Heart Rate Modulation by Social Contexts in Greylag Geese (*Anser anser*)

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Physical activity is generally considered as most relevant for modulating heart rate (HR). The authors show here that HR is not only modulated by physical activity but even more by social contexts. HR modulation in three free-ranging, socially embedded, male greylag geese fitted with implanted radio-transmitters was investigated. Measured HR ranged from 40 beats per minute (bpm) during rest to a maximum over 400 bpm during takeoff. Almost the same maximum HRs (400 bpm) were reached during social interactions, which however, generally require less bodily action. Mean HR during social interactions (agonistic interactions, vocalizations) was significantly higher than during behaviors with a less obvious social context (e.g., resting, comfort or feeding behavior), but with comparable physical activity involved. The authors also found significant and consistent differences in HR between the three focal individuals, probably because of individual behavioral phenotype. Our results show that social context has a strong modulatory effect on the sympathico-adrenergic activity in a social bird and conclude that particularly the latter may pose considerable energetic costs.

Keywords: heart rate, social modulation of heart rate, physical activity, individual differences, greylag geese

Heart rate (HR) is a highly variable physiological parameter modulated by various factors (Bastian, 1984; Odum, 1941). Particularly important HR modulators are physical activity, season and time of the day (Arnold, Ruf, & Kuntz, 2006; Boyd, Bevan, Woakes, & Butler, 1999; Dressen, Grün, & Hendrichs, 1990; Moen, 1978; Nilsson et al., 2006) as well as ambient temperature and thermoregulation (Arnold et al., 2006; Bartholomew, Hudson, & Howell, 1962; Müller, 1982). Therefore, HR may be considered as a parameter integrating all relevant internal and external stimuli an individual has to cope with at any given time. Besides glucocorticoid modulation, HR is also a direct indicator for the sum of stressors (allostatic load: McEwen & Wingfield, 2003). Generally, physical activity received most attention, because of its clear connection to energy expenditure (Wieser, 1986). In a number of studies HR indeed covaried with bodily action (red deer *Cervus elaphus*: Arnold et al., 2004; monkeys *Macaca mulata* and *Papio hamadryas*: Tatoyan & Cherkovich, 1972). HR modulation and oxygen consumption have repeatedly shown to be correlated with physical activity (Bevan, Woakes, & Butler, 1994; Bevan, Woakes, Butler, & Croxall, 1994; Bishop, Ward, Woakes, & Butler, 2002; Green et al., 2001; Ward, Bishop, Woakes, & Butler, 2002), but the relationship between HR and oxygen consumption generally varies among individuals (Nolet, Butler, Masman, & Woakes, 1992) or situations (Wooley, 1978). This made HR an attractive parameter for investigating the energetics of behavior (Brackenburry, 1984; Brown & Adams, 1984; Ferns, Macalpine-Lenny, & Gross-Custard, 1980). The basic assumption of all these studies was that physical activity is the most important factor modulating HR.

Consequently, most studies in birds focused on flight, which is one of the energetically most demanding behaviors. In greater white-fronted geese (*Anser albifrons*), HR has been shown to rise from 112 beats per minute (bpm) during resting to a maximum of 447 bpm during flight (Ely, Ward, & Bollinger, 1999). Kanwisher et al. (1978) also presented evidence for a pronounced HR increase in free-ranging herring gulls (*Larus argentatus*) during flight.

Social stimuli are known to be among the most potent stressors for social vertebrates, affecting both the HPA- and the sympathico-adrenergic system (de Vries, Glasper, & Detillion, 2003). The "slow" HPA-axis response is characterized by glucocorticoid synthesis within minutes whereas the activation of the "fast" sympathico-adrenergic-axis results in a release of catecholamines and modulation of HR and blood pressure in less than a second (von Holst, 1998). These two stress axes are regulated relatively independent from each other (Nephew, Kahn, & Romero, 2003; S. Kralj-Fiser, unpublished data). As HR is modulated beat-to-beat and HR responses can be related to single events, HR monitoring may be useful for two reasons: first, to evaluate the relevance of particular social stimuli or contexts for individuals, and second, as an indicator of the energetic cost.

HR increases during agonistic interactions in birds were only reported anecdotally up to now (Ely et al., 1999; Kanwisher et al., 1978), presenting examples of HR-modulation in parallel to certain events, without much quantification or statistical analysis of these responses in individuals or populations. In the present study, we analyze the context-specific modulation of HR in free-living, socially embedded greylag goose males. We sampled HR and behavior repeatedly in each of three focal individuals in similar situations for statistical analysis. In addition, we determined individual "basal" HR during resting, and then quantified the up-regulation of HR by physical activity as well as by social interactions and contexts. However, physical activity and social context cannot be fully separated. Much physical activity occurs in a social setting (e.g., during agonistic encounters) and physical activity (e.g., walking, flying) is never free of a social connotation in geese. Only in so called 'bystander situations,' which means the focal individual watching a relevant event without being actively involved, the social context can be fully separated from physical activity. For example, in a resting goose, HR may be up-regulated because of a close-by third party interaction, with no observable behavioral change in the focal individual (Wascher, Scheiber, & Kotrschal, submitted).

In this report we concentrate on situations where physical activity of comparable intensity is either clearly paired with, or relatively independent of a social context. We expected that behaviors shown in an explicitly social context (e.g., vocalizations) would correlate with a significantly higher HR relative to behaviors shown in a standard flock situation (e.g., resting or feeding behavior), which are also "social" in a sense that the focal individual is embedded within the flock and close to its partner, but not directly involved in 'social behavior.' We also predicted HR modulation during social interactions to be influenced by the intensity of an encounter as well as by the type of interaction (focal individual either attacking or being the target of an attack). In addition, we expected individual variability and consistency in HR responses, according to 'individual behavioral phenotype' (sensu Koolhaas et al., 1999). Because of our small sample size (three individuals), the latter connection necessarily remains anecdotical.

Method

The Flock

A nonmigratory flock of greylag geese was introduced in the Almtal (Upper Austria) by the late Konrad Lorenz in 1973. The geese 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 the study, the flock consisted of approximately 170 individuals, marked with colored leg bands for identification.

The flock is supplemented with pellets and grain twice daily. Both hand-raised and goose-raised flock members are habituated to the close presence of humans and neither show avoidance if approached up to 1m distance, nor do they excrete elevated levels of corticosterone metabolites following such situations (Scheiber et al., 2005) or significantly change HR when familiar humans approach (C. Wascher, unpublished data).

Transmitter Technology and Implantation Technique

Three focal individuals were fitted with a fully implanted sensor-transmitter package without external antennas or repeater, weighing approximately 60 g with a battery lifetime of 18 months. The HR was instantaneously transmitted on a beat-to-beat basis over distances up to 100 m as well as stored in the implant over its entire lifetime (Prinzinger et al., 2002). A pulse-interval modulated signal of carrier frequency pulses was formed. The transmission frequency was in the 150 MHz range (2 m-band). To save battery only every second heartbeat was transmitted. The transmitter was calibrated to record and transmit in the range of 30 to over 400 bpm. An industrial RF tracking receiver module and a control board developed at the Research Institute of Wildlife Ecology was used to receive HR and body temperature data. Data were transferred to a commercial laptop computer via a serial interface (RS 232).

The electronic package measured $60 \times 30 \times 11$ mm and was implanted by an experienced team of veterinarians into the abdominal cavity and fixed intraperitoneally (Walzer et al., 2000). Two electrode leads with a length of approximately 10 cm each connected the electronic package and the electrode plates, which were approximately 8 mm in diameter and 1 mm thick. The electrodes were fixed toward the lower rib cage near the heart. This was approved by animal experimental license (GZ68.210/41-BrGT/2003) of the Austrian government. The advantages of abdominally implanted transmitters are obvious. The alternative are harnesses, for example, in a study on mallards (*Anas platyrhynchos*) impaired the survival and return rates of females with harnesses compared to females with implanted transmitters (Dzus & Clark, 1996). Furthermore, in Canada geese (*Branta canadensis parvipes*; Hupp et al., 2003) as well as in blue-winged teal (*Anas discors*; Garrettson, Rohwer, & Moser, 2000) the behavior of animals with implanted radio transmitters in contrast to animals equipped with backpacks, did not significantly differ from nonimplanted geese.

Twenty hours after implantation the geese were released and returned to the flock and 2 to 7 days after the surgery they had fully recovered from the surgery (flying as untreated animals, normal body temperature). They could not be distinguished from nonimplanted geese neither in looks nor in their behavior. All geese returned to and were accepted by their familiar social environment (partner, family) immediately after release.

Data Collection

The three focal males were matched in age (individual 1 and 3: 5 years, individual 2: 4 years of age) and heterosexually paired. Individual 1 had offspring for 23 days (May, June). All three individuals where located in the upper third segment of the flock dominance hierarchy (individual 1: 13, individual 2: 15, individual 3: 31; Weiβ, Kotrschal, Frigerio, Hemetsberger, & Scheiber, in press). HR and behavior was recorded simultaneously by one of us (CW) at a maximal distance of 10 m from the focal individual. The following behaviors were recorded using OBSERVER 4.1.126 (Noldus, 2003) software: locomotion (walk, swim, run, takeoff, fly, including body postures float, lay, and stand), vocalization (scream, cackle, greeting partner, triumph ceremony), comfort behavior (preening, shaking, bathing), feeding (grazing, picking grain, drinking), resting behavior (beak under wing, resting), vig-

ilance behavior (head up, extreme head up, beak up) and agonistic interactions (threat, attacking, being attacked; Lorenz, 1991). For statistical analysis we choose six categories of frequently occurring behaviors (agonistic interactions, vocalizations, head up, resting, comfort, and feeding behavior). Additionally, we compared different types of locomotion, including floating, laying, and standing, during head up behavior. We distinguished between three intensities of agonistic interactions and included also threat postures without any locomotory activity. The three intensities of agonistic interactions were defined as intensity 1: goose standing, laying, floating, or walking toward another goose in a threat posture. Intensity 2: goose running toward another goose without body contact. Intensity 3: fight with body contact (e.g., biting, wing beating). Every change in behavior and locomotion was noted and could afterward be assigned to the simultaneous HR.

We characterized the three focal individuals along the 'proactive-reactive' axis behaviorally (Koolhaas et al., 1999) according to their active social involvement (agonistic encounters and vocalizations) and affiliative tendencies toward their mates (closer to partner in postconflict situations compared to matched-control situations; de Waal & Yoshihara, 1983; Veenema, 2000). More agonistically involved, but less socially affiliated, individuals were characterized as "proactive" and vice versa. Thereby, we classified individual 1 most proactive and individual 3 most reactive.

Data was taken daily over a period of 4 months (April-July), starting with the feeding at 8:00 a.m., observing for a minimum of 30 minutes, up to a maximum of 2.5 hours per individual per day. On rainy days, no data could be collected because of the sensibility of the technical equipment. The sequence of data collection from individuals was randomized. Recordings were taken in a radius of 1.5 km around the research station. Time spent observing each focal differed between the three birds because they were not always present at the study site.

Statistical Analysis

Data were analyzed using the SPSS 12.0.1 (2003) statistical package. Results of all tests are given two-tailed and significance was set to $p = .05$. As data partly deviated from normal distribution, we resorted to nonparametrical tests. For statistical analysis, we choose means instead of maxima, because HR peaks were highly variable and thus we felt that means would provide more reliable information. To evaluate HR variation within different behaviors, intensities of agonistic interactions or between attacking versus being attacked, we compared mean HR values using a Friedman's two-ways ANOVA of variance by ranks, and applied Wilcoxon signed-ranks test post hoc (Siegel & Castellan, 1998). To ensure independence of data, we calculated a mean value for each behavior per observation session. Only behaviors that lasted for at least 2 seconds per session were included in the analysis. We performed separate statistical tests within each individual. We calculated pooled p values across the individuals, using Fisher's method for combined probabilities (Bugnyar & Kotrschal, 2002; Heinrich & Pepper, 1998; Sokal & Rohlf, 1981) for coping with low number of individuals. Individual differences in HR were analyzed using Kruskal-Wallis-one-way analysis of variance and post hoc Mann–Whitney-U tests. Effect sizes (Cohen's d; d) have been calculated using effect size calculator (Devilly, 2004). Bonferroni-corrections were not employed, because this increases the probability of type II error without significantly decreasing the probability of Type I error (Nakagawa, 2004).

Results

Physical Modulation of HR in Standard Flock Situations

Mean HR of the three focal individuals differed significantly according to the type of locomotor activity, which had no obvious social context (Table 1; Figure 1A). During the first second of flight (takeoff) mean HR was at 306 bpm, whereas mean HR during other locomotory behaviors was around 100 bpm. The HR was already greatly increased seconds before takeoff. For example, in individual 2 maximum HR during preparation for departure increased to 244 bpm 19 seconds before takeoff. Maximum HR during takeoff in this case reached 344 bpm. Hence, besides locomotion itself, preparation for action may greatly increase HR.

Social Modulation of HR

Mean HR of the three focal gander differed significantly in a range of behaviors (Table 2; Figure 1B). Mean HR during agonistic interactions (156.68 bpm) was almost double the mean HR during resting (84.44 bpm). Mean HRs during behaviors in a clearly defined social context were significantly higher than mean HRs during behaviors in which social context was less obvious, although the locomotory effort seemed comparable between these two contexts. Maximum HR during agonistic interactions (intensity 1: focal individual walking toward another goose in a threat posture) approached 400 bpm. This is almost as high as HR during takeoff (see Figure 2).

Table 1

Mean Heart Rate of the Three Focal Individuals During Different Locomotory Behaviors and Postures Compared With Fisher's Combined Probability Test

	Lay	Swim	Stand	Walk	Takeoff
Float	n.s.	n.s.	$\chi^2 = 15.899, p = .025, d = 1.113$	$\chi^2 = 19.484, p = .005, d = 1.338$	$\chi^2 = 23.182, p < .001, d = 5.047$
Lay		n.s.	$\chi^2 = 12.81, p = .05, d = 0.944$	$\chi^2 = 19.152, p = .005, d = 1.137$	$\chi^2 = 23.182, p < .001, d = 5.034$
Swim			n.s.	$\chi^2 = 12.705, p = .05, d = 0.886$	$\chi^2 = 23.182, p < .001, d = 4.962$
Stand				n.s.	$\chi^2 = 23.182, p < .001, d = 4.832$
Walk					$\chi^2 = 23.182, p < .001, d = 4.666$

Notes. $n_1 = 12, n_2 = 4, n_3 = 4$). In addition to significance (p), effect sizes (Cohens'd; d) are given. n.s. = nonsignificant.
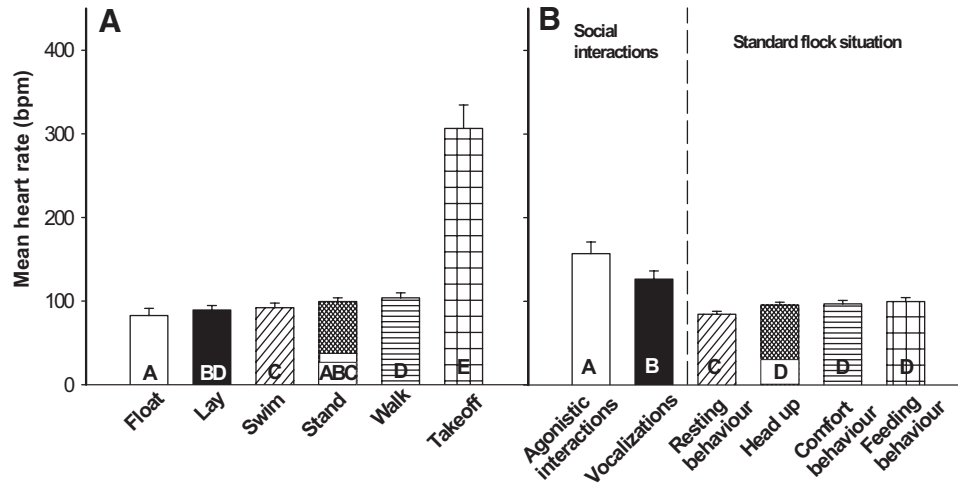
Figure 1. (A) Mean heart rate (HR) $\pm$ 95% confidence interval (CI) in three greylag ganders during different locomotory behaviors including the body postures float, lay, and stand during head up **(B)** Mean HR $\pm$ 95% CI during different behaviors. Different letters are indicating significant differences between the different behaviors.

HR was significantly higher when individual 1 actively attacked an opponent than when he was attacked himself (Wilcoxon's-signed rank test: z = −2.311, p = .021, n = 46, d = 0.477). The same seemed to be the case in the other two individuals, but probably because of the low number of events recorded (individual 2: 26 interactions, individual 3: 12 interactions) there was no significant difference between attacking and being attacked. In individual 1 we also found significantly different mean HRs between the three different intensities of agonistic interactions (Friedman-test: p = .029, df = 2, χ^2 = 7.091). HR during attacks with intensity 1 was significantly lower than during attacks with intensity 2 (Wilcoxon's-signed rank test: z = −2.401, p = .016, n = 11, d = 1.027) and intensity 3 (Wilcoxon's-signed rank test: z = −2.490, p = .013, n = 11, d = 1.425). When being attacked, HR in individual 1 was significantly lower during intensity 1 than intensity 2 (Wilcoxon's-signed rank test: z = −3.696, p < .001, n = 20, d = 1.29). Again, such a difference did not show in individuals 2 and 3, probably because of limited sample size

(individual 2: 4 interactions, individual 3: 5 interactions of higher intensity).

We found significant differences between different kinds of vocalizations (Fisher's combined probability: n_1 = 10, n_2 = 8, n_3 = 4; χ^2 = 15.624, p < .001). Mean HR during "cackling" was significantly lower than during "screaming" (Fisher's combined probability: n_1 = 10, n_2 = 8, n_3 = 4; χ^2 = 10.918, p = .01, d = 0.464), "greeting" the partner (Fisher's combined probability: n_1 = 10, n_2 = 8; χ^2 = 10.21, p = .01, d = 1.02) and "triumph ceremony" (Fisher's combined probability: n_1 = 10, n_2 = 8, n_3 = 4; χ^2 = 21.449, p < .001, d = 0.772).

Individual Differences

Mean HR in five of six behavioral categories differed significantly between the three focal individuals. Mean HR during agonistic interactions, vocalizations, resting behavior, head up, and comfort behavior differed, HR during feeding behavior did not between the three

Table 2

Mean Heart Rate of the Three Focal Individuals During Different Behaviors Compared With Fisher's Combined Probability Test

	Vocalizations	Resting behavior	Feeding behavior	Comfort behavior	Head up
Agonistic interactions	χ^2 = 19.7, p = .005, d = 0.645;	χ^2 = 41.446, p < .001, d = 1.7	χ^2 = 35.557, p < .001, d = 1.511	χ^2 = 40.06, p < .001, d = 1.497	χ^2 = 40.062, p < .001, d = 1.556
Vocalizations		χ^2 = 41.446, p < .001, d = 1.296	χ^2 = 24.236, p < .001, d = 1.037	χ^2 = 33.468, p < .001, d = 1.016	χ^2 = 31.805, p < .001, d = 1.097
Resting behavior			χ^2 = 30.963, p < .001, d = 0.355	χ^2 = 28.474, p < .001, d = 0.554	χ^2 = 29.001, p < .001; d = 0.36
Feeding behavior				n.s.	n.s.
Comfort behavior					n.s.

Notes. n_1 = 23, n_2 = 13, n_3 = 22. In addition to significance (p), effect sizes (Cohens' *d*; d) are given. n.s. = nonsignificant.
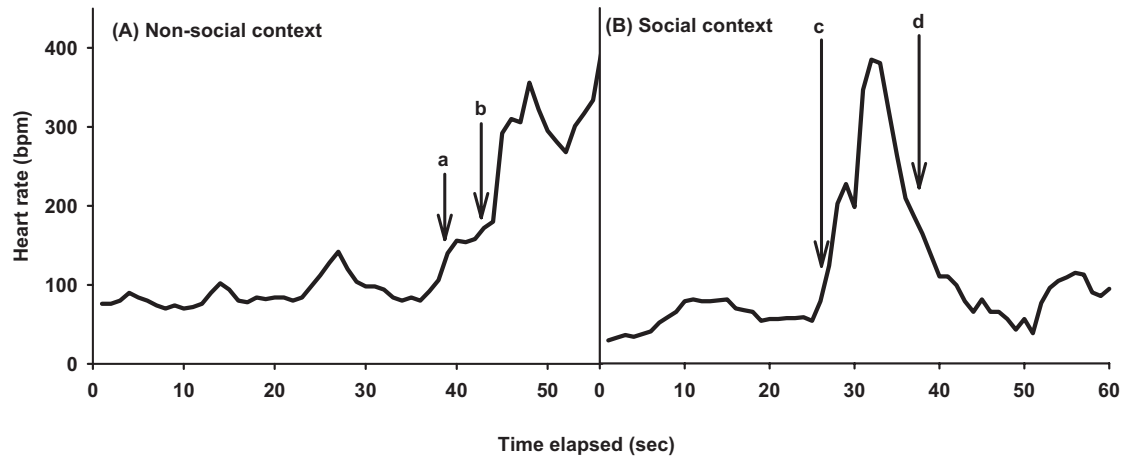
Figure 2. Single examples of heart rate modulation. (A) Departure event of focal individual 1. At the first arrow (a) behavior changed from head up to preflight synchronisation behavior, the second arrow (b) marks the actual departure. Recording ends when the individual had left the recording range. (B) Attack by focal individual 1. The goose showed the behavior head up when interaction of intensity 1 started (marked by arrow c). The end of the interaction is marked by arrow (d).

focal individuals. Differences between individuals were consistent across behaviors (Kruskal-Wallis-test: $n_1 = 23$, $n_2 = 13$, $n_3 = 22$; agonistic interactions: $p < .001$, $df = 2$, $\chi^2 = 24.333$; vocalizations: $p = .002$, $df = 2$, $\chi^2 = 12.30$; resting: $p = .009$, $df = 2$, $\chi^2 = 9.453$; preening: $p < .001$, $df = 2$, $\chi^2 = 22.145$; head up: $p = .002$, $df = 2$, $\chi^2 = 12.559$). Individual 1 was significantly higher in HR than individual 2 in 1 of 6 behaviors and individual 3 was lower in HR in 5 of 6 behaviors (Table 3; Figure 3).

Discussion

As expected, HR in the three focal greylag ganders was strongly modulated by both, physical activity and in particular by social interactions (40 to over 400 bpm). Highest HR because of physical activity was reached during the first seconds of flight, but may decrease during flight (Butler & Woakes, 1980; Ely et al., 1999). In herring gulls, for example measured HR during flight was nearly as low as at rest (Kanwisher et al., 1978). In our study, we were only able to measure HRs during flight for a few seconds, because of the low range of the receiving equipment. Compared

with the minimum HR of 40 bpm during rest, HR increased 10-fold. However, HR rose already before departure, associated with the synchronization behavior with other flock members before takeoff. This may indicate both, emotional arousal in preparation of departure and a pretakeoff 'physiological warm up' (Black, 1988).

Previous studies report even subtle physical activity or body posture affecting HR (Cacioppo et al., 1994; Marler, 1996). In retrospect it cannot be excluded, that HR increases were attributed to postures, when in fact they were rather related to a different stimulus context (i.e., social). Except for takeoff, HR differences between behaviors, locomotions, or body postures were small. For example, floating involves no active body movements, whereas swimming does. We therefore predicted higher mean HR during the latter, which was not the case. The same was true for standing versus walking.

Our results indicate that social context may not only mask potential subtle differences in HR because of locomotory activity, but may be the most modulating factor of HR in general. Compared with mean HR during takeoff, mean HR during social

Table 3

Heart Rate Differences Between the Three Focal Individuals Compared With Mann-Whitney-U Tests

	Individual 1 - 2	Individual 1 - 3	Individual 2 - 3
Agonistic interactions	$p = .043$, $z = -2.025$, d = 0.592	$p < .001$, $z = -4.768$, d = 1.352	$p = .009$, $z = -2.595$, d = 0.68
Vocalizations	n.s.	$p = .041$, $z = -2.048$, d = 0.746	$p = .032$, $z = -2.151$, d = 0.518
Resting behavior	n.s.	$p = .003$, $z = -2.974$, d = 0.526	$p = .049$, $z = -1.980$, d = 0.268
Resting behavior	n.s.	n.s.	n.s.
Comfort behavior	n.s.	$p < .001$, $z = -4.064$, d = 0.734	$p < .001$, $z = -3.892$, d = 0.589
Head up	n.s.	$p = .022$, $z = -2.293$, d = 0.445	$p < .001$, $z = -3.414$, d = 0.745

Notes. $n_1 = 23$, $n_2 = 13$, $n_3 = 22$. In addition to significance (p), effect sizes (Cohens'*d*; d) are given. n.s. = nonsignificant.
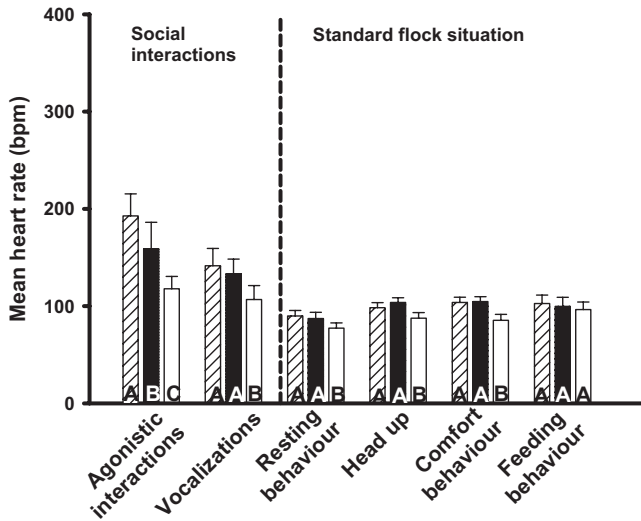
Figure 3. Differences in heart rate (HR) between the three focal individuals. Notched bars: Individual 1, black bars: Individual 2, open bars: Individual 3. The *x*-axis shows different behaviors, the *y*-axis displays the mean HR ± 95% confidence interval in beats per minute (bpm). Different letters are indicating significant differences between the individuals.

interactions was lower, but maximum HR was similar to those reached during takeoff. Behaviors shown in a social context (e.g., agonistic interactions, vocalizations) were generally characterized by significantly higher mean HR than those shown in a nonsocial context (e.g., resting, comfort behavior, feeding behavior, head up), although the physical activity may have been relatively similar in both categories. This indicates that much of HR modulation, particularly in social contexts may be caused by some kind of 'emotional involvement,' probably in anticipation of bodily activity rather than by muscle action directly.

HR during attacks could of course, be explained partly by bodily action. Especially in aggressive encounters of intermediate or high intensity pronounced muscular activity, such as running, was involved. Still, the highest recorded HR during an agonistic interaction (400 bpm) was associated with an interaction of low-intensity. Mean HR when walking was approximately 100 bpm. Therefore, the increase during this agonistic interaction was four times higher than expected from the physical activity performed. This implies that the motivational background of an agonistic interaction, which may be related to the importance of a particular interaction for the individual involved, affected HR much more than physical activity per se.

Mean HR increased with the intensity of an attack. This may be partly attributed to differences in physical activity between the three intensities. Although behavior and physiology may be regulated independently, we suggest that in this case the relative low physical activity involved in "low intensity" interactions in general is caused by a moderate motivation resulting from a moderate importance of this interaction to the focal individual, which also produces only moderate HRs. In cases, when low-intensity attacks are accompanied by relatively high HRs, this plausibly supports motivational effects, independent of observable behavioral expression.

In addition to intensity, the type of interaction also mattered. For example, HR during agonistic encounters was generally higher

when the focal individual attacked an opponent than when it was attacked itself, although similar amounts of physical activity are performed by both the attacker and the target. This indicates that motivation (i.e., the emotional value of an interaction) is the main causal factor for HR modulation. In this respect, also the identity of the opponent might have an influence onto HR. Independent of flock size, social clusters are maintained long-term, creating the likelihood that opponents already have a dyadic history of different interactions (Black, Prop, & Larsson, 2007).

Also, interactions of the same intensity, with comparable locomotory effort resulted in different HRs. The same was found in rats, where winners showed higher catecholaminergic responses than losers (Sgoifo et al., 2001). Attacking another individual may be associated with a higher emotional load than being attacked. This is not surprising, because the attacker needs to overcome an internal threshold to become active. In contrast, the target becomes activated only via the opponent's attack.

HR was shown to correlate well with oxygen consumption in birds (Butler et al., 2004; Froget et al., 2001; Ward et al., 2002). Hence, high HRs in social interactions indicate high energetic investment into the social domain and therefore, their relevance for a social animal. During the reproductive season, when most of this data was collected, lost interactions may be associated with a loss of access to nesting sites, food or even the pair partner (Kotrschal et al., 2005; Weiß et al., in press). Finally, males in particular should generously invest into the social domain as a precondition for reproductive success. Females on the other hand, are expected to be more energy-efficient with regards to social interactions, because their reproductive potential is more determined by turning energy into viable offspring (Loonen et al., 1999).

According to "coping style" theory (Koolhaas et al., 1999; Korte et al., 2005), individuals should vary in their behavioral and physiological responses to challenges, and these differences should be consistent over time and situations. We indeed, found significant differences in HR between our three focal individuals. Independent of the HR recordings, we characterized the individual behavioral phenotype along the proactive-reactive axis. Our HR data indeed fit the predictions from the coping style theory. The individual characterized as most "reactive" had a significantly lower HR than the two individuals characterized as more proactive (see Figure 3). Our findings are in line with another study, which showed that personality traits are behaviorally as well as physiologically manifested in free-roaming, socially embedded greylag geese. In this study, the authors found frequencies of aggressive behavior, retreat, proximity to the female partner as well as vigilance to be repeatable and excretion of corticosterone as well as testosterone metabolites consistent across social situations as well as time (Kralj-Fiser et al., 2007). Hence, our results hint at the possibility that HR modulation in geese also may be related to individual behavioral phenotype.

We conclude that, at least in male greylag geese, social stimuli and the related motivational context may have even a more pronounced effect on HR modulation than mere physical activity.

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