Heart rate responses to agonistic encounters in greylag geese, *Anser anser*

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As in most social groups, agonistic interactions of various intensities are common in a goose flock. This may cause social stress, modulating heart rate (HR), which may serve as a measure of energetic investment and also of individual emotional involvement. We investigated HR responses to social encounters in 24 free-living greylag geese in an intact social environment. We recorded 1602 social interactions of various intensities in which the focal individual either attacked another member of the flock or was attacked itself. We analysed five HR parameters (mean HR, maximum HR, HR increase, duration until maximum, time until the baseline value was reached again). Generally, HR scaled positively with increasing intensity of agonistic interactions as well as with increasing duration. Individuals showed higher HRs when attacking than when being attacked. In addition, focal individuals responded with a greater HR increase when confronted with an opponent winning a higher percentage of interactions than itself. Repeated agonistic interactions against a specific opponent were related to greater HR responses than single events and focal individuals responded more strongly to male opponents than to females. Our results indicate a differential HR response depending on the intensity and duration of an interaction as well as the identity of the opponent. This differential physiological investment may reflect differences in emotional involvement depending on the social context of a particular agonistic interaction.

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Social context affects individual behaviour (Blanchard et al. 2001; Stefanski 2001; Bartolomucci et al. 2005), physiology (Eisermann 1992; Blanchard et al. 1993; Levine 1993; Creel 2001; Abbott et al. 2003; de Vries et al. 2003;) and immune status (von Holst 1998; Zuk & Johnsen 1999; Larson et al. 2001; Stefanski 2001). Agonistic encounters are energetically costly, which may influence an individual's decision whether to engage in such interactions or not (Parker & Rubenstein 1981; Briffa & Elwood 2001, 2005;). For example, the duration and intensity of an encounter may be influenced by the physical condition and the motivation of the individuals involved (Parker 1974). While it may be beneficial to disguise one's motivational state behaviourally (Maynard Smith & Parker 1974), this is hardly possible with physiological responses, for example heart rate (HR; Wascher et al. 2008a, b), which will reflect the relevance of an event for a focal individual and the emotional involvement of a participant (Listerman et al. 2000).

Heart rate is known to be influenced by a range of factors (Odum 1941; Moen 1978; Nimon et al. 1995; Korte et al. 1999; Zhang & Sannajust 2000; Hagen et al. 2005), especially by physical activity (Tatoyan & Cherkovich 1972; Arnold et al. 2004) and social context (Kanwisher et al. 1978; Aureli et al. 1999; Ely et al. 1999). Also, HR is closely related to energy expenditure (Ferns et al. 1980; Nolet et al. 1992; Weimerskirch et al. 2002) and, therefore, can be used to estimate energetic investment in the social domain. In greylag geese, HR is strongly modulated by social contexts (Wascher et al. 2008a), even in the absence of any observable physical activity (Wascher et al. 2008b). We investigated whether, and in what way, characteristics of an agonistic interaction modulate the physiological investment of a particular individual.

Greylag geese live in a complex social system where families dominate pairs and pairs dominate unpaired individuals (Lamprecht 1986). Social allies support each other actively in agonistic interactions as well as passively, via their mere presence. This influences the physiological stress response (glucocorticoid excretion) and has motivational effects for the individual, which result in enhanced success in agonistic interactions as well as increased feeding rates (Frigerio et al. 2003; Weiß & Kotrschal 2004; Scheiber et al. 2005b; Weiß et al. 2008). Agonistic interactions of different intensities and duration occur frequently within a flock of greylag geese and individuals are involved to different degrees, depending on sex (Black & Owen 1989; Lorenz 1991), social embedding (Weiß & Kotrschal 2004; Scheiber et al. 2005b), rank (Gregoire & Ankney 1990), 'personality' (Kralj-Fiser et al. 2007) and season (Hirschenhauser et al. 1999; Kotrschal et al. 2000).

Based on our previous results, we predicted that the HR of individuals in agonistic encounters will depend on the physical

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activity involved (Wascher et al. 2008a), but even more on the individual relevance of an interaction (Wascher et al. 2008b). We expected HR responses to agonistic encounters to vary with the identity of the opponent (e.g. rank, sex). Effects of intensity and duration of an interaction, as well as the identity of the opponents, on HR have been investigated under laboratory conditions (e.g. Aureli et al. 1999; Marchant et al. 1995a). The present study is the first to show how social encounters influence HR in a group of free-flying greylag geese, in an intact social environment. Our geese do not live in an enclosure, with a given group composition, and, therefore, individuals are free to choose their preferred social allies and they can avoid social encounters. Hence, our results reflect the relevance of encounters in a fully representative social context.

METHODS

Study Site

A nonmigratory flock of greylag geese was introduced in the Almtal, Upper Austria, by Konrad Lorenz in 1973. The geese are unrestrained and roam the valley between the Konrad Lorenz research station and a lake approximately 10 km to the south, where they roost at night. At the time of data collection, the flock consisted of approximately 150 individuals, marked with coloured leg bands for identification.

The flock is supplemented with pellets and grain twice daily at 0800 and 1500 hours during the winter months and at 1700 hours during the summer months. Both hand-raised and goose-raised flock members are habituated to the close presence of humans and they neither show avoidance if approached up to 1 m distance nor excrete elevated levels of corticosterone metabolites following such situations (Scheiber et al. 2005a) or significantly change HR when familiar humans approach (C.A.F. Wascher, unpublished data).

Transmitter Technology and Implantation Technique

Twenty-five individuals were implanted with sensor-transmitter packages without external antennas or repeater, weighing approximately 60 g, with a battery lifetime of approximately 18 months. General information about focal individuals (sex, pair bond status, index of winning interactions and baseline HR) is given in Table 1. Both HR and body core temperature were instantaneously transmitted on a beat to beat basis over distances up to 100 m as well as stored as 2 min means in the implant over its lifetime (Prinzinger et al. 2002). The transmitter was calibrated to record and transmit in the range of 30 to over 500 beats/min. An industrial RF tracking receiver module and a control board developed at the Research Institute of Wildlife Ecology, Vienna, Austria, was used to receive HR and body temperature data. Data were transferred to a commercial laptop computer via a serial interface (RS 232).

Implantations were conducted from 18 May to 14 September 2005 in five sessions of five individuals each. Geese were caught opportunistically on the day before implantation or on the same day in the morning and kept together in a large outdoor aviary with access to a small pond and food or were isolated in transport boxes (depending on the time until surgery). The electronic package was implanted into the abdominal cavity by an experienced team of veterinarians in a properly equipped surgery room at the veterinary clinic Cumberland in Gmunden, the closest clinic to the study site. For anaesthesia the geese were randomly assigned to three groups. Group 1 received medetomidine (0.1 mg/kg), ketamine (10 mg/kg) and butorphanol (1 mg/kg), group 2 received midazolam (3 mg/kg) and ketamine (30 mg/kg) and group 3 received midazolam (3 mg/kg), ketamine (30 mg/kg) and butorphanol (0.5 mg/kg), all given intramuscularly. Endotracheal intubation was done if

necessary following mask induction and anaesthesia was maintained with isoflurane in 100% oxygen delivered with a semiopen anaesthesia system. For surgery, the geese were placed in dorsal recumbency. A standard ventral midline celiotomy approach 1 cm caudal of the sternum was used with an incision length of 4 cm. The transmitter and one of the two electrodes were fixed in the coelum and the incision for the second electrode was placed subcutaneously near the axilla. The electrode was then subcutaneously pulled from the coelum through a subcutaneous tunnel prepared with a sterile gynaecological catheter (4 mm in diameter) and fixed to the subcutis. After the proper function of the transmitter was ensured, the abdominal wall and skin incisions were closed with sutures of absorbable material (U. Auer, I. Wiederstein & W. Zenker, unpublished data; W. Zenker, U. Auer, G. Fluch, F. Schober & I. Wiederstein, unpublished data).

After surgery, geese were housed individually in transport boxes overnight to recover from anaesthesia. All 25 individuals were released into the flock the morning after implantation, after veterinary inspection. They returned to, and were accepted by, their social partners immediately after release. One female disappeared the night after release and was probably taken by a fox, the main natural predator of geese at the study site. The geese had fully recovered from the surgery after 2–7 days (flying as untreated animals, normal body temperature and HR): they could not be distinguished from nonimplanted geese in looks or behaviour (unpublished data). The implantation was conducted under a licence issued by the Austrian Ministry of Science. To exclude possible effects of the surgery on behaviour or HR, data taking started at the earliest 3 weeks after surgery.

Data Collection

The HR and behaviour (Noldus 2002) of 24 focal individuals (16 males, 8 females) were recorded simultaneously by one of us (C.W.) at a maximal distance of 10 m from the focal individual. We recorded all interactions in which a focal individual was involved, regardless of whether it attacked an opponent or was attacked by another flock member. In all cases of interactions reported here, the initiator of the interaction was also the winner. We differentiated between five intensities of agonistic encounters. Intensity 1: one individual briefly touched or was touched by another individual with the beak, without any locomotion involved. Such interactions occurred most frequently in the context of feeding, when flock members stayed very close to one another. Intensity 2: threat without any locomotion involved. Intensity 3: one individual walked towards another individual in threat posture. Intensity 4: an individual ran or flew towards its opponent. Intensity 5: fight with severe biting and wing beating. (For a detailed ethogram see also Lorenz 1991.) The study period lasted for 18 months between June 2005 and November 2006 and during this period a total of 286 h of HR and behavioural data were collected by C.W. from individual focal animals. Recordings were taken in a radius of 1.5 km around our research station. We recorded a total of 2885 agonistic encounters, in 1602 of which the identity of the opponent could be recorded. Therefore we based our statistical analysis on these interactions.

An index of winning interactions for each individual was evaluated independently of this study by B.M.W. (in September 2005, January, February and August 2006). Data were collected on 5 consecutive days in each period by scan sampling the flock for agonistic interactions during the morning and afternoon feeding, when the entire flock was present and active. For each observed interaction the identities of the winner and loser and the intensity of the interaction were noted. The individual that retreated was designated the loser of an interaction; in more than 99% of cases, the individual being attacked also lost the interaction. In September 2005 a total of 1723

Table 1
Mean baseline HR, 4 s before the onset of an aggressive encounter in beats/min, sex, pair bond status and index of winning interactions of the 24 focal individuals

	Sex	Pair bond status	Index of winning interactions*	Baseline HR
Armando	Female	Paired	80	141
Balu	Female	Paired	79	130
Blossom	Male	Unpaired	84	117
Boston	Male	Paired	61	146
Celine	Female	Paired	17	117
Corrie†	Male	Unpaired	124	115
—	—	Paired	120	128
Edes	Male	Paired	81	128
Gantenbein	Female	Paired	40	130
Halas	Male	Paired	16	108
Jacky	Female	Paired	98	120
Jana	Female	Paired	92	122
Jesaja	Female	Paired	71	128
Juniper	Male	Unpaired	67	131
Keiko	Male	Paired	50	139
Lanzelot	Female	Unpaired	113	132
Little	Male	Unpaired	70	132
Loki	Male	Paired	38	184
Löwenherz	Female	Paired	111	99
Sinus	Male	Paired	48	101
Smoky	Male	Paired	51	83
Spiro	Male	Paired	26	163
Terri	Male	Paired	73	145
Tian	Male	Paired	128	127
Tristan	Male	Paired	22	123

* Index of winning calculated for all members of the flock (approximately 150 individuals); Number 1 wins the highest percentage of interactions, 150 the lowest; mean indices of all seasonal phases for the 24 focal individuals are given.

† One male lost its partner during the course of the study period (March 2006). Therefore baseline HR is given for when it was paired as well as when it was unpaired.

interactions were observed ($\overline{X} \pm SD = 23.9 \pm 13.5$, range 5–65 per individual), in January 2006 2250 interactions ($\overline{X} \pm SD = 21.5 \pm 14.1$, range 7–75 per individual), in February 2006 1778 interactions ($\overline{X} \pm SD = 24.0 \pm 19.8$, range 6–125 per individual) and in August 2006 1554 interactions ($\overline{X} \pm SD = 21.2 \pm 12.2$, range 5–91 per individual). Because the dominance hierarchy of the geese is not strictly linear, we did not order individuals from highest to lowest ranking, but instead calculated the percentage of won interactions (number of interactions won/number of interactions lost).

Analysis

We analysed the mean HR during an interaction, maximum HR in response to an interaction, HR increase, time (s) from baseline to maximum and duration of HR increase (s), which is the time from maximum until the 'baseline value' is reached again. The maximum HR is the highest HR value during or after an interaction before the 'baseline value' is reached again. We took the 'baseline value' to be the momentary HR 4 s before the start of an event, because HR was significantly higher at 2 s than at as 3 s before the event (Wilcoxon signed-ranks test: $Z = -3.238$, $N = 24$, $P = 0.01$) but did not change significantly from 4 to 3 s before an interaction ($Z = 1.645$, $N = 24$, $P = 0.103$). To calculate the HR increase we subtracted the 'baseline value' from the maximum HR. For the duration of the HR response we calculated the time (s) until HR returned to the 'baseline' value after the onset of an event.

Data were analysed using the GenStat 10.1 statistical package (VSN International Ltd, Hertfordshire, U.K.). We conducted a generalized linear mixed model (GLMM) for each of the HR parameters (above) and applied the restricted maximum likelihood (REML) procedure for repeated sampling with an unbalanced design. We present Wald statistics for REML, because the change in deviance when dropping a term from the model approximates a chi-square

distribution (Foerster & Kempenaers 2005). In all models we included first-order interaction terms in the model. We sequentially deleted fixed terms in order of decreasing significance. Only terms with $P < 0.1$ remained in the final model. 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).

RESULTS

Characteristics of Interaction Influencing HR

All five HR parameters analysed (mean HR, maximum HR, HR increase, duration from baseline to maximum and time from maximum to baseline) increased with the duration of an agonistic encounter (HR increase, Fig. 1, Table 2). Mean HR, maximum HR and HR increase in response to an interaction rose with increasing intensity of the interaction (HR increase, Fig. 2a, Table 2). The HR increase was more pronounced if the focal individual was actively attacking than when being attacked (Fig. 2b, Table 2).

Characteristics of Opponent Influencing HR

The HR response of the focal individual was higher when interacting with an individual winning a higher percentage of interactions than itself, compared with an individual winning a lower percentage of interactions than itself (Fig. 2c, Table 2). When a focal individual was involved in repeated interactions with one specific opponent, mean HR, maximum HR and duration of the HR increase were higher, the greater the number of interactions with this opponent (Table 2). Heart rate increase and time until maximum HR was reached during agonistic interactions were significantly higher when the focal individual was attacking a male than a female opponent (Fig. 2d, Table 2), but pair bond status or whether the opponent and the focal individual were the same or different sexes did not affect the HR response (Table 2).

Characteristics of Focal Individual Influencing HR

Maximum HR and HR increase in response to agonistic encounters were significantly greater in single than in paired individuals (Table 2). The only sex difference in focal males and females was in the duration until maximum HR was reached: it took males longer to reach maximum HR than females (Table 2).
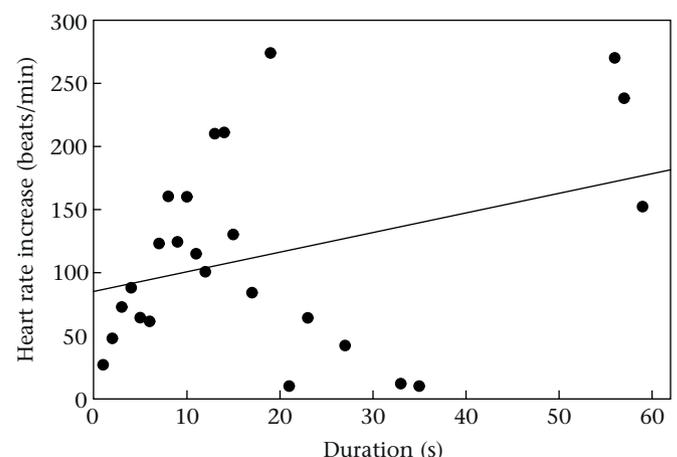

Figure 1. Correlation between the duration of an encounter and heart rate increase (beats/min).

Table 2
Factors affecting five heart rate (HR) parameters (mean HR in beats/min (bpm), maximum HR in bpm, HR increase in bpm, duration until maximum is reached (s), time until baseline is reached) in response to agonistic encounters

	Duration		Intensity		Type of interaction		Number of interactions		Winning index		Status				Sex				Sex difference	
											Focal individual		Opponent		Focal individual		Opponent			
	W	P	W	P	W	P	W	P	W	P	W	P	W	P	W	P	W	P	W	P
Mean	2.85	<0.001	121.84	<0.001	0.19	0.666	22.44	0.014	472.42	<0.001	3.60	0.059	0.85	0.357	0.59	0.444	2.13	0.545	2.13	0.545
Maximum	153.01	<0.001	174.18	<0.001	3.75	0.053	20.02	0.03	371	<0.001	4.46	0.035	2.66	0.103	0.69	0.406	4.51	0.212	0.17	0.679
HR increase	182.84	<0.001	205.35	<0.001	8.74	0.003	12.49	0.254	369.39	<0.001	6.44	0.011	0.95	0.331	1.07	0.3	9.74	0.021	0.01	0.905
Duration to maximum	427.51	<0.001	7.43	0.115	0.01	0.923	8.3	0.599	205.43	0.911	0.78	0.377	0.01	0.928	5.82	0.016	9.78	0.021	0.59	0.442
HR decrease	108.96	<0.001	85.31	<0.001	0.03	0.863	29.44	0.001	400.89	0.001	2.12	0.145	0.14	0.709	0.53	0.468	4.73	0.193	0.35	0.553

Results of the generalized linear mixed model are shown. Results in bold remained in the final model. Duration: duration of the interaction (range 1–57 s); intensity: intensity of interaction (1 = low intensity; 5 = high intensity); type of interaction: focal individual attacking another flock member or being attacked by an opponent; number of interactions: number of interactions in which the focal individual was involved with a particular other flock member (1–13); winning index: index of whether focal individual won a higher or lower percentage of interactions; status: pair bond status of focal individual and opponent; sex difference: whether focal individual was confronted with a same-sex or a different-sex opponent. W = Wald statistic.

DISCUSSION

In accordance with a previous study (Wascher et al. 2008a), we showed HR to be strongly modulated by social interactions. In this study, we investigated how and to what degree characteristics of the interaction, the focal individual and the opponent influenced the HR response. Heart rate was modulated by two main factors. First, the HR response to social interactions was strongly affected by the intensity and duration of the interaction, which we interpret as an activation of the sympathicoadrenergic system following an
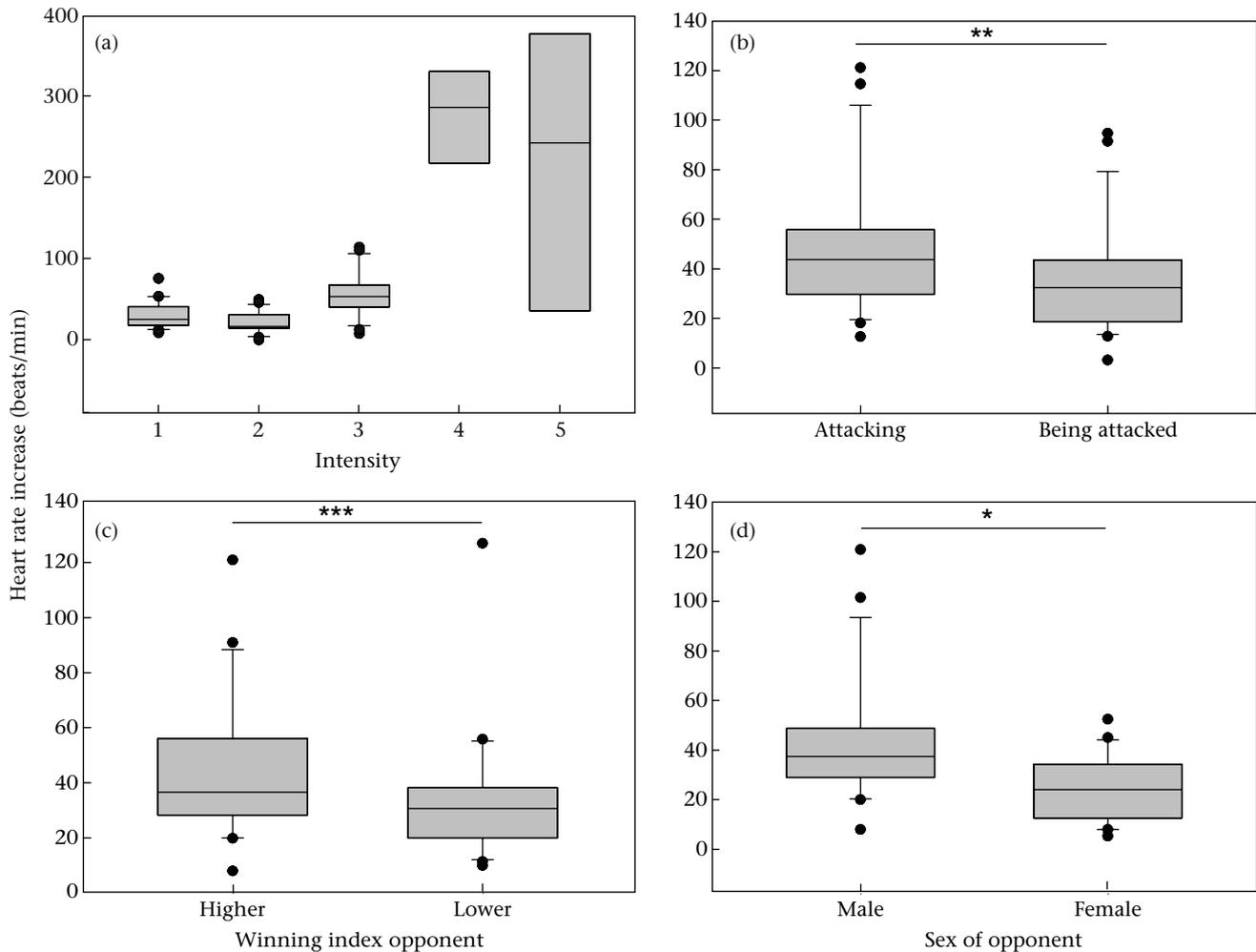

Figure 2. Heart rate increase (beats/min) (a) during agonistic encounters of different intensities, (b) during attacking versus being attacked, (c) during agonistic encounters with opponents winning a lower or higher percentage of interactions than the focal individual and (d) in relation to opponent's sex. In (a): intensity 1: peck, short body contact mostly during high-density situations such as feeding (N = 413); intensity 2: threat posture without body movement (N = 611); intensity 3: walking towards the opponent in threat posture (N = 561); intensity 4: interaction with pronounced physical activity such as running or flying (N = 13); intensity 5: severe fight with body contact such as biting or wing beating (N = 4). Box plots show the median and the interquartile range from the 25th to the 75th percentiles. Whiskers above and below the box indicate the 10th and 90th percentiles. Black circles indicate outliers. $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

increased metabolic demand (Obrist 1981). Second, HR is also indicative of the motivational state of an individual and used to estimate the level of responsiveness to different kinds of stimuli (Listerman et al. 2000). We found the HR of individuals differed between interactions, which cannot be fully explained by the physical activity involved. Therefore, we suggest such differential HR responses provide information about the psychological state of an individual (Blix et al. 1974). For example, we found a higher HR in individuals actively attacking compared to individuals being attacked. Our observations suggest that on both sides, the amount of physical activity involved in such an interaction is not too dissimilar, but the motivational states of the two individuals are certainly different. This we have shown in a previous study in greylag geese (Wascher et al. 2008a), as have studies on other species (pigs, *Sus scrofa domestica*: Marchant et al. 1995b; rats, *Rattus norvegicus*: Sgoifo et al. 2001). For the target individual, predictability and controllability are low, which could explain the HR differences between attacker and target of an interaction, because these two factors are known to be strong HR modulators (Weiss 1970; Désiré et al. 2006).

Also, we found that characteristics of the opponent, such as sex and percentage of winning interactions (an operational equivalent of dominance rank) influenced the focal individuals' HR in an agonistic interaction. The HR was significantly higher when the focal individual interacted with an individual winning a higher percentage of interactions than itself (i.e. with a higher-ranking individual). In such interactions, the risk of being defeated is high and the control over the situation by the focal individual is lower, compared to interactions with opponents winning a lower percentage of interactions. Similar HR responses in interactions with higher-ranking individuals have been reported in rhesus macaques, *Macaca mulatta* (Aureli et al. 1999) and the status of focal individuals has been shown to affect HR, for example in squirrel monkeys, *Saimiri sciureus* (Candland et al. 1970), rhesus macaques and baboons, *Papio hamadryas* (Cerkovich & Tatoyan 1973), cynomolgus monkeys, *Macaca fascicularis* (Kaplan et al. 1990) and rabbits, *Oryctolagus cuniculus* (Eisermann 1992). In our study HR was, in fact, not so much influenced by the dominance status of the focal individual itself, as estimated by the percentage of winning interactions, but rather by its relationship with the opponent.

These results indicate that individuals flexibly evaluate the relevance of single encounters and modulate their physiological stress response according to the outcome of this evaluation. In immediate response to any stressor an increase in HR and blood pressure is triggered via the sympathetic nervous system and the release of catecholamines into the blood stream (Stoddard et al. 1986; Sapolsky 1992). The activation of the stress system is energetically costly and frequent/chronic activation may even negatively affect an individual's reproductive success (Bowman et al. 1978; Mendl et al. 1992). Therefore, it is crucial for an individual to respond adequately, particularly to social stressors. We suggest that the differential HR response depending on characteristics of the opponent reflects such a sociophysiological optimization. Our results indicate that the risk of losing an interaction was the main determinant of HR modulation. Only when this risk was high (e.g. male rather than a female opponent, opponent winning a higher percentage of interactions than the focal individual) did individuals show a pronounced up-regulation of HR, important in preparing the body for action (Axelrod & Reisine 1984). In low-risk situations (e.g. low-ranking opponent), such physiological effort and, hence, energy expenditure are not needed to win a contest, and HR increases remain moderate.

It is not only characteristics of the opponent that determine the physiological investment of an individual in an interaction, but also characteristics of the focal individual. Maximum HR and HR increases in response to an agonistic interaction were greater in singletons than in paired individuals. Active social support in agonistic interactions, as well as passive social support via the mere presence of a social ally, reduces stress, by affecting the activation of the hypothalamic–pituitary–adrenocortical system (Frigerio et al. 2003; Weiß & Kotrschal 2004; Scheiber et al. 2005b, 2009). We propose that the greater HR responses to agonistic encounters in unpaired individuals may reflect their lack of adequate social support and, hence their increased risk of being defeated (Lamprecht 1986). Such an increased investment in the social domain of unpaired individuals may not only imply direct costs, such as the risk of injuries or the loss of resources, but will also generate indirect effects, for example, the energy invested in interactions constraining an individual's investment in reproduction.

In greylag geese, such energy constraints on reproduction are expected to be greater in females than in males, as body condition of females influences reproductive parameters, such as clutch size and number of eggs (Hemetsberger 2001). However, in contrast to our expectations, we did not find higher HR responses to social interactions in males than in females. Only the time until the maximum HR was reached was longer in males. Little is known about sex differences in sympathicoadrenergic activation in response to social stressors, as most studies performing HR measurement have focused on only one sex (Candland et al. 1970; MacArthur et al. 1979; Marchant et al. 1995b; Aureli et al. 1999). If at all, we would expect such sex differences in HR over longer periods of time, but as our results show, not necessarily in response to acute challenges. However, when the opponent was a female, HR response was significantly lower than when the opponent was a male. This fits with the social patterns: males are generally more aggressive than females (Black & Owen 1989; Lorenz 1991) and female rank within a pair bond is determined by the male's performance (Weiß et al. 2008), which, in turn, is affected by the individual support provided by the female, mainly just because of her presence (Black & Owen 1986; 'motivational effect': Lamprecht 1986).

In conclusion, our results suggest that greylag geese evaluate the relevance of single agonistic encounters according to the risk of being defeated, which is determined by the sex and percentage of winning interactions of the opponent as well as the pair bond status of the focal individual itself. The physiological stress response, as measured by HR, is flexibly modulated by these parameters, which may help individuals to optimize their investment in the social domain and may be beneficial in terms of an individual's energy expenditure, health and reproductive success.

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