Influence of socially involved hand-raising on life history and stress responses in greylag geese

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Animals are hand-raised in a variety of contexts, including experimental research. This has been criticized frequently as producing animals with species-untypical behaviour. Here we compare life histories of 330 hand-raised and 631 goose-raised Greylag geese from a free-flying flock to determine whether hand-raising affected life history, reproductive variables and behaviour. We found little differences in life histories (e.g. male age, age at pair bond) or reproductive variables (e.g. number of eggs, egg weight, number of young hatched and fledged) of hand-raised and goose-raised geese. However, hand-raised females had lower life expectancies than goose-raised ones, mainly due to predation during breeding. Hand-raised geese were stressed significantly less during social, handling and predator stress, were attacked less by conspecifics and were less vigilant than goose-raised geese. We conclude that hand-raising resulted in geese with species-typical life histories but reduced stress responses. This makes hand-raised geese cooperative partners for research, but also more vulnerable when exposed to predators.

Keywords: hand-raising; greylag goose; *Anser anser*; life-history; reproductive success; stress

1. Introduction

Animals are hand-raised or socialized with humans early in their lives in a number of contexts and for a variety of purposes, such as support of dwindling populations in the wild, to stock game for hunting, for re-establishing populations (Kotrschal 1999; Whitmore & Marzluff 1998) or for research. Most hand-raising, for example in parrots, is done for creating tame pets, i.e. to provide the basis for trustful social relationships with humans. Also, early post-partum socialization is necessary

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in cats and dogs (weeks 3–8) to enable them to engage in trustful relationships with their human caretakers later in life (Scott & Fuller, 1965; Turner, 2000). The amount and quality of early post-partum handling generally correlates positively with effective stress coping in adulthood (Macrì & Würbel, 2006), i.e. sufficient early handling results in calm animals well suited for interacting with humans. Animal subjects employed in scientific investigations are frequently hand-raised and socialized with humans early on to make them trustful, calm and cooperative. This is often the case in ethological studies in general and in cognition research in particular, where animals need to be relaxed and non-fearful of the human experimenter as well as of the experimental situation (Kitaysky et al., 2006).

It has been proposed that hand-raising may constrain learning (Hinde & Stevenson-Hinde, 1973), but does not seem to change behaviour in a fundamental way (Lorenz, 1988). Particularly strong heritable traits seem relatively inert against modification due to the environment during early ontogeny (Tinbergen, 1951). For example, hand-raising has been shown not to affect neuroanatomy in marsh wrens *Cistothorus palustris* (Kroodsma & Canady, 1985) or avoidance of aposematic prey by great tits *Parus major* (Lindström et al., 1999). In golden eagles *Aquila chrysaetos*, growth of hand-raised chicks and wild nestlings did not differ (Collopy, 1986). In sandhill cranes *Grus canadensis*, hand-raised individuals survived better in the wild than their parent-raised conspecifics (Ellis et al., 2000).

Hand-raising seems to reduce human-generated stress responses and regular handling of young birds can reduce their fear responses to people (Barnett et al., 1994; Collette et al., 2000; Jones & Waddington, 1993). For example, hand-raised red-legged kittiwakes *Rissa brevirostris* showed no fear or measurable stress during a learning experiment (Kitaysky et al., 2006). Hand-raised grey-faced petrel *Pterodroma macroptera gouldi* chicks that were subjected to a standardised blood sampling procedure showed a reduced cortiocosterone response compared to parent-raised chicks (Adams et al., 2005). Via these mechanisms, hand-raising may thus create cooperative animals for research, as they are less prone to be fearsome or stressed by experimental setups and interactions with humans.

Although hand-raising has advantages when cooperative animals are needed, it may distort results pertaining to demographics, life-history evolution or ecological investigations, if hand-raised individuals, for example, alter the age distribution within a population or lead to higher mortality of individuals through predators. Interpretation of the results obtained from hand-raised animals, therefore, needs to be taken cautiously when applying it to conspecific wild populations. For instance, animals raised by hand or artificially, for release, i.e. for support of wild populations may suffer from reduced growth (Bird & Clark 1983), health problems (Nearenberg et al. 1985) and reduced fitness and enhanced mortality in comparison to parent-reared offspring (Brittas et al., 1992; Hill & Robertson, 1988;

Page et al., 1989; Putaala & Hissa, 1998). One reason may be that they differ in basic morphology and physiology (Putaala & Hissa, 1995), as well as in behavioural phenotype (Vilhunen et al., 2008). Increased mortality may also be a result of impaired predator avoidance. Animals raised by humans are not exposed to potential predators during ontogeny (Vilhunen et al., 2005), and will likely be less skilled in appropriately responding to predators. A similar argument may also apply to foraging skills (Fritz et al., 1999).

Critiques of the hand-raising approach maintain that epigenetic mechanisms may affect brain maturation to a certain extent and thereby, may shift the behavioural/cognitive performance as compared to individuals raised by their conspecific parents in the wild (Bering, 2004). Hence, results from animals, such as the Grey parrot "Alex" *Psittacus erithacus* (Pepperberg, 1999; Pepperberg, 2006) may not exactly reflect the performance of individuals in the wild, but they are certainly valid to show the behavioural/cognitive potentials inherent to a certain individual and thereby being indicative of a species' potential.

Greylag geese *Anser anser* show a complex social organization, featuring long-term parent-offspring bonds (Lorenz, 1988; Weiß et al., 2008; Scheiber et al., 2009) and a female-centred clan organization (Frigerio et al. 2001). Ever since K. Lorenz established the greylag goose flock at the Konrad Lorenz Research Station (KLF) in Grünau, geese have been hand-raised to make collaborative partners for research. Objections raised against this method include that it is "unnatural" and may result in individuals behaving "untypically". Based on over 30 years of data on life histories and social behaviour of nearly 1000 male and female greylag geese, and additional experimental data, we wanted to determine, whether hand-raised geese are similar to parent-raised controls in aspects of life history, behaviour, and stress response to human observers.

2. Material and methods

2.1 Study area and study population

Konrad Lorenz and co-workers introduced a non-migratory flock of greylag geese into the valley of the River Alm in 1973 (Lorenz, 1988; Hemetsberger, 2001; Kotrschal et al., 2006). 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. Since 1973 the flock size ranged from 110–170 individuals, with 961 ($N_{males} = 420$, $N_{females} = 440$, $N_{individuals\ of\ unknown\ sex} = 101$) different geese in total until 2009. Approximately one third of these individuals ($N = 330$, $N_{males} = 117$, $N_{females} = 140$, $N_{individuals\ of\ unknown\ sex} = 73$) were hand-raised. All geese are marked individually with coloured leg bands. 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. Feeding is done year-round to keep the flock accessible to humans and to discourage migration in the fall. As in other populations, natural predation, mainly by Red Foxes *Vulpes vulpes* is common and may account for losing up to 10% of the flock per year. Most predatory events occur on the nests during laying and breeding in March and April (Hemetsberger, 2001). The presence or absence of all individuals and changes in the social status are recorded every second day; in addition B.M. Weiß has monitored the dominance hierarchy of the whole flock three times per year since 1992. Geese breed in open nests on islands or along the river, or in one of the 21 relatively predator-safe nest boxes provided by the KLF, which are located around the research station, the nearby Cumberland game park as well as a breeding area 'Oberganslbach' (OGB), where the majority of families also raise their young. For each nest, every new egg is numbered consecutively, weighed and its length and width (mm) measured before onset of incubation. After hatching, families are monitored daily to determine number of young and to check on their proper development. Close to fledging at eight weeks of age, goslings are caught by hand or in a stationary aviary for ringing and taking body measurements such as weight and tarsus length. Life history data such as hatching site and date, number of siblings, first pair bond, partner changes, reached age and reproductive data such as nest site, nest site changes, number of eggs, and hatched and fletched goslings per year were recorded from the entire flock since its establishment.

2.2 The KLF hand-raising tradition

In most years, up to three groups of goslings are hand-raised, each by a single human foster parent, to keep the flock accessible to humans and for various scientific reasons. Eggs are obtained from either our own flock or other goose populations to increase genetic diversity. Goslings hatch in an incubator and get into contact with their human foster parent already during the hatching process. With an average of 5–7 goslings (range 3–11) per human foster parent, hand-raised groups are similar in size to those of wild goose families. Goslings are always hand-raised with brood mates to avoid sexual imprinting on humans. Goslings within a hand-raised group may stem from different nests, i.e. are social, but no genetic siblings, and may differ in age up to 5 days. After hatching is completed, goslings remain with their foster parent 24 hours/day until they fledge approximately ten weeks later. During this time the spatio-temporal pattern of the hand-raised groups follows that of the wild goose families. Like goose mothers, foster parents brood their goslings in the first weeks and spend the daylight hours walking them along meadows and shallow streams for feeding, in the same area where also the wild families raise their young. Hand-raised goslings spend the nights in a heated compartment next to their foster parent's bed, with food and water provided *ad libitum*. Shortly before fledging, they spend the nights on the ponds of the raising area together with the wild goose families. The sibling groups fully integrate into the flock, when it re-assembles after adult geese have finished moult. During this time, human foster parents reduce the amount of time spent with the goslings and typically leave 2–4 weeks after fledging. Goslings then follow the rest of the flock, but spend ample time with other, familiar humans (e.g. people working with the geese on a day-to-day basis) when around the research station for much of their first year and retain a life-long basic confidence towards humans.

2.3 Behavioural data collection

Behavioural protocols consisted of 7 min continuous sampling (Martin & Bateson, 1986) of 43 adult greylag geese (21 males and 22 females, 23 hand-raised and 20 goose-raised geese) from different social categories (paired without offspring or singletons). Data were collected with a Psion Organiser and The Observer 2.0 software (Noldus Information Technology, Wageningen, The Netherlands). Five behavioural protocols per focal animal were recorded (total 215 protocols). To standardise data collection, observations started half an hour after feeding, when the geese spread over the meadows around the Research Station, and ended when the focal animals began to rest, i.e. approximately from 8:30 to 9:00. During data collection, the observer stood at the edge of the foraging area, approximately 5 meters from one focal individual. The following behaviours were considered: vigilance, including "head up" and "extreme head up" (Lazarus, 1978; Lazarus & Inglis, 1978; Lorenz, 1988) and agonistic interactions, such as threats, attacks or fights (Raveling, 1970; Lorenz, 1988), distinguishing the passive or active role of the observed goose. The short duration of each of these events and their recognisable onsets and ends allowed this form of data collection. The frequency of occurrence per 7-min protocols was analysed later on.

2.4 Stress experiments

In addition, we performed experiments, in which focal geese were exposed experimentally to three different types of stressors: (a) a high-density feeding situation, (b) exposure to a predator and (c) handling stress. Experiments (a) and (b) were performed three times each over a period of six weeks, with one experiment being performed per week. The type of stressor, the sequence in which the different stressors were applied, the social density of the subjects, as well as the day of data collection was chosen at random. During social density stress, geese are fed with the same amount of food spread over about one quarter of the regular feeding area. This is perceived stressful by the geese and results in increased excretion of faecal immuno-reactive corticosterone metabolites (Scheiber et al., 2005a). To investigate stress responses to a predator, geese were exposed to a leashed dog for 4 minutes. Different dogs were used for each of the three repeats to avoid habituation. For both the social and the predator stress experiments, focal individuals were the same 43 adult greylag geese as above. All of them experienced the stressors at the same time. Handling stress was investigated by hand-catching a goose and keeping it immobile for 3 minutes. For catching, geese were not chased but were caught while feeding from the hand. This happened near the house wall, in order to hide the caught goose from the rest of the flock. Only 20 individuals (8 males and 12 females, 15 hand-raised and 5 goose-raised) could be caught, and no more than three geese were caught on the same day. On stress days we investigated the adrenocortical response of the focal geese to determine their stress response by measuring levels of faecal immuno-reactive corticosterone metabolites ('BM' thereafter, for terminology see Kime, 1995). Four to five faecal samples per individual per situation were collected within 2.5 hours after exposure to a particular stressor. Faecal samples were stored at -20^{0}C for determination of BM (see below) within two hours after collection. No faecal samples could be collected from a hand-raised male after exposure to a predator, which reduced the sample size to 42 individuals.

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

For the past fifteen years stress levels of the Grünau greylag geese where determined through enzyme immuno assay (EIA) of faecal corticosterone (Kotrschal et al., 1998, 2000; Möstl et al., 1987). Details of the procedure and cross-reactivities were published elsewhere (Kotrschal et al., 1998). In brief, to determine stress levels in this study, BM was determined with antibodies recognizing 11β, 21OH, 20-oxo-corticosterone metabolites (Möstl et al., 2005). The sensitivity of the assay was less than 0.3 pg/well and concentration limits for reliable measurements ranged from 4 to 50 pg/well (Frigerio et al., 2001). Intra- and inter-assay variations were determined with homogenized pool samples. Mean intra-assay coefficient of variation was 12.6 %, mean inter-assay coefficient of variation was 28.1%. These values are characteristic for EIA procedures on faeces (Frigerio et al., 2001).

2.6 Sample size and statistical analysis

In total, we analyzed life history and social data of 961 individuals ($N_{males} = 420$, $N_{females} = 440$, $N_{individuals\ of\ unknown\ sex} = 101$) living in the KLF flock over the past 30 years. Life-history records were incomplete for some individuals, therefore the N used for the various analyses differed, depending on the available information.

Data were not normally distributed (Shapiro-Wilk, $p < 0.05$) and were analyzed using Mann-Whitney-U (MW-U) tests or Chi-square tests. Levels of significance were corrected according to Bonferroni post-hoc tests when necessary. All significances are given two-tailed. All tests were conducted with SPSS 15.0.

3. Results

3.1 Anticipated average life expectancy

Including all individuals of known sex, the anticipated average life expectancy for males was generally higher than for females (MW-U with Bonferroni correction, $N_{males} = 315$, $N_{females} = 368$, $U = 52605.5$, $p = 0.037$). Hand-raised males live as long as goose-raised males ($N_{males} = 117$, $N_{females} = 200$, $U = 10458.5$, $p = 0.495$, Figure 1a). However, hand-raised females succumbed at an earlier age than goose-raised females ($N_{hand\text{-}raised} = 140$, $N_{goose\text{-}raised} = 229$, $U = 13196$, $p = 0.015$, see Figure 1a).

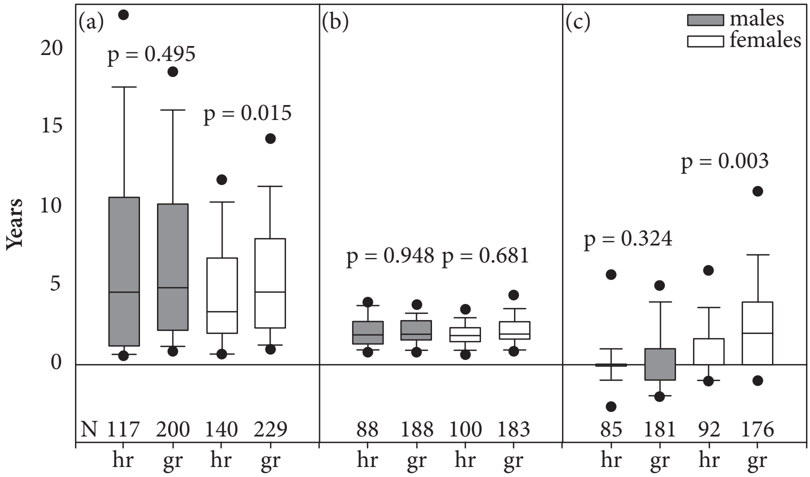

Figure 1. Age at death (a), age at first pair-bond (b) and age difference between pair partners (c) in hand-raised (hr) and goose-raised (gr) Greylag Geese. Lines indicate median and inter-quartile range; whiskers range between 10th and 90th percentile. Full circles represent data outside 5th and 95th percentile

3.2 First pair bond

Neither sex nor upbringing influences when geese paired for the first time (males: $N_{hand\text{-}raised} = 88$, $N_{goose\text{-}raised} = 188$, $U = 7653$, $p = 0.948$; females: $N_{hand\text{-}raised} = 100$,

$N_{goose\text{-}raised}$ = 183 U = 8356.5, p = 0.681; see Figure 1b). On average, males and females paired when about two years old. In males, age of prospective partners at first pairing did not differ between hand-raised vs. goose-raised individuals ($N_{hand\text{-}raised}$ = 85, $N_{goose\text{-}raised}$ = 181, U = 6813, p = 0.324, Figure 1c). Hand-raised females, however, acquired partners from their own age cohort, whereas goose-raised females had partners that were on average 2.5 years older ($N_{hand\text{-}raised}$ = 92, $N_{goose\text{-}raised}$ = 176, U = 5465, p = 0.003, see Figure 1c).

Overall, the first pair bonds lasted about three years (Mean ± SE = 2.96 ± 0.14), with no significant differences related to sex or upbringing (N_{males} = 261, $N_{females}$ = 262, U = 33428.5, p = 0.659; males: $N_{hand\text{-}raised}$ = 97, $N_{goose\text{-}raised}$ = 165, U = 6999, p = 0.400; females: $N_{hand\text{-}raised}$ = 97, $N_{goose\text{-}raised}$ = 165, U = 7137, p = 0.144). Generally, the first pair bond was heterosexual (males 66.8%, females 83.9%). While females never formed homosexual pair bonds, males occasionally paired with another male (depending on the sex-ratio, see Kotrschal et al., 2006). Other forms of bonds, comprising of trios (two males and one female or one male and two females) and harems (1 male, 2+ females), occurred on occasion, i.e. in less than 10% of all observed first time pairings.

The kind of raising did not influence what type of pair bond females engaged in (X^2 = 0.595, p = 0.440), but it did so in males (X^2 = 6.261, p = 0.044). Compared to goose-raised males, hand-raised males appeared to engage in other forms of bonds (trios, harems) more often when pairing for the first time (see Figure 2).

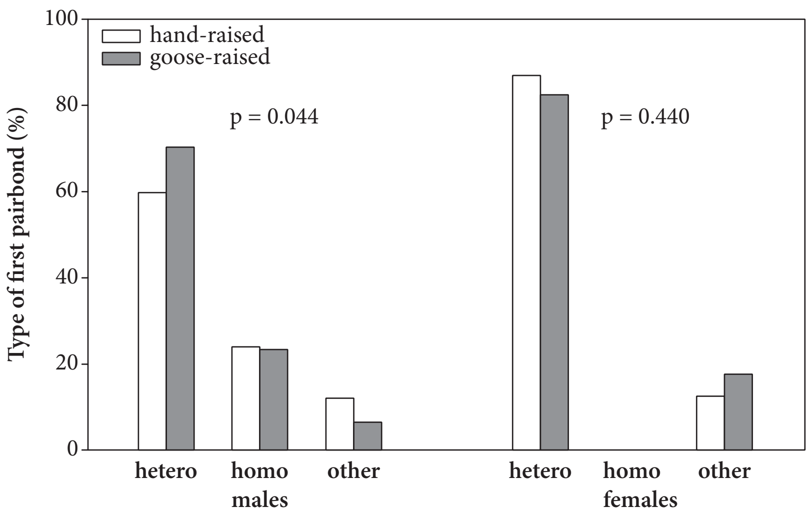

Figure 2. Type of first pair bond in hand-raised (hr) and goose-raised (gr) male and female Greylag Geese in percent

3.3 Reproductive variables

Hand-raised and goose-raised females did not differ in the number of eggs laid per clutch (Mean ± SE = 4.99 ± 0.16, $N_{hand\text{-}raised} = 42$, $N_{goose\text{-}raised} = 62$, U = 1266, p = 0.664). Also egg weight did not differ between hand-raised and goose-raised females (Mean ± SE = 169.61 ± 1.36, $N_{hand\text{-}raised} = 18$, $N_{goose\text{-}raised} = 39$, U = 298, p = 0.367). Upbringing of females did neither influence the percentage of hatched eggs ($N_{hand\text{-}raised} = 56$, $N_{goose\text{-}raised} = 93$, U = 2565.5, p = 0.876), nor the number of goslings fledged ($N_{hand\text{-}raised} = 56$, $N_{goose\text{-}raised} = 93$, U = 2554.5, p = 0.834).

3.4 Stress physiology and behaviour

In all experimental stress situations (social density, handling and predator stress), hand-raised geese excreted fewer immuno-reactive corticosterone metabolites (BM) than goose-raised geese (social density: $N_{hand\text{-}raised} = 23$, $N_{goose\text{-}raised} = 20$, U = 134, p = 0.020; handling: $N_{hand\text{-}raised} = 5$, $N_{goose\text{-}raised} = 15$, U = 3, p = 0.003; predator: $N_{hand\text{-}raised} = 20$, $N_{goose\text{-}raised} = 22$, U = 139, p = 0.043, see Figure 3). Not surprising, differences between hand-raised and goose raised geese were most pronounced during handling. Furthermore, hand-raised geese were less vigilant during the induced stressful situations relative to goose-raised geese ($N_{hand\text{-}raised} = 20$, $N_{goose\text{-}raised} = 23$, U = 92, p = 0,001, see Figure 4). Furthermore, hand-raised geese were less often targets of attacks by conspecifics than goose-raised geese ($N_{hand\text{-}raised} = 20$, $N_{goose\text{-}raised} = 23$, U = 108, p = 0.002, Figure 4).

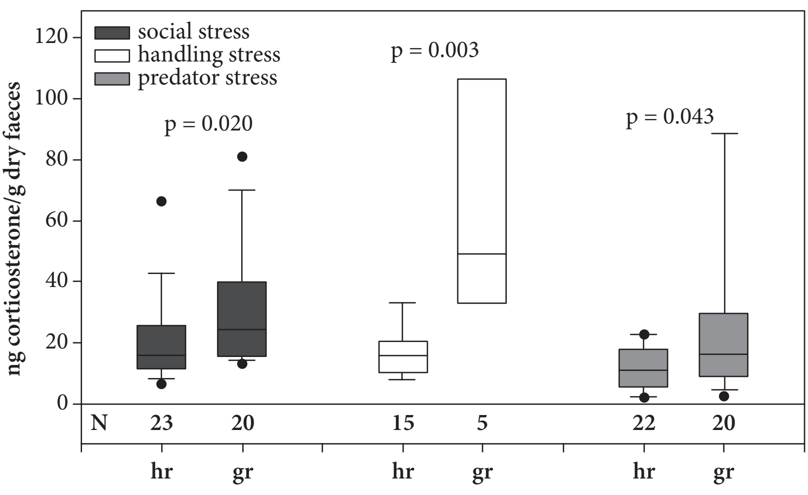

Figure 3. Excreted corticosterone in different stress situations of hand-raised (hr) and goose-raised (gr) Greylag Geese. Lines indicate median and inter-quartile range; whiskers range between 10th and 90th percentile. Full circles represent data outside 5th and 95th percentile

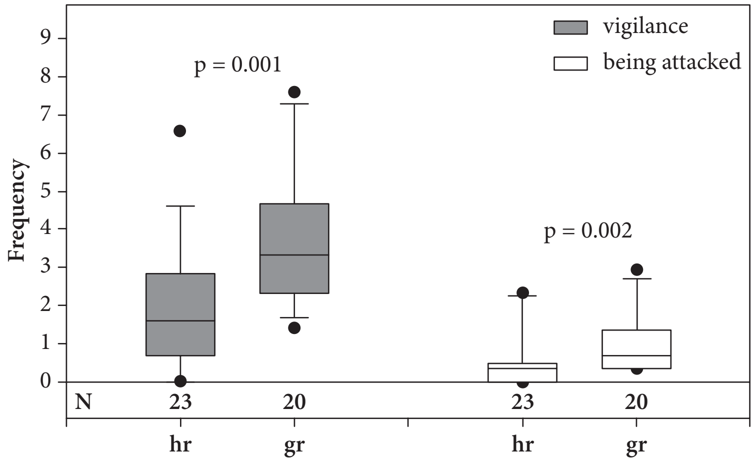

Figure 4. Frequency of vigilance and being attacked of hand-raised (hr) and goose-raised (gr) Greylag Geese. Lines indicate median and inter-quartile range; whiskers range between 10th and 90th percentile. Full circles represent data outside 5th and 95th percentile

4. Discussion

In the present study we show that the hand-raised and goose-raised greylag geese of the KLF flock did not differ in most aspects of their life histories over the past 30 years, and that hand-raised geese generally showed reduced physiological and behavioural reactivity to different types of stressors. This is certainly advantageous in some contexts like close contact with humans, as it results in cooperative individuals which are not affected negatively. Also, a reduced stress response in socially challenging situations like a tight feeding flock is likely to be advantageous. We showed previously that social allies may modulate corticosterone excretion by means of social support. Such social allies may be both, the conspecifics as well as the human foster parent in case of hand-raised geese. Thus, juvenile geese experienced a reduced stress response in experimentally induced challenging situations (Frigerio et al., 2003; Scheiber et al., 2005b). Hand-raised and goose-raised young benefited from social support in a similar manner, thereby enhancing their success in agonistic interactions as well as increasing their feeding rates (Weiß & Kotrschal, 2004). However, hand-raised individuals showed reduced stress responses also in a predator context. Females are particularly vulnerable to predation during breeding, and mortality of females in our flock indeed peaks during the breeding season, with almost 50% of females being preyed upon when on the nest in March and April (Hemetsberger, 2002). This is the most likely cause for the observed lower life expectancy of females compared to males and supports the idea that mortality of breeding females could be the key factor explaining the often found male bias in wild waterfowl populations (e.g. Blums & Mednis, 1996).

Mortality of breeding females may also be the reason why hand-raised females, but not males in our flock had a lower life expectancy than goose-raised individuals, a finding that parallels results in ring-necked pheasants *Phasianus colchicus* (Hill & Robertson, 1988). This is most likely due to the fact that goose-raised females prefer safe nest boxes, whereas hand-raised females are more likely to choose relatively unsafe sites (Hemetsberger, 2002). This may seem counter-intuitive at first. However, Hemetsberger (2002) found that females tended to breed frequently in an area and nest type in which they hatched themselves. Hence, as hand-raised females hatched in an incubator, they lack the early experience of a natural nest site. Furthermore, a lack of exposure to predators in early life and thus reduced opportunities to observe and learn appropriate reactions may be the reason why hand-raised individuals excreted fewer stress hormones and were less vigilant when confronted with a dog as a model predator. These reduced stress responses may put hand-raised females at even greater risk when choosing an unsafe nest site and may thus result in the increased mortality of hand-raised compared to goose-raised females. In general, the behavioural contexts most affected by hand-raising appear to be related to reproduction (e.g. Myers et al., 1988). This seems to be the case in species with a complex social system, such as the Western lowland gorilla *Gorilla gorilla gorilla*, where mother-raised, zoo-born females produced more offspring and used more reproductive opportunities than hand-raised zoo-born females, whereas rearing had no effect on the reproductive success of zoo-born males (Ryan et al., 2002). In our study, reproductive output of hand-raised females did not differ from that of goose-raised females. Also, age at first pair bond and pair bond duration were similar, but goose-raised females tended to form pair bonds with older males, while hand-raised females tended to pair with males from the same age cohort. In barnacle geese *Branta leucopsis*, first-time pair bonds were typically formed between partners of the same age cohort (Black & Owen, 1995), thus paralleling our results in hand-raised rather than goose-raised females. The differences in mate choice observed in hand-raised and goose-raised females may have been due to e.g. differences in intra-sexual competitive abilities but remain to be explored in more detail. For instance, one should take into consideration the identity and life history of the partner as well, as also social associations in early life may shape future mate preferences (Choudhury & Black, 1994; Black et al., 2007). Similarly, in males, the type of the first pair bond differs between hand-raised and goose-raised individuals. While both hand-raised and goose-raised males formed heterosexual pair bonds more often than other types of bonds, this was more pronounced in goose-raised males. Homosexual pair bonds were formed at similar rates, but hand-raised males formed pair bonds with more than one partner more often than goose-raised males. Comparable to age differences in female geese and their partners, hand-raised males may have differed from goose-raised males in attractiveness or intra-sexual competitive abilities, but again, mate choice patterns remain to be explored in the future.

These findings leave us with the question why humans seem to be reasonably adequate social foster parents for geese despite the fact that humans and birds split phylogenetically approximately 320 million years ago. Comparative organismic biology has produced evidence of brain homologies and social convergence in physiological systems. The ability to socialize across-species is probably facilitated by a common “social toolbox” (Kotrschal et al., in press), including conservatively maintained vertebrate brain structures and functions (i.e. Goodson, 2005; Panksepp, 2005), a conservative “social physiology” (i.e. McEwen & Wingfield, 2003; deVries, 2002) and a universal attachment system (Curley & Keverne, 2005).

We conclude that adequately hand-raised geese exhibit life history characteristics, which are in most instances indistinguishable from their goose-raised conspecifics. Hand-raised geese, however, showed less pronounced stress responses during handling, social stress and in a predator context compared to their goose-raised conspecifics in the same flock. Hence, raising conditions should be taken into account when addressing certain questions. However, hand-raising generally makes suitable partners for research, allowing for experimental work in close association with humans in a field setting.

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