Published in final edited form as:

Horm Behav. 2009 January ; 55(1): 133–138. doi:10.1016/j.yhbeh.2008.09.006.

Benefits of family reunions: Social support in secondary greylag goose families

Isabella B.R. Scheiber^{a,*}, Kurt Kotrschal^{a,b}, and Brigitte M. Weiß^a

^aKonrad Lorenz Forschungsstelle für Ethologie, Fischerau 11, 4645 Grünau im Almtal, Austria

^bDepartment for Behavioural Biology, University of Vienna, Austria

Abstract

Social interactions are among the most potent stressors. However, social allies may diminish stress, increase success in agonistic encounters and ease access to resources. We studied the role of social support as a major mechanism for individual stress management in families of free-ranging greylag geese (*Anser anser*). Greylag geese are long-term monogamous, live in a female-bonded social system, and fledged offspring stay with their parents until the next breeding season ('primary families'). Should parents then fail to fledge young, subadults might rejoin them in summer after molt is completed ('secondary families'). We have previously shown that primary greylag goose families reap benefits from active social support in agonistic encounters, and also excrete lower levels of immuno-reactive corticosterone metabolites (CORT, 'passive social support'). Here we investigated how far active and passive social support continues in secondary goose families. Although we found that active support in agonistic encounters was almost absent in secondary families, subadult male geese won an increased number of agonistic encounters due to the mere presence of their secondary family. Particularly adult and subadult females benefited from passive social support through decreased CORT, whereas males did not. Decrease in the hormonal stress response during challenging situations, induced by social allies, may help the females' long-term energy management, thereby improving the odds for successful future reproduction. We discuss whether joining a secondary family may be an alternative tactic for young geese towards optimizing their start into a complex social life.

Keywords

Anser anser; Immuno-reactive corticosterone metabolites; Extended family bond; Greylag goose; HPA-axis; Secondary family; Social support; Stress management

Introduction

Social life presents challenges to group-living individuals, because social interactions are known to be among the most potent stressors (DeVries et al., 2003; Wascher et al., 2008). On the other hand, social allies may buffer stress. Two types of social support, which are not mutually exclusive, have been described so far: "active" social support in agonistic encounters (e.g. Horrocks and Hunte, 1983; Pereira, 1992), and the stress-reducing effects of the presence of a social ally through "passive" social support (e. g. von Holst, 1986; Levine, 1993a,b; Sachser et al., 1998; Sapolsky, 1992; Smith et al., 1998). This was found in primates (e. g. Berman, 1980; Datta, 1983a,b; Bernstein and Ehardt, 1985, 1986; Horrocks

and Hunte, 1983; Netto and van Hooff, 1986; Pereira, 1992), non-primate mammals (von Holst, 1986, 1987; Hennessy and Ritchey, 1987; Arnold and Dittami, 1997) and, recently, in birds, including geese (Emery et al., 2007; Frigerio et al., 2003; Scheiber et al., 2005a; Weiß and Kotrschal, 2004).

Geese and other social birds form large flocks and show complex social relationships (Fox et al., 1995; Kotrschal et al., 2005; Rutschke, 1982; Schneider and Lamprecht, 1990). Similar to primates, greylag geese (*Anser anser*) exhibit a female-bonded social system (Frigerio et al., 2001; Weiß et al., 2008). Dominance rank in flocks of geese is affected by the active social support pair partners or family members provide for each other (Black and Owen, 1986, 1989; Boyd, 1953; Hanson, 1953; Lazarus and Inglis, 1978; Raveling, 1970; Scheiber et al., 2005a; Stahl, 2001). Parents typically provide active assistance for their young in encounters with other flock members (Black and Owen, 1986, 1989; Kotrschal et al., 1993; Lorenz, 1988; Lorenz et al., 1978; Scheiber et al., 2005a), but juveniles and females of several species of geese were more successful in agonistic interactions even when the male parent or partner was nearby but did not interfere actively (Boyd, 1953; Lamprecht, 1986a,b, 1991; Raveling, 1970). In hand-raised juvenile greylag geese, the mere presence of a human social ally not only enhanced success in agonistic interactions, and increased feeding rates, but also modulated excreted corticosterone levels, whereby excreted corticosterone decreased or increased depending on the identity of the human ally (Frigerio et al., 2003; Weiß and Kotrschal, 2004). Similarly, greylag families with more than two young were involved in fewer agonistic interactions than families with just one offspring, mainly through active social support, and excreted significantly fewer immuno-reactive corticosterone metabolites during socially stressful situations (Scheiber et al., 2005a). In both, hand-raised and goose-raised family groups, these effects decreased with increasing age of the juveniles (Scheiber et al., 2005a; Weiß and Kotrschal, 2004).

Prolonged parent–offspring bonds and extended family groups are prevalent in territorial communal breeders (Brown, 1987), but communal breeding is rare in waterfowl (Lombardi, 1998). Yet, extended family bonds that last beyond independence of offspring are described for several waterfowl species including geese (*Anser* sp.). Juvenile geese are known to remain with their parents after independence for at least part of their first year (e.g. Elder and Elder, 1949; Lorenz et al., 1978; Philips, 1916; ‘primary family’) and may even rejoin for a second year if parents fail to reproduce (‘secondary family’, Lorenz, 1988).

Primary families are characterized by close proximity between family members, socio-positive behaviors, e.g. greeting and performance of triumph ceremonies towards one another, and virtually no aggression within the family (Scheiber et al., 2005a; Weiß et al., 2008). Keeping contact with parents increases juvenile geese’ odds of surviving (Black et al., 2007; Raveling et al., 2000). In Canada geese (*Branta canadensis*), juveniles, which experienced long-term stability in family associations, especially those in large families, were more successful in rearing a brood of their own as two year olds (Raveling et al., 2000). However, not only the offspring seems to profit from the extended goose family bond. Parental barnacle geese (*Branta leucopsis*), which associated with their young until spring, were more likely to return with a new set of offspring the next year than did parents that split with their young earlier. By associating with at least one gosling, parents maintained the high social rank afforded to family units, and gained access to prime feeding areas. Juvenile geese that remained in the family into the spring season assisted parents in fighting for foraging space as well as competitor and predator detection (Black and Owen, 1989; Lamprecht, 1986a).

Young geese rarely remain with their parents for longer than 1 year (Boyd, 1959; Ely, 1993; Prevett and MacInnes, 1980; Raveling, 1969; Warren et al., 1993), but may rejoin parents if

their next breeding attempt was unsuccessful (Lorenz, 1988). While it may be assumed that primary and secondary families engage in extended bonds for the same reasons, the mechanisms behind and the potential benefits of such family reunions have not been studied in detail (see Weiß et al., 2008 for a review). Indications, that secondary families benefit from similar effects as primary families stem from hand-raised greylag geese, where the mere presence of a human social ally in close proximity increased feeding rates and success in agonistic interactions, but did not seem to influence excreted corticosterone metabolite levels of subadults (Frigerio et al., 2003; Weiß and Kotrschal, 2004). Here we wanted to determine whether parent and offspring roles in primary and secondary greylag goose families are similar with respect to the exchange of active and passive social support (Scheiber et al., 2005a).

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 (Hemetsberger, 2001; Lorenz, 1988). 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 150 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 (Hemetsberger, 2001; Kotrschal et al., 1992).

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 monitored continuously since 1973. Geese breed in the valley, either at natural nest sites or in relatively predator-safe nest boxes provided by the KLF. In some years a few geese are carefully hand-raised to keep the flock accessible to humans. Both hand-raised and goose-raised flock members are habituated to the close presence of humans. Geese do not show avoidance behavior if approached up to 1 m distance, nor do they excrete elevated levels of immuno-reactive corticosterone metabolites (Scheiber et al., 2005a,b; D. Frigerio, unpubl.) or show significant heart rate changes when familiar humans approach, as could be determined by 25 geese implanted with heart rate transmitters (C. Wascher, unpubl.). This indicates that human observers do not cause measurable arousal and probably will not negatively affect agonistic motivation even in the goose-raised geese.

Usually secondary families are formed only if parents do not raise concurrent young. Data collection took place from August 2004 to February 2005 (two secondary families), as well as from August 2005 to February 2006 (eight secondary families) to reach a sufficiently large sample size. In total, we collected data from 45 individuals: 10 adult males, 10 adult females, and 25 subadults, which were surviving offspring from the primary family units of the previous year, regardless of whether they had formed a secondary family unit in the year of data collection or not. Out of 25 subadults five males and seven females rejoined their parents, whereas eight males and five females did not. In two families three subadults rejoined their parents, in two families two subadults rejoined, in two families one subadult rejoined, whereas in the remaining four families no subadult rejoined (Table 1).

Data collection

Data from secondary families were collected similarly to the ones taken from primary families (Scheiber et al., 2005a). In brief, behavioral protocols and fecal samples were

collected during three periods between August 2004 and February 2005 and August 2005 and February 2006, respectively. These three periods pertained to different seasonal phases: (a) re-establishment of the flock in the fall (August–September) when the dominance hierarchy is rein-stated after molt; (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 (I.S.) observed all agonistic interactions of the members of one focal family during morning feedings on two consecutive 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 ($\sim 40 \text{ m}^2$). Social density stress feeding has been shown to introduce a competitive feeding situation (Kotrschal et al., 1993) resulting in an increased excretion of immuno-reactive corticosterone metabolites (Scheiber et al., 2005b; D. Frigerio, unpubl.) relative to control days. A family was observed for the entire time it spent in the feeding area, or for a maximum of 1 h, whichever occurred first, and all agonistic interactions were recorded. An agonistic interaction was defined as an encounter between two geese, in which one of them evoked withdrawal behavior from the opponent. The withdrawing goose was considered the loser of the interaction, the goose which evoked the withdrawal was considered the winner. 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 social 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). Interactions could also be won or lost by an individual without any evident interference by another family member (interaction won without active support). In addition, one of us (B.W.) has been monitoring dominance rank as measured by % interactions won ('rank') of all geese in the flock three times per year over the past 15 years. These independently collected rank data were used in one analysis.

We collected feces for extraction of immuno-reactive corticosterone metabolites (CORT) of all individuals within the focal family for 3 h from the beginning of the feeding situation by tracking them individually. In geese, fecal samples represent an integrated, proportional record of the plasma level within a time period of 2–4 h prior to defecation (Hirschenhauser et al., 2000a,b; Krawany, 1996). Our endocrine data thus include the corticosterone situation during and short after the morning feedings. As geese defecate approximately every 20 min (Kotrschal et al., 2000; Scheiber et al., 2005b) and variation between individual samples tends to be high in geese, we attempted to collect short series of three fecal samples per individual on control days, and four samples on social density stress days, to counteract variability in excreted CORT over time to provide more reliable results (Scheiber et al., 2005b). This, however, was not always possible. Ranges and mean $\pm$ standard deviation of consecutive fecal samples per individual per observation period were: re-establishment of the flock: control: 1–9 samples (3.6 ± 1.3); stress: 1–9 samples (4.8 ± 2.0); stable winter flock: control: 1–6 samples (3.3 ± 1.2); stress: 1–8 samples (3.6 ± 1.7); disintegration of the flock: control: 1–5 samples (3.0 ± 1.0); stress: 2–6 samples (3.4 ± 1.0). To avoid the effect of diurnal variation, individual fecal 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 feces in geese is not entirely possible, we collected and analyzed always feces with a minor urine fraction. Samples were frozen within 1 h after collection at -20°C .

Extraction of immuno-reactive corticosterone metabolites and determination of hormone metabolite levels

Fecal samples (0.5 g) were extracted in methanol and assayed with enzyme immuno assay (Kotrschal et al., 1998, 2000; Möstl et al., 1987). Details of the procedure and cross-reactivities were published elsewhere (Kotrschal et al., 1998). A new group-specific antibody was developed recently, recognizing other groups of metabolites (i.e. 5 β , 3 α , 11 β -diol glucocorticoid metabolites) than the previously used antibodies recognizing 11 β , 21OH, 20-oxo-corticosterone metabolites (Möstl et al., 2005). The new assay is considerably more sensitive, resulting in higher peak values (Frigerio et al., 2004). Concentration limits for reliable measurements ranged from 7.25 ng/g to 501.4 ng/g immuno-reactive corticosterone metabolites. Intra- and inter-assay coefficients of variations were determined from homogenized pool samples. Mean intra- and inter-assay coefficients of variation were 9.8% and 13.9%, respectively.

Data analyses

Over the three seasonal phases we observed a total of 965 agonistic interactions, 295 during re-establishment of the flock, 228 during the stable winter flock, and finally 372 when the flock disintegrated into pairs. Out of all 965 agonistic interactions, adult females ($N=10$) were involved in 184 interactions, adult males ($N=10$) in 286 interactions, subadult females ($N=12$) in 245 interactions, and subadult males ($N=13$) in 250 interactions. As variation between individuals as well as individual samples tends to be high in geese, we analyzed hormonal data by computing a Δ CORT value. This was calculated as CORT (social density stress)–CORT (control) per individual and seasonal phase. Δ CORT values can, therefore, either be positive, indicating a higher corticosterone metabolite excretion during social density stress feeding, equal zero, or be negative, indicating a higher corticosterone metabolite excretion during control feeding.

First, we determined the occurrence of primary and secondary families from 1992 to 2007, and analyzed, whether a correlation exists between the quantities of primary and secondary families in the given time interval calculating a Kendall's τ rank correlation coefficient (Fredricks and Nelsen, 2007).

To compare the observed frequencies of agonistic interactions won or lost with or without social support by family members between primary (1°) and secondary (2°) families, we conducted a C^2 -Test. To determine, if subadult geese won more agonistic interactions, if their parents were merely present, but did not interfere, we constructed a generalized linear mixed model (GLMM) and applied the restricted maximum likelihood (REML) procedure for repeated sampling with an unbalanced design. The model was constructed with the binomial variable 'won-lost' as the response variate, 'family affiliation' and 'identity of subadult individual' as random terms, and 'individual rejoined yes/no', 'seasonal phase', 'sex', 'feeding regime (control/stress)', 'rank fathers' and 'rank mothers' as fixed terms. We present Wald statistics, because the change in deviance when dropping a term from the model approximates a X^2 -distribution (Foerster and Kempnaers, 2005). In all models we included first order interaction terms and removed them if $p>0.1$. Excluded terms were re-entered one by one into the final model to confirm that they did not explain a significant part of the variation (Poesel et al., 2006). Only terms with $p<0.1$ remained in the final model. As the random terms 'family relation' was aliased with 'identity of subadult individuals', we excluded the former from the GLMM.

Hormonal data (Δ CORT values) were not normally distributed when analyzed with Shapiro–Wilk Tests for Normality ($p<0.05$). We conducted four generalized linear mixed models (GLMMs with standard least square personality) and applied the REML procedure

for repeated sampling with a balanced design and present Wald statistics. Only terms with $p < 0.1$ remained in the final model. We re-entered excluded terms one by one into the final model and removed them once more if they did not explain a significant part of the variation. We constructed the first GLMM with ' Δ CORT adult females' as the response variate, 'individual identity adult female' as a random term, and 'season' and 'offspring rejoined (yes-no)' as fixed terms. We assembled the other three GLMMs accordingly for subadult females, adult males, and subadult males, respectively.

Results

From 1992 to 2007 primary families ($N=76$) have been more common than secondary families ($N=27$) in the Grünau flock of greylag geese (mean $\pm$ S.E per year and range of primary and secondary families: 4.93 ± 0.96 , 0–13 primary families; 1.86 ± 0.49 , 0–6 secondary families). The number of secondary families correlates positively with the number of primary families of the previous year (Kendall's τ rank correlation: $N_{\text{prim. fam.}}=16$; $N_{\text{sec. fam.}}=15$, $T=0.57$, $p=0.009$).

Agonistic interactions and active social support in primary versus secondary families; success in agonistic encounters of subadult geese in a secondary family

A comparison of agonistic interactions between primary and secondary families revealed that active social support was significantly less common in secondary families (primary families: 38% of 4474 interactions, secondary families: 1.5% of 965 interactions, χ^2 -Test: $\chi^2=488.85$, $df=1$, $p<0.001$). Still, agonistic interactions were won more frequently if subadult geese had rejoined their parents in a secondary family (64% of 249 interactions won) than if subadults had not joined (51% of 237 interactions won, Wald statistic=4.08, $df=1$, $p=0.048$). Also, subadult males were more likely to win agonistic encounters than subadult females (Wald statistic=6.58, $df=1$, $p=0.018$; GLMM with individual identity as a random factor to account for repeated measures within individuals; $N=486$ agonistic interactions won without active social support in 25 subadult individuals).

Corticosterone and passive social support

Both adult and subadult females, but not males, profited from passive social support through joining secondary families. Adult females in secondary families excreted less CORT during the social density stress situation, than females, whose young had not rejoined (Δ CORT < 0 , GLMM 1: Wald statistic=23.73, $df=1$, $p=0.0008$, Fig. 1a. Here, and in the following three models, GLMM with individual identity as a random factor to account for repeated measures within individuals; $N=30$ Δ CORT values in 10 individuals). Also subadult females excreted less CORT during social density stress when rejoining their parents (Δ CORT < 0 , GLMM 2: Wald statistic=9.69, $df=1$, $p=0.0055$, Fig. 1b, $N=36$ Δ CORT values in 12 individuals). Such benefits from passive social support, however, were neither detectable in adult males (Δ CORT > 0 , GLMM 3: Wald statistic=0.40, $df=1$, $p=0.54$, Fig. 1c, $N=30$ Δ CORT values in 10 individuals) nor in subadult males (Δ CORT > 0 , GLMM 3: Wald statistic=1.10, $df=1$, $p=0.31$, Fig. 1d, $N=39$ Δ CORT values in 13 individuals). In all four GLMMs, seasonal phases had no influence on Δ CORT (adult females: Wald statistic=1.14, $df=1$, $p=0.34$; subadult females: Wald statistic=2.35, $df=1$, $p=0.12$; adult males: Wald statistic=2.21, $df=1$, $p=0.14$; subadult males: Wald statistic=0.49, $df=1$, $p=0.63$), and were excluded from the final models.

Discussion

For the first time we provide evidence for the functional significance of secondary family formation in greylag geese. We have shown that subadult geese as well as their parents

profit from being part of a secondary family. Although active social support hardly occurred, young male greylag geese enjoyed an enhanced dominance rank when part of a secondary family unit. In contrast, females, but not males enjoyed dampened glucocorticoid responses during stressful situations when part of a secondary family. This was true for both, family females and female offspring. Although, generally social density stress induces an increase in CORT excretion, this was not the case in primary families either (Scheiber et al., 2005a), probably due to a closer distance maintained between family members (I. Scheiber, unpubl. data).

Females are more energy-restrained over the course of the year than males and we suggest that an effective corticosterone management may allow females to optimize their body condition. This may result in production of larger clutches and/or heavier eggs in adult females, whereas offspring might be able to compete for a high-quality mate and may reproduce successfully at an early age. This hypothesis is supported by studies in a number of animals, which showed that glucocorticoid levels negatively relate to body condition, survival and reproductive success (e.g. alpine marmot, *Marmota marmota*: Arnold and Dittami, 1997; black-browed albatross, *Thalasarche melanophris*: Angelier et al., 2007; harlequin duck, *Histrionicus histrionicus*: Perfito et al., 2002; American kestrels, *Falco sparverius*: Sockman and Schwabl, 2001; Galapagos marine iguanas, *Amblyrhynchus cristatus*: Romero and Wikelski, 2001). Body condition, in turn, influences reproductive parameters like the number or size of eggs laid (lesser snow geese, *Anser caerulescens caerulescens*: Ankney and MacInnes, 1978; barnacle geese: Black et al., 2007; greylag geese, Hemetsberger, 2001), and large females seem to pair at an earlier age (barnacle geese, Black and Owen, 1989b; Choudhury and Black, 1993).

Secondary family units seem to be social alliances that provide similar, yet somewhat less pronounced advantages as primary families (Scheiber et al., 2005a). Still, only ~1/3 of all young rejoin their parents for a second year, regardless whether or not they are in the company of siblings (Weiß et al., 2008). One of the major factors that, indeed, influenced whether subadults – regardless of their sex – rejoined their parents was whether or not parents had bred successfully again (Weiß et al., 2008). The other major determinant of rejoining parents was the pair-bond status of subadults. Subadult geese, which were already pair-bonded at the age of 1 year, were significantly less likely to rejoin their parents than those, which were still single. Paired individuals receive social support from their mate and, although pairs typically rank lower than secondary families, such early bonded individuals thereby have good chances for an early first breeding attempt (Weiß et al. 2008). The only four individuals that were either already pair-bonded or being pursued by a potential mate over the course of this study were female, and neither of these rejoined their parents.

As current or future energetic costs of reproduction are usually higher for females than males in birds and mammals (Adkins-Regan, 2005), we would expect that females should not only be the ones to benefit more from a reduction in HPA-activity, but also that subadult female greylag geese should be more likely to rejoin their parents than subadult males. This finding is supported by observations in white-fronted geese (*Anser albifrons*), where females remained with their parents for an average of 2 years, while males left the family at a mean age of 1.65 years (Warren et al., 1993). Although a higher rate of female offspring rejoined their parents in studies on white-fronted and greylag geese, these results were not significant (Warren et al., 1993; Weiß et al., 2008).

We suggest that social support in primary and secondary goose families may be considered as some kind of helping behavior, i.e. that subadult geese are ‘motivational and/or physiological helpers’ of their parents. In communal breeding systems, helpers generally feed nestlings or fledglings, but can also incubate or defend the nest or territory, and helpers

are often related to the focal breeding pair (Brown, 1987). Whereas there is hardly any need to help raise younger siblings in precocial species, the mere presence of subadult offspring in secondary families has beneficial effects on both adult males and females. In communal breeders, the shortage of vacant breeding territories of sufficient quality and a low probability of finding a mate are among the major constraints to independent breeding (Hatchwell and Komdeur, 2000). Similarly, in geese the availability of high-quality mates as well as predator-safe nest sites may influence whether subadult geese are able to form pair bonds at a young age or rejoin the parents for another year or longer.

Motivational components (Lamprecht, 1986a) are most likely the main proximate function in the formation of secondary families. Via their enhanced agonistic motivation, males benefit from winning agonistic interactions through the mere presence of their social allies, thereby climbing higher in rank than comparable individuals outside secondary family units (Weiß et al., 2008). Females, on the other hand, may reap benefits from a reduction in CORT merely via their motivational state produced by being in a spatially tight social unit with bonding partners ('Triumphgeschreigemeinschaft', Fischer, 1965). Costs of the formation of a secondary family can probably be neglected from the parents' point of view, as they hardly interfere in agonistic interactions nor provide assistance in defending food sources, therefore, accepting yesteryear young should always be beneficial for parents. Subadult geese, on the other hand, have to make the choice of trying to court a potential future mate at an early age or forming a secondary family with their parents. We, therefore, suggest that the formation of secondary families may be viewed as an alternative tactic of subadult geese, where individuals associate with former allies when no appropriate mate is available. Retaining a family unit may allow both, parents and offspring, to maintain a high social status and to enjoy the benefits of a social alliance as discussed above. Via our novel insight in the potential functions of secondary families, we have also contributed to unravel the causes for long-term family formation in geese in general.

Acknowledgments

We gratefully acknowledge financial support from the FWF (Projects 18601-B17, 18744-B03), by the "Verein der Förderer", and the "Herzog von Cumberland Stiftung". D. Frigerio and J. Dittami promoted discussions on the topic. For help in collecting fecal samples we are thankful to C. A. Wascher and I. Nedelcu. C. Siutz prepared the fecal samples for analysis. Enzyme immuno assays were conducted in the laboratory of E. Möstl at the Department of Biochemistry of the Veterinary University of Vienna by A. Kuchar.

References

- Adkins-Regan, E. Hormones and Animal Social Behavior. Princeton University Press; Princeton, NJ: 2005.
- Angelier F, Weimerskirch H, Dano S, Chastel O. Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behav. Ecol. Sociobiol.* 2007; 61:611–621.
- Ankney CD, MacInnes CD. Nutrient reserves and reproductive performances of female lesser snow geese. *AUK.* 1978; 95:459–471.
- Arnold W, Dittami JP. 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. Parent–offspring relationship in wintering barnacle geese. *Anim. Behav.* 1989; 37:187–198.
- Black, JM.; Prop, J.; Larsson, K. Wild Goose Dilemmas: Population Consequences of Individual Decisions in Barnacle Geese. Branta Press; Groningen, NL: 2007.
- Boyd H. On encounters between wild white-fronted geese in winter flocks. *Behaviour.* 1953; 5:85–130.
- Boyd H. The composition of goose populations. *Ibis.* 1959; 101:441–445.
- Brown, JL. Helping and Communal Breeding in Birds. Princeton University Press; Princeton, NJ: 1987.
- Choudhury S, Black JM. Mate-selection behaviour and sampling strategies in geese. *Animal Behaviour.* 1993; 46:747–757.
- 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.
- DeVries AC, Glasper EF, Detillion CE. Social modulation of stress responses. *Physiol. Behav.* 2003; 79:399–407. [PubMed: 12954434]
- Elder WH, Elder NL. Role of the family in the formation of goose flocks. *Wilson Bull.* 1949; 61:133–140.
- Ely CR. Family stability in greater white-fronted geese. *Auk.* 1993; 110:425–435.
- Emery NJ, Seed AM, von Bayern AMP, Clayton NS. Cognitive adaptations of social bonding in birds. *Philos. T. R. Soc. B.* 2007; 362:489–505.
- Fischer H. Das Triumphgeschrei der Graugans (*Anser anser*). *Z. Tierpsychol.* 1965; 22:247–304. [PubMed: 5833824]
- Foerster K, Kempnaers B. Effects of testosterone on male-male competition and male-female interactions in blue tits. *Behavioral Ecology and Sociobiology.* 2005; 57:215–223.
- 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.
- Fredricks GA, Nelsen RB. On the relationship between Spearman's rho and Kendall's tau for pairs of continuous random variables. *J. Stat. Plan. Inference.* 2007; 137:2143–2150.
- 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.
- 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, 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]
- Hanson HC. Inter-family dominance in Canada geese. *Auk.* 1953; 70:11–16.
- Hatchwell BJ, Komdeur J. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour.* 2000; 59:1079–1086. [PubMed: 10877885]
- Hennessy MB, Ritchey RL. Hormonal and behavioral attachment responses in infant guinea pigs. *Developmental Psychobiology.* 1987; 20:613–625. [PubMed: 3691968]
- Hemetsberger, J. Die Entwicklung der Grünauer Graugansschar seit 1973. In: Kotrschal, K., et al., editors. *Konrad Lorenz und seine verhaltensbiologischen Konzepte aus heutiger Sicht*. Filander Verlag; Fürth: 2001. p. 249–260.
- 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.

- Holst, v.D. Psychosocial stress and its pathophysiological effects in tree shrews (*Tupaia belangeri*). In: Schmidt, TH., et al., editors. Biological and Psychological Factors in Cardiovascular Disease. Springer; Berlin: 1986. p. 508-516.
- 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.
- 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, Hirschenhauser K, Möstl E. The relationship between social stress and dominance is seasonal in greylag geese. *Anim. Behav.* 1998; 55:171-176. [PubMed: 9480683]
- 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.; Weiß, BM. Homosociality in greylag geese. In: Vasey, P.; Sommer, V., editors. Homosexual Behaviour in Animals: An Evolutionary Perspective. Cambridge University Press; Cambridge, UK: 2005.
- Krawany, M. Die Entwicklung einer nichtinvasiven Methode zum Nachweis von Steroidhormonmetaboliten im Kot von Gänsen. Institute of Biochemistry, Veterinary University of Vienna; Vienna, Austria: 1996. PhD thesis Institute of Biochemistry
- 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. Factors influencing leadership: a study of goose families (*Anser indicus*). *Ethology*. 1991; 89:265-274.
- 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. N.Y. Acad. Sci.* 1993b; 697:61-69. [PubMed: 8257023]
- Lombardi, J. Comparative Vertebrate Reproduction. Springer Verlag; Berlin: 1998.
- 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.
- Möstl E, Meyer HHD, Bamberg E, Hegel von 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.Y. Acad. Sci.* 2005; 1046:17-34. [PubMed: 16055841]
- 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.
- Perfito N, Schirato G, Brown M, Wingfield JC. Response to acute stress in the Harlequin duck (*Histrionicus histrionicus*) during the breeding season and moult: relationships to gender, condition, and life-history stage. *Can. J. Zool.* 2002; 80:1334-1343.
- Philips JC. Behavior and make up of the migratory flocks of Canada Geese. *Auk*. 1916; 33:24-27.

- Poesel A, Kunc HP, Foerster K, Kempenaers B. Early birds are sexy: male age, dawn song and extrapair paternity in blue tits, *Cyanistes* (formerly *Parus*) *caeruleus*. *Anim. Behav.* 2006; 72:531–538.
- Prevett JP, MacInnes CD. Family and other social groups in snow geese. *Wildl. Monogr.* 1980; 71:1–46.
- Raveling DG. Social classes of Canada geese in winter. *J. Wildl. Manage.* 1969; 33:304–318.
- Raveling DG. Dominance relationships and agonistic behavior of Canada geese in winter. *Behaviour.* 1970; 37:291–319.
- Raveling DG, Sedinger JS, Johnsson DS. Reproductive success and survival in relation to experience during the first two years in Canada geese. *Condor.* 2000; 102:941–945.
- Romero LM, Wikelski M. Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Nino events. *Proc. Natl. Acad. Sci. U. S. A.* 2001; 98:7366–7370. [PubMed: 11416210]
- 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. *Psychoneuroendocrinology.* 1998; 23:891–904. [PubMed: 9924743]
- Sapolsky, RM. Neuroendocrinology of the stress response. In: Becker, J., et al., editors. *Behavioural Endocrinology*. MIT University Press; Cambridge, MA: 1992.
- Scheiber IBR, Weiß BM, Frigerio D, Kotrschal K. Active and passive social support in families of greylag geese (*Anser anser*). *Behaviour.* 2005a; 142:1535–1557. [PubMed: 21984839]
- 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. N.Y. Acad. Sci.* 2005b; 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.
- 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]
- Sockman KW, Schwabl H. Plasma corticosterone in nestling American kestrels: effects of age, handling stress, yolk androgens, and body condition. *Gen. Comp. Endocrinol.* 2001; 122:205–212. [PubMed: 11316426]
- 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]
- Warren SM, Fox AD, Walsh A, O'Sullivan P. Extended parent–offspring relationships in Greenland white-fronted Geese (*Anser albifrons flavirostris*). *Auk.* 1993; 110:145–148.
- Wascher CA, Arnold W, Kotrschal K. Heart rate modulation by social contexts in greylag geese (*Anser anser*). *J. Comp. Psychol.* 2008; 122:100–107. [PubMed: 18298287]
- 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.
- Weiß, BM.; Kotrschal, K.; Frigerio, D.; Hemetsberger, J.; Scheiber, IBR. Birds of a feather stay together: extended family bonds and social support in greylag geese (*Anser anser*). In: Ramirez, RN., editor. *Family Relations: Issues and Challenges*. Nova Science Publishers; New York: 2008.

Fig. 1.

Δ corticosterone immuno-reactive metabolites (Δ CORT=CORT social density stress minus CORT control in ng/g) of (a) adult female, (b) subadult female, (c) adult male and (d) subadult male greylag geese in secondary families. Positive values indicate higher CORT excretion during social density stress than during control, negative values indicate lower CORT excretion during social density stress than during control. Note the different scaling on the y-axes. Asterisks mark significant differences, ** $p < 0.01$, *** $p < 0.001$.

Table 1

Ten greylag goose focal families, with observation period, number of juveniles when in the primary family unit, and number of subadult geese, which rejoined the secondary

Family number	Observation period: August–February	Number of offspring in primary family	Number of offspring in secondary family
1	2004/2005	3	3
2	2004/2005	3	3
3	2005/2006	5 ^a	2
4	2005/2006	5	2
5	2005/2006	2	1
6	2005/2006	2	0
7	2005/2006	2	0
8	2005/2006	2	0
9	2005/2006	1	1
10	2005/2006	1	0

^aDenotes a family, in which one of the subadults died during the summer of 2005, before a secondary family formed.