
Repeatability=r between three repeats of the same test situation of an individual's behavioral and hormonal parameters in "low density feeding condition" (LDF), "high density feeding condition" (HDF) and "low density post-feeding situation" (LDPF)

Variable	"LDF"		"HDF"		"LDPF"	
	r	P	r	P	r	P
Frequency of aggressive behaviors	0.655	<0.001*	0.602	0.001*	0.512	0.004*
Frequency of being attacked	0.381	0.025	0.331	0.043	−0.114	0.708
Frequency of retreat behaviors	0.512	0.004*	0.110	0.265	0.085	0.308
Frequency of vigilance behaviors	0.450	0.010*	−0.145	0.766	−0.082	0.642
Percentage of time spent in locomotion	−0.217	0.881	0.117	0.253	0.046	0.380
BM levels	0.480	0.006*	0.188	0.157	Not sampled	
TM levels	0.062	0.349	−0.017	0.507	Not sampled	

Number of individuals=10. BM=excreted immuno-reactive corticosterone metabolites, TM=excreted immuno-reactive testosterone metabolites. *Significant result after Bonferroni correction.

taken. Besides, the time of these measurements was different for each goose. These may have an effect on excreted BM levels, making them non-comparable with the first two trials. However, there was some trend for repeatability of BM responses between the first two repeats of the "high density feeding condition" (repeatability: $r=0.413$, $N=10$, $P=0.094$). We found no consistency of TM in the "high density feeding condition" (repeatability: $r=-0.017$, $N=10$, $P=0.507$) and handling (repeatability: $r=-0.230$, $N=10$, $P=0.754$).

Consistency of behavioral and physiological parameters across different test situations

Frequencies of aggressive behaviors and being attacked correlated across all social situations (Table 2). Occurrence of retreating tended to be consistent between the "low density feeding" and "low density post-feeding" situations, as well as between the "high density feeding" and "low density post-feeding" conditions (Table 2). Males' vigilance behaviors correlated between the "low density feeding" and the "high density feeding condition" (Table 2). We found a tendency for consistency of the BM responses between the "high density feeding condition" and the handling trials (Pearson: $r=0.415$, $N=10$, 2 repeats, $P=0.069$; Fig. 3A) as well as the TM responses (Pearson: $r=0.404$, $N=10$, 2 repeats, $P=0.077$; Fig. 3B).

Correlation between aggressiveness within the social context and struggling duration during handling

Tendencies for positive correlations were found between the struggling duration during handling and aggressiveness in the "low density feeding" (Spearman: $r_S=0.593$, $N=10$, $P=0.071$; Fig. 3C) and the "low density post-feeding" conditions (Spearman: $r_S=0.579$, $N=10$, $P=0.079$; Fig. 3C), but not in the "high density feeding condition" (Spearman, $r_S=0.406$, $N=10$, $P=0.244$). General aggression in social conditions tended to

correlate with the struggling duration of the first handling trial (Spearman, $r_S=0.574$, $N=10$, $P=0.10$).

Variability of an individual's aggression level in the social context

The most aggressive individual showed the highest frequency of aggressive behaviors in four out of nine social test conditions (SD=1), while the least aggressive individual had the lowest aggression level in six out of nine social test conditions (SD=0.65). Individuals with intermediate levels of aggressiveness were less stable; their aggressiveness varied between standard deviations of 1.91 and 2.59. Two individuals from either extreme, showed significantly lower SD than intermediary individuals ($F_{1,8}=7.532$, $P=0.025$).

Discussion

Here, repeatability of baseline ("low density feeding condition") and stress-induced corticosterone metabolite levels in free-roaming birds was shown for the first time. A very high degree of BM consistency was found in the individuals' responses to handling (repeatability: $r=0.77$), a standard stress situation presumably mimicking a predation event (Silverin, 1998). This is in accordance with results in captive great tits, where a repeatability of plasma corticosterone levels in response to handling was found (Cockrem and Silverin, 2002a). In great tits, however, individuals' baseline levels of plasma corticosterone were not consistent (Cockrem and Silverin, 2002a), whereas in geese, also the baseline levels of excreted BM ("low density feeding condition") were highly repeatable (repeatability: $r=0.48$). Moreover, individual BM responses showed consistency across different test situations. Repeatability of corticosterone excretion may indicate a genetic basis (Falconer, 1996) of individual variation in corticosterone responses to environmental stimuli in greylag geese, and thus, agree with the results of studies on selection lines in other species of birds (turkeys, *Meleagris gallopavo*, Brown and Nestor, 1973; chickens, Edens and Siegel, 1975; Japanese quail, *Coturnix coturnix japonica*, Satterlee and Johnson, 1988). Taking into account that individuals' BM levels and responses are repeatable and of limited plasticity, we suggest that corticosterone modulation may be causally involved in generating or maintaining consistent personality traits (e.g. Sih et al., 2004) in free-roaming geese. Also, differential perception of the situation among individuals, which may be related to personality (Sapolsky, 1994), is likely to contribute to consistent individual variation in corticosterone excretion. Correlation between personality traits and HPA (re)activity was shown in rodents (Koolhaas et al., 1999; Veenema et al., 2003) and great tits (Carere et al., 2003). Androgens may be another physiological process related to personality (e.g. Koolhaas et al., 1997). We, however, found no significant repeatability of TM, probably due to seasonal variation. Nevertheless, individuals tended to show inter-test consistency in testosterone responses, suggesting individuality in TM modulation as well.
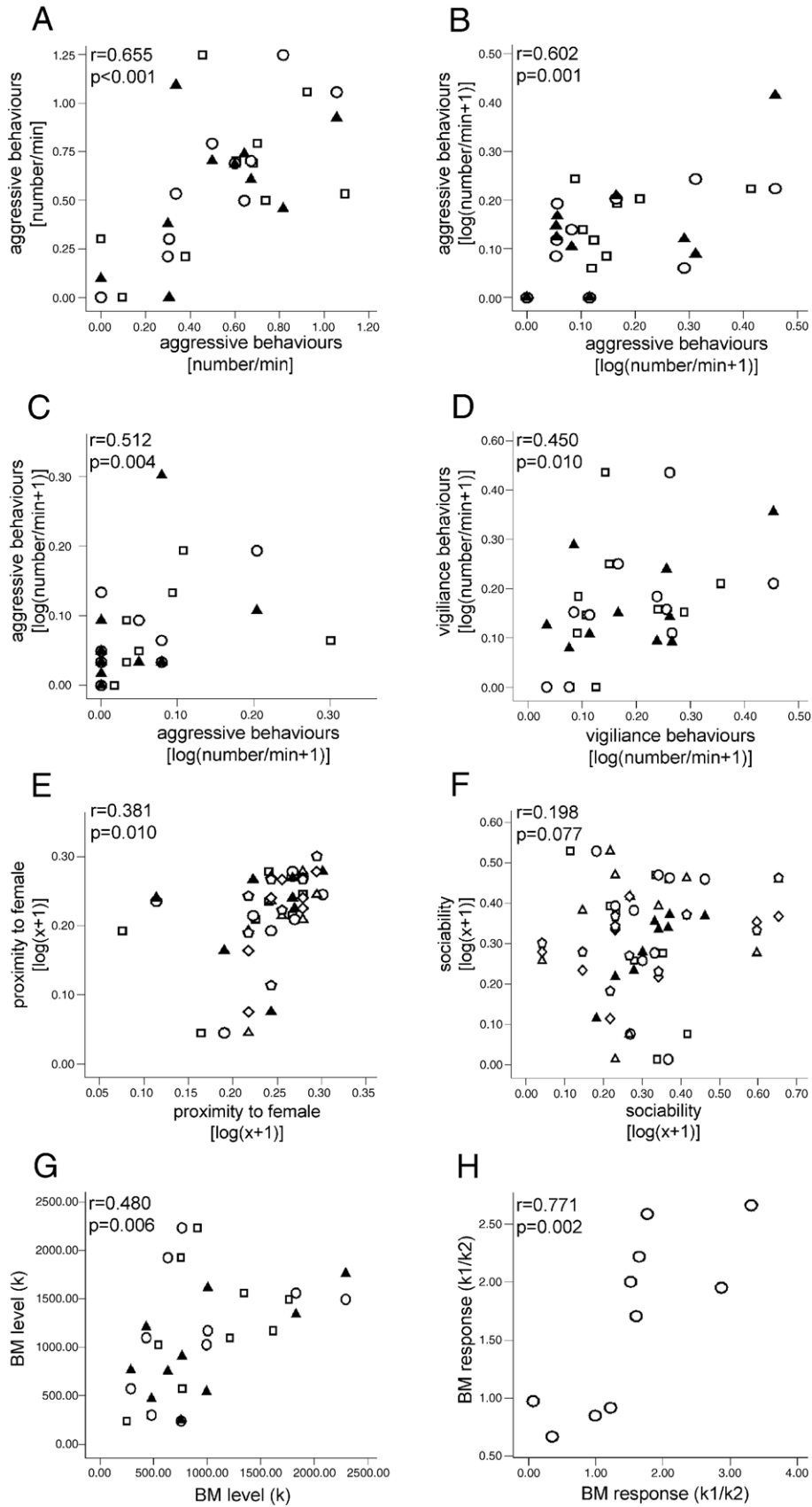
Table 2
Inter-test consistency of an individual's behavioral responses between different social situations

Variable	"LDF" vs. "HDF"		"LDF" vs. "LDPF"		"HDF" vs. "LDPF"	
	r_S	P	r_S	P	r_S	P
Frequency of aggressive behaviors	0.635	<0.001*	0.933	<0.001*	0.599	<0.001*
Frequency of being attacked	0.540	0.002*	0.490	0.006*	0.519	0.003*
Frequency of retreat behaviors	0.345	0.065	0.236	0.209	0.350	0.058
Frequency of vigilance behaviors	0.516	0.004*	0.074	0.699	0.125	0.512
Percentage of time spent in locomotion	−0.120	0.741	0.283	0.428	−0.105	0.582

In order to increase the between individual variance and to account for within individual variability, data from all three repeats of the same test situation were combined (for discussion, see Liu and Liang, 1992; Fleeson, 2004). Number of individuals = 10; 3 repeats of each situation; $N = 30$. *Significant result after Bonferroni correction.

Defining traits related to personality in group-living animals is difficult, as it is unclear to what extent behavioral responses of individuals are influenced by social relationships (e.g. von Holst, 1998; DeVries et al., 2003; Scheiber et al., 2005a) and conversely, how much personality characteristics will affect social relationships (Hinde, 1979). Very high consistency in aggressiveness over time and across different social situations implies that aggressiveness may be a heritable component of geese' personality, similar to what was shown in rodents (Benus et al., 1991; Koolhaas et al., 1999, 2001), great tit (Carere et al., 2005b) and primates (Fairbanks et al., 2004). On the other hand, the stability of aggressiveness might be a consequence of the social hierarchy, which places consistent demands upon individuals to conform. Stability of geese' aggressiveness (repeatabilities = 0.51–0.66; correlation coefficients = 0.60–0.93) was in general higher than stability of personality traits observed in other species, such as boldness in wild bighorn sheep (repeatability = 0.36, Réale et al., 2000) or exploratory behavior (repeatability = 0.27–0.48, Dingemanse et al., 2002) and risk-taking behavior (repeatability = 0.26, van Oers et al., 2004a) in wild-caught great tit. Such high stability is probably due to individual and social factors. Yet, aggressiveness tended to correlate with struggling duration during handling, at least in two out of the three social contexts. Assuming that aggressiveness and active defense may be based on the same underlying "coping" trait (e.g. Hessing et al., 1993, 1994; Koolhaas et al., 1999, 2001), we suggest that aggressiveness was modulated and

potentially masked, but not overridden by the social environment. Furthermore, repeatability of "proximity to the female partner" and "sociability" may result from stable affiliative tendencies of the observed individuals and/or their female partner/other flock members. Similar to other studies in birds, where the degree of "social attachment" was shown to be related to "proactivity/reactivity" (Carere et al., 2001; Daisley et al., 2005), non-aggressive focal ganders were more "social", although less attached to their female partners, than aggressive ones (Kralj-Fišer et al., unpublished). On the other hand, an individual's tendency to be vigilant is probably not strictly related to personality, despite being repeatable. According to Lorenz (1988), certain ganders are considerably more vigilant than other members of the flock. Increased vigilance often occurs when ganders guard offspring. Therefore, repeatability/consistency of vigilance may be a sign of a family role rather than being a trait of individual differences related to personality.

Studies aimed at investigating, whether personality traits are context-general or context-specific, gave mixed results. Several studies tested whether different traits are correlated in more than one context (e.g. Dingemanse and de Goede, 2004), whereas others, like this one, asked whether single behaviors show consistency within and across different contexts (e.g. van Oers et al., 2005b). Ganders' responses to different tests were of different intensity, e.g. the level of aggressiveness during competitive feeding was higher than during rest. However, aggressiveness and being attacked were consistent across all social test situations, whereas vigilance and retreat were predictable only across certain situations. In cases, behaviors were predictable across different situations but not over repeats of the same situation. These seemingly paradoxical results suggest a short-term inter-situational consistency. Individuals probably changed frequency of certain behaviors according to the temporal variation in their environment, e.g. increased vigilance in the presence of an unfamiliar person, while aggressiveness was more intrinsically robust. Contradictory findings that behavioral traits sometimes seem domain-general and sometimes domain-specific may be due to different individuals' reaction norms for different traits (De Jong, 1990; Lynch and Walsh, 1998). The expression of an individual's behavioral phenotype may vary on different points of the environmental axis (van Oers et al., 2005a). Therefore, it seems of crucial importance to examine these traits in appropriate test conditions.

It was shown that personality-related traits particularly manifest in mildly stressful or challenging situations (Suomi et al., 1996; Koolhaas et al., 2001). This is probably an explanation for the low consistency of behaviors in the relaxed, "low density post-feeding situation". However, it was difficult to produce a challenging condition in the flock context. According to BM

Fig. 2. Overlay scatter plots of behavioral frequencies and BM levels between repeats of the same test situation. (A) Aggressiveness in "low density feeding condition" (repeatability: $r = 0.655$, $N = 10$, $P < 0.001$); (B) aggressiveness in "high density feeding condition" (repeatability: $r = 0.602$, $N = 10$, $P = 0.001$); (C) aggressiveness in "low density post-feeding situation" (repeatability: $r = 0.512$, $N = 10$, $P = 0.004$); (D) vigilance in "low density feeding condition" (repeatability: $r = 0.450$, $N = 10$, $P = 0.010$); (E) proximity to the female partner for distance up to 2 m during rest (repeatability: $r = 0.381$, $N = 8$, $P = 0.010$); (F) "sociability" for distance up to 2 m during rest (repeatability: $r = 0.198$, $N = 10$, $P = 0.077$); (G) baseline level of BM (repeatability: $r = 0.480$, $N = 10$, $P = 0.006$); (H) BM response to handling (repeatability: $r = 0.771$, $N = 10$, $P = 0.002$). BM = fecal immuno-reactive corticosterone metabolites. Symbols in graphs A–G represent measured variables plotted between all possible pairs of repeats in a given test situation: □ repeat one plotted against repeat two, ○ repeat one plotted against repeat three, ▲ repeat two plotted against repeat three, △ repeat one plotted against repeat four, ◇ repeat two plotted against repeat four, ⌂ repeat three plotted against repeat four.
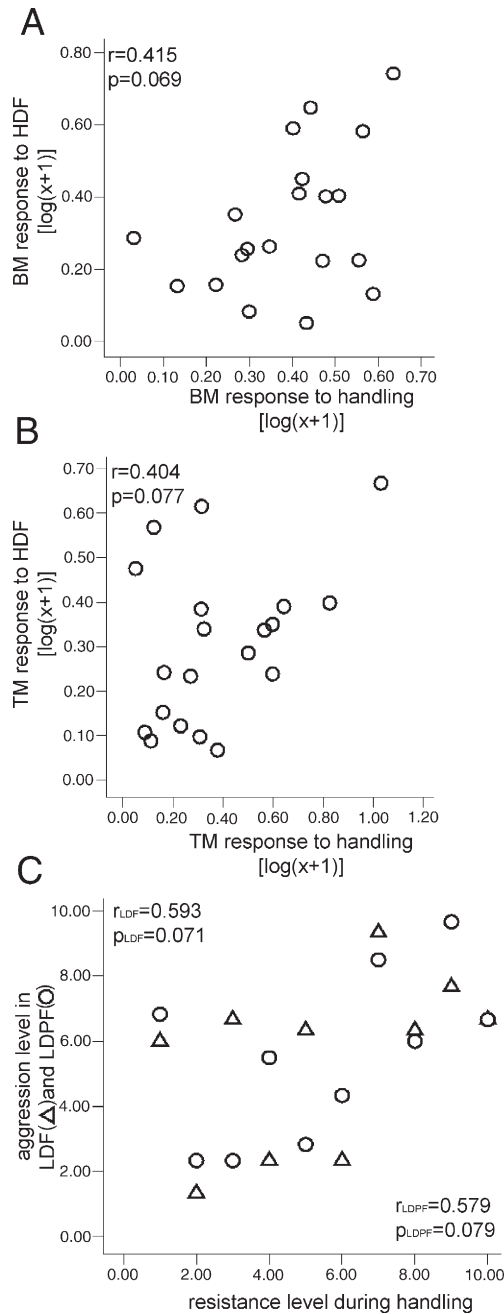
Fig. 3. (A) Correlation of BM responses between handling and the "high density feeding condition" (Pearson: $r=0.415$, $N=10$, 2 repeats, $P=0.069$); (B) correlation of TM responses between handling and the "high density feeding condition" (Pearson: $r=0.404$, $N=10$, 2 repeats, $P=0.077$); (C) correlation between resistance level during handling and aggression level in the "low density feeding condition" (Spearman: $r_S=0.593$, $N=10$, $P=0.071$); and correlation between resistance level during handling and aggression level in "low density post-feeding situation" (Spearman: $r_S=0.579$, $N=10$, $P=0.079$).

values of the "high density feeding condition", all individuals might not have always perceived the situation as a threat, which is probably a consequence of individual experience and different social embedding (e.g. "social support", Scheiber et al., 2005a). We hypothesize that a goose, which feeds in the middle of the flock during the high density condition is being constrained in moving around freely, and may be more stressed than a goose

feeding at the edge of the flock, where it has the possibility of quickly escaping or avoiding conflict situations. The perception of a threat also may depend on the quality of relationships with the neighboring geese, particularly if a goose is feeding in the middle of the flock and cannot avoid confrontations.

Another methodological problem is habituation to stressful conditions. Along these lines, geese struggled only briefly during the second and the third handling trial. Consequently, it was difficult to measure the duration of struggling precisely, which may be a reason for an inconsistent result of behavioral responses to repeated handling. The consistency of this behavior during comparable tests was found in laying hens (manual restraint, van Hierden et al., 2002) and bighorn sheep (docility during handling: repeatability=0.65–0.66, Réale et al., 2000), whereas results were mixed for pigs (Hessing et al., 1993, 1994; Forkman et al., 1995; Ruis et al., 2000). Still, the resistance during the first handling trial was certainly not affected by habituation and therefore was probably appropriate for measuring individual resistance levels. The second handling test had a low predictive power, which was also the case in group-living pigs (e.g. Ruis et al., 2000).

Defining personality traits by their consistency may be problematic because some individuals may be more stable in their behavior than others (Bem and Allen, 1974; Kagan et al., 1988; Wilson et al., 1994; Carere et al., 2005a,b). For example, there may be more consistency towards the extremes of personality traits and more context-related variability in between. Behavioral and physiological consistency was, indeed, most convincingly shown in animals that were genetically selected for extreme phenotypes (see reviews by Koolhaas et al., 1999, 2001). In pigs for example, only extreme phenotypes fulfilled the criteria of the coping styles theory (Ruis et al., 2000). We investigated personalities in unselected individuals of the same social category, intermediate in ranks, which are also generally intermediate in their aggressiveness. Also, inter-individual differences in aggression levels were rather small. However, despite very high repeatability/consistency of aggressiveness, ganders with intermediate level of aggressiveness varied significantly more in their aggressive behavior than the two most and the two least aggressive individuals.

We conclude that aggressiveness and "affiliative tendencies" may be heritable personality traits in geese, whereas very high repeatability and consistency of corticosterone excretion may indicate heritable physiological processes that constrains the behavioral plasticity of an individual.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yhbeh.2006.10.006.

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