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Active and passive social support in families of greylag geese (*Anser anser*)

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Summary

In general, support by social allies may reduce stress, increase success in agonistic encounters and ease access to resources. Social support was mainly known from mammals, particularly primates, and has been studied in birds only recently. Basically two types are known: (i) ‘active social support’, which describes the participation of a social ally in agonistic encounters, and (ii) ‘passive social support’ in which the mere presence of a social ally reduces behavioural and physiological stress responses. In greylag geese (*Anser anser*) offspring stay with their parents for an entire year or even longer and therefore are a candidate avian model to study support by social allies. We investigated the effects of active and passive social support in ten families (ten males, ten females, 33 juveniles) in a free-roaming, semi-tame flock of greylag geese. Focal individuals were observed during three time periods: (i) re-establishment of the flock in the fall, (ii) stable winter flock, and (iii) disintegration of the flock and break-up of family bonds. We recorded all agonistic interactions of the members of one focal family during morning feedings for two consecutive days: a control day, in which food was distributed widely, and a social density stress situation, in which the same amount of food was spread over a much smaller area. In addition, we collected faeces of all individuals within this family for three hours from the beginning of the feeding situation for determining excreted corticosterone immuno-reactive metabolites by enzyme immuno assay. We found that the small families, *i.e.* pairs with one or two accompanying young, were involved in more agonistic interactions, mainly through the lack of active social support, as compared to large families in the same situation. Members of greylag goose families lost agonistic encounters significantly less often when actively supported. In addition, the excretion of corticosterone metabolites was significantly decreased in large families during a social density stress situation, probably as an effect of passive social support. Via such a socially induced decrease in hormonal stress response during challenging situations, an individual’s long term energy management may benefit.

Keywords

active social support; agonistic interaction; *Anser anser*; immunoreactive corticosterone metabolites; enzyme immuno assay (EIA); Greylag goose; passive social support; social ally; social density stress

Introduction

Von Holst (1998) describes stressors as “all social and non-social stimuli that are challenging or threatening to the survival, health, and reproductive success of animals and that are, therefore, an essential part of natural selection”. Social interactions are among the

most potent stressors (DeVries et al., 2003). On the other hand, social contact with allies may buffer stress. Depending on the social situation, social challenges may affect individuals differently across all members of a group (DeVries, 2002; DeVries et al., 2003; McEwen & Wingfield, 2003; Goymann & Wingfield, 2004). Therefore, it is crucial to understand the means employed by individuals to gain advantages over others in the competition for food and reproductive success. One possibility is through the support of, and by, social allies, a phenomenon common in primates (e.g., Berman, 1980; Datta, 1983a, b; Horrocks & Hunte, 1983; Bernstein & Ehardt, 1985, 1986; Netto & van Hooff, 1986; cercopithecine societies, Pereira, 1992) as well as non-primate mammals (von Holst, 1986; Hennessy & Ritchey, 1987; Arnold & Dittami, 1997).

Two kinds of benefits by social alliances, which are not mutually exclusive, have been described: ‘active’ social support in agonistic encounters (e.g., Horrocks & Hunte, 1983; Pereira, 1992), and ‘passive’ social support through the stress-reducing effects of the presence of a social ally (e.g., von Holst, 1986; Sapolsky, 1992; Levine, 1993a, b; Sachser et al., 1998; Smith et al., 1998). Particularly the passive supportive effects of social allies are less clear in birds than in mammals (Dugatkin, 1997). Generally, three conditions are considered necessary for the development of social support systems (von Holst, 1998): (a) complex social organization, (b) long-term relationships with bonding partners, and (c) matrilineal.

Geese and other social birds form large flocks and show complex social relationships (Rutschke, 1982; Schneider & Lamprecht, 1990; Fox et al., 1995; Kotrschal et al., 2005). For example, geese engage in long-term pair and family bonds, in which juveniles stay with their parents until the next breeding season in the following spring (Lorenz et al., 1978; Lamprecht, 1987; Hemetsberger, 2001). Similar to primates, greylag geese (*Anser anser*) seem to live in a female-bonded social system (Frigerio et al., 2001). In goose flocks, families dominate pairs in aggressive encounters and pairs tend to win against single individuals (e.g., Black & Owen 1986; Lamprecht 1986a, b, 1991; Kotrschal et al., 1993). The dominance rank of a family is determined by the gander (male), the agonistic motivation of which is related to the number of offspring (Lamprecht, 1986a, b). This suggests that in geese, dominance rank is affected by the active social support pair partners or family members may provide for each other. This was indeed found in several goose species (white-fronted geese, *Anser albifrons albifrons*, Boyd, 1953; Canada geese, *Branta canadensis*, Hanson, 1953; Raveling, 1970; pink-footed geese, *A. brachyrhynchus*, Lazarus & Inglis, 1978; barnacle geese, *B. leucopsis*, Black & Owen, 1986, 1989; Stahl et al., 2001). Also, parents are known to provide active assistance for their young in encounters with other flock members until the next breeding season (Black & Owen, 1986, 1989; Kotrschal et al., 1993). Juveniles and females of several species of geese were more successful in agonistic interactions when the gander was nearby, even if not actively interfering (white-fronted geese, Boyd, 1953; Canada geese, Raveling, 1970; bar-headed geese, *Anser indicus*, Lamprecht, 1986a, b, 1991). This was experimentally confirmed with hand-raised greylag geese with humans as models for conspecific allies (Weiß & Kotrschal, 2004). Therefore, social support in geese not only includes physical co-operation, but also motivational effects on both the supportee and the opponent (Lamprecht, 1986a, b, 1991).

Social interactions and social status usually modulate the pituitary-adrenocortical “slow” stress response in mammals and birds (Wingfield & Silverin, 1986; Kotrschal et al., 1998, 2000; Creel, 2001; DeVries, 2002; DeVries et al., 2003). Frigerio et al. (2003) studied the effects of passive social support on individual stress levels and success in agonistic interactions of juvenile hand-raised greylag geese for one year. They found that the mere presence of a human social ally modulated excreted corticosterone levels and enhanced success in agonistic interactions. Weiß & Kotrschal (2004) established that both, success in

agonistic interactions and feeding rates increased with decreasing distance to the human social ally. These social support effects decreased with increasing age of the juveniles.

In continuation of the latter studies, we aimed to investigate experimentally mechanisms and functions of social alliances within greylag geese. We hypothesized that family members would benefit from social support, in a similar way to hand-raised juvenile greylag geese (Frigerio et al., 2003; Weiß & Kotrschal, 2004). We expected higher success in agonistic interactions when family members were actively or passively supported, and predicted a modulation of stress levels of focal individuals during competitive feeding situations. As subadult geese usually loosen their social bonds with their parents at the end of their first year (Rutschke, 1982; Lorenz, 1988; Choudhury & Black, 1993), we expected decreasing effects of active and passive social support towards the end of the first year.

Materials and methods

Study area and study population

A non-migratory flock of greylag geese was introduced into the valley of the River Alm in 1973 by Konrad Lorenz and co-workers (Lorenz, 1988; Hemetsberger, 2001). Individuals are unrestrained and roam the valley between the Konrad Lorenz Forschungsstelle (KLF) and a lake approximately 10 km to the south, where they roost at night. At the time of data collection, the flock consisted of around 170 geese, which were all individually marked with colored leg bands. As in other populations, natural predation, mainly by red foxes (*Vulpes vulpes*) and golden eagles (*Aquila chrysaetos*), is common and may account for losing up to 10% of the flock per year (Kotrschal et al., 1992; Hemetsberger, 2001).

The flock is supplemented with pellets and grain twice daily on the meadows around the research station, with low quantities from spring to fall, and with sustaining amounts during winter. Individual life history data and social backgrounds of all individuals have been continuously monitored since 1973. In addition to hand-raising, geese readily breed in the valley, either at natural nest sites or breeding boxes provided by the KLF. Both hand-raised and goose-raised flock members are habituated to the close presence of humans and neither show avoidance if approached up to 1 m distance, nor do they excrete elevated levels of immunoreactive corticosterone metabolites following such situations (D. Frigerio, unpubl. data; Scheiber et al., 2005), nor do they significantly change heart rates when familiar humans approach (Wascher, 2005). This indicates that human observers do not cause stress and, for example, probably will not negatively affect agonistic motivation even in the goose-raised geese.

Ten focal families were studied in 2003, all raising at least one offspring (range: 1-6 juveniles, $\bar{x} \pm \text{SE}: 3.3 \pm 0.52$ juveniles) to fledging. These were the focus of this work. Families varied in number of young. In total, we collected data from 53 individuals: 10 adult males, 10 adult females, and 33 juveniles. The latter hatched between April 13th and May 25th 2003 (Table 1). Of these 10 families, one female and three juveniles disappeared in December 2003, reducing the number of families to 9 for the final data collection period.

Data collection

Behavioural protocols and faecal samples were collected during three periods between August 2003 and February 2004 which pertained to three different seasonal phases: (a) re-establishment of the flock in the fall (August-September) when the dominance hierarchy is reinstated after moult; (b) stable winter flock (October-November), when the dominance hierarchy is well established, and (c) disintegration of the flock into pairs and loosening of parent-offspring bonds (January-February) due to the pairs preparing for breeding. One of us

observed all agonistic interactions of the members of one focal family per day during morning feedings on two continuous days, a control day, when food was distributed widely ($\sim 150 \text{ m}^2$), and a social density stress situation, in which the same amount of food was spread over approximately a quarter of that area ($\sim 40 \text{ m}^2$). This situation has been shown to introduce a competitive feeding situation (Kotrschal et al., 1993; Scheiber et al., 2005; D. Frigerio, unpubl. data) and actually results in an increased excretion of immunoreactive corticosterone metabolites (Scheiber et al., 2005). A family was observed for the entire time it spent in the feeding area, or for a maximum of one hour, whichever occurred first. During the observation we recorded which focal individual was involved in an agonistic interaction, the social category (family, paired, single) as well as the sex of the opponent, and whether the interaction was won or lost with or without active support. We define interactions won or lost with active support, if at least one family member assisted the focal individual in an interaction. This assistance was often a supportive shouting display by the rest of the family, with each individual stretching the neck forward towards the opponent (Lorenz, 1988), very likely followed by a parental attack towards the winner of the initial interaction in case a juvenile lost (interaction won with active support). Interactions could also be won or lost by an individual without any interference by another family member (interaction won without active support).

In addition, we collected faeces for extraction of immunoreactive corticosterone metabolites (CORT) of all individuals within the focal family for three hours from the beginning of the feeding situation by tracking them from the onset of the feeding situation. In geese, faecal samples represent an integrated, proportional record of the plasma level within a time period of 2-4 hours prior to defecation (Krawany, 1996; Hirschenhauser et al., 2000a). As geese defecate approximately every 20 minutes (Kotrschal et al., 2000; Scheiber et al., 2005) and variation between individual samples tends to be high in geese, we attempted to collect short series of at least three samples of faeces per individual per observation day, to counteract variability in excreted CORT over time to provide more reliable results (Scheiber et al., 2005). This, however, was not always possible. Ranges of consecutive fecal samples per individual per observation period were: re-establishment of the flock: 1-10 samples; stable winter flock: 2-9 samples; disintegration of the flock: 1-9 samples. To avoid the effect of diurnal variation, individual faecal samples were collected only during late morning hours. Our sampling started well after the endogenous corticosterone early morning peak (Schütz et al., 1997). As separation of urine and faeces in geese is not entirely possible, we collected and analysed always faeces with a minor urine fraction. Samples were frozen within 1 hour after collection at -20°C .

Extraction of immunoreactive corticosterone metabolites and determination of hormone metabolite levels

Faecal samples (0.5 g) were extracted in methanol as described by Kotrschal et al. (1998). We assayed faecal samples with enzyme immuno assay (EIA, Möstl et al., 1987; Kotrschal et al., 1998, 2000). Details of the procedure and cross-reactivities were published elsewhere (Kotrschal et al., 1998). A new group-specific antibody was developed (E. Möstl, 2005) recognizing other groups of metabolites (i.e., 5β , 3α , 11β -diol glucocorticoid metabolites) than the previously used antibodies recognizing 11β , 210H , $20\text{-oxo-corticosterone}$ metabolites. The new assay is considerably more sensitive, resulting in higher peak values (Frigerio et al., 2004). Faecal samples of the first seasonal phase were analysed using the old assay as described in Kotrschal et al. (1998), whereas faecal samples of the second and third seasonal phase were analysed using the new assay as described in Frigerio et al. (2004). Concentration limits for reliable measurements ranged from 0.1 ng/g to 92.8 ng/g immunoreactive corticosterone metabolites for the old assay in seasonal phase 1, 0.15 ng/g to 250.5 ng/g for the new assay in seasonal phase 2, and 11.1 ng/g to 217.05 ng/g for the

new assay in seasonal phase 3, respectively. Intra- and inter-assay coefficients of variations were determined from homogenized pool samples. For the old assay the intra-assay coefficient of variation was 13.3% and the inter-assay coefficient of variation was 14.1%. For the new assay the mean intra-assay coefficient of variation was 7.4% and the inter-coefficient of variation was 14.4% for seasonal phase 2. The mean intra-assay coefficient of variation was 10.3% and the inter-coefficient of variation was 13.2% for seasonal phase 3. These values are in the typical range for EIA procedures on faeces, because the number of steps necessary increase total variation.

Data analyses

Over the three seasonal phases we observed a total of 2452 agonistic interactions, 1145 during re-establishment of the flock, 906 during the stable winter flock, and finally 401 when the flock dis-integrated into pairs. Out of all 2452 agonistic interactions, females ($N=10$) were involved in 462 interactions, males ($N=10$) in 995 interactions, and juveniles ($N=33$) in 995 interactions. Mean percentages of agonistic interactions won with active social support were calculated per adult focal individual, using the following formula: number of agonistic interactions won with active support $\times 100$ / total number of agonistic interactions. Similar values were calculated for agonistic interactions won without active support, agonistic interactions lost with active support, and agonistic interactions lost without active support. For juveniles we calculated a mean per family per period accordingly to control for differences in offspring number in the different families. Hormonal data were analysed by computing a Δ CORT value. This was calculated as $\bar{x}$ CORT social density stress $- \bar{x}$ CORT control either per individual for either parent or a family mean for sibling groups to correct for differences in offspring number in the ten families.

Data were analysed using the SPSS statistical program (Version 11.0.1, 2001). Results of all tests are all given two-tailed and level of significance is set to $p = 0.05$. Only significant values ($p < 0.05$) are displayed in the figures. Not all behavioural data were normally distributed (Shapiro-Wilk tests for normality: control seasonal phase 3: $W = 0.661$; $N = 9$; $df = 9$; $p < 0.001$). Therefore, we calculated observed agonistic interactions per minute for each family and correlated these with family size in different seasonal phases using regression analyses. Although interactions won and lost during different control and social density stress feeding situation in each seasonal phase add up to 100%, there are relative differences between wins and losses with or without active social support. Therefore, we present data both for interactions won and lost. Percentages of interactions won and lost with and without active social support were analysed using Wilcoxon signed rank tests repeatedly for 'control' and 'social density stress' days as well as different seasonal phases.

As CORT data were obtained from two different enzyme immuno assays, we chose not to combine them but analysed them according to seasonal phases. Hormonal data (Δ CORT values) were normally distributed when analyzed with Shapiro-Wilk tests for normality ($p > 0.05$). Best fit relationships were calculated to investigate whether correlations existed between family size and excreted immunoreactive corticosterone metabolites. Data were analysed for females, males, and sibling groups of juveniles as well as different seasonal phases.

Results

Agonistic interactions and active social support

There was considerable variation in the number of observed agonistic interactions per minute in males, females and juveniles (Table 2). Males were significantly more often

involved in agonistic interactions compared with females and juveniles, whereas females and juveniles were generally involved similarly often (Table 2).

Furthermore, we found considerable variation in the number of observed agonistic interactions per focal family (Figure 1). Smaller families (one and two juveniles) were involved in more agonistic interactions in stress situations (Figure 1, right panels) and marginally so in controls (Figure 1, left panels) in all three seasonal phases. We observed that greylag geese won encounters through active social support frequently, and juveniles were the ones to benefit most (Figure 2). During re-establishment of the flock and when the flock was stable in the winter, juveniles won significantly more often when actively supported during social density stress (Figure 2 right panels), but not controls. The same was partially true for females, which won significantly more often when actively supported during the social density stress situation in the stable winter flock (Figure 2 middle panels). In contrast, males won encounters generally without active social support (Figure 2 left panels). During disintegration of the flock in the spring, active social support ceased in females, males, and juveniles both in controls and social density stress (Figure 2, lower panels). Results from all Wilcoxon tests are presented in Table 3.

In addition, members of greylag goose families lost agonistic encounters significantly less often, when actively supported (Figure 3), and again, differences in juveniles were most pronounced (Table 3).

Corticosterone and benefits of passive social support

Hormonal stress response was correlated with social context in greylag goose families. CORT increased with decreasing family size over all three seasonal phases in females, males, and when the flock re-established also in the juveniles (Figure 4a-e, g, h). Whereas families with few young excreted more CORT during the social density situation, this was not the case in families with a larger number of young ($\Delta \text{CORT} = 0$), indicating that passive support by social allies was more pronounced in larger families. When the flock was stable in the winter and when it disintegrated in the spring, however, results in the juveniles were reversed: ΔCORT decreased with decreasing family size. In other words, young of larger families excreted more CORT during stress, whereas juveniles of smaller families gained benefits through passive social support (Figure 4f, i). During disintegration of the flock, one family (Family 5, Table 1) showed particularly interesting CORT results. The female and the four young (one male, three females), but not the male, deviated from the patterns shown by the other families. Whereas the young geese had relatively high ΔCORT values, implying higher than average stress levels, the female's value was extremely low.

Discussion

Our data show a level of complexity of social support hitherto described mainly in mammals (Sapolsky, 1992, 1998; Levine, 1993a, b; von Holst, 1998). From fledging in July, to family disintegration, the next February, greylag offspring are embedded in family units. They profit particularly from active social support (i.e., family interference in agonistic interactions). Passive social support (i.e., dampening the excretion of immunoreactive corticosterone metabolites – CORT) was mainly found in offspring right after fledging, during the early summer flock situation. Parents, in contrast, win most of their agonistic interactions without active support by other family members, but seem to profit from passive social support due to motivational effects (Lamprecht, 1986a) over the entire time the family unit exists. Glucocorticoids are, indeed, major endocrine switches for channelling energy into behaviour (Nagra et al., 1963; Sturkie, 1986; Landys-Ciannelli et al., 2004). Therefore, passive social support can be regarded a prime major mechanism for efficient individual stress management. This mechanism explains why in geese successful reproduction

increases rather than decreases the prospects for successful future reproduction (Cooke et al., 1995; Hemetsberger, 2002).

Our present data may also explain the apparent paradox that geese in general and greylag geese in particular tend to tolerate the integration of unrelated goslings within their own group of offspring (Kalmbach et al., 2005). In general, unrelated young should only be accepted, if benefits of raising them exceed costs. This indeed seems to be the case. Costs of additional offspring should be low in geese, because goslings are not fed by their parents. On the plus side, an increase of gosling group size may not only increase the safety of own offspring (Dehn, 1990), but that the company of a large offspring group may substantially benefit parental stress management and hence necessarily, energy balance.

Several studies suggested that larger brood size may be advantageous in geese (Raveling, 1970; Lamprecht, 1986a; Gregoire & Ankney, 1990; Loonen et al., 1999), but social support as a crucial mechanism behind this was never investigated. Our data show that family size mattered in regard to both active and passive social support. Small families had more agonistic encounters per minute, mainly due to being attacked more often (B. Weiß & I. Scheiber, unpubl. data), than did families with three or more young. Flock members generally seem to avoid agonistic encounters with members of large families (B. Weiß & I. Scheiber, unpubl. data). These are therefore, less exposed to stressful social stimuli. However, not only did large families benefit from active social support, the larger the family, the less CORT was excreted particularly during social density stress feedings. Our findings suggest that, although generally social density stress induces an increase in CORT excretion (Scheiber et al., 2005), this is not the case in parental geese. For greylag goose parents a closer distance maintained to their offspring during the social density stress feeding situation seems to reduce stress because parents are in no need to check on their young (I. Scheiber, unpubl. data).

From a gosling's perspective, there is hardly an alternative to staying within the family unit as long as possible. The alternative would be fending for itself in a relatively hostile flock environment. Indeed, the goslings' reward for providing passive social support service for their parents is mainly receiving active social support in agonistic interactions over the summer flock and winter flock periods. As an effect, juveniles, by and large, assume the family rank position established by their parents, particularly by the male (Scott, 1980; Lamprecht, 1986a, b, 1991). In contrast to parents, offspring CORT levels increase towards spring, probably in preparation for integration into the flock. Our study corresponds with findings in hand-raised juvenile greylag geese, where the presence of social allies has advantageous effects for individual greylag geese in number of interactions won, elevated feeding rates (Frigerio et al., 2003; Weiß & Kotrschal, 2004), and in a modulation of the hormonal stress response (Frigerio et al., 2003).

CORT management directly influences fitness in a number of animals. In marmots, for example, Arnold & Dittami (1997) showed that with a larger number of subordinate sons in the group, dominant males had lower glucocorticoid concentrations, whereas the concentration of glucocorticoids increased with an higher number of unrelated subordinate males in the group. Furthermore, they found that males with high corticosteroid levels in spring gained less mass during the following summer, which could result in a lower winter survival as well as in decreased reproductive success in the following year. It is well documented, that corticosterone promotes the mobilization of lipids (Nagra et al., 1963; Landys-Ciannelli et al., 2004). Particularly for female geese, the breakdown of stored lipids over the winter may constrain their ability to build eggs in the following spring.

Within a flock, the relationship between social dominance and corticosteroids may change as social conditions and functional demands change with the annual cycle (Sapolsky, 1983; Hirschenhauser et al., 2000b; see also DeVries et al., 2003). Males, females and juveniles seem to benefit physiologically from a stable social rank. These advantages evidently continue in females until the flock disintegrates in the spring. In contrast, juvenile geese of large families showed the decrease in CORT only in the summer flock situation. Offspring from larger families might experience more stress and hence higher CORT levels compared with offspring from small families due to two reasons. First, the increase in CORT in larger families may reflect sibling competition within the family as the individual juveniles start to establish an independent position in the flock hierarchy (B. Weiß & I. Scheiber, unpubl. data). This should be more pronounced in relatively large sibling groups. Second, the higher CORT in juveniles of larger families during the latter two seasonal phases may reflect a shift in their social status. Although the flock situation seems stable, young geese become increasingly independent from their parents with only their siblings as allies. Whereas juveniles of small families can often be found in close proximity of at least one of their parents until the end of the mating season, offspring from large families usually have to establish a dominance position within the flock often without support from their parents (B. Weiß & I. Scheiber, unpubl. data). In the one family, whose CORT patterns differed from the others during the disintegration of the flock phase (family 5), for example, the subadult geese were still with their parents, while at this point other young ones had already split off from their parents. The subadult geese showed increased CORT values which may have been due to social stress caused by a male challenging their parents' pair bond during that time. In contrast, the female benefited from passive social support due to the prolonged stay with her offspring with a low CORT relative to the other females.

Potentially confounding to our findings may be that dominance rather than actual family size *per se* could explain our results. It is well documented for various species of geese that statistically, large families rank higher than small ones (Raveling, 1970; Gregoire & Ankney, 1990; Loonen et al., 1999). However, the relationship between family size and rank was less clear in Bewick's swans (Scott, 1980) and semi-captive greylag geese (Lamprecht, 1986a and references therein). Also in this study individual families did not rank linearly according to number of offspring. The two largest families, with six and five juveniles, respectively, ranked seventh and tenth out of all ten families. This is probably an effect of the rank of the gander (Lamprecht, 1986a) at the time of data collection (i.e., October 2003; B. Weiß, unpubl. data). A similar argument applies to females choosing to pair with a dominant male at the time of mate selection. It was shown in barnacle geese that partners were not primarily chosen according to dominance rank position within the flock (Choudhury & Black, 1993), probably because all single individuals are low-ranking by that time, and will rise in rank only after they paired. In addition, pairs apparently need to establish a workable relationship (Black & Owen, 1988), including hormonal compatibility (Hirschenhauser et al., 1999).

To conclude, we have shown that similar to mammals, social support has several positive effects on the supportees in greylag geese, parents and offspring, and that these effects may vary systematically with season. We suggest that social support within the family unit may have decisive fitness consequences, particularly for both, parents and offspring. We suggest active and passive social support as major mechanisms determining social organization in greylag geese.

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References

- Arnold W, Dittami J. Reproductive suppression in male alpine marmots. *Anim. Behav.* 1997; 53:53–66.
- Berman CM. Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *Int. J. Primatol.* 1980; 1:153–170.
- Bernstein IS, Ehardt C. Agonistic aiding: Kinship, rank, age, and sex influences. *Am. J. Primatol.* 1985; 8:37–52.
- Bernstein IS, Ehardt C. The influence of kinship and socialization on aggressive behaviour in rhesus monkeys (*Macaca mulatta*). *Anim. Behav.* 1986; 34:739–747.
- Black JM, Owen M. Determinants of social rank in goose flocks: Acquisition of social rank in young geese. *Behaviour.* 1986; 102:129–146.
- Black, JM.; Owen, M. Variations in pair bond and agonistic behaviours in barnacle geese on the wintering grounds. In: Weller, MW., editor. *Waterfowl in the winter*. University of Minnesota Press; Minneapolis: 1988. p. 39-57.
- Black JM, Owen M. Parent-offspring relationship in wintering barnacle geese. *Anim. Behav.* 1989; 37:187–198.
- Boyd H. On encounters between wild white-fronted geese in winter flocks. *Behaviour.* 1953; 5:85–130.
- Choudhury S, Black JM. Mate-selection behaviour and sampling strategies in geese. *Anim. Behav.* 1993; 46:747–757.
- Cooke, F.; Rockwell, RF.; Lank, DB. *The snow geese of La Perouse Bay*. Oxford University Press; Oxford: 1995.
- Creel S. Social dominance and stress hormones. *Trends Ecol. Evol.* 2001; 16:491–497.
- Datta, SB. Relative power and the acquisition of rank. In: Hinde, RA., editor. *Primate social relationships*. Blackwell Sci. Publ.; Boston: 1983a. p. 93-102.
- Datta, SB. Relative power and the maintenance of dominance. In: Hinde, RA., editor. *Primate social relationships*. Blackwell Sci. Publ.; Boston: 1983b. p. 103-111.
- Dehn MM. Vigilance for predators: Detection and dilution effects. *Behav. Ecol. Sociobiol.* 1990; 26:337–342.
- DeVries AC. Interaction among social environment, the hypothalamic-pituitary-adrenal axis, and behavior. *Horm. Behav.* 2002; 41:405–413. [PubMed: 12018936]
- DeVries AC, Glasper EF, Detillion CE. Social modulation of stress responses. *Physiol. Behav.* 2003; 79:399–407. [PubMed: 12954434]
- Dugatkin, LA. *Cooperation among animals*. Oxford University Press; Oxford: 1997.
- Fox AD, Boyd H, Bromley RG. Mutual benefits of associations between breeding and non-breeding white-fronted geese, *Anser albifrons*. *Ibis.* 1995; 137:151–156.
- Frigerio D, Dittami J, Möstl E, Kotrschal K. Excreted corticosterone metabolites co-vary with ambient temperature and air pressure in male greylag geese (*Anser anser*). *Gen. Comp. Endocrinol.* 2004; 137:29–36. [PubMed: 15094333]
- Frigerio D, Weiß BM, Dittami J, Kotrschal K. Social allies modulate corticosterone excretion and increase success in agonistic interactions in juvenile hand-raised greylag geese (*Anser anser*). *Can. J. Zool.* 2003; 81:1746–1754.
- Frigerio D, Weiß BM, Kotrschal K. Spatial proximity among adult siblings in greylag geese (*Anser anser*): Evidence for female bonding? *Acta Ethol.* 2001; 3:121–125.
- Goymann W, Wingfield JC. Allostatic load, social status and stress hormones: The costs of social status matter. *Anim. Behav.* 2004; 67:591–602.

- Gregoire PE, Ankney CD. Agonistic behavior and dominance relationships among lesser snow geese during winter and spring migration. *Auk*. 1990; 107:550–560.
- Hanson HC. Inter-family dominance in Canada geese. *Auk*. 1953; 70:11–16.
- Hemetsberger, J. Die Entwicklung der Grünaauer Graugansschar seit 1973. In: Kotrschal, K.; Müller, G.; Winkler, H., editors. Konrad Lorenz und seine verhaltensbiologischen Konzepte aus heutiger Sicht. Filander Verlag; Fürth: 2001. p. 249–260.
- Hemetsberger, J. Populationsbiologische Aspekte der Grünaauer Graugansschar (*Anser anser*). University of Vienna; 2002. Dissertation
- Hennessy MB, Ritchey RL. Hormonal and behavioral attachment responses in infant guinea pigs. *Develop. Psychobiol.* 1987; 20:613–625.
- Hirschenhauser K, Möstl E, Kotrschal K. Withinpair testosterone covariation and reproductive output in greylag geese (*Anser anser*). *Ibis*. 1999; 141:577–586.
- Hirschenhauser K, Möstl E, Peczely P, Wallner B, Dittami J, Kotrschal K. Seasonal relationships between plasma and fecal testosterone in response to GnRH in domestic ganders. *Gen. Comp. Endocrinol.* 2000a; 118:262–272. [PubMed: 10890566]
- Hirschenhauser K, Möstl E, Wallner B, Dittami J, Kotrschal K. Endocrine and behavioral responses of male Greylag Geese (*Anser anser*) to pairbond challenges during the reproductive season. *Ethology*. 2000b; 106:63–77.
- von Holst, D. Psychosocial stress and its pathophysiological effects in tree shrews (*Tupaia belangeri*). In: Schmidt, TH.; Dembroski, TM.; Blümchen, G., editors. Biological and Psychological Factors in Cardiovascular Disease. Springer; Berlin: 1986. p. 508–516.
- von Holst D. The concept of stress and its relevance for animal behavior. *Adv. Behav.* 1998; 27:1–131.
- Horrocks J, Hunte W. Maternal rank and offspring in vervet monkeys: An appraisal of the mechanisms of rank acquisition. *Anim. Behav.* 1983; 31:772–782.
- Kalmbach E, van der Aa P, Komdeur J. Adoption as a gosling strategy to obtain better parental case? Experimental evidence for gosling choice and age-dependency of adoption in greylag geese. *Behaviour*. 2005; 142:1515–1533.
- Kotrschal K, Dittami J, Hirschenhauser K, Möstl E, Peczely P. Effects of physiological and social challenges in different seasons on fecal testosterone and corticosterone in male domestic geese (*Anser domesticus*). *Acta Ethol.* 2000; 2:115–122.
- Kotrschal K, Hemetsberger J, Dittami J. Vigilance in a flock of semi-tame Greylag Geese (*Anser anser*) in response to approaching eagles *Haliaeetus albicilla* and *Aquila chrysaetos*. *Wildfowl*. 1992; 43:215–219.
- Kotrschal K, Hemetsberger J, Dittami J. Food exploitation by a winter flock of greylag geese: Behavioral dynamics, competition and social status. *Behav. Ecol. Sociobiol.* 1993; 33:289–295.
- Kotrschal, K.; Hemetsberger, J.; Weiß, BM. Homosociality in greylag geese. In: Vasey, P.; Sommer, V., editors. Homosexuality behaviour in animals: An evolutionary perspective. Cambridge University Press; Cambridge, UK: 2005.
- Kotrschal K, Hirschenhauser K, Möstl E. The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* 1998; 55:171–176. [PubMed: 9480683]
- Krawany, M. Die Entwicklung einer nichtinvasiven Methode zum Nachweis von Steroidhormonmetaboliten im Kot von Gänsen. Institute of Biochemistry, Veterinary University of Vienna; Austria: 1996. PhD thesis
- Lamprecht J. Structure and causation of the dominance hierarchy in a flock of bar-headed geese (*Anser indicus*). *Behaviour*. 1986a; 96:28–48.
- Lamprecht J. Social dominance and reproductive success in a goose flock (*Anser indicus*). *Behaviour*. 1986b; 97:50–65.
- Lamprecht J. Female reproductive strategies in bar-headed geese (*Anser indicus*): Why are geese monogamous? *Behav. Ecol. Sociobiol.* 1987; 21:297–305.
- Lamprecht J. Factors influencing leadership: A study of goose families (*Anser indicus*). *Ethology*. 1991; 89:265–274.

- Landys-Ciannelli MM, Ramenofsky M, Piersma T, Castricum Ringing Group, Wingfield JC. Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, *Limosa lapponica*. *Physiol. Biochem. Zool.* 2004; 75:101–110. [PubMed: 11880983]
- Lazarus J, Inglis IR. The breeding behaviour of the pink-footed goose: Parental care and vigilant behaviour during the fledging period. *Behaviour.* 1978; 65:62–88.
- Levine S. The influence of social factors on the response of stress. *Psychother. Psychosom.* 1993a; 60:33–38. [PubMed: 8234640]
- Levine S. The psychoendocrinology of stress. *Ann. NY Acad. Sci.* 1993b; 697:61–69. [PubMed: 8257023]
- Loonen MJJ, Bruinzeel LW, Black JM, Drent PJ. The benefit of large broods in barnacle geese: A study using natural and experimental manipulations. *J. Anim. Ecol.* 1999; 68:753–768.
- Lorenz, K. Hier bin ich – wo bist du? Ethologie der Graugans. Piper Verlag; München: 1988.
- Lorenz, K.; Kalas, S.; Kalas, K. Das Jahr der Graugans. Piper Verlag; München: 1978.
- McEwen B, Wingfield JC. The concept of allostasis in biology and biomedicine. *Horm. Behav.* 2003; 43:2–15. [PubMed: 12614627]
- Möstl E, Meyer HHD, Bamberg E, von Hegel G. Oestrogen determination in feces of mares by enzyme immunoassay on microtitre plates. *Proc. Symp. Analysis Steroids Sopron Hungary.* 1987:219–224.
- Möstl E, Rettenbacher S, Palme R. Measurement of corticosterone metabolites in birds' droppings: An analytical approach. *Ann. N.* 2005
- Nagra B, Breitenbach RP, Meyer RK. Influence of hormones on food intake and lipid deposition in castrated pheasants. *Poul. Sci.* 1963; 42:770–775.
- Netto, WJ.; van Hooff, JARAM. Conflict interference and the development of dominance relationships in immature *Macaca fascicularis*. In: Else, JG.; Lee, PC., editors. Primate ontogeny, cognition and social behaviour. Cambridge University Press; New York, N.Y.: 1986. p. 291–300.
- Pereira, ME. The development of dominance relations before puberty in cercopithecine societies. In: Silverberg, J.; Gray, JP., editors. Aggression and peacefulness in humans and other primates. Oxford University Press; Oxford: 1992. p. 117–149.
- Raveling DG. Dominance relationships and agonistic behavior of canada geese in winter. *Behaviour.* 1970; 37:291–319.
- Rutschke E. Stability and dynamics in the social structure of the greylag goose (*Anser anser*). *Aquila.* 1982; 89:39–55.
- Sachser N, Dürschlag M, Hirzel D. Social relationships and the management of stress. *Psychoneuroendocrinol.* 1998; 23:891–904.
- Sapolsky RM. Individual differences in cortisol secretory patterns in the wild baboon: Role of negative feedback sensitivity. *Endocrinology.* 1983; 133:2263–2267. [PubMed: 6315347]
- Sapolsky, RM. Neuroendocrinology of the stress response. In: Becker, J.; Breedlove, S.; Crews, D., editors. Behavioural endocrinology. MIT University Press; Cambridge, MA: 1992.
- Sapolsky, RM. Why zebras don't get ulcers: An updated guide to stress, stress-related disease and coping. Freeman; New York, NY: 1998.
- Scheiber IBR, Kralj S, Kotrschal K. Sampling effort/frequency necessary to infer individual acute stress responses from fecal analysis in greylag geese (*Anser anser*). *Ann. NY Acad. Sci.* 2005; 1046:154–167. [PubMed: 16055849]
- Schneider JM, Lamprecht J. The importance of biparental care in a precocial, monogamous bird, the bar-headed goose (*Anser indicus*). *Behav. Ecol. Sociobiol.* 1990; 27:415–419.
- Schütz K, Wallner B, Kotrschal K. Diurnal patterns of steroid hormones from feces in greylag goslings (*Anser anser*). *Adv. Ethol.* 1997; 32:66.
- Scott DK. Functional aspects of the pair bond in winter in Bewick's swans (*Cygnus columbianus bewickii*). *Behav. Ecol. Sociobiol.* 1980; 7:323–327.
- Smith TE, McGreer-Whitworth B, French J. Close proximity of the heterosexual partner reduces the physiological and behavioral consequences of novel-cage housing in black tufted-ear marmosets (*Callithrix kuhli*). *Horm. Behav.* 1998; 34:211–222. [PubMed: 9878270]
- SPSS. SPSS for Windows. Version 11.0.1. SPSS, Inc.; 2001. p. 1989–1991.

- Stahl J, Tolsma P, Loonen MJJ, Drent RH. Subordinates explore but dominants profit: Resource competition in high Arctic barnacle goose flocks. *Anim. Behav.* 2001; 61:257–264. [PubMed: 11170715]
- Sturkie, PD. *Avian physiology*. 4th edn. Springer Verlag; New York: 1986.
- Wascher, C. Einfluss sozialer Interaktionen auf die Herzfrequenz bei Grangänsen (*Anser anser*). Dept. of Biology, Karl-Franzens University; Graz, Austria: 2005. MSc. thesis
- Weiß BM, Kotrschal K. Effects of passive social support in juvenile greylag geese (*Anser anser*): A study from fledging to adulthood. *Ethology*. 2004; 110:429–444.
- Wingfield JC, Silverin B. Effects of corticosterone on territorial behavior of free-living male song sparrows (*Melospiza melodia*). *Horm. Behav.* 1986; 20:405–417. [PubMed: 3793022]

Figure 1.

Mean observed agonistic interactions per minute of ten families of greylag geese sorted by number of offspring. Data were collected during control (left panels) and social density stress (right panels) in three different seasonal phases: re-establishment of the flock (upper panels), stable winter flock (middle panels), disintegration of the flock and family break-up (lower panels). Linear regression lines, samples sizes and significance values are given in the upper left corner of the panels. Missing values in the lower two panels are due to the loss of three young: the first one in the family with six offspring, reducing it to a family with five offspring, the second one in the family with two offspring, reducing it to a family with one offspring, and the last in one of the two families with initially one offspring, eliminating it from the analysis.

Figure 2.

Agonistic encounters of males, females, and offspring groups won with and without active social support. Data were collected during control (light boxes) and social density stress (dark boxes) in three different seasonal phases: re-establishment of the flock (upper panels), stable winter flock (middle panels), disintegration of the flock and family break-up (lower panels). Significance values were calculated with Wilcoxon test statistics, and only significant differences are indicated. Boxes show medians as well as 25% and 75% quartiles. Whiskers indicate the range between the 10th and 90th percentiles. Solid circles indicate data outside the 10th and 90th percentiles.

Figure 3.

Agonistic encounters of males, females, and offspring groups lost with and without active social support. Data were collected during control (light boxes) and social density stress (dark boxes) in three different seasonal phases: re-establishment of the flock (upper panels), stable winter flock (middle panels), disintegration of the flock and family break-up (lower panels). Significance values were calculated with Wilcoxon test statistics, and only significant differences are indicated. Boxes show medians as well as 25% and 75% quartiles. Whiskers indicate the range between the 10th and 90th percentiles. Solid circles indicate data outside the 10th and 90th percentiles.

Figure 4.

Δ immunoreactive corticosterone metabolites (Δ CORT = $\bar{x}$ CORT social density stress minus $\bar{x}$ CORT control in ng/g) of ten males, females, and mean = Mf offspring groups of greylag geese sorted by number of offspring during three sampling periods: re-establishment of the flock (upper panels), stable winter flock (middle panels), disintegration of the flock and family break-up (lower panels). Formulas of best fit relationships, sample sizes, p values and trend lines are given. Missing values in the lower two panels are due to the loss of three young: the first one in the family with six offspring, reducing it to a family with five offspring, the second one in the family with two offspring, reducing it to a family with one offspring, and the third one in one of the two families with initially one offspring, which therefore had to be eliminated it from the analysis.

Table 1

Greylag goose focal families with the year the parents were hatched, the year since the male and female were breeding together, the hatching date and number of focal offspring given.

Family number	Mother hatched in/ raised by	Father hatched in/ raised by	Paired since	Hatching date offspring	Number of hatched offspring	Number of fledged offspring
1	1998 Goose	1998 Goose	2001	13. April 2003	7	6
2	1996 Human	1998 Goose	2000	20. April 2003	7	5
3	1993 Human	1992 Goose	1996	29. April 2003	6	4
4	1993 Goose	1993 Human	2000	28. April 2003	5	4
5	2000 Goose	1999 Goose	2001	12. May 2003	4	4
6	1999 Goose	1999 Human	2000	23. April 2003	4	3
7	1999 Human	1999 Human	2000	23. April 2003	7	3
8	1995 Human	1996 Goose	1998	02. May 2003	4	2
9	1998 Goose	1998 Goose	1999	20. April 2003	4	1
10	2000 Goose	1998 Goose	2001	10. May 2003	3	1

Table 2

The mean frequencies of all agonistic interactions for males, females, and offspring separately per seasonal phase and experimental situation. Significant differences of posteriori multiple ranges Tukey tests are indicated by different letters, (a-c).

Seasonal phase	Experimental situation	Males ($\bar{x} \pm SE$)	Females ($\bar{x} \pm SE$)	Offspring ($\bar{x} \pm SE$)	ANOVA statistics
Re-establishment of the flock	control	26.10 $\pm$ 2.96 (a)	12.5 $\pm$ 1.97 (b)	6.64 $\pm$ 0.75 (c)	$F_{2,50} = 42.20$
	social density stress	18.10 $\pm$ 3.58 (a)	10.8 $\pm$ 1.98 (b)	7.61 $\pm$ 0.68 (b)	$F_{2,50} = 10.64$
Stable winter flock	control	22.00 $\pm$ 3.28 (a)	10.10 $\pm$ 2.50 (b)	5.94 $\pm$ 0.51 (b)	$F_{2,50} = 27.32$
	social density stress	14.70 $\pm$ 2.75 (a)	7.90 $\pm$ 1.83 (b)	4.94 $\pm$ 0.46 (b)	$F_{2,50} = 15.23$
Flock disintegration/ family break up	control	10.11 $\pm$ 2.76 (a)	2.33 $\pm$ 0.33 (b)	2.63 $\pm$ 0.26 (b)	$F_{2,45} = 15.34$
	social density stress	10.56 $\pm$ 1.38 (a)	3.11 $\pm$ 0.87 (b)	2.90 $\pm$ 0.30 (b)	$F_{2,45} = 35.58$

Table 3

Statistical results of interactions won and lost with or without active social support for males, females, and offspring separately per seasonal phase and experimental situation. For all tests, Wilcoxon z and p values are presented.

Seasonal phase situation	Experimental	Interactions won		
		Males	Females	Offspring
Re-establishment of the flock	control	$z = -2.293$ $p = 0.022$	$z = -1.859$ $p = 0.063$	$z = -1.120$ $p = 0.263$
	social density stress	$z = -0.420$ $p = 0.674$	$z = -1.126$ $p = 0.260$	$z = -2.395$ $p = 0.016$
Stable winter flock	control	$z = -1.680$ $p = 0.093$	$z = -0.867$ $p = 0.386$	$z = -1.599$ $p = 0.110$
	social density stress	$z = -1.612$ $p = 0.107$	$z = -2.330$ $p = 0.017$	$z = -2.322$ $p = 0.017$
Flock disintegration/ family break up	control	$z = -2.689$ $p = 0.007$	$z = -2.754$ $p = 0.006$	$z = -2.666$ $p = 0.008$
	social density stress	$z = -2.675$ $p = 0.007$	$z = -2.636$ $p = 0.008$	$z = -2.668$ $p = 0.008$
Interactions lost				
Re-establishment of the flock	control	$z = -2.023$ $p = 0.043$	$z = -1.153$ $p = 0.249$	$z = -2.666$ $p = 0.008$
	social density stress	$z = -2.366$ $p = 0.018$	$z = -2.201$ $p = 0.028$	$z = -2.599$ $p = 0.009$
Stable winter flock	control	$z = -1.965$ $p = 0.049$	$z = -1.992$ $p = 0.046$	$z = -2.701$ $p = 0.007$
	social density stress	$z = -1.612$ $p = 0.107$	$z = -1.753$ $p = 0.080$	$z = -2.142$ $p = 0.032$
Flock disintegration/ family break up	control	$z = -1.342$ $p = 0.180$	$z = -1.633$ $p = 0.102$	$z = -2.524$ $p = 0.012$
	social density stress	$z = -1.826$ $p = 0.068$	$z = -1.604$ $p = 0.109$	$z = -2.524$ $p = 0.012$