

Social allies modulate corticosterone excretion and increase success in agonistic interactions in juvenile hand-raised graylag geese (*Anser anser*)

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Abstract: In mammals, support by a social partner may reduce stress levels and ease access to resources. We investigated the effects of the passive presence of a nearby social ally on excreted corticosterone immunoreactive metabolites and behaviour in juvenile graylag geese (*Anser anser*). Two groups of hand-raised juveniles ($N_1 = 9$, $N_2 = 3$) were tested over 1 year by positioning humans of different familiarity (i.e., the human foster parent, a familiar human, a nonfamiliar human, no human) at a standard distance to the focal geese. Their success in agonistic interactions significantly decreased with age and with decreasing familiarity of the accompanying human. The humans present modulated the excretion of corticosterone immunoreactive metabolites, with the strongest effects recorded after fledging when corticosterone metabolites were also positively correlated with agonistic behaviour. This suggests that a human foster parent may provide similar supportive benefits as goose parents do in natural families. We discuss the benefits of social alliances with regard to the integration into the flock, access to resources, and life history.

Résumé : Chez les mammifères, le support d'un partenaire social peut réduire les niveaux de stress et faciliter l'accès aux ressources. Nous avons étudié les effets de la présence passive à proximité d'un allié social sur l'excrétion des métabolites immunoréactifs de la cortisone et sur le comportements chez de jeunes oies cendrées (*Anser anser*). Deux groupes de jeunes élevés à la main ($N_1 = 9$, $N_2 = 3$) ont été évalués au cours d'une année en plaçant des humains de familiarité variable (i.e., le parent adoptif humain, un humain familier, un humain inconnu, aucun humain) à une distance standard des oies ciblées. Le succès des oies dans les interactions agonistiques décroît significativement avec l'âge et augmente avec la familiarité du compagnon humain. La présence des humains affecte l'excrétion des métabolites immunoréactifs de la cortisone et les effets les plus forts se manifestent après l'envol, un moment où métabolites de la cortisone est en corrélation positive avec le comportement agonistique. Ces observations laissent croire que le parent adoptif humain apporte sans doute les mêmes bénéfices de support que le font les parents naturels dans les familles d'oies. La discussion porte sur les bénéfices des alliances sociales sur l'intégration des jeunes dans la bande, sur l'accès aux ressources et sur le cycle biologique.

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Introduction

Social support is generally defined by the stress-reducing effect of the presence of a familiar social partner (for a review see von Holst 1998). At the functional level, social support may positively affect individual status and access to resources. A number of primate studies have shown the behavioural implications of support by close kin as allies in agonistic encounters (e.g., Japanese macaques, *Macaca fasciata* (Kawai 1958); vervet monkeys, *Cercopithecus aethiops* (Horrocks and Hunte 1983); Rhesus monkeys, *Macaca mulatta* (Berman 1980; Bernstein and Ehardt 1985, 1986); macaques, *Macaca fascicularis* (Netto and van Hooff 1986)).

In contrast, the supportive effects of social allies are less clear in birds (Dugatkin 1997). Geese and other social birds form large flocks and show complex social relationships (e.g., Rutschke 1982; Schneider and Lamprecht 1990; Fox et al. 1995). In geese, families dominate pairs in aggressive encounters and pairs tend to win against single individuals. Hence, social status in geese seems to be positively affected by the number of individuals in the social unit (e.g., white-fronted geese, *Anser albifrons albifrons* (Boyd 1953); Canada geese, *Branta canadensis* (Hanson 1953); pink-footed geese, *Anser brachyrhynchus* (Lazarus and Inglis 1978); barnacle geese, *Branta leucopsis* (Black and Owen 1986; Stahl et al. 2001)). Offspring benefit from parental vigilance and assistance in encounters with other flock members for much of their first year (Black and Owen 1989a, 1989b; Kotrschal et al. 1993; Warren et al. 1993; Fox et al. 1995), and juveniles as well as females were found to be more successful in agonistic interactions when the gander was nearby, even if not actively interfering (Boyd 1953; Raveling 1970; Lamprecht 1986). The primary mechanisms possibly involved were physical cooperation and motivational effects (Lamprecht 1986).

In general, social interactions as well as social status may modulate the pituitary–adrenocortical stress response (for

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reviews see Wingfield et al. 1997; von Holst 1998; Creel 2001). The social environment affects individual stress levels in mammals (e.g., dwarf mongooses, *Helogale parvula*, and wild dogs, *Lycaon pictus* (Creel et al. 1993); olive baboons, *Papio anubis* (Altmann et al. 1995)) as well as in birds (e.g., song sparrows, *Melospiza melodia* (Wingfield and Silverin 1986); pied flycatchers, *Ficedula hypoleuca* (Silverin 1998a); geese (Kotrschal et al. 1998, 2000)). For mammals, it has been shown that the presence of a familiar social partner may reduce the magnitude of a stress response in acutely challenging situations (i.e., high-density population, presence of an intruder in the group, etc., in squirrel monkeys, *Saimiri sciureus* (Levine 1993a), and guinea-pigs, *Cavia aperea f. porcellus* (Sachser et al. 1998)). Therefore, the (active) supportive effects of social partners in agonistic encounters, as repeatedly shown in primates and geese, and the stress-reducing effect of the presence of a social partner by (passive) social support, as shown in mammals, may represent different kinds of benefits yielded by social alliances.

In our semi-tame flock of graylag geese (*Anser anser*), social relationships have been monitored since 1973. In recent years, social patterns of excreted immunoreactive steroid metabolites have been investigated (e.g., Kotrschal et al. 1998; Hirschenhauser et al. 1999a, 1999b, 2000a; Frigerio et al. 2001a). A well-established hand-raising tradition (Lorenz 1988) provides the opportunity to experimentally investigate mechanisms and functions of social alliances by using human models of different familiarity to the focal, socially human-imprinted geese (Hess 1973). Such manipulations are unfeasible with free-living natural parent-offspring groups and, therefore, the role of alliances within a flock remained speculative and eluded experimental testing (Warren et al. 1993; Fox et al. 1995). To our knowledge, the present study is the first experimental contribution on the physiological and behavioural effects of the presence of social allies in birds.

We tested the effect of the nearby passive presence of a social ally on excreted corticosterone immunoreactive metabolites (BM) and on agonistic behaviour of juvenile hand-raised graylag geese during competitive feeding situations that are known to be stressful for the animals (Frigerio and Kotrschal 1999). We expected humans (foster parent, familiar, and nonfamiliar human) to modulate stress levels of focal individuals and also their success in agonistic interactions with nonallies in a familiarity-dependent way. The temporal patterns of such effects were also considered during the focals' first year of life. Subadult geese usually loosen their social bonds with their parents at the end of their first winter in favour of establishing new bonds with their forthcoming mates (Rutschke 1982; Choudhury and Black 1993). Therefore, we expected decreasing effects of all supporting humans on excreted BM and on behaviour, particularly towards the end of the first year.

Materials and methods

Animals

The nonmigratory flock of graylag geese studied was introduced into the Alm valley in Upper Austria by Konrad Lorenz and coworkers in 1973 (Lorenz 1988). Animals are unrestrained and subject to natural selection. Losses to natu-

ral predators (mainly foxes, *Vulpes vulpes*, in spring and golden eagles, *Aquila chrysaetos*, in winter) may account for up to 10% of the flock per year (Hemetsberger 2001). During daytime, the geese can be found at the meadows and ponds close to the research station where they are also provided with supplemental food twice a day, year-round. At night, the birds roost on a lake approximately 10 km south of the research station. All animals in the flock are marked with an individual combination of coloured leg rings, which allows continuous monitoring of individuals' social behaviour and life history.

Every year two groups of goslings are experimentally hand-raised. This happens in the same area where the wild families also raise their offspring (Lorenz 1988). From hatching to fledging, the human foster parents (one person per sibling group) stay permanently with their goslings and their daily spatiotemporal activity patterns follow those of the goose families. After fledging, at 9–10 weeks after hatching, the human foster parent leaves and the juvenile sibling groups integrate into the flock. Later on, they establish (and maintain) social bonds with goose partners and raise offspring in a manner indistinguishable from goose-raised geese (Hemetsberger 2002).

The present study is based on 12 hand-raised geese from two different sibling groups ($N_1 = 9$, $N_2 = 3$). Sibling groups were defined as individuals raised together by the same human foster parent regardless of genetic relatedness (Weigmann and Lamprecht 1991). All individuals hatched in May 1996 (Table 1) and were individually marked with coloured leg rings. Because of prolonged daily contacts, the two groups were well acquainted with each other as well as with both human foster parents. All individuals fledged in August 1996. Four of the focal individuals disappeared in their first winter (Table 1). The remaining eight were still alive at the end of data collection in October 1997 (Table 1).

Data collection

Behavioural protocols and faecal samples were collected during four periods between August 1996 (after fledging) and October 1997 (after reintegration of the flock following their first wing-feather moult; Table 2). During each sampling period, data were collected over 12 subsequent days and consisted of four treatments of 3 days each. At each treatment a different human supporter was present (Table 2) during the regular morning and evening (0800 and 1600, respectively) food provisioning to the flock. This person had different social relationships with the focal animal and was either its human foster parent (treatment A), a familiar human (the human foster parent of the second sibling group, treatment B), or a known but nonfamiliar human (treatment C). The nonfamiliar human was played by four different people (one per sampling period) who the focal geese may have seen before but were not individually habituated to. In the specific context of our flock, if the human foster parent and the familiar human were considered members of the group, the nonfamiliar human was seen as an outsider. In the fourth treatment (D), no human was present. Logistic necessities (i.e., constraints in people's availability) did not allow the experimental setup to be fully randomized and, therefore, treatment A was always first and treatment D never second (Table 2). During data collection, the human foster parent,

Table 1. Focal individuals of juvenile hand-raised graylag geese, *Anser anser*, and their life-history characteristics.

Sibling group	Goose ID	Date (day.month.year)	Sex
1	Ta.	09.05.96	Female
	Ska.	09.05.96	Male
	Ke.	09.05.96	Male
	L.S.	10.05.96	Female
	Ki.*	14.05.96	Unknown
	Je.	14.05.96	Female
	In.†	14.05.96	Unknown
	Tli.	15.05.96	Female
2	Chi.‡	15.05.96	Unknown
	Smi.§	22.05.96	Unknown
	He.	22.05.96	Male
	Pa.	23.05.96	Male

*Goose Ki. died Dec. 1996.

†Goose In. disappeared Sept. 1996.

‡Goose Chi. disappeared Oct. 1996.

§Goose Smi. disappeared Oct. 1996.

familiar human, or nonfamiliar human supporters placed themselves at the feeding area (approximately 50 m²), within approximately 3 m of the focal sibling groups and remained passive (i.e., they were neither moving around nor actively joining the focal individuals in any of their agonistic interactions) over the whole period of observation. Behavioural observations of individual agonistic interactions were taken from a covered observation post approximately 10 m off the feeding area.

Behavioural protocols consisted of continuous individual focal sampling of agonistic interactions with other flock members. Data collection started after all the food was distributed and ended when the focals began to rest after feeding. Food (wheat and pellets) was usually distributed over approximately 50 m², creating a competitive feeding situation (Kotrschal et al. 1993). The duration of the behavioural sampling periods was 17.2 ± 4.1 (mean ± SD) min.

For the assessment of excreted BM, individual faecal samples were collected daily from the resting animals approximately 30–90 min after the morning behavioural data collection, when BM excretion usually peaks in geese following a challenge (i.e., injection of adrenocorticotrophic hormone or gonadotrophin-releasing hormone and presence of unfamiliar individuals in the group of geese; Krawany 1996; Kotrschal et al. 2000; Hirschenhauser et al. 2000b). Furthermore, this was late enough in the day to avoid the endogenous BM early morning peak (Schütz et al. 1997). Samples were frozen at –20 °C within 1 h after collection (Hirschenhauser 1998). During the sampling period, 10 ± 0.25 (mean ± SE) samples per individual were collected (total *N* = 368). It was not always possible to sample all individuals on the same day.

Because repeated and regular collection of blood in the field was neither feasible nor advisable owing to potential feedback on the parameters to be measured (Miller et al. 1991), circulating corticosterone levels remained unknown. However, because experiments with domestic geese showed deterministic relationships between plasma steroids and their metabolites in the faeces (Hirschenhauser et al. 2000b; Kotrschal et al. 2000), we were confident that our faecal BM

levels were representative of plasma corticosterone levels 1–2 h before defecation.

Faecal steroid assay

Faecal samples (0.5 g) were extracted in methanol and hydrolysed as described by Kotrschal et al. (1998). Excreted BM were assayed by enzyme immunoassay (EIA, Möstl et al. 1987). Details about the procedure and cross-reactivities were published elsewhere (Kotrschal et al. 1998). Concentration limits for reliable measurements ranged from 0.5 to 98.2 ng/g. Intra- and inter-assay coefficients of variations were determined by homogenized pool samples. Mean intra-assay coefficient of variation was 13.8%; mean inter-assay coefficient of variation was 15.7%. Such values are typical for EIA procedures on faeces, because the number of steps involved in the procedure increases total variation.

Data analysis

Mean percentages of agonistic interactions won were calculated per focal individual, treatment, and period as follows: percentage of interactions won = (number of agonistic interactions won / total number of agonistic interactions) × 100. Mean excreted BM values were calculated per focal individual, treatment, and period.

Data were analysed using the SPSS statistical program (Pfeifer 1991). Results of all tests are two-tailed and levels of significance are corrected using the Bonferroni post-hoc tests when necessary (Rice 1989). Both behavioural and hormonal data were not normally distributed (Kolmogorov–Smirnov; agonistic interactions: *Z* = 2.52, *N* = 360, *P* < 0.0001; excreted BM: *Z* = 3.151, *N* = 368, *P* < 0.0001). Therefore, the behavioural percentages were arcsine transformed and the hormonal values were log transformed (Zöfel 1992). Parametric one-way ANOVA was used to investigate the effect of the four different treatments on excreted BM and behaviour within and between sampling periods. Furthermore, as family size might positively affect social interactions in geese, the possible effect of the different size of the two sibling groups was considered for each period. Correlations between hormone levels and behavioural parameters were calculated using Pearson's correlation coefficient.

To compare the supportive effects of the different treatments on excreted BM between sampling periods and to avoid a confounding effect owing to excreted BM basal seasonal levels (see Kotrschal et al. 1998), the percent difference in excreted BM (BM response) was calculated per treatment as

$$\frac{BM_{\text{treatment } x, \text{ season } x} - BM_{\text{treatment } x, \text{ season } 1}}{BM_{\text{treatment } x, \text{ season } 1}} \times 100$$

where the value at fledging (i.e., August 1996, period 1) is considered basal.

Results

After fledging

After fledging (i.e., August 1996; Table 2), the person present significantly affected the percentage of agonistic interactions won ($F_{[3,124]} = 15.468$, *P* < 0.0001; Fig. 1a), as

Table 2. Periods of data collection between August 1996 and October 1997.

Sampling period	Flock size (no. of individuals)	Sequence of treatments	Life-history context
After fledging, August 1996	140	Human foster parent, nonfamiliar human, familiar human, no human	Integration into the flock, tight sibling group
First winter, December 1996	135	Human foster parent, familiar human, no human, nonfamiliar human	Individuals fully integrated, sibling group becomes looser
First spring, February 1997	135	Human foster parent, nonfamiliar human, no human, familiar human	Individuals sexually immature, loose sibling group
Second autumn, October 1997	120	Human foster parent, familiar human, nonfamiliar human, no human	Reunion of the sibling group within the flock frame

Note: Each of the four treatments consisted of 3 consecutive sampling days.

well as excreted BM levels ($F_{[3,140]} = 4.567$, $P = 0.004$; Fig. 1b). Specifically, the presence of the human foster parent significantly increased the percentage of interactions won compared with all other observed treatments (Bonferroni post-hoc test; human foster parent vs. familiar human, $P < 0.0001$; human foster parent vs. nonfamiliar human, $P < 0.0001$; human foster parent vs. no human, $P < 0.0001$; Fig. 1a). Percentages of interactions won were similar when the focals were accompanied by either a familiar human or a nonfamiliar human, and were lowest when no human was present (Fig. 1a). The size of the sibling group had no effect on the percentages of agonistic interactions won ($F_{[1,11]} = 0.247$, $P = 0.63$).

When the familiar human was present, excreted BM was lower than with the human foster parent or with a nonfamiliar human (Bonferroni post-hoc test; familiar human vs. human foster parent, $P = 0.038$; familiar human vs. nonfamiliar human, $P = 0.001$; Fig. 1b). However, excreted BM levels in the presence of the human foster parent were similar to those with no human (Fig. 1b). This may be explained by the fact that only after fledging were the percentages of interactions won correlated positively and significantly with excreted BM when the focal individuals were accompanied by their human foster parent (Pearson's correlation; human foster parent, $r = 0.689$, $N = 12$, $P = 0.013$; familiar human, $r = -0.483$, $N = 12$, $P = 0.811$; nonfamiliar human, $r = 0.23$, $N = 12$, $P = 0.471$; no human, $r = 0.033$, $N = 12$, $P = 0.92$; Fig. 2). Hence, it seems that the presence of the human foster parent enhanced the percentage of interactions won, which in turn increased the levels of excreted BM. Furthermore, no significant effect of the size of the sibling group was observed on excreted BM ($F_{[1,11]} = 0.208$, $P = 0.658$).

First winter flock

During their first winter (i.e., December 1996; Table 2), the presence of different humans still affected the percentages of agonistic interactions won by the focal animals ($F_{[3,64]} = 5.706$, $P = 0.002$; Fig. 1c), as well as excreted BM levels ($F_{[3,70]} = 5.024$, $P = 0.003$; Fig. 1d); also, percentages of interactions won still gradually declined with familiarity as observed in summer 1996 (Fig. 1a). Specifically, the focal individuals won significantly less interactions in the absence of any human than with the foster parent present (Bonferroni post-hoc test; no human vs. human foster parent, $P = 0.001$; Fig. 1c). Group size had no influence on the percentage of interactions won ($F_{[1,7]} = 1.96$, $P = 0.211$).

Excreted BM was lower when the nonfamiliar human was present than in the presence of a familiar human (Bonferroni post-hoc test; nonfamiliar human vs. human foster parent, $P = 0.016$; nonfamiliar human vs. familiar human, $P = 0.026$; Fig. 1d). No differences in excreted BM were observed between the two sibling groups ($F_{[1,7]} = 0.568$, $P = 0.48$).

First spring

In the yearlings (i.e., February 1997; Table 2), the percentage of interactions won still decreased with familiarity ($F_{[3,74]} = 3.575$, $P = 0.018$; Fig. 1e), but this was not reflected in excreted BM patterns ($F_{[3,66]} = 1.157$, $P = 0.333$; Fig. 1f). Again, no differences were found when controlling for the effect of the size of the sibling group (agonistic interactions, $F_{[1,7]} = 0.552$, $P = 0.485$; BM, $F_{[1,7]} = 0.036$, $P = 0.855$).

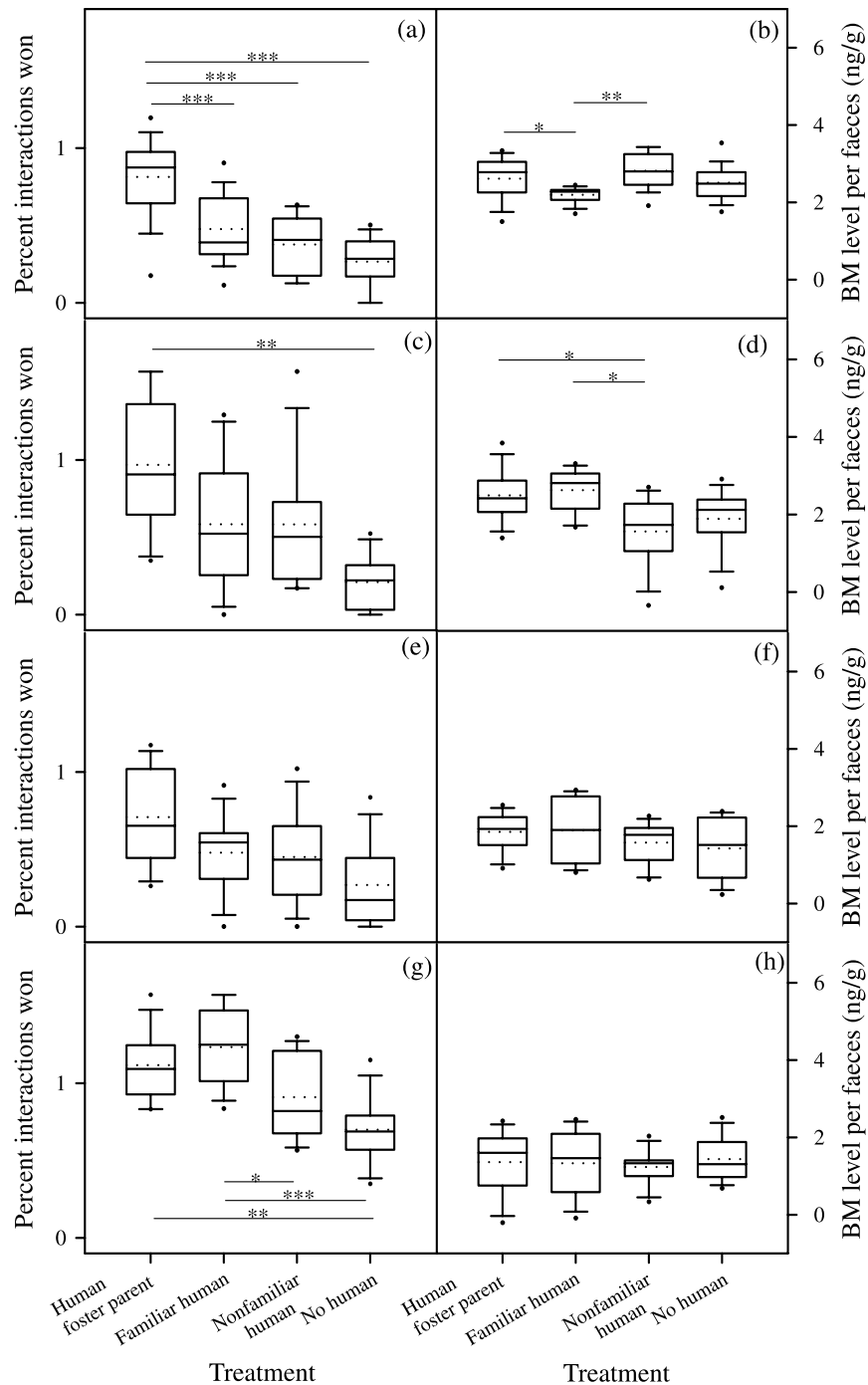
Second winter flock

In their second autumn (i.e., October 1997; Table 2), the presence of different humans still affected the percentage of interactions won ($F_{[3,82]} = 9.668$, $P < 0.0001$; Fig. 1g). However, this was not reflected in excreted BM ($F_{[3,70]} = 1.123$, $P = 0.946$; Fig. 1h). Focal individuals showed significantly higher percentages of interactions won in the company of the foster parent or the familiar human than with a nonfamiliar human or no human (Bonferroni post-hoc test; human foster parent vs. no human, $P = 0.003$; familiar human vs. nonfamiliar human, $P = 0.04$; familiar human vs. no human, $P < 0.0001$; Fig. 1g). No behavioural or hormonal differences were found between the two groups (agonistic interactions, $F_{[1,7]} = 0.018$, $P = 0.899$; BM, $F_{[1,7]} = 0.004$, $P = 0.949$).

Temporal patterns

Finally, we compared the effect of each treatment on excreted BM among the four sampling periods. The percentage of BM response to each treatment significantly decreased with age (i.e., the four sampling periods) in each of the four treatments considered (human foster parent, $F_{[3,28]} = 5.47$, $P = 0.004$ (Fig. 3a); familiar human, $F_{[3,28]} = 3.684$, $P = 0.024$ (Fig. 3b); nonfamiliar human, $F_{[3,28]} = 9.071$, $P < 0.0001$ (Fig. 3c); no human, $F_{[3,28]} = 4.095$, $P = 0.016$ (Fig. 3d)), but the amplitude of decrease was greater in the presence of the human foster parent or familiar human than in the presence of the nonfamiliar human or no human.

Fig. 1. Percent interactions won (arcsine transformed) and levels (log transformed) of excreted corticosterone immunoreactive metabolites (BM) during the four sampling periods (after fledging, August 1996 (a, b); during the first winter, December 1996 (c, d); during the first spring, February 1997 (e, f); during the second autumn, October 1997 (g, h)) and during the four experimental treatments (human foster parent, familiar human, nonfamiliar human, no human) in juvenile hand-raised graylag geese, *Anser anser*. Boxplots indicate the median and interquartile ranges; dotted lines indicate the arithmetic means; whiskers indicate the range between the 10th and 90th percentiles; solid circles indicate data outside the 10th and 90th percentiles; and the horizontal bars indicate which groups are significant (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

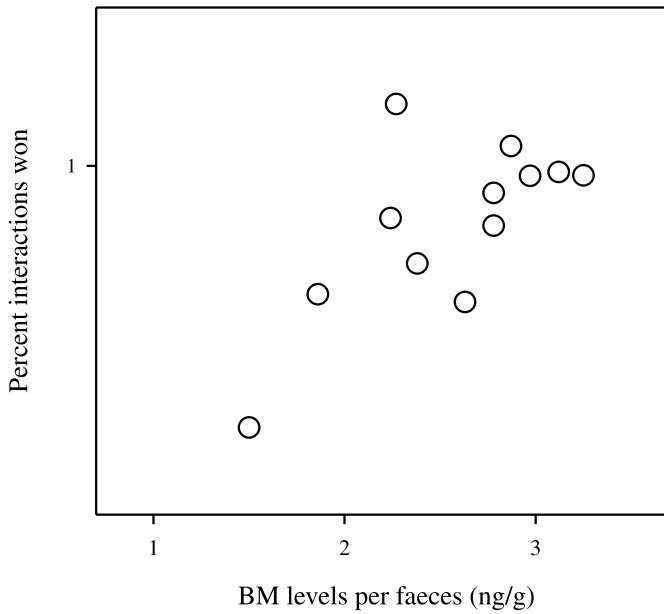


Discussion

Social stimuli are among the most potent modulators of the hypothalamic–pituitary–adrenal axis in vertebrates (Sapolsky

1992; De Vries 2002). Glucocorticoids are not only involved in the stress response but also affect sex steroids and life-history decisions (Silverin 1998b; Wingfield et al. 1994, 1997). The presence of familiar social partners may reduce

Fig. 2. Excreted BM levels (log transformed) and percent agonistic interactions won (arcsine transformed) during the first sampling period (after fledging, August 1996) of juvenile hand-raised graylag geese in the presence of the human foster parent (Pearson's correlation coefficient, $r = 0.689$, $P = 0.013$).



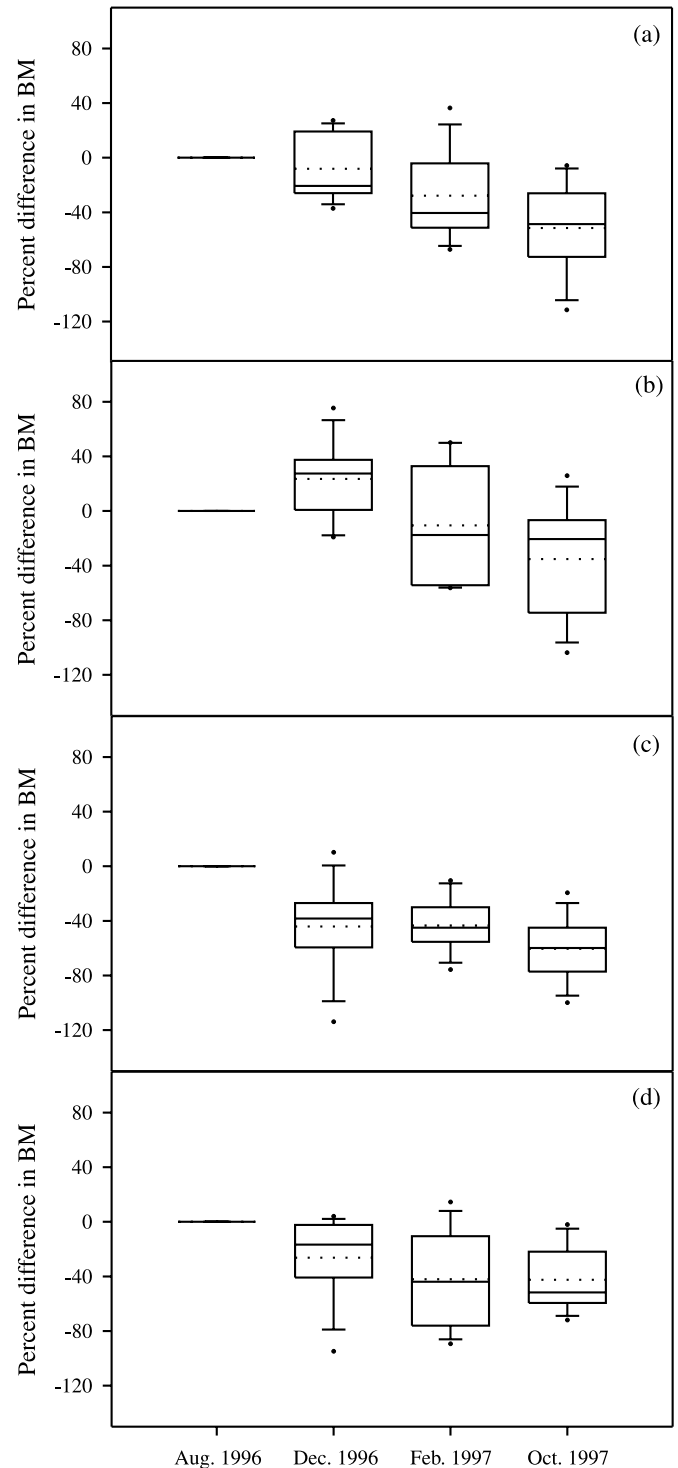
or eliminate the stress response in acutely challenging situations, such as agonistic interactions over food and social turnover (Levine 1993a; von Holst 1998).

In the present study, hand-raised juvenile graylag geese (i.e., human socially imprinted geese; Lorenz 1937) responded hormonally and behaviourally to the passive presence of humans of different familiarity. This shows that graylag geese are able to distinguish between different human individuals. The presence of a social ally clearly affected agonistic interactions and modulated individual stress levels as reflected by excreted amounts of BM (Fig. 1). These behavioural and physiological effects of the presence of a parent-mimicking social ally dynamically changed during the individuals' development (Fig. 3).

At the time of fledging, goslings join the flock, which is reaggregating after the breeding season and moult (Rutschke 1982). Social-integration processes produce stressful situations during which social bonds might have buffering effects (e.g., Sachser et al. 1998; for a review see von Holst 1998). By December 1996 (our second sampling period), the hand-raised geese were fully integrated into the flock (Table 2). Still, the presence of either familiar human (human foster parent or familiar human) produced similar physiological and behavioural effects as in the preceding season (Figs. 1a–1d).

After December 1996, the positive supportive effects of the social ally on behavioural and physiological parameters gradually decreased (Figs. 1e–1f). In February 1997, although still sexually immature, the hand-raised focal individuals were involved in sexual and courtship behaviours toward prospective goose mates (D. Frigerio and B. Weiss, personal observations). Therefore, similar to wild geese (Lorenz 1988), our hand-raised focals seemed to loosen their

Fig. 3. Comparison of the percent difference in excreted BM in juvenile hand-raised graylag geese between sampling periods in the presence of the human foster parent (a), familiar human (b), nonfamiliar human (c), and no human (d). Boxplots indicate the median and interquartile ranges; dotted lines indicate the arithmetic means; whiskers indicate the range between the 10th and 90th percentiles; solid circles indicate data outside the 10th and 90th percentiles.



social bonds to their (foster) parents in favour of contacts with their new social/sexual partners (Table 2).

In summer, after their first moult of wing feathers, the hand-raised focal individuals of both groups reaggregated into a single group (Table 2). This is quite normal, as pair formation in graylag geese occurs at the earliest when they are 2 years old, and juvenile geese may resume their tight kin-bonds with siblings or even parents for a second year (Lorenz 1988). Although familiar humans (human foster parent and familiar human) still had a significant effect on the percentage of interactions won (Figs. 1*g*–1*h*), it seemed that the hand-raised geese were able to assert their social status within the flock even without human presence because the percentages of interactions won in the presence of a nonfamiliar human and no human remained high (Fig. 1*g*).

Physical cooperation (i.e., active support) as well as motivational effects induced by the presence of the social ally (i.e., passive support) have been suggested as mechanisms of social alliances in geese (Lamprecht 1986). In the present study, the experimental setup excluded any participation of the human present in the social interactions of the focal individuals. Therefore, increased success in agonistic interactions in the presence of (familiar) humans can only be attributed to (passive) motivational effects. Alternatively, the presence of any human might have decreased agonistic motivation of the goose-raised opponents. This seems unlikely, as the flock is habituated to the close presence of human observers. Nevertheless, this may be considered an indirect benefit of the presence of a respected ally, whether it is a familiar human or a motivated and aggressive goose parent (Lamprecht 1986).

Furthermore, physical cooperation (i.e., active support) by the siblings could not be excluded. In fact, proximity among the siblings may enhance the chances of actively supporting each other in case of being attacked (Scott 1980*a*, 1980*b*; Black and Owen 1985; Lamprecht 1986). In geese, adult females stay closer to their sisters than expected by chance (Frigerio et al. 2001*b*), and among goose-raised juveniles the distances to family members predicted the outcome of most interactions (Weiss and Kotschal 2001). Although data about the distance between the siblings are not available for this study, the size of the sibling group did not have an effect on both parameters measured (excreted BM and behaviour). We suggest that the two sibling groups were well acquainted with each other and behaved as a single unit so that during feeding (and data collection) they were quite close to each other.

Even though the human foster parent was expected to have, via social support, the greatest stress-reducing effect (Cobb 1976; Levine 1993*a*, 1993*b*; Sachser et al. 1998; von Holst 1986, 1998), her/his presence was always associated not only with a high percentage of agonistic interactions won but also with increased excreted BM levels (Fig. 1). This was unexpected, but it may be explained by a linear and positive relationship between agonistic interactions and BM excretion (Fig. 2). The great arousal associated with the increased number of agonistic interactions won in the presence of the foster parent may have up-regulated corticosterone levels. Additionally, in our experiments the supporting person was not interfering at all, the opposite of what a goose parent would do (and what the offspring might ex-

pect). Hence, the hand-raised focals may have been motivated to interact by the presence of their foster parent, but the lack of active support may have caused increased stress levels as reflected in the excreted BM levels (Fig. 2). Furthermore, it cannot be excluded that the effort of the focal geese in monitoring the position of their most important social ally (i.e., the human foster parent) contributed to the increase in excreted BM levels, as this person, in contrast to goose parents, did not change position in response to the movements of his/her offspring. In fact, adrenal steroids such as corticosterone may be involved in cognitive functions (McEwen and Sapolsky 1995), and graylag goslings being attentive to and performing an operational task excreted higher BM than unsuccessful individuals (Pfeffer et al. 2002).

Among the possible functions of social alliances, enhanced competitiveness for food has also been suggested by other goose studies (e.g., Raveling 1970; Black and Owen 1985; Black et al. 1996). In our semi-tame flock, hand-raised juveniles spent more time feeding in the presence of a familiar human than with a nonfamiliar human (Weiss and Kotschal 1997). Efficient feeding as a gosling or juvenile may be extremely important, because it may affect life-history traits such as adult body size and reproductive success (Sadlier 1969; Pereira 1988; Owen and Black 1990; Cooke et al. 1995; Hemetsberger 2001). At a physiological level, both food uptake and energy management are modulated by corticosterone (Norris 1997; Silverin 1986, 1998*b*). Therefore, social alliances may yield both behavioural and physiological benefits.

In conclusion, our data show that juvenile hand-raised graylag geese enjoy distinct benefits from the passive presence of familiar humans in terms of access to resources, agonistic interactions, and with respect to individual glucocorticoid levels, energy management. As deterring effects of the human presence on the behaviour of the rest of the flock are unlikely, we suggest that, with respect to agonistic interactions, a human foster parent may be a valid model of goose parents because he/she may provide similar benefits for his/her hand-raised geese.

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