

RESEARCH PAPERS

Effects of Passive Social Support in Juvenile Greylag Geese (*Anser anser*): A Study from Fledging to Adulthood

Brigitte M. Weiß & Kurt Kotrschal

Konrad Lorenz Forschungsstelle für Ethologie, Grünau/Almtal, Austria

Abstract

In general, support by social allies may reduce stress, increase an individual's status and facilitate access to resources. In Greylag geese (*Anser anser*), offspring stay with their parents for an entire year or even longer and thereby enjoy social support in encounters with other flock members. We investigated the influence of spatial distance to one's allies on the outcome of agonistic encounters in a natural flock situation for a total of 12 sibling groups after fledging. In addition, we tested two groups of hand-raised juvenile geese over a time span of 1½ yr. Passive (i.e. not interfering) human supporters of different familiarity were placed at a standard distance during food provisionings, which produced a tight flock situation. Success in agonistic interactions increased with decreasing distance to members of their social unit. The hand-raised juveniles were more successful in agonistic interactions and showed increased feeding rates when accompanied by a familiar human than when alone or with a non-familiar human. The effect of the presence of familiar humans on success in agonistic encounters significantly decreased with increasing age, while feeding rates remained elevated. The positive effects of social support were particularly evident in females. We conclude that social support has similar effects and functions in the highly social greylag geese as reported for social mammals.

Corresponding author: Brigitte M. Weiß, Konrad Lorenz Forschungsstelle, A-4645 Grünau 11, Austria. E-mail: a9400355@unet.univie.ac.at (or) klf.gruenau@telecom.at

Introduction

Social support by close kin as allies in agonistic interactions is a phenomenon well known in primates (e.g. rhesus monkeys, *Macaca mulatta*, Berman 1980; Datta 1983a,b; Bernstein & Ehardt 1985, 1986; vervet monkeys, *Cercopithecus aethiops*, Horrocks & Hunte 1983; Japanese macaques, *Macaca fuscata*, Kawai 1958; macaques, *Macaca fascicularis*, Netto & van Hooff 1986). The reduction of

physiological and behavioural stress responses as an effect of the presence of a familiar social partner (Levine 1993a,b; von Holst 1998) may allow socially supported individuals to improve their status and enjoy direct benefits by gaining access to resources otherwise accessible only under considerable agonistic pressure. Hence, social support may increase access to food, may positively affect energy budgets and thereby enhance survival (Ekman et al. 2000) and reproductive success.

Greylag geese form large flocks and show complex social organization. They develop dominance relationships and show family structures and female-bonded clans similar to many primates (Lorenz 1988; Frigerio et al. 2001). Families dominate pairs in agonistic encounters and pairs tend to win against single individuals. This suggests that in geese, dominance rank is affected by social support pair partners or family members may provide for each other (e.g. white-fronted geese, *Anser albifrons albifrons*, Boyd 1953; Canada geese, *Branta canadensis*, Hanson 1953; Raveling 1970; pink-footed geese, *Anser brachyrhynchus*, Lazarus & Inglis 1978; barnacle geese, *Branta leucopsis*, Black & Owen 1986, 1989a,b; Stahl et al. 2001).

In primates, social support typically involves active interference by close kin in aggressive encounters (e.g. Horrocks & Hunte 1983; Pereira 1992). In geese, too, parents provide active assistance for their young in encounters with other flock members until the next breeding season (Black & Owen 1989a,b; Kotrschal et al. 1993). In addition, 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, *A. albifrons albifrons*, Boyd 1953; Canada geese, *B. canadensis*, Raveling 1970; bar-headed geese, *Anser indicus*, Lamprecht 1986). Therefore, social support in geese not only includes physical co-operation, but also motivational effects on both the supportee and the opponent (Lamprecht 1986). However, the benefits of passive social support have never been experimentally investigated in juvenile geese.

In the semi-tame Grünau flock of greylag geese, individual life histories and social relationships have been monitored since 1973. Detailed knowledge of individuals allows observing the influence of spatial distance to social allies on the outcome of agonistic interactions. However, manipulating the structure of social units without disturbing the variables to be measured is not feasible with natural parent-offspring groups. The well-established Grünau hand-raising tradition (Lorenz 1988; A. Bisenberger, K. Pfeffer & B. M. Weiss, unpubl. data) provides the basis for investigating mechanisms and functions of social support. A workable alternative to the manipulation of wild greylag families is the use of socially human-imprinted (Hess 1973), hand-raised geese in a natural flock situation and of human supporters, whose familiarity and/or distance to the focal individuals can be varied. Our experimental approach allows us to distinguish between active and passive mechanisms of support and to quantify its effects at different developmental stages.

With this approach, 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 1 yr. They found that the mere presence of a human social ally modulated excreted corticosterone levels and enhanced success in agonistic interactions. At present we aim at investigating individual aspects and temporal dynamics of the behavioural effects of social support from fledging to sexual maturity. While Frigerio et al. (2003) described agonistic success rates of the juvenile geese we also analysed rates of aggression, individual feeding and the influence of distance to human and conspecific allies on the outcome of agonistic interactions. In addition, success in agonistic interactions was also investigated in goose-raised juveniles and was compared with the results of the hand-raised geese. As sub-adult geese loosen social bonds with their parents at the end of their first winter and establish new bonds with forthcoming mates (Lorenz 1988), we expected decreasing effects of social support on the outcome of agonistic interactions and feeding rates towards the end of the first year. Our findings are consistent with these predictions.

Methods

Animals

The studied flock of Greylag geese (*Anser anser*) was introduced into the valley of the river Alm by Konrad Lorenz and co-workers in 1973 (Lorenz 1988, Hemetsberger 2001). The flock is non-migratory but individuals are unrestrained and roam the valley between the Konrad Lorenz Research Station (KLF) and a lake 10 km to the south, which is used as a night roost. Over the years, flock size varied between 120 and 160 individuals. As in other populations, losses to natural predators (mainly foxes and golden eagles) may account for up to 10% of the flock per year (Kotrschal et al. 1992, Hemetsberger 2001). To keep the flock accessible, supplemental food is provided at the meadows around the KLF twice a day, year-round. All individuals are marked with coloured leg rings and are habituated to the close presence of humans. Individual life histories and social backgrounds have been routinely monitored since the introduction of the geese. For varying scientific reasons, usually, two groups of goslings per year are hand-raised in the same area, where also most wild geese raise their goslings (Lorenz 1988). Between hatching and fledging, hand-raised goslings are in permanent company of their human foster parent and their daily spatio-temporal activities follow those of the goose families. They are in contact with the flock from hatching and after fledging fully integrate into the flock. Raising goslings in sibling groups and early contact with the flock avoids sexual misprinting of hand-raised geese. They establish pair bonds with goose-partners and raise offspring, indistinguishable from the goose-raised geese. However, hand-raised individuals maintain a life-long confidence towards certain humans (the foster parent and other well known humans), but otherwise do not behave significantly different than the goose-raised geese (Hemetsberger 2002, B. M. Weiß & K. Kotrschal

unpubl. data). At the time of data collection approximately 25% of the flock members were hand-raised.

In addition, the goose-raised flock members are fully habituated to the close presence of humans and neither showed avoidance if approached as close as at 1 m distance, nor did they excrete elevated levels of corticosterone metabolites following such situations (D. Frigerio, unpubl. data). This indicates that human presence does not cause stress and probably does not negatively affect agonistic motivation of the non-hand-raised geese.

The present study is based on observations of 10 goose-raised sibling groups (one to seven juveniles, total $n = 34$) and two groups of hand-raised siblings ($n_1 = 9$, $n_2 = 3$, total $n = 12$). Sibling groups are defined as individuals raised together by the same parent(s) from hatching, irrespective of genetic relatedness. All goose-raised individuals hatched in spring 1998 (Appendix). The hand-raised individuals hatched in May 1996 (Appendix). Due to frequent contact before fledging, the two hand-raised groups were well acquainted with each other as well as with both human foster parents. Four of the 12 hand-raised juveniles disappeared between the first and second sampling period, probably because of predation and/or natural dispersal. Of the remaining eight, four established pair bonds with greylag mates before the end of this study (Appendix).

Data Collection

Behavioural protocols of goose-raised juvenile geese consisted of continuous focal sampling of agonistic interactions with other flock members. For each observed interaction, we recorded the winner and loser, and distances between the interacting juvenile and its family members. As the instigator won most interactions (usually more than 99%; B. M. Weiß, unpublished observations), we equate instigation with winning in this study. Distances were coded relative to flock density: 1 = the social allies were the nearest neighbours to the interacting focal (usually < 1 m), 2 = at least one, but not all social allies were the nearest neighbour(s) to the interacting focal (usually 1–3 m), 3 = at least one of the social allies was within visual range of the focal individual, but none were its nearest neighbours (usually 3–10 m), 4 = all social allies were hidden from the view of the interacting focal (usually > 10 m). As siblings always kept close proximity to each other, focal animals in a protocol were all juveniles of one particular sibling group.

Data on goose-raised individuals were collected during the food provisionings of the flock at the KLF in the mornings and afternoons, on eight consecutive days in Sept. 1998, which was about 2 mo after the goose-raised juveniles fledged. Observations started after all the food (wheat and pellets) was distributed over approximately 50 m², and ended when the focal individuals began to rest after feeding. The mean duration for the behavioural sampling periods was 18.8 ± 1.6 ($\bar{X} \pm SE$) minutes.

Behavioural protocols of hand-raised focal individuals were collected in the presence of different human supporters. The humans had different social

relationships with the focal animals and either were the human foster parent (treatment A), or a familiar human (the human foster parent of the second sibling group; treatment B), or a known but non-familiar human (treatment C). Supporter C was generally a person whom the focal geese might have seen before but to whom they were not individually habituated. In a fourth treatment (D) no human was present.

Protocols consisted of continuous focal sampling of agonistic interactions with other flock members as well as instantaneous focal sampling of feeding in 1-min sample intervals. During data collection, supporters A, B, or C placed themselves in the centre of the feeding area, thereby keeping the distance to the focal geese below 5 m, and kept passive and silent. Agonistic interactions were recorded in the same manner as for the goose-raised juveniles. The two hand-raised sibling groups were observed simultaneously, as they usually kept in close proximity to the other group. Therefore, treatment A for sibling group 1 equalled treatment B for group 2 and vice versa. Data were taken from a hide approximately 10 m off the feeding area, so that no human other than the supporter was visible for the geese during data collection.

Behavioural protocols of the hand-raised juveniles were collected during six sampling periods over a time span of 18 mo (Table 1), from fledging (Aug. 1996, age 3 mo) to adulthood (Feb. 1998, age 21 mo). During each sampling period, data were collected over 12 subsequent days, consisting of three consecutive days per treatment. At each treatment a different human supporter was present (Table 1) during the regular morning and evening food provisioning to the flock. As for the goose-raised juveniles, observations started after all the food was distributed, and ended when the focal individuals began to rest after feeding. The mean duration for the behavioural sampling periods was 18.8 ± 0.5 ($\bar{X} \pm \text{SE}$) minutes in summer/fall (Aug.–Oct.) and 15.1 ± 0.5 ($\bar{X} \pm \text{SE}$) minutes in winter (Dec.–Feb.).

In Dec. 1997 (age 19 mo) the flock avoided our feeding area for several days, probably due to the presence of a wintering golden eagle in the area, and data collection on 12 consecutive days was not possible. Hence, no data with supporter C were taken. Logistic reasons did not allow us to fully randomize the treatment sequence and therefore treatment A was always first except once and treatments C and D were never first (Table 1).

Data Analysis

Data were analysed using the SPSS[®] statistical program (Pfeifer 1991). Results of all tests are given two-tailed. Most behavioural data were normally distributed (Kolmogorov–Smirnov: *goose-raised*: distance to father: $Z = 1.15$, $n = 50$, $p = 0.144$; distance to mother: $Z = 0.73$, $n = 68$, $p = 0.656$; distance to siblings: $Z = 0.77$, $n = 64$, $p = 0.602$; *hand-raised*: distance to foster parent: $Z = 0.76$, $n = 24$, $p = 0.610$; distance to siblings (in hand-raised): $Z = 0.67$, $n = 24$, $p = 0.754$; distance to second sibling group: $Z = 0.68$, $n = 24$, $p = 0.739$; percentage of won agonistic interactions: $Z = 0.60$, $n = 104$, $p = 0.861$; feeding

Table 1: Sampling periods for hand-raised focal animals. Flock size (number of individuals) and the sequence of treatments are indicated

Sampling period	Flock size	Treatment	Life-history context
1 Aug. 1996 (after fledging)	140	A C B D	3 mo old, integration into the flock, tight sibling groups
2 Dec. 1996 (first winter)	135	A B D C	7 mo old, individuals fully integrated, sibling groups become looser
3 Feb. 1997 (first spring)	135	A C D B	9 mo old, individuals sexually immature, loose sibling groups
4 Oct. 1997 (second summer)	120	A B C D	17 mo old, re-union of the sibling groups
5 Dec. 1997 (second winter)	120	A D B	19 mo old, first individuals paired, loose sibling groups
6 Feb. 1998 (second spring)	120	C A B D	21 mo old, individuals sexually mature, no more sibling groups

A, human foster parent; B, familiar human; C, non-familiar human; D, no human.

rate: $Z = 0.59$, $n = 104$, $p = 0.874$; effect on agonistic interactions: $Z = 1.13$, $n = 49$, $p = 0.155$; effect on feeding rates: $Z = 0.95$, $n = 54$, $p = 0.321$). For those that were not, logarithmic transformation (Zöfel 1992) was performed (Kolmogorov–Smirnov after transformation: won interactions per minute: $Z = 0.53$, $n = 46$, $p = 0.945$; lost interactions per minute: $Z = 0.98$, $n = 46$, $p = 0.290$; total n of interactions per minute: $Z = 0.88$, $n = 46$, $p = 0.426$).

Parametric repeated-measures ANOVA was used to compare mean distances between focal animals and their social allies in won and lost agonistic interactions. As in the goose-raised juveniles, we analysed distances between hand-raised juveniles and their allies only after fledging. The effects of treatment on the number of won and lost interactions, percentage of won interactions and on feeding rates were investigated with multivariate ANOVA for repeated measures. As comparisons of agonistic interactions per treatment in the first four sampling periods are included elsewhere (Frigerio et al. 2003), we pooled the data for treatments A and B and for C and D, respectively, and compared the data over all six sampling periods.

To measure the effect of human allies on agonistic behaviour and feeding rates we calculated the support effect as the increase of values in treatment AB (foster parent and familiar human) compared with treatment CD (non-familiar human and no human) per individual and sampling period. Agonistic interactions: effect = (fraction won in treatment AB – fraction won in treatment CD)/fraction won in treatment CD \times 100; feeding rates: effect = (fraction of time spent feeding in treatment AB – fraction of time spent feeding in treatment CD)/fraction of time spent feeding in treatment CD \times 100. This allowed us to compare support effects corrected for potential seasonal changes of rank or feeding rates. Changes in the support effect over time and the influence of sex were investigated with repeated-measures ANOVA and Pearson correlations.

To test for status differences, we calculated individual mean over the last two periods for the eight focals surviving beyond the end of the study. We used parametric one-way ANOVA to test for status differences.

Results

Goose-raised Juveniles

Shortly after fledging, we observed 17 ± 2.11 ($\bar{X} \pm \text{SE}$) agonistic interactions per goose-raised focal individual, or 578 interactions in total. There was considerable variation in the amount of observed agonistic interactions per minute both within and between families (Table 2). Goose-raised juveniles were significantly closer to their father, mother and siblings when winning agonistic

Table 2: Observed agonistic interactions per minute ($\bar{X} \pm \text{SE}$) within and between sibling groups

Group	N	Interactions/min.
1	12	0.129 \pm 0.017
2	3	0.106 \pm 0.026
3	7	0.393 \pm 0.064
4	4	0.255 \pm 0.022
5	5	0.337 \pm 0.072
6	5	0.183 \pm 0.046
7	4	0.313 \pm 0.031
8	3	0.282 \pm 0.014
9	2	0.829 \pm 0.2
10	2	0.6 \pm 0.071
11	1	0.31
12	1	0.87
h.r.	15	0.118 \pm 0.011
g.r.	34	0.437 \pm 0.077
total	49	0.384 \pm 0.08

h.r., between hand-raised sibling groups; g.r., between goose-raised sibling groups; total, between all sibling groups. Groups 1 and 2 were hand-raised.

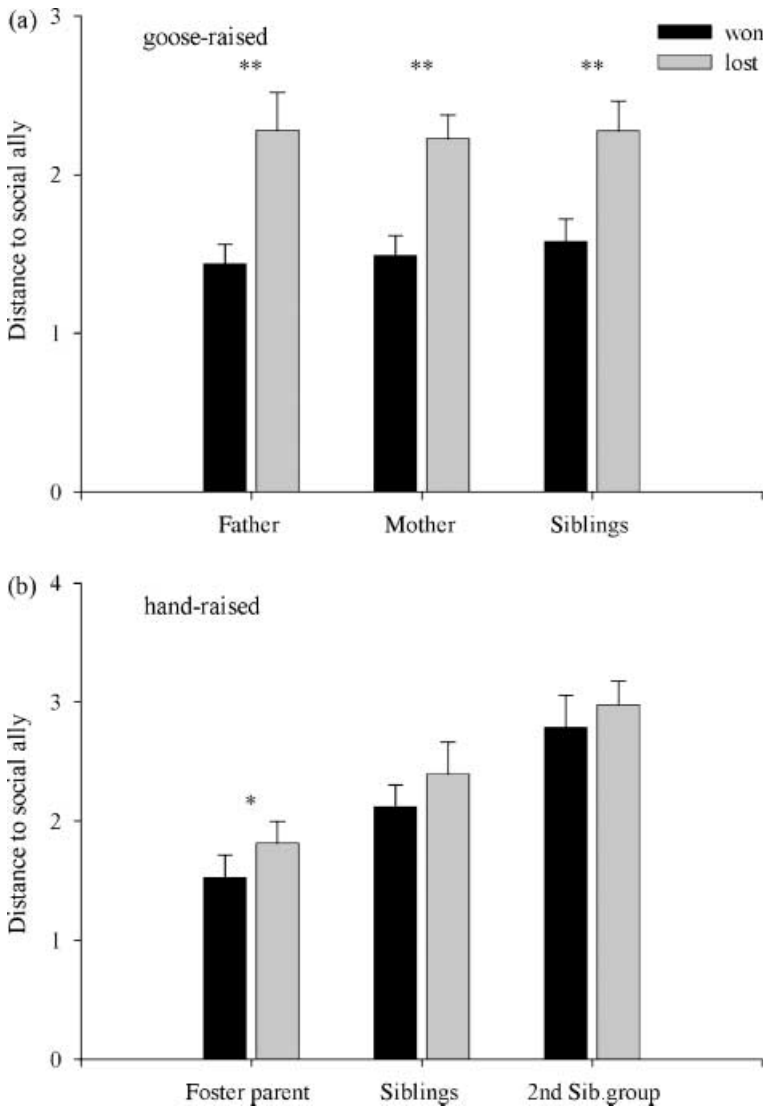


Fig. 1: Distance to social allies during agonistic interactions in goose-raised (a) and hand-raised (b) juvenile greylag geese after fledging. Bars show mean distance category and 95% confidence interval. Asterisks indicate statistically significant differences in distance between won and lost agonistic interactions: * $p < 0.05$, ** $p < 0.01$

encounters than when losing encounters with other flock members (father: $F_{1,24} = 40.93$, $p < 0.001$; mother: $F_{1,33} = 68.94$, $p < 0.001$; siblings: $F_{1,31} = 41.22$, $p < 0.001$; Fig. 1a).

Neither the number of agonistic interactions won per minute nor the number of lost agonistic interactions per minute correlated with the size of the family clan

(Pearson, $n = 34$, won: $r_s = -0.197$, $p = 0.265$; lost: $r_s = -0.067$, $p = 0.707$). Male juveniles won more agonistic interactions per minute than female juveniles ($F_{1,32} = 12.39$, $p = 0.001$). Males and females did not differ in the amount of lost interactions per minute ($F_{1,32} = 0.87$, $p = 0.359$).

Hand-raised Juveniles

In the presence of a human ally, we observed 25.9 ± 2.95 ($\bar{X} \pm \text{SE}$) agonistic interactions per hand-raised juvenile shortly after fledging. With 0.12 ± 0.015 ($\bar{X} \pm \text{SE}$) interactions per minute, the hand-raised focal individuals were significantly less often engaged in agonistic interactions than the goose-raised juveniles (0.37 interactions, $F_{1,44} = 33.09$, $p < 0.001$).

After fledging, hand-raised juveniles were significantly closer to their human foster parent when successfully displacing other flock members than when being displaced themselves ($F_{1,11} = 8.35$, $p = 0.015$; Fig. 1b). Contrary to goose-raised juveniles, there were no significant differences in the distance to siblings in won or lost agonistic interactions ($F_{1,11} = 2.03$, $p = 0.182$; Fig. 1b). In addition, the distance between the two hand-raised groups did not differ for won and lost interactions ($F_{1,11} = 1.02$, $p = 0.335$, Fig. 1b).

Between fledging and sexual maturity, hand-raised juveniles generally won a higher number of agonistic interactions per minute in treatment AB (foster parent or familiar human) than in treatment CD (non-familiar human or no human; $F_{1,6} = 8.95$, $p = 0.02$). The focal animals were displaced more often by their flock members (i.e. all other geese except family members) in treatment CD than in the presence of their human allies, but this difference was not significant ($F_{1,6} = 4.71$, $p = 0.067$). Consequently, the percentage of interactions won was significantly higher in treatment AB than in treatment CD ($F_{1,6} = 37.02$, $p < 0.001$). Moreover, feeding rates of hand-raised juveniles were higher when these were in company of their human allies (treatment AB; $F_{1,6} = 147.57$, $p < 0.001$).

The support effect, i.e. the increase in success between treatments AB and CD, differed significantly between sampling periods (percentage of interactions won: $F_{5,6} = 5.54$, $p = 0.001$; feeding rates: $F_{5,6} = 8.27$, $p < 0.001$). The effect of passive social support on success in agonistic interactions significantly decreased with increasing age of the hand-raised focal individuals (Pearson, $n = 49$, $r = -0.462$, $p = 0.001$; Fig. 2a). The positive effects on the feeding rates of juveniles significantly increased with time (Pearson, $n = 52$, $r = 0.537$, $p < 0.001$; Fig. 2b).

The effect of social support on success in agonistic encounters of hand-raised juveniles was significantly higher for females than for males ($F_{1,6} = 12.61$, $p = 0.012$; Fig. 3). Increases in feeding rates, however, were not significantly different between sexes ($F_{1,6} = 0.34$, $p = 0.579$).

For the last two sampling periods, when sibling units had disintegrated, mean support effects on success in agonistic interactions and feeding rates were compared between paired ($n = 4$) and unpaired ($n = 4$) hand-raised focal individuals. Although it seemed that unpaired individuals profited more

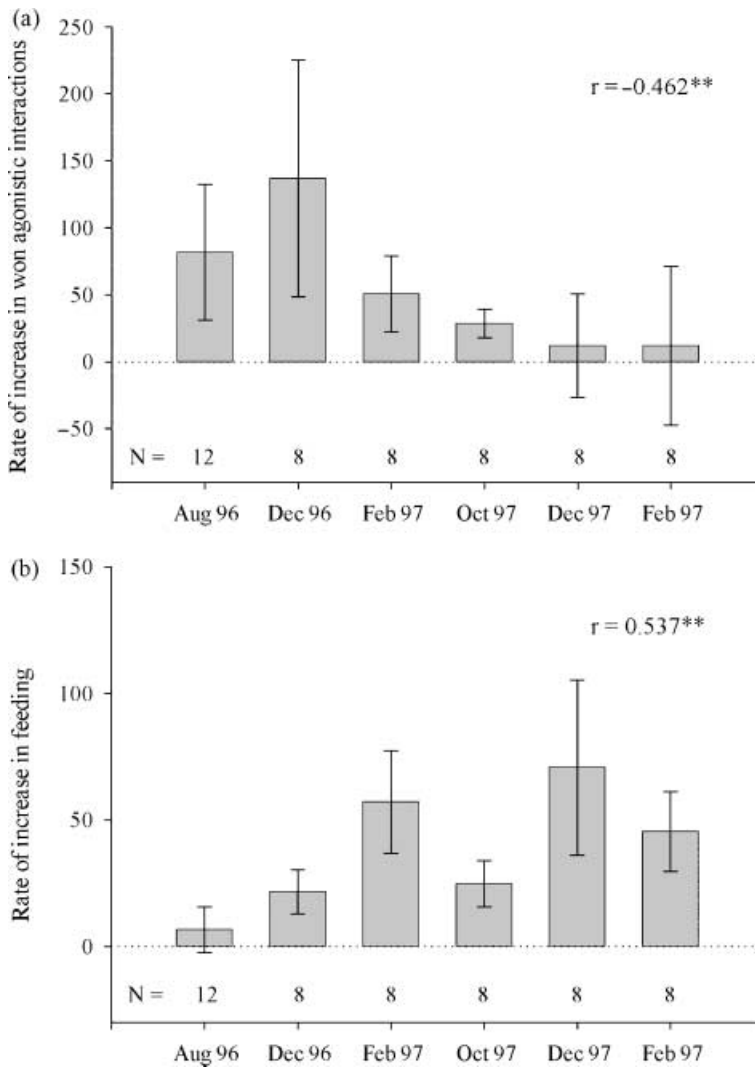


Fig. 2: Effects of social support by human allies on agonistic interactions (a) and feeding rates (b) of hand-raised geese from fledging to adulthood. The increase in agonistic interactions won (a) or feeding rates (b) from situations without (treatment CD) to situations with human allies (treatment AB) is plotted on the y-axes. Bars show mean and 95% confidence intervals. In Feb. 1997, Dec. 1997 and Feb. 1998 one individual won no agonistic interactions in treatment CD. Calculation of the support effect was not possible and the n was reduced to 7 in those periods. $**p < 0.01$

from the presence of their allies in agonistic interactions and feeding rates than paired ones (Fig. 3), differences were not significant (percentage of won interactions: $F_{1,6} = 3.40$, $p = 0.115$; feeding rates: $F_{1,6} = 1.92$, $p = 0.215$).

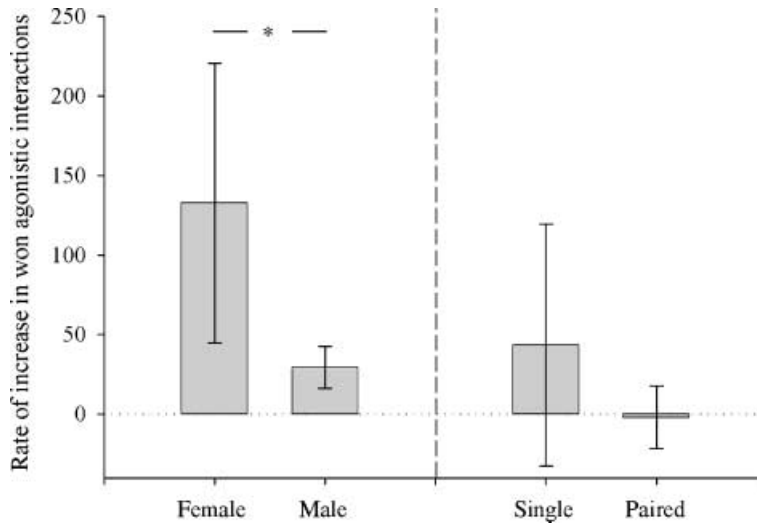


Fig. 3: Sex- and social status-dependent differences of support effects (AB vs. CD) in agonistic interactions. Bars show mean and 95% confidence intervals. Asterisks indicate statistically significant differences in the rate of increase in won agonistic interactions: * $p < 0.05$

Discussion

Our results indicate that the presence of social allies has beneficial effects for individual greylag geese. Even if not actively interfering, a social ally in close proximity increases both the proportion of agonistic interactions won as well as feeding rates in a competitive situation. This parallels results in many social animals, particularly primates, where success in agonistic interactions depends on the position, number, and dominance rank of allies (Scott 1980a,b; Lamprecht 1986) and a high rank enhances competitiveness for food (Pereira 1992; Black et al. 1996; Höjesjö et al. 1998). In a parallel study we found that the mere presence of social allies also reduced the amounts of excreted corticosterone metabolites in the geese in question (Frigerio et al. 2003; cf. Kotschal et al. 1998). Hence, the stress-reducing effect of social support as known from mammals (Levine 1993a,b; von Holst 1998; Sapolsky 1998), is found in this social bird as well.

Close proximity to a conspecific parent or a human foster parent enhanced success in agonistic interactions in both the goose-raised and the hand-raised juveniles. This indicates that human foster parents are suitable models of goose parents, and that geese are able to discriminate between individual humans. The role of siblings, however, seems to differ in goose-raised and hand-raised groups. While goose-raised juveniles were closer to their siblings when winning agonistic interactions, no such effect was apparent in the observed hand-raised geese. A possible reason for this is that the human foster parents represent the 'highest-ranking flock members' and are thus far more powerful allies than any conspecifics. This may cause the hand-raised juveniles

to rely more on support from their human foster parent than goose-raised juveniles may rely on support by their goose parents. In goose families also, the parents seem to be more important allies than siblings, as a higher number of siblings did not enhance the number of interactions won per minute in the goose-raised juveniles.

With the foster parent as a 'super-ally' it may seem surprising that the hand-raised juveniles in this study interacted significantly less than the goose-raised focal individuals. Maybe they did not have to, because they reached their goals with less aggression than the goose-raised juveniles, or these hand-raised geese were inherently less aggressive than offspring from goose families. In addition, it cannot be excluded that because data collection on the hand-raised geese occurred only 2 wk after fledging, they might still have been in the process of integrating into the flock. Therefore, they may have spent more time with looking after, and keeping close proximity to, clan members (Weiss 2000) and less with interactions and even feeding. Furthermore, the human foster parents did not actively interfere during data collection, while the actively interacting goose parents may have enhanced aggression in their young.

As is the case in previous studies (e.g. Lamprecht 1986; Pereira 1988), we were not able to distinguish between the effects of active and passive social support in the goose-raised juveniles. However, using human supporters and socially human-imprinted geese allowed this distinction to be made. As the humans did not actively interfere, the differences in the support treatments were solely due to passive support, which may increase the agonistic motivation of the supportee or decrease the likelihood of flock members to attack individuals with high-ranking allies on their side (Lamprecht 1986). In our study, the increased motivation of the supportees was reflected by the increase of attacks successfully initiated by the focal animals when their foster parent or a familiar human was close by. Such motivational effects may depend on a certain pre-experience of active support, and the possibility of interference by a powerful ally when needed. Indeed, before fledging, hand-raised focal individuals were occasionally agonistically defended by the hand-raisers against attacks from flock members. The potential of allies to interfere is a major tactical factor in primates (Berman 1983; Horrocks & Hunte 1983). Greylag geese were also found to specifically attack individuals that had previously displaced a member of their own social unit (Weiss 2000).

Surprisingly, the effect of social support on agonistic interactions and feeding rates was not highest right after fledging, but increased towards the first winter. Geese may go through a process of learning which flock members have a powerful ally on their side, be it a familiar human or an agonistically motivated goose parent. This is supported by the fact that our focal geese tended to be subject to fewer attacks in the presence of their human allies, but not when an unfamiliar human was close by. Alternative, although not mutually exclusive, explanations include higher energy constraints during winter time or a habituation phase after fledging, in which the juveniles invest more time into keeping up the close proximity to their family members and spend less time feeding and interacting with other flock members.

Because the effects of social support on agonistic interactions decreased over time with decreasing affiliation to the human foster parent and to the siblings, it may seem surprising that the effects of social support on feeding rates did not decrease, but on the contrary, even tended to increase over time. However, such a pattern fits the matricentral clan organization of greylag geese. Particularly, female offspring stay closer to their kin than expected by chance, even after forming pair bonds (Frigerio et al. 2001), while the males essentially follow their female mates. Within the clan, agonistic interactions and thus, displacement from a food source, are rare (Weiß 2000), although threat displays and attacks between clans are common (B. M. Weiß & K. Kotrschal, unpubl. data). Not only the gander shields disturbances from his female and thus furthers her feeding (Lamprecht 1987). The same function may be attributed to the matricentral clan in general. This makes sense, as females are more energy-restrained over the year than males. For example, the number of eggs laid depends on body condition acquired during the winter flock (lesser snow geese, *Anser caerulescens caerulescens*, Ankney & MacInnes 1978; Owen & Black 1990; greylag geese, *A. anser*, Hemetsberger 2001).

Large females seem to pair at an earlier age (barnacle geese, *B. leucopsis*, Black & Owen 1989b; Choudhury & Black 1993). Hence, early social support could boost an individual's value as a mate and early mating of a female would grant her uninterrupted social support, providing such individuals with a head start over life history. Even the access to a high-quality mate (Hirschenhauser et al. 2000) and therefore, lifetime reproductive success (Hemetsberger 2002) may be affected by the quality of social support early in life history. Such complex social and life history mechanisms may contribute to the fact that < 10% of the females in the Grünau flock raise more than 10 offspring to fledging and that approximately two-thirds of all females remain without success (Hemetsberger 2001), which is similar in wild flocks (Rutschke 1982). To date, three of the four females surviving past the end of the study successfully hatched young and two of them raised more than 10 offspring to fledging. Despite their youth, they are among the most successful females in the flock.

Hence, it seems that similar to mammals, social support has positive fitness consequences for supportees. Especially early in life, stress reduction, high rank position and benefits with respect to feeding will positively affect individual energy budgets and may allow more energy to be channelled into growth, which, in turn, may positively affect life history and lifetime reproductive success. But still, as our present sample size is low, such far-reaching functional conclusions remain speculative.

Acknowledgements

We gratefully acknowledge financial support by FWF-Project P10483-BIO, by the 'Verein der Förderer' and sponsorship by MAYR-Schulmöbel. D. Frigerio and B. Weiß hand-raised the two sibling groups. L. Dittami, J. Hemetsberger, M. Stöwe, A. Tintner and K. Tuckova acted as unfamiliar

supporting persons for the geese. We thank J. Daisly, D. Frigerio, I. Scheiber and two anonymous referees for helpful comments on the manuscript. Our special thanks go to the focal individuals and all other geese in the flock for their (almost) permanent co-operation.

Literature Cited

- Ankney, C. D. & MacInnes, D. C. 1978: Nutrient reserves and reproductive performance of female lesser snow geese. *Auk* **100**, 670–679.
- Berman, C. M. 1980: Early agonistic experience and rank acquisition among free-ranging infant Rhesus monkeys. *Int. J. Primatol.* **1**, 153–170.
- Berman, C. M. 1983: Early differences in relationships between infants and other group members based on mother's status: their possible relationship to peer-peer rank acquisition. In: *Primate Social Relationships* (Hinde, R. A., ed.). Blackwell Sci. Publ., Boston, pp. 154–159.
- Bernstein, I. S. & Ehardt, C. 1985: Agonistic aiding: kinship, rank, age, and sex influences. *Am. J. Primatol.* **8**, 37–52.
- Bernstein, I. S. & Ehardt, C. 1986: The influence of kinship and socialization on aggressive behaviour in Rhesus monkeys (*Macaca mulatta*). *Anim. Behav.* **34**, 739–747.
- Black, J. M. & Owen, M. 1986: Determinants of social rank in goose flocks: acquisition of social rank in young geese. *Behaviour* **102**, 129–146.
- Black, J. M. & Owen, M. 1989a: Parent–offspring relationships in wintering Barnacle geese. *Anim. Behav.* **37**, 187–198.
- Black, J. M. & Owen, M. 1989b: Agonistic behaviour in Barnacle goose flocks: assessment, investment and reproductive success. *Anim. Behav.* **37**, 199–209.
- Black, J. M., Choudhury, S. & Owen, M. 1996: Do Barnacle geese benefit from lifelong monogamy. In: *Partnership in Birds* (Black, J. M., ed.). Oxford Univ. Press, Oxford, pp. 91–117.
- Boyd, H. 1953: On encounters between White-fronted geese in winter flocks. *Behaviour* **37**, 291–319.
- Choudhury, S. & Black, J.M. 1993: Mate-selection behaviour and sampling strategies in geese. *Anim. Behav.* **46**, 747–757.
- Datta, S. B. 1983a: Relative power and the acquisition of rank. In: *Primate Social Relationships* (Hinde, R. A., ed.). Blackwell Sci. Publ., Boston, pp. 93–102.
- Datta, S. B. 1983b: Relative power and the maintenance of dominance. In: *Primate Social Relationships* (Hinde, R. A., ed.). Blackwell Sci. Publ., Boston, pp. 103–111.
- Ekman, J., Bylin, A. & Tegelström, H. 2000: Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behav. Ecol.* **11**, 416–420.
- Frigerio, D., Weiss, B. & Kotrschal, K. 2001: Spatial proximity in adult sibling groups: evidence for female bonding in Greylag geese (*Anser anser*)? *Acta Ethol.* **3**, 121–125.
- Frigerio, D., Weiss, B., Möstl, E. & Kotrschal, K. 2003: Social allies modulate corticosterone excretion and increase success in agonistic interactions in juvenile hand-raised graylag geese (*Anser anser*). *Can. J. Zool.* **81**, 1746–1754.
- Hanson, H. C. 1953: Inter-family dominance in Canada geese. *Auk* **70**, 11–16.
- Hemetsberger, J. 2001: Die Entwicklung der Grünaauer Gänseschar seit 1973. In: *Konrad Konrad Lorenz und seine verhaltenbiologischen Konzepte aus heutiger Sicht* (Kotrschal, K., Müller, G. & Winkler, H., eds). Filander Verlag, Fürth, pp. 249–260.
- Hemetsberger, J. 2002: *Populationsbiologische Aspekte der Grünaauer Graugansschar (Anser anser)*. PhD Thesis, Inst. Zoology, Univ. Vienna, Austria.
- Hess, E. H. 1973: *Imprinting. Early Experience and the Developmental Psychobiology of Attachment*. Van Nostrand Reinhold Company, New York, USA.
- Hirschenhauser, K., Möstl, E., Wallner, B., Dittami, J. & Kotrschal, K. 2000: Endocrine and behavioural response of male Greylag geese (*Anser anser*) to pairbond challenges during the reproductive season. *Ethology* **106**, 63–77.
- Höjesjö, J., Johnsson, J. I., Pettersson E. & Järvi, T. 1998: The importance of being familiar: individual recognition and social behavior in Sea trout (*Salmo trutta*). *Behav. Ecol.* **5**, 445–451.
- von Holst, D. 1998: The concept of stress and its relevance for animal behaviour. *Adv. Study Behav.* **27**, 1–131.

- Horrocks, J. & Hunte, W. 1983: Maternal rank and offspring rank in Vervet monkeys: an appraisal of the mechanisms of rank acquisition. *Anim. Behav.* **31**, 772—782.
- Kawai, M. 1958: On the system of social ranks in a natural troop of Japanese monkeys. I. Basic rank and dependent rank. In: *Japanese Monkeys: A Collection of Translations* (Altman, S. A., ed.). Publ. by the editor, Chicago, pp. 105—112.
- Kotschal, K., Hemetsberger, J. & Dittami, J. 1992: Vigilance in a flock of semi-tame Greylag geese (*Anser anser*) in response to approaching eagles (*Haliaeetus albicilla* and *Aquila chrysaetos*). *Wildfowl* **43**, 215—219.
- Kotschal, K., Hemetsberger, J. & Dittami, J. 1993: Food exploitation by a winter flock of Greylag geese: behavioral dynamics, competition and social status. *Behav. Ecol. Sociobiol.* **33**, 289—295.
- Kotschal, K., Hirschenhauser, K. & Möstl, E. 1998: The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* **55**, 171—176.
- Lamprecht, J. 1986: Structure and causation of the dominance hierarchy in a flock of Bar-headed geese (*Anser indicus*). *Behaviour* **96**, 28—48.
- Lamprecht, J. 1987: Female reproductive strategies in Bar-headed geese (*Anser indicus*): Why are geese monogamous? *Behav. Ecol. Sociobiol.* **21**, 297—305.
- Lazarus, J. & Inglis, I. R. 1978: The breeding behaviour of the Pink-footed goose: parental care and vigilant behaviour during the fledging period. *Behaviour* **65**, 62—88.
- Levine, S. 1993a: The influence of social factors on the response to stress. *Psychother. Psychosom.* **60**, 33—38.
- Levine, S. 1993b: The psychoendocrinology of stress. *Ann. N.Y. Acad. Sci.* **697**, 61—69.
- Lorenz, K. 1988: *Hier bin ich -wo bist Du?* Ethologie der Graugans. Piper, München.
- Netto, W. J. & van Hooff, J. A. R. A. M. 1986: Conflict interference and the development of dominance relationships in immature *Macaca fascicularis*. In: *Primate Ontogeny, Cognition and Social Behavior* (Else, J. G. & Lee, P. C., eds). Cambridge Univ Press, New York, pp. 291—300.
- Owen, M. & Black, J. M. 1990: *Waterfowl Ecology*. Blackie, Glasgow, London, UK.
- Pereira, M. E. 1988: Agonistic interactions of juvenile Savanna baboons I. Fundamental features. *Ethology* **80**, 152—171.
- Pereira, M. E. 1992: The development of dominance relations before puberty in cercopithecine societies. In: *Aggression and Peacefulness in Humans and other Primates* (Silverberg, J. & Gray, J. P., eds). Oxford Univ. Press, Oxford, pp. 117—149.
- Pfeifer, A. 1991: *Datenanalyse mit SPSS/PC+4.0*. R. Oldenbourg Verlag GmbH, Munich, Germany.
- Raveling, D. G. 1970: Dominance relationships and agonistic behavior of Canada geese in winter. *Behaviour* **37**, 291—319.
- Rutschke, E. 1982: Stability and dynamics in the social structure of the Greylag goose (*Anser anser*). *Aquila* **89**, 39—55.
- Sapolsky, R.M. 1998: *Why Zebras don't get Ulcers: An Updated Guide to Stress, Stress-related Disease and Coping*. Freeman, New York.
- Scott, D. K. 1980a: Functional aspects of the pair bond in winter in Bewick's swans (*Cygnus columbianus bewickii*). *Behav. Ecol. Sociobiol.* **7**, 323—327.
- Scott, D. K. 1980b: Functional aspects of prolonged parental care in Bewick's swans. *Anim. Behav.* **28**, 938—952.
- Stahl, J., Tolsma, P. H., Loonen, M. J. J. E. & Drent, R. H. 2001: Subordinates explore but dominants profit: resource competition in high Arctic barnacle geese flocks. *Anim. Behav.* **61**, 257—264.
- Weiß, B. 2000: *Social Support in Juvenile Greylag Geese (Anser anser)*. Masters Thesis, Univ. Vienna, Austria.
- Zöfel, P. 1992: *Statistik in der Praxis*, 3rd edn. UTB, Stuttgart, Germany.

Received: February 26, 2003

Initial acceptance: May 17, 2003

Final acceptance: January 12, 2004 (L. Sundström)

Appendix

Focal individuals and their life history characteristics (sibling group; code for the individual, sex if known: m = male, f = female; month and year of hatch; parents: f.p. = human foster parent, g/g = both parents goose-raised, h/h = both parents hand-raised, g/h = mother goose-, father hand-raised, h/g = mother hand-, father goose-raised, h/0 = mother hand-raised, no social father). Italic writing marks hand-raised juveniles that disappeared or died between the first and second sampling period, those marked with an asterisk formed pair bonds in Nov. 1997.