Physiological implications of pair-bond status in greylag geese

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In group-living vertebrates, reliable social allies play a decisive role in dealing with stressors. For example, support by social allies is known to dampen glucocorticoid responses. It remains unknown, however, how social embedding affects the sympatho-adrenergic axis as indicated by heart rate (HR) in non-human animals. We studied the relationships between HR, pair-bond status and distance from the partner in twenty-five free-ranging greylag geese (Anser anser) in a natural social environment. In three individuals, we investigated HR responses following partner loss. Overall, we found a context- and sex-dependent difference in HR between paired and unpaired individuals, paired males having a lower HR during agonistic encounters, and unpaired females having a lower HR during resting. Also, in paired females HR increased with increasing distance from the partner. Our data suggest that HR is modulated by pair-bond status in greylag geese in a context- and sex-dependent manner, which may be representative for social vertebrates in general. Despite the low sample size, the present study indicates that proper social embedding may optimize an individual's physiological investment in the social domain. This reduces individual energy expenditure and may benefit health and reproductive success.

Keywords: pair-bond status; social support; heart rate; greylag goose; Anser anser

1. INTRODUCTION

In group-living vertebrates, social partners are an important factor against stress and consequently in keeping the costs of social life low [1,2]. In fact, a key mechanism in dealing with stress is social support, which affects behaviour [2,3], physiology [4,5] and immune status [6,7]. In humans, social support reduces cardiovascular reactivity to acute stressors [8,9]. In non-human animals, social isolation was found to increase [10,11], and grooming to reduce, heart rate (HR) [12,13]. However, there have been few investigations of the effects of pair-bond status on the sympathico-adrenomedullary stress response. Also, most studies have been conducted under laboratory conditions, where individuals are forced into certain conditions (e.g. isolated and not-isolated). Here, we emphasize the effect of pair-bond status on HR in a socially complex bird, the greylag goose, living in its natural social environment, where individuals can actively choose with whom to interact. In these long-term monogamous birds, pair-partners remain in close proximity throughout the year [14,15]. Families are typically dominant over pairs, which dominate singletons [16]. Social allies (i.e. partner and family) provide social support to each other [17,18]. Social stressors have been shown to be among the strongest modulators of HR [19], scaling with the relevance of a stressor [20,21]. We therefore predicted higher HR in unpaired than in paired individuals, particularly in males and during stressful situations. Furthermore, we expected that HR would increase with spatial distance between partners, and report HR changes following partner loss owing to predation, which constitutes a particularly stressful event in the life of a long-term monogamous animal.

2. METHODS

A non-migratory flock of greylag geese was introduced into the Almtal (Upper Austria) in 1973. The flock is supplemented with focal twice daily and consisted of approximately 150 marked individuals in 2005. Birds are habituated to the close presence of humans [22]. In 2005, 25 individuals were fitted with fully implanted sensor–transmitter packages (Austrian animal experiment law GZ 6210.41-BaGT/2003; see [21]).

(a) Data collection

Over 18 months, HR and all behaviours (e.g. feeding, attentional states, preening and agonistic encounters) of 25 focal individuals (15 males and 10 females) were recorded simultaneously for a total of 286 h, encompassing all daylight hours. In seven individuals, pair-bond status changed, therefore they appear in both categories (paired and unpaired). In February 2006, HR and behaviour of 16 individuals (nine males, seven females; 12 paired individuals, four male singletons) were recorded during morning feedings (08.00) on a control day, when food was distributed widely (approx. 150 m²), and a social density day, when food was spread over only approximately 40 m². In two males and one female, we recorded HR on five consecutive days for 10 min each following partner loss owing to predation, and compared this with five ‘control’ recordings each before and two months after the partner was lost. In one male, we were only able to record HR and behaviour on 4 days in each period. Further details on transmitter technology, implantation and data collection are provided as electronic supplementary material.

(b) Statistical analysis

We used generalized linear mixed models (GLMMs) with Poisson error distribution and log link function. Response variables were the heart-beat HRs during the overall observation period and the feeding experiment. Date, time, behaviour, locomotion, distance to group, distance to partner, sex, age, rank, rearing type (hand-raised versus goose-raised), pair-bond status, pair-bond type (male–female, male–male, female–female–male), food density and the interactions between behaviour × food density, behaviour × pair-bond status, sex × pair-bond status, behaviour × sex × pair-bond status and distance × sex served as fixed factors. To account for repeated measures, individual and pair identity were included as random factors. We used second-order Akaike’s information criterion (AICc) to choose the best model, starting with all main effects and interactions between factors [23]. DAIc and AICc weights are presented in the electronic supplementary materials. For post hoc comparisons, we divided differences between parameter estimates by the standard error (s.e.) differences between pairs and interpreted the output as a t-test, with the degrees of freedom equal to the residual of the model [24]. All tests were two-tailed and were performed in SPSS v. 19.0.

3. RESULTS

Over 18 months of data taking, HR during agonistic encounters was significantly higher in paired than in
unpaired males but not females, whereas in females but not in males, HR was higher in paired individuals during rest (behaviour × sex × pair-bond status: d.f. = 99, \( F = 834.481 \), \( p < 0.001 \); figure 1). Also, HR was increased in females but not in males, when the pair-partner was farther than 1 m away (pair-partner × sex: d.f. = 14, \( F = 4728.875 \), \( p < 0.001 \); figure 2).

During the feeding experiment, HR was higher when high food density forced geese to feed closely together (d.f. = 1, \( F = 2531.407 \), \( p < 0.001 \). In three individuals,
a HR decrease was observed after the loss of the pair-partner compared with a control situation before (mean ± s.d.: 19.5 ± 6.73%). Two months after the partner loss, HR was still reduced compared with the control situation before (mean ± s.d.: 13.178 ± 20.023%). For additional results and figure see the electronic supplementary material.

4. DISCUSSION
To our knowledge, we provide the first evidence for effects of social allies on HR in birds. As predicted, in social situations, paired males generally appeared less reactive to stressors than those without allies, and in particular, in a dense feeding situation, which is a stressful for all individuals, as shown in a higher HR compared with control feedings. The HR difference between paired and unpaired individuals during agonistic interactions was found in males but not in females. Generally, HR responses to agonistic encounters were higher in males, and as stress responses are energetically costly [25,26], responding adequately to stressors is crucial for them in terms of an individual’s fitness, and well-being [27]. We suggest that social support, i.e. the presence of the partner, is the main factor for keeping HR low, particularly in females [2,5]. In paired females, HR increased in a nonlinear way if the partner was farther than 1 m away, potentially because providing support in agonistic encounters is constrained by increasing distance. Interestingly, paired females had a significantly higher HR than unpaired females during resting, which we presently cannot explain.

We also recorded HR responses of three individuals after the loss of their partner. Despite the small sample size, these are unique data from free-living animals. The loss of the partner is probably the most traumatic event for long-term monogamous animals, including humans, and may trigger a severe and long-lasting depression-like syndrome, with bradycardia as one of the symptoms [28]. Short-term bradycardia in response to a severe stressor has been shown in animals (e.g. rats [29]; squirrel monkeys [30]; white-tailed deer [31]). We found HR to decrease after a predator took the partner, whereby the decrease lasted for months after the stressful event, not just seconds or minutes. This supports that partner loss may trigger long-term depressive-like syndromes in geese, which has already been observed by Konrad Lorenz.

Despite the relatively low number of individuals, our results show physiological consequences of the social bond in geese, which have been described in mammals and may be representative for social vertebrates in general [32]. This adds to our understanding why it pays for geese to stay permanently with the partner. Singleton in a goose flock are not only lowest in the dominance hierarchy [16], they are also most reactive to social stressors.

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