



# Hormonal correlates of being an innovative greylag goose, *Anser anser*

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A number of studies have focused on the spread of foraging innovations within animal populations, but only rarely have individual dispositions of becoming innovative been considered. With two groups of individually marked, hand-reared greylag goslings we investigated hormonal and behavioural correlates related to the individual's ability to perform operant tasks. During individual tests 6 weeks after hatching, goslings were given small food containers covered by lids. In the following winter the sibling groups were tested in a social set-up at a food dispenser, which the geese could activate by pulling a flap. We analysed individual faecal samples collected at 2, 6 and 12 weeks of age, and also after the individual tests, for excreted corticosterone and testosterone metabolites by enzyme immunoassay. During the individual test, 18 of 23 individuals learned to remove the lids. These 18 birds excreted higher faecal corticosterone concentrations than their respective controls 2 weeks after hatching. At the food dispensers, only four males became food producers; all the others scrounged. These four were in the group of 18 that were successful in the individual test and again tended, although not significantly, to have higher faecal corticosterone 2 weeks after hatching than the scroungers. In one of the groups, excreted corticosterone increased and excreted testosterone decreased after the individual test. Goslings successfully removing lids at 6 weeks raised their faecal corticosterone to a significantly greater extent than the unsuccessful individuals. Our results suggest that becoming an innovator may be contingent upon individual coping styles.

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The ability to innovate, that is, to develop new or modified behaviour patterns, is regarded as an important component of behavioural plasticity, vital to the fitness of individuals with generalist or opportunistic lifestyles living in variable environments (Kummer & Goodall 1985; Lefebvre et al. 1997, 1998). The best-known examples of innovative behaviours spreading through free-living animal populations via different social-learning mechanisms are related to the extraction, preparation and processing of food (Laland & Reader 1999), such as potato and wheat washing by Japanese macaques, *Macaca fuscata* (Kawai 1965), tool use in different primate species (Goodall 1964; Beck 1980; McGrew 1994; Whiten et al. 1999), milk bottle opening by great tits, *Parus major* (Fisher & Hinde 1949; Sherry & Galef 1990), and pine cone stripping in black rats, *Rattus rattus* (Terkel 1996). Lefebvre et al. (1997, 1998) listed numerous examples of innovations in birds and showed that even though these are phylogenetically widespread, innovation frequency in

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different taxa is related to relative forebrain size (Lefebvre et al. 1997, 1998; Lefebvre 2000).

Innovations typically involve particular individuals, who learn individually to perform the new behaviour. Such innovators may become models for other group members causing the behaviour to spread through social-learning mechanisms (Heyes & Galef 1996; Fritz & Kotrschal 1999). They also act as producers of food, which can then be used by scroungers (producer-scrounger systems; Barnard & Sibly 1981; Giraldeau & Caraco 2000).

Little is known about the starting conditions of innovations, that is, the factors channelling particular individuals into the roles of innovators/model/producers and others into the roles of observer/scrounger. In a study with guppies, *Poecilia reticulata*, Laland & Reader (1999) found that females were more likely to innovate than males, smaller fish more likely than larger fish and food-deprived fish more likely than nondeprived. However, apart from these differences related to sex, size and motivation they found that individuals who repeatedly innovated in the past were more likely to do so again

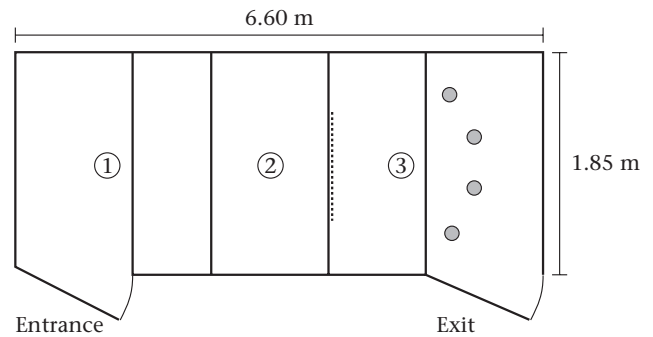
than past noninnovators. Thus, at least in guppies some individuals seem to express 'personality' differences in their tendency to innovate.

The expression of individual behavioural and physiological phenotypes or 'coping styles' is defined as the way individuals cope behaviourally and physiologically with environmental and social challenges, irrespective of life history state, sex or motivational state. The existence of different coping styles has been shown for various animal species including humans (Wilson et al. 1994; von Holst 1998; Koolhaas et al. 1999). In mice, *Mus musculus*, and rats, *Rattus norvegicus*, for example, aggressive individuals ('proactive copers') entrain more rigid routines, spend less time exploring novel environments and are less alert to changing stimuli in known environments than less aggressive individuals ('reactive copers'; Benus et al. 1987, 1990, 1991; Koolhaas et al. 1999). Similar patterns have been found in great tits ('fast copers' and 'slow copers': Verbeek et al. 1994, 1996; Drent & Marchetti 1999), domestic pigs, *Sus scrofa domestica* (Hessing et al. 1994) and the lion-headed cichlid, *Steatocranus casuarius* (Budaev et al. 1999).

Proactive copers (Koolhaas et al. 1999) tend to respond to challenges with only minor changes in glucocorticoids, but with considerable androgen modulation and vice versa in reactive copers. Such individual differences in hormonal responses may, in turn, within minutes feed back on individual behaviour, attention, readiness to learn and central learning mechanisms (Yerkes & Dodson 1908; Orchinik et al. 1991; Brown 1994; Breuner et al. 1997, 1998; von Holst 1998; Orchinik 1998; Koolhaas et al. 1999; Mendl 1999).

We have observed the spread of the ability to trigger a food dispenser in a free-living, semitame flock of greylag geese for more than 3 years (J. Fritz & K. Kotschal, unpublished data). As these birds live in affiliative social units of pairs, families or sibling groups (Lorenz 1979; Lamprecht 1986; Fritz et al. 2000), their members scrounge without interference. Usually one or two individuals within such groups operate the food dispenser whereas the others exclusively scrounge.

This raised the question whether individuals become innovators/producers or scroungers just by chance, or whether there is indeed a relationship with coping style (Clark & Ehlinger 1987; Wilson et al. 1994). To tackle this question, we experimentally hand-reared two sibling groups of greylag geese and, when they were 6 weeks old, tested individual performance in a simple learning situation. After fledging, these birds integrated into the unrestrained flock of greylag geese, which, during the following winter, was given a food dispenser. In parallel, we monitored individual patterns of excreted corticosterone and testosterone metabolites from hatching to fledging. The appropriate null hypothesis would be that a random selection of individuals from a population would, simply by chance, be confronted with stimulus situations furthering individual learning, making them innovators. In contrast, our working hypothesis was that the individual propensity to innovate has a deterministic underpinning, related to differences in the individual hormonal response to challenges.



**Figure 1.** Plan of the test arena with three compartments: (1) entrance and waiting compartment for the sibling group; (2) compartment to single out individuals; (3) test arena and exit. The three compartments were divided by removable barriers and surrounded by an opaque wooden fence (1 m high). Four grey plastic containers were placed at equal distances of 1 m to the entrance of the test arena.

## METHODS

### Subjects

In 1973, a free-living, nonmigratory flock of ca. 100 greylag geese was introduced into the Upper Austrian valley of the river Alm (Lorenz 1979). Over the initial years, this flock assumed stable spatiotemporal patterns and increased to more than 150 individuals. Birds are individually marked with coloured leg rings, are habituated to the presence of humans and are continuously monitored for social interactions. For a number of reasons, sibling groups of goslings are hand-reared every year in the nursing area of the flock by human foster parents.

All goslings in this study were hatched in an incubator within a week in late April 1999 and were assigned to sibling groups, one containing 13 individuals (nine males, four females; reared by A. Bisenberger), the second with 10 individuals (three males, seven females; reared by one of the authors, K.P). These two groups were kept under near-natural conditions from hatching to fledging. Goslings spent the nights together with their foster parent in a small hut. Foster parents stayed with their goslings 24 h/day for at least 10 weeks, walking them during the day to graze and to make contact with other members of the flock present in the area. For positive conditioning to the forthcoming test situation, goslings were regularly provided with preferred food (chicken starter) inside the test arena (see below). We genetically sexed goslings from feather samples taken at the age of 7 weeks.

### Individual Test

#### Experimental set-up

The experimental arena was situated adjacent to one of the huts mentioned above and consisted of a wooden floor,  $6.6 \times 1.85$  m surrounded by an opaque wooden fence (Fritz et al. 2000; Fig. 1). The arena was subdivided into three compartments, the first for group entry and waiting. A removable opaque barrier separated the

second, central compartment, used to single out individuals for testing, from the first one. The third compartment was the test arena proper, separated from the second again by a removable transparent barrier. From there, the subjects could leave the arena after testing. Because of pretest training, all goslings were well acquainted with this procedure. During tests the subjects could always see their human foster parent and were habituated to the presence of the experimenter (J.F.), who had regularly joined the groups since hatching. In this way we could separate individuals in the experimental arena for some minutes without causing social distress (as would have been indicated by distress calls). As goslings are relatively inactive around noon, we conducted arena experiments between 0830 and 1200 hours and between 1630 and 2000 hours. At least 2 h ahead of each experiment the birds were deprived of chicken starter.

### Procedure

Four grey plastic containers, 4.7 cm high and 7.0 cm in diameter, were placed in a crescent-shaped arrangement at equal distances of 1 m to the entrance of the test arena. Small amounts of granular chicken starter (ca. 5 g) in the containers served as a reward.

We tested goslings at 4–6 weeks. Two sessions per day were run with each individual. A single session consisted of a 'motivation trial' followed by two 'test trials', both identical in procedure and set-up except for the containers. During the motivation trial these were uncovered, allowing the individual free access to the food reward, whereas during the test trials they were covered by lids with a small handle.

After singling out an individual in the central compartment of the arena, we started a trial by removing the barrier to the test compartment and allowing the bird to enter. The experimenter stood behind the containers. Each time the subject pecked twice at the food (training trials) or removed a lid and pecked twice at the food (test trials) the experimenter removed this container. Thereby, movement to other containers was stimulated and the amount of food gained per container was standardized. A trial ended after all four containers were removed or after 30 s whichever occurred first. Then the gosling was called back into the central compartment by the foster parent, who offered water and greens, which are much less attractive than the chicken starter used in the containers. Meanwhile the experimenter prepared the next trial. One session consisted of two such individual trials. All goslings had at least 10 sessions (20 trials). We finished this experiment when a particular gosling had reached the 'learning criterion', defined as opening all four lids within one trial. With goslings that did not reach this criterion within the initial 10 sessions, we continued until they finally succeeded or until a maximum of 20 sessions was reached, which was the case in five out of 23 individuals.

### Data collection

All experiments were videotaped (Digital Handycam Sony DCR-VX700E). From tape we recorded the following

parameters for each test trial: (1) contact latency, that is the time from entering the arena to the first bill contact with a container; birds that did not touch containers during a trial were given a maximum score of 30 s (mean contact latency  $\pm$  SD =  $3.11 \pm 3.97$  s); (2) number of visits, that is the approach to a container with a distance below one length of the individual, either with or without contact; (3) number of containers opened; and (4) route length, that is the sum of all distances between the containers visited until all four were opened or the 30-s period had ended. The distance between two adjacent containers we defined as 1, with one container in between as 2, etc. Thus, the minimal route length to exploit all four containers was 3.

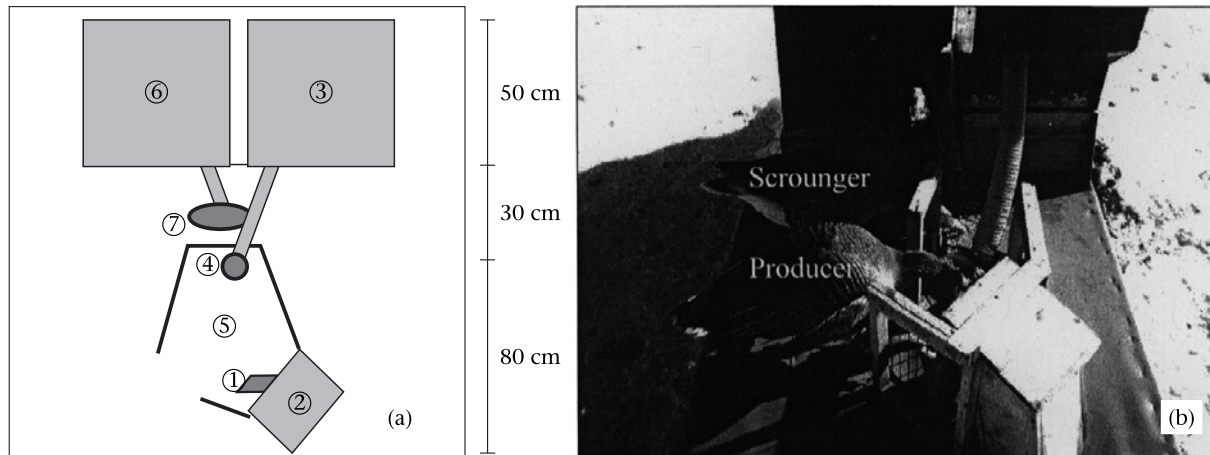
### Performance at the Food Dispenser

After fledging, at approximately 3 months of age, the juveniles integrated into the flock and were regularly present at the institute building. In winter of the same year, we staged a producer–scrounger experiment (J. Fritz & K. Kotrschal, unpublished data). When an individual pulled a flap at a computer-controlled food dispenser (Fig. 2) grain became available for the producer and, in a controllable way, also for the other individuals around it (scroungers). Producer and scrounger patches were close together, but were separated by a transparent partition (Fig. 2). The food dispenser was regularly active between 0900 and 0400 hours on 46 days, from 12 December 1999 to 12 March 2000. When active, data were collected twice a day for a mean  $\pm$  SD of  $19 \pm 3$  min each.

The dispenser was monopolized sequentially by social units, that is, groups of socially related individuals (Lamprecht 1986), such as families as the highest-ranking social units in goose flocks (Lorenz 1979; Kotrschal et al. 1998; Hirschenhauser et al. 1999a), monogamous pairs and sibling groups (fledged, unpaired adolescent geese up to 2 years, either not accompanied by their parents or hand-reared such as those we worked with). Usually, one or two individuals of any social unit became producers by learning how to trigger the dispenser, whereas all the others remained scroungers. Hence, there was a minority of producers and a majority of scroungers, as found in other producer–scrounger systems (Giraldeau & Caraco 2000; Lefebvre 2000). This was also the case in the two sibling groups that participated in the individual test described above.

### Faeces Sampling and Hormone Analysis

We took faecal samples at 2 (posthatching), 6 (6-week control) and 12 weeks (postfledging), each within a period of 5 days (see Table 1 for sample sizes). To avoid the endogenous early morning peak in excreted corticosterone (Schütz et al. 1997), we collected individual faecal samples between 0930 and 1200 hours and froze them at  $-20^{\circ}\text{C}$  within 2 h of collection. At the age of 6 weeks a further sample was taken 5–90 min after the final test session from each of the goslings (postexperimental). This time period after the session was chosen because it yields



**Figure 2.** Diagrammatic plan view (a) and photograph (b) of the feeder used. It consisted of two identical dispensers (40×50 cm area and 60 cm high; 2, 4), which were controlled via specific computer software. Pulling an orange flap (4×8 cm; 1), fixed at the front of a wooden box (2), activated both dispensers simultaneously. One dispenser (3) released ca. 1 g of grain (the producer's patch, 4), into the producer's compartment (5). The other dispenser (6) released ca. 3 g of grain outside the compartment (the scrounger's patch, 7). The transparent partition was made of wire mesh (35 cm high). Only half the body of a goose fitted into the compartment, blocking the entrance to it (22 cm) and, thereby, excluding the other geese (see 2b).

**Table 1.** Faecal sampling for hormone analysis: periods, mean age of the individuals at time of collection (weeks after hatching) and the mean±SD number of samples per individual

Sampling period	Age (weeks)	Samples/individual
Posthatching*	2	6.52±1.08
6-week control*	6	7.57±1.67
Postexperimental†	6	6.04±1.33
Postfledging*	12	6.00±0.00

\*Faecal samples were always collected over a period of 5 days.

†Samples were taken 5–90 min after the final test session for each of the goslings.

the peak corticosterone excretion after a challenge (Krawany 1996; Kotrschal et al. 2000).

The method of analysing steroid hormones from goose faeces is well established and evaluated. Steroid surges in the plasma caused by challenges are reliably reflected in the faeces (Hirschenhauser et al. 2000; Kotrschal et al. 2000). We used this noninvasive approach mainly to avoid handling the birds, which would have influenced hormone levels. Also, faecal samples reveal an integrated, proportional record of the plasma levels within ca. 1–2 h prior to defecation and, thereby, avoid the potential short-term fluctuations of hormones in the blood. Steroid metabolites are excreted via hepatic or renal pathways. Because it is not possible to separate faeces from the minor amounts of urine in goose droppings, we analysed both together for excreted corticosterone and testosterone metabolites (BM and TM).

Faecal samples (0.5 g) were extracted with 2.5 ml of water plus 3 ml of methanol, hydrolysed with a mixture of glucuronidase/arylsulphatase (Merck 4114), and determined by enzyme immunoassay (EIA, Möstl et al. 1987).

Kotrschal et al. (1998) and Hirschenhauser et al. (1999a, b) describe in detail the assays for corticosterone and testosterone, respectively, and their excreted metabolites. Concentration limits for reliable measurements ranged from 7 to 520 pg/well for corticosterone (B) and its metabolites (BM) and from 0.5 to 43 pg/well for testosterone (T) and its metabolites (TM). Intra- and interassay variations were determined from homogenized pool samples. The mean intra-assay coefficient of variation was 18.3% for B and 13.5% for T, and the mean interassay coefficient of variation was 24.4% for B and 40.8% for T. For every individual and sampling period we calculated the means of hormone metabolite concentrations. In addition, we calculated the percentage increase from the 6-week control to the postexperimental samples.

### Body and Competitive Weights

During the individual tests, 4–6 weeks after hatching, we weighed the goslings four to six times by luring individuals on to a digital scale by offering greens.

The ability to innovate could also be influenced by dominance rank, especially as becoming dominant is contingent on coping style (Koolhaas et al. 1999). However, as hardly any agonistic interactions occur within sibling groups, determining a rank order is neither feasible nor relevant. As an alternative, we determined competitive weight during feeding with a box (10 × 20 cm area and 64 cm high), filled with chicken starter, which we gave to the gosling groups in the test arena. This box had one small rectangular opening (4 cm diameter) at the top, allowing only one gosling at a time to obtain access to the food. The sessions, lasting 2 min each, were videotaped. From the tape we analysed the percentage feeding time per session for each gosling. With both groups we had 12 sessions.

**Table 2.** Statistical analysis of group and sex differences in the faecal corticosterone metabolites (BM) and testosterone metabolites (TM)

Sampling period	BM	TM
<b>Group differences</b>		
Posthatching	Lower in group 1 ( $U=3$ )*	Lower in group 1 ( $U=9$ )*
6-week control	Lower in group 1 ( $U=10$ )*	Lower in group 1 ( $U=24$ )*
Postexperimental	Lower in group 1 ( $U=29$ )*	No significant difference ( $U=50$ )*
<b>Sex differences</b>		
Posthatching	No significant difference ( $U=33$ )†	Higher in females ( $U=22$ )†
6-week control	Higher in females ( $U=28$ )†	No significant difference ( $U=38$ )†
Increase from 6-week control to postexperimental	Lower in females ( $U=30$ )†	No significant difference ( $U=46$ )†

\*Mann–Whitney  $U$  tests:  $N_1=13$  (group 1),  $N_2=10$  (group 2); sequential Bonferroni correction, error rate 5%.

†Mann–Whitney  $U$  tests:  $N_1=12$  (males),  $N_2=11$  (females); sequential Bonferroni correction, error rate 5%.

## Data Analysis

We used nonparametric statistical procedures. Means per sampling periods for the hormones and means of the two test trials per session for the individual tests were analysed. To compare the B and T hormone values, analysed from the same faecal samples, between the gosling groups (Table 2) we used the sequential Bonferroni correction to assess the type I error rate by adjusting the significance level downwards in relation to the number of tests (Wright 1992). We chose an experimentwise error rate of 5%. Statistical analyses were carried out with the SPSS statistical package. All data are given as means  $\pm$  SD and statistical tests are two tailed.

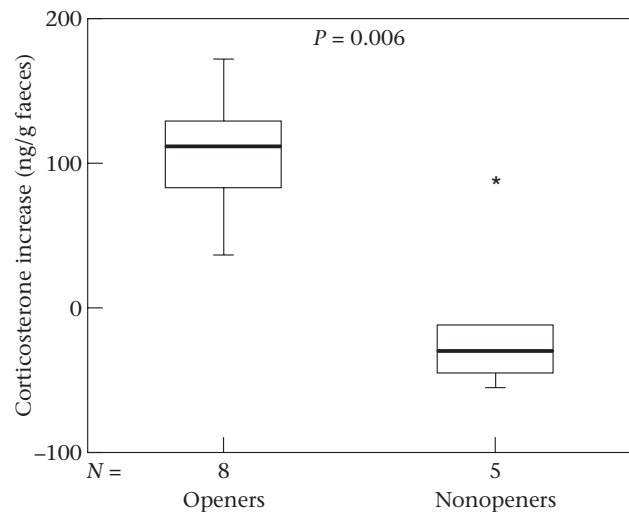
## RESULTS

### Individual Tests (Age 4–6 Weeks)

Eighteen of 23 individuals (10 males, eight females) reached the learning criterion (opening all four lids within one trial) within 20 sessions (on average after  $5.2 \pm 3.2$  sessions). All five individuals that did not learn to open the lids (two males, three females) were members of sibling group 1. Thus, we compared ‘openers’ and ‘nonopeners’ only within this sibling group.

During the first motivation trial, that is, when the birds entered the experimental arena and were confronted with the uncovered containers individually for the first time, those five individuals that did not learn to open the containers showed a nonsignificant trend towards a longer route than those of the same group that did open them (Mann–Whitney  $U$  test:  $U=8$ ,  $N_1=8$ ,  $N_2=5$ ,  $P=0.078$ ).

In sibling group 1 the concentration of excreted faecal corticosterone metabolites (BM) was significantly higher in the postexperimental samples than in the controls (mean increase:  $63.56 \pm 76.58\%$ ; Wilcoxon signed-ranks test:  $T=14$ ,  $N=13$ ,  $P=0.03$ ). This increase was higher in birds that successfully opened containers than the unsuccessful ones (Mann–Whitney  $U$  test:  $U=2.0$ ,  $N_1=8$ ,  $N_2=5$ ,  $P=0.006$ ; Fig. 3; the extreme value in Fig. 3 was included in the test). In group 2, the BM increase was not

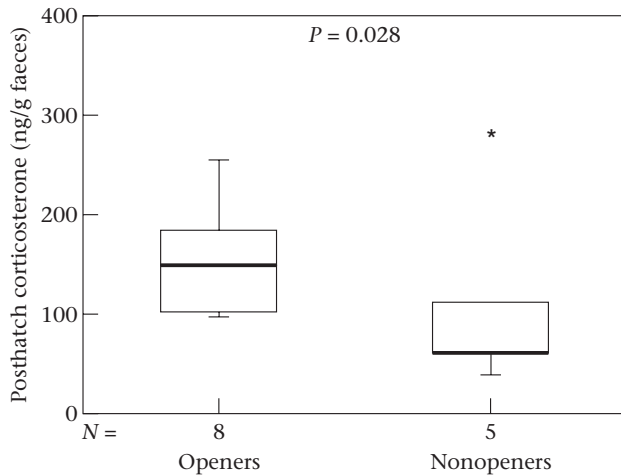


**Figure 3.** The increase in faecal corticosterone metabolites from 6-week control to postexperimental samples. Individuals in sibling group 1 that learned to open containers (openers) are compared with those that did not (nonopeners). Box plots show median, 25 and 75% quartiles and range of data; the asterisk indicates an outlying value for bird 9.

significant (mean increase  $49.02 \pm 91.62\%$ ; Wilcoxon signed-ranks test:  $T=16$ ,  $N=10$ , NS).

For sibling group 1 the concentration of excreted faecal testosterone metabolites (TM) was significantly lower in the postexperimental sample than in the pre-experimental control (mean decrease  $33.90$ – $37.63\%$ ; Wilcoxon signed-ranks test:  $T=12$ ,  $N=13$ ,  $P=0.02$ ). For sibling group 2 the decrease was not significant (Wilcoxon signed-ranks test:  $T=13$ ,  $N=10$ , NS). In sibling group 1 the unsuccessful ones showed a nonsignificant trend for a stronger TM decrease from control to postexperimental than the successful ones (Mann–Whitney  $U$  test:  $U=7.0$ ,  $N_1=8$ ,  $N_2=5$ ,  $P=0.065$ ).

For group 1 posthatching faecal BM concentrations (age 2 weeks) were significantly higher in individuals that opened containers 4 weeks later than in individuals that did not, if one extreme outlier was excluded (female 13, Fig. 4; Mann–Whitney  $U$  test:  $U=3.0$ ,  $N_1=8$ ,  $N_2=4$ ,  $P=0.028$ ; including this extreme value:  $U=11.0$ ,  $N_1=8$ ,



**Figure 4.** Posthatching faecal corticosterone values of individuals at 2 weeks of age. Individuals in sibling group 1 that later, during individual tests at 4–6 weeks of age, learned to open containers (openers) are compared with individuals that did not (nonopeners). Box plots show medians, 25 and 75% quartiles and range of data; the asterisk indicates an outlying value for bird 13.

$N_2=5$ ,  $P=0.188$ ). Posthatching faecal TM concentrations did not differ significantly between future openers and nonopeners (Mann–Whitney  $U$  test:  $U=19.0$ ,  $N_1=8$ ,  $N_2=5$ ,  $P=0.943$ ).

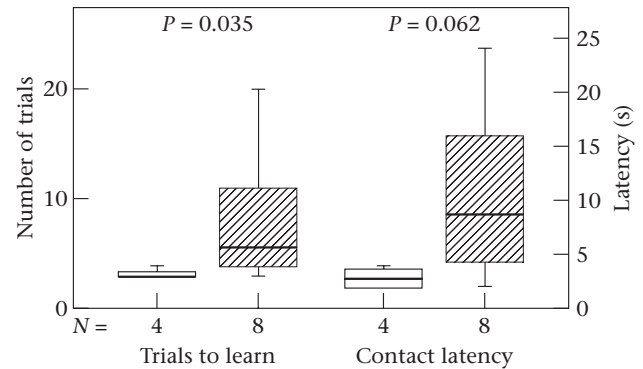
### Body and Competitive Weights

For group 1 mean body weight during the time of the individual test (age 4–6 weeks) did not differ significantly between individuals that reached the learning criterion ( $1839 \pm 260$  g) and those that failed ( $1865 \pm 298$  g; Mann–Whitney  $U$  test:  $U=16.0$ ,  $N_1=5$ ,  $N_2=8$ ,  $P=0.622$ ). In addition, mean body weight did not correlate with either posthatching faecal BM (Spearman rank correlation:  $r_s = -0.32$ ,  $N=13$ ,  $P=0.28$ ) or the BM difference between the 6-week control and the postexperimental sample (Spearman rank correlation:  $r_s=0.04$ ,  $N=13$ ,  $P=0.89$ ).

Individual feeding time (percentage of time feeding as a measure of competitive weight) at the limited food resource did not correlate with either posthatching faecal BM (Spearman rank correlation:  $r_s=0.33$ ,  $N=13$ ,  $P=0.26$ ) or the BM difference between the 6-week control and the postexperimental sample (Spearman rank correlation:  $r_s=0.18$ ,  $N=13$ ,  $P=0.55$ ). In addition, individual feeding time did not correlate with the number of sessions to reach the learning criterion during the individual test (Spearman rank correlation: group 1:  $r_s = -0.34$ ,  $N=13$ ,  $P=0.26$ ; group 2:  $r_s=0.11$ ,  $N=10$ ,  $P=0.76$ ) and did not differ significantly between male producers and scroungers at the feeding dispensers (Mann–Whitney  $U$  test:  $U=11$ ,  $N_1=4$ ,  $N_2=8$ ,  $P=0.40$ ).

### Group and Sex Differences

Faecal hormone metabolites (BM and TM) differed significantly between the sexes as well as between the



**Figure 5.** Number of trials to reach the learning criterion and contact latency during the individual test at 4–6 weeks of age for males that were producers (□) or scroungers (▨) during social tests at 8–11 months of age. Box plots show medians, 25 and 75% quartiles and range of data.

gosling groups (Table 2). However, these differences did not confound the previous analyses of the individual tests, since the proportions of individuals that reached the learning criterion and those that failed were similar for both sexes, and we analysed only within-group differences.

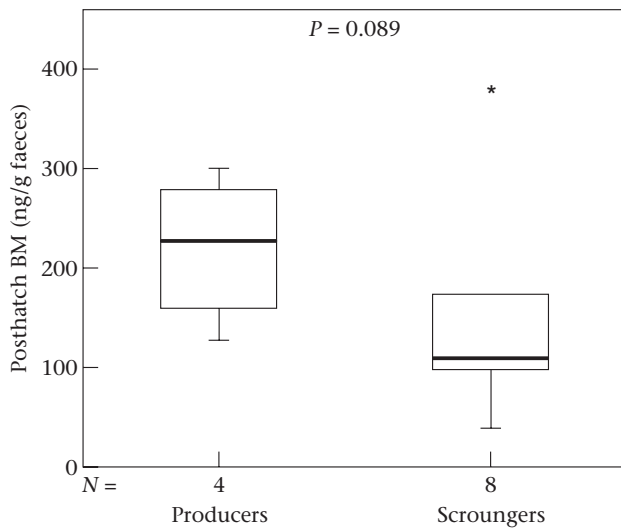
### Social Tests (Age 8–11 Months)

Five of 23 individuals (three females, two males), for unknown reasons, never fed at the food dispenser. From the remaining 18 individuals, four (two of each group) learned how to trigger the dispenser, whereas 14 never produced food on their own, but scrounged after one of the producers had triggered it. This proportion (producers:scroungers=1:3.5) parallels the proportion of food assigned to the producer or the scroungers, respectively (1:3). Thus, a producer's share of food was similar to that of a scrounger, minimizing potential effects of competition over access to food between producer and scroungers. This equilibrium distribution was similar to that for different family units at the same dispenser (J. Fritz & K. Kotrschal, unpublished data).

The four producers had all learned to open the containers in the individual test at ca. 6 weeks. All four were males, which differs significantly from an expected proportion of producers based on the given sex ratio (2.1 males:1.9 females; chi-square test:  $\chi^2_1=11.15$ ,  $P=0.001$ ). Because of this sex bias we compared the performance and hormone values of producers only with the male scroungers of both groups.

The producers at the food dispenser had a significantly shorter learning phase during the individual tests 9 months earlier than the scroungers (Mann–Whitney  $U$  test:  $U=4.0$ ,  $N_1=4$ ,  $N_2=8$ ,  $P=0.035$ ; Fig. 5). There was also a nonsignificant trend for future producers to have a shorter contact latency during the individual test than future scroungers (Mann–Whitney  $U$  test:  $U=5.0$ ,  $N_1=4$ ,  $N_2=8$ ,  $P=0.062$ ; Fig. 5).

Posthatching BM at the age of 2 weeks showed a non-significant trend to be higher in future producers



**Figure 6.** The posthatch faecal corticosterone (BM) values (at 2 weeks of age) for males that were producers or scroungers during the social tests (at 8–11 months). Box plots show medians, 25 and 75% quartiles and range of data; the asterisk indicates an outlying value for bird 16.

than in future scroungers (Mann–Whitney  $U$  test:  $U=6.0$ ,  $N_1=4$ ,  $N_2=8$ ,  $P=0.089$ ; Fig. 6; the extreme value in Fig. 6 was included in the test). Posthatching faecal TM concentrations did not differ significantly between future producers and scroungers (Mann–Whitney  $U$  test:  $U=10.0$ ,  $N_1=4$ ,  $N_2=8$ ,  $P=0.368$ ).

## DISCUSSION

Our results reveal consistent differences in hormonal and behavioural traits between greylag goslings that succeeded in solving operant tasks and their siblings that did not, either individually at 6 weeks or in a social context at 11 months.

At 11 months old, only four males out of 23 individuals began to produce food at the dispensers. All the others resorted to scrounging. Nine months earlier, at 4–6 weeks, these producers had a significantly shorter learning phase and also tended to have a shorter contact latency than scroungers, although this was not significant. This points to a contingency between individual behavioural dispositions and the probability of becoming a producer or a scrounger in our affiliative greylag sibling groups. In dominance-structured groups the probability of becoming either a producer or a scrounger seems to be mainly related to rank (Theimer 1987; Caraco et al. 1989; Barta & Giraldeau 1998; Giraldeau & Caraco 2000). Owing to the near lack of agonistic interactions, as is characteristic of affiliative groups, we could not establish meaningful rank orders in our gosling groups. We also found no relationship between competitive weight and performance, either in the individual setting or in the social setting.

The goslings' learning performance correlated with the amount of excreted corticosterone metabolites in the faeces (BM). In the four producers at the food dispenser we found a nonsignificant trend to excrete more

BM 2 weeks after hatching than scroungers. All four producers were also among the 18 goslings that were successful in the individual tests at 6 weeks and whose excreted BM levels 2 weeks after hatching were also significantly higher than in scroungers.

Such individual consistency parallels results by Laland & Reader (1999), whose previous innovator guppies were more likely to innovate again than previous noninnovators, and may reflect distinct behavioural strategies to cope with challenges (Benus et al. 1987; Hessing et al. 1994). It remains unclear, however, whether our innovators should be classified as 'proactive' or 'reactive' copers (Koolhaas et al. 1999). Relatively short latencies to approach a task would indicate proactive coping, whereas the general high reactivity to environmental stimuli would be a typical feature of reactive copers. We found no significant differences between our innovators and the others with respect to testosterone modulation. This may either support the hypothesis that these innovators were 'reactive' individuals (Koolhaas et al. 1999) or simply be due to our animals not being sexually mature or our tasks not having a sexual/social context.

The significant increase in the excretion of corticosterone metabolites (BM) and the significant decrease in the excretion of testosterone metabolites (T) in the post-experimental samples compared with the 6-week control samples in group 1 shows a general response to the individual test situation. The BM increase was significantly higher in the successful birds than the unsuccessful ones of the same group. Since the postexperimental samples were taken at a time when the successful individuals had already learned to open the containers, these birds received the reward and, hence, were highly motivated to continue with their performance, which was not the case for the unsuccessful, unrewarded individuals. Therefore, such motivational differences may have caused the higher increase in BM in the successful birds. Alternatively, the higher increase in BM excretion in the lid openers may reflect a general disposition of these individuals to increase corticosterone (B) more than their unsuccessful group members when confronted with a challenge. In this way, individual disposition to modulate B in response to environmental challenges would significantly affect the initial conditions for becoming an innovator/producer or not.

Corticosterone is released in stressful situations (von Holst 1998). Besides B, corticotrophin-releasing factor (CRF) and adrenocorticotrophic hormone (ACTH) are modulated by attention and, in turn, may affect attention (e.g. van Wimersma Greidanus & Rigter 1989). Short-term activation of the glucocorticoid system seems to enhance memory consolidation processes (Mendl 1999), since moderate B concentrations enhance reorganization of synapses and dendrites (Sapolsky 1992). This suggests a contingency between faecal BM and the disposition to learn and innovate. Moderately increased systemic B may prime memory formation about the environment. Cognitive performance is supposed to be best when an individual is in some intermediary state of stress or arousal (Mendl 1999). In this sense, the higher concentrations of excreted BM in the posthatching samples of

the later innovators may indicate their responsiveness to environmental stimuli (Koolhaas et al. 1999). In turn, such individual hormonal response may facilitate learning to solve a task via trophic effects on the nervous system (van Wimersma Greidanus & Rigter 1989; Dukas & Clark 1995) and may promote consistent attentiveness to tasks.

As the juveniles were individually trained to open our containers, there was no opportunity to scrounge at other individuals that had already opened them. Hence, a majority of individuals learned to produce in the individual test (Giraldeau et al. 1994). At the food dispensers, however, in a social setting, only two individuals in each sibling group produced. This fits a general producer–scrounger equilibrium (Barnard & Sibly 1981; Giraldeau & Caraco 2000), which depends on the proportion of individuals in a group that choose to produce or take the opportunity to scrounge. The individual lid-opening test without scrounging opportunities probably discriminated against those five birds that were least likely to become producers. In contrast, the social setting at the food dispenser test probably favoured the four most innovative individuals, all of them males.

This male bias at the dispenser is in contrast to Reader & Laland's (2000) study, where guppy innovators were female. Since they found sexual differences in solving novel tasks only in adult guppies, they assumed that this might reflect a motivational difference that was due to reproductive investment. No sex difference in performance was found in the juvenile guppies, as was the case in geese. In a previous experiment with greylag goslings, Fritz et al. (2000) found that socially human-imprinted, juvenile female greylag geese learned an operant task faster via stimulus enhancement than males when tutored by a human model. The four male innovators at our food dispenser, in contrast, learned to pull the flap individually. These limited data may indicate that, within the affiliative groups of geese, the roles of innovators/producers may mainly be assumed by males, whereas the females may be more likely than males to learn socially.

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