Macaques attend to scratching in others

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Self-directed behaviours in primates as a response to increasing psychological or physiological stress are a well-studied phenomenon. There is some evidence that these behaviours can be contagious when observed by conspecifics, but the adaptive function of this process is unclear. The ability to perceive stress in others and respond to it could be an important part of sustaining cohesiveness in social primates, but spontaneously acquiring stress-related behaviours (and potentially emotional states) from all group mates via contagion could be maladaptive. To investigate this, a group of captive Barbary macaques, *Macaca sylvanus*, were presented with videos of conspecifics engaging in self-directed behaviour (scratching) and neutral behaviour. Behavioural responses as a result of exposure to the stimuli were compared (1) between familiar and unfamiliar individuals, and (2) within familiar individuals to consider the modulating effects of social relationships. Our results did not show contagious scratching in this species. However, there were differences in how individuals attended to the scratching stimuli. Subjects were more attentive to scratching videos than to neutral videos and familiar than unfamiliar individuals. Within the familiar individuals, subjects were more attentive to those to whom they were weakly bonded. We suggest that increased attention to scratching behaviours may be adaptive in order to monitor and avoid stressed group mates, whose subsequent behaviour may be unpredictable and aggressive. Monitoring group mates who are not allies may also be adaptive as they may pose the biggest risk. These findings will help increase our understanding of subtle cues that can be communicative in primates, and also the evolutionary steps towards understanding others.

Keywords: communication, displacement, self-directed behaviour, signal, stress,

In a wide range of animal taxa, humans included, individuals produce self-directed behaviours that often appear irrelevant to current activities (Tinbergen, 1952). Although a social function of these behaviours is yet to recognized, these behaviours, which, for example, include scratching, face touching, self-grooming and yawning in primates (Mohiyeddini, Bauer, & Semple, 2013; Pavani, Maestripieri, Schino, Turillazzi, & Schucci, 1991; Schino, Troisi, Perretta, & Monaco, 1991; Troisi, 1999), have been shown to reliably indicate the presence of both psychological and physiological stress (Maestripieri, Schino, Aureli, & Troisi, 1992; Troisi, 2002). Mice, *Mus musculus*, presented with a novel environment increase chewing behaviours irrelevant to that of feeding or escape in response to stress (Hennessy & Foy, 1987). Many bird species increase rates of preening in stressful situations, for example when disturbed while resting (Delius, 1988). High rates of scratching follow intense intragroup aggression in macaques, particularly in the victims (Filippo Aureli, van Schaik, & van Hoof, 1989) and chimpanzees, *Pan troglodytes*, scratch more frequently when the difficulty of cognitive tasks increases (Leavens, Aureli, Hopkins, & Hyatt, 2001) or when frustration is induced through an unsolvable task (Waller, Misch, Whitehouse, & Herrmann, 2014). Thus, in some contexts, there is a demonstrable relationship between stress and self-directed behaviour in animals.

Unhelpfully, the term stress is used variably throughout the literature, to describe situations from mild stimulation to extreme adverse conditions (Koolhaas et al. 2011). Here, we define stress as a biological response elicited to cope with disruptions to an animal's homeostasis (Moberg 1999), and a natural and common response to challenges animals face in their environment. We separate stress from distress, which can be observed after prolonged periods of extreme stress, and leading to often unnatural, exaggerated and stereotyped behaviours (e.g. feather plucking in parrots and trichotillomania in humans, van Zeeland et al. 2009). The behaviours associated with stress, however, are usually variants of normal functional behaviours (e.g. self-grooming, which also serves a hygienic function, (Maestripieri et al. 1992)

Our current understanding of the adaptive value of these behaviours is that they function to reduce the physiological stress response, playing an important role in how animals cope with stress (Koolhaas et al., 1999). For example, increasing chewing and gnawing behaviours attenuates physiological stress responses of rodents, including a reduced activation of stress-associated neural systems (Berridge, Mitton, Clark, & Roth, 1999) and endocrinological responses (Hennessy & Foy, 1987). In bushbabies, *Otolemur garnettii*, individuals that perform increased scent marking in response to stress exhibit a lower cortisol response, and therefore appear to cope with stress more effectively (Watson, Ward, Davis, & Stavisky, 1999), and in human males, those who engage in increased self-directed behaviours during stressful events report lower experienced stress afterwards (Mohiyeddini et al. 2013). The evidence for self-directed behaviours as a coping mechanism is convincing; what we do not know, however, is whether or not these behaviours are socially relevant.

When scientists focus on behaviours that are associated with underlying emotional states there is a tendency to focus on the feelings of the actor and subsequently ignore the potential responses these behaviours may elicit in the receiver (Waller & Micheletta, 2013). Historically, this has been particularly true for the study of facial expression (Darwin, 1872; Fridlund, 1994), and may also be the case for the study of self-directed behaviour. To understand the evolution of stress behaviours, it is imperative to fully explore their functional value and not only their causal value (Tinbergen, 1952). One proposal is that these behaviours could also have a social function by providing information to a social audience about internal states (Bradshaw, 1993). If so, self-directed behaviours may not just function as a coping mechanism, but could be an important aspect of the social repertoire of some gregarious animals. Specifically within the primates, a communicative function of stress behaviours has been proposed (Bradshaw, 1993; Maestripieri et al., 1992; Nakayama, 2004; Waller et al., 2014), but empirical evidence remains elusive.

Although a social function of self-directed behaviours remains undocumented in any species, we do know that these behaviours can, in some cases, be contagious when observed by others. A contagious response has been reported following the observation of both yawning (dogs, *Canis familiaris*, Joly-Mascheroni et al. 2008; budgerigars, *Melopsittacus undulatus*, Gallup et al. 2015; chimpanzees, Anderson et al. 2004; gelada baboons, *Theropithecus gelada*, Palagi et al. 2009) and scratching (rhesus macaque, *Macaca mulatta*, Nakayama 2004; Japanese macaque, *Macaca fuscata*, Feneran et al. 2013). In a handful of these examples, the contagious response has been sensitive enough to be triggered experimentally through the presentation of videos (Feneran et al., 2013; Paukner & Anderson, 2006) and, particularly for the primates, have been discussed mostly alongside the subject's (and species') capacity for empathic behaviours (Lehmann, 1979). However, spontaneous acquisition of stress behaviours (and therefore potentially the acquisition of stress itself) may lack adaptive value. Cognitive function and decision making are significantly impaired in stressed individuals (McEwen & Sapolsky, 1995) and prolonged stress has many recognized negative effects on health (Sapolsky, 1996). If cognitive function and decision making are impaired in the individuals surrounding a stressed animal, this may not produce an optimal social environment that allows for the mitigation of stress or may not allow for a response to stressed group mates in a way that would be the most advantageous. Responding to the stress of others spontaneously through emotional contagion, therefore, has the potential to be a maladaptive strategy. Instead, a more adaptive strategy could be to monitor these behaviours in others and respond to them in a facultative way that is functional (such as a positive or negative social interaction) and provides an advantage for one or all individuals.

If responses to stress behaviours go beyond contagious affect and, instead, elicit functional responses in others, we could expect both the production of a signal and the response to it to be influenced by the sender–receiver relationship (Guilford &

Dawkins, 1991; Micheletta et al., 2012). Signals often occur more frequently if the audience contains key social partners (Slocombe et al., 2010), and the response to signals can become stronger as social relationships become more important (Micheletta & Waller, 2012). By addressing how social relationships affect the production and response to communicative behaviours, we can, as a first step, begin to understand their function. A stronger response by friends or kin could suggest a function to facilitate cooperative efforts (Micheletta et al., 2012; Slocombe et al., 2010), whereas a stronger response by competitors could suggest that a signal functions to facilitate competition (Muroyama & Thierry, 1998). In the context of stress, by attending and responding to the stress behaviours of friends and kin, individuals could capitalize on important opportunities to manage social relationships and maintain a cohesive social group (Clay & de Waal, 2013). Conversely, monitoring the potential stress in competitors could provide opportunities to maximize competitive efforts by being able to taking advantage of another's weakness (Byrne & Whiten, 1989).

Assessing when and how animals respond to the negative emotions of conspecifics could significantly contribute to our understanding of sociality, and has the potential to inform us regarding the evolutionary steps that may have led to the ability to understand others. In the following experiment, we aimed to assess whether behaviours directly related to stress are socially functional, and whether or not these lead to responses in observers. As a species characterized as highly gregarious and cooperative (Thierry, Singh, & Kaumanns, 2004) the Barbary macaque, *Macaca sylvanus*, provides an excellent model for the study of social behaviour in animals. We predicted that the macaques would respond to the stress behaviours of others, particularly those with whom they had close social bonds, and in a way that may provide further opportunities for cooperation.

<H1>Methods

<H2>*Subjects and housing*

This study was conducted between February and December 2015. We tested six, unrelated adult Barbary macaques (two males, four females) currently living in a social group at the Monkey Haven, Isle of Wight, U.K. Subjects had free access to a naturalistic, grassy outdoor area (20 x 12 m and 4 m high), filled with trees, logs, ropes, swings and a waterfall. New novel enrichment devices were provided to the animals weekly. Animals also had free access to a smaller outdoor area (5 x 5 m and 4 m high), and a heated indoor area (5 x 3 m and 3 m high). Subjects could be separated into each of the areas as needed; however, the smaller outdoor area was used for all experiments. Prior to this study, all subjects had been exposed to cognitive testing and were habituated to the presence of the experimenter. Macaques were fed daily with assorted fruits and vegetables, nuts, cereals, seeds and commercial monkey pellets. Water was available ad libitum. Our experiments never impacted on the normal dietary and husbandry routines of the animals.

<H2>*Stimuli and apparatus*

For each animal, we prepared 20 experimental videos: 10 scratching videos and 10 neutral videos. Half featured a familiar individual (another Monkey Haven group mate) and half featured an unfamiliar individual (a Barbary macaque from an unknown group). Animals were not exposed to any videos of themselves throughout the experiment. Each video was 3 min long, and was composed of five unique occurrences of scratching (or other neutral behaviour, see below) from a single individual, presented randomly and repeated four times within a video; each scratching occurrence was separated by a blank screen. Scratching was defined as the raking or dragging of fingers or toes over the skin in a repetitive motion, whereas neutral behaviour was defined as a lack of explicit social behaviour or extreme physical movement other than vigilance. Scratching that occurred directly after a conflict or disturbance in the group was favoured in the selection process in case there were any hitherto undocumented differences between stress-induced scratching and hygienic scratching. Neutral stimuli with qualitatively similar movement (i.e. brief limb movements) were favoured in an attempt to match the scratching videos and control for simple differences in stimuli salience. Neutral clips were chosen from the same videos as the scratching stimuli to minimize the effects of background information.

Videos of the unfamiliar Barbary macaques were collected at the Trentham Monkey Forest (Trentham, U.K.); individuals at the Monkey Haven had no previous exposure to these animals. The unknown individuals were five randomly chosen adult males. All videos (both for the stimuli and for the experiments) were collected with a Panasonic HDC-SD700 video camera and were presented on a 19” Elo Monitor (refresh rate, 75 hz; videos presented at 24 fps). Stimuli were cropped around the animal to reduce excess background information and muted using Adobe Premier Pro CC 2014.

<H2>*Experimental Procedure*

Here, we modified an experimental procedure commonly used to test for yawn contagion (Anderson et al., 2004). A monitor was positioned outside the enclosure with a video camera above it; this provided an accurate record of both the animal's behaviours and where it was looking during experimental trials. Animals were free to enter our test area voluntarily and approach the experimenter. Once an animal had arrived at the experimental apparatus, the door to the test area was closed and other individuals in the group were locked out. Subjects could leave the test area voluntarily at any point during the experiment, but other individuals could not enter. If any animal chose to leave, the session was aborted and repeated on a different day. After a short delay, allowing the animal to settle in the new area, the experiment would begin. Data were collected opportunistically, and were dependent on the motivation of the animals on a test day. Two videos were presented in each experimental session, one scratching video (SC) and one neutral video (N), of which one was of a familiar individual (F) and one was of an unfamiliar individual (UF) allowing four possible video combinations in each session: FSC & UFN, UFN & FSC, UFSC & FN and FN & UFSC. The video combination presented to the animals in a session was selected at random, to nullify any effects of presentation order. The identity of the individual in the videos was also randomized, until subjects had been tested with all individuals on each video type at least twice and a maximum of four times (depending on the motivation of the subject).

All sessions were videotaped, and followed this procedure: (1) presentation of first video, (2) 3 min observation period, (3) presentation of second video, (4) 3 min observation period. During the observation periods the screen was switched off, and the picture remained blank. After the second observation period, subjects were encouraged to leave the test area and were not tested again for at least 2 h. To increase motivation in the experiment, and to keep subjects seated next to the screen, animals were rewarded with a piece of cereal after the presentation of every stimulus. Rewards were given during the blank screen between stimuli, and reward rate remained uniform across videos (20 rewards per video). Other individuals could not see the videos during testing, but could remain in visual and auditory contact with each other. Only a single experimenter was present at any time, and remained as neutral as possible throughout testing. The animals were never rewarded for a particular response, and the experimenter was careful not to act in a way that could influence the behaviour or attention of the subject. The experimenter did not make eye contact with the animals, remained silent at all times and maintained a neutral expression. A video example of the procedure can be found in the Supplementary material.

<H2>Video coding

All videos were coded using BORIS (Behavioral Observation Research Interactive Software, Friard & Gamba 2016). From the videos, we calculated the rate of scratching, the subject’s attention to the video and the subject’s orientation towards the rest of their group. Attention to the video was defined as the duration of gazing at the screen by the subject (Fig. 1). Orientation towards the group was defined as the duration of gazing by the subject towards the rest of its group mates. Owing to lack of motivation (i.e. the animal would not enter the test area), one subject was dropped from the analysis, and analyses were conducted on the remaining five individuals only. A naïve observer coded 10% of the videos to assess interobserver reliability using the intraclass correlation coefficient. We found significant agreement on both the rate (ICC = 0.871, N = 41, P <0.001) and duration (ICC = 0.992, N = 29, P <0.001) of coded behaviour.

<H2>Measures of relationship quality

To measure social bonds within a dyad, we recorded the frequency of contact sitting and the frequency of grooming interactions between all individuals. Data were collected every 10 min using the instantaneous scan sampling method (Altmann, 1974) resulting in a total of 272 scans over the course of the experiment. Scans were taken during days when experimental trials were not occurring. These data were then used to calculate a composite sociality index (CSI, or friendship index, see Silk et al. 2006); this index provides us with a measure of affiliation between each dyad relative to the rest of the group, and is a commonly used measure of friendship in primates. To calculate the dominance rank, all agonistic interactions with a clear outcome were recorded ad libitum, including conflict and displacement. The outcomes of 64 agonistic interactions were collected during the study. Individuals were then ranked according to their normalized David's score (David, 1987), giving each individual a rank from 1 to 5, where 1 is the highest rank.

<H2>Data Analysis

We used a generalized linear mixed-model analysis (GLMMs), applying random intercept/slope models. In our first model, which was applied to the full data set, we included video type (scratching video, neutral video), familiarity (familiar, unfamiliar) and the rank of observer as predictors, including interactions between video type and familiarity. We also included the ID of the subject, and the ID of actor in the video as random factors. In our second model, which was applied to familiar trials only, we included CSI (index of friendship with actor) and rank difference (rank of subject – rank of actor) to the model to assess for the effects of social relationships on behaviour. Again, the ID of the subject and the ID of the actor in the video were included as random factors. Here, the dependent variables were rates of scratching, attention to the video and orientation towards the rest of the group. We fitted GLMMs using the function lmer provided by the package lme4 for RStudio Version 0.99 for R version 3.1.3 (Bates et al. 2014; R Core Team 2014) . We assessed overall fit of the model by comparing our full models to a reduced model including only the intercept and random factors using a likelihood ratio test (LRT, function anova). We considered the significant effects of predictors only if the full model was a significant improvement from the reduced model.

Rates of scratching during the presentation of the video were compared with the rates of scratching during the 3 min after the video with a paired *t* test. As we found no difference in scratching when comparing these first and second observation periods (*t* test: $t_{7.7} = -1.178$, $P = 0.274$), scratching data from each of these two periods were pooled for subsequent analysis

<H2>*Ethical note*

This study received approval from the Animal Welfare and Ethical Review Body (AWERB), University of Portsmouth. Subjects were never food deprived prior to experimental trials. Animals always participated voluntarily and were kept to normal daily husbandry schedules predetermined by zoo staff throughout the study. All work conforms to the ASAB/ABS ethical guidelines for the treatment of animals in behavioural research.

<H1>Results

<H2>Influence on rates of scratching

Our first model, which included video type, familiarity and rank of the observer, was not a significant improvement from the null model (LRT: $X^2_3 = 1.049$, $P = 0.790$) indicating poor explanatory value of these predictors on the subjects' rates of scratching.

Our second model, which included the CSI and the rank difference between the actor and observer, was also not a significant improvement from the null model (LRT: $X^2_3 = 1.49$, $P = 0.684$) again indicating poor explanatory value of these predictors on the subjects' rates of scratching.

<H2>Influence on the attention to the video

Our first model, which included video type, familiarity and rank of the observer, was a significant improvement from the null model (LRT: $X^2_3 = 28.17$, $P < 0.001$)

indicating good explanatory value of the predictors on the subject's attention. Overall, video type was a significant predictor of attention (*t* = 2.03, *P* = 0.046). Subjects attended to scratching videos for longer (mean = 35.38 s, SE = 3.89) than neutral videos (mean = 25.78 s, SE = 3.14). Familiarity was also a significant predictor of attention (*t* = -4.46, *P* <0.001). Subjects attended to familiar videos (mean = 35.90 s, SE = 4.44) for longer than unfamiliar videos (mean = 29.33 s, SE = 2.54; Fig. 2). No significant interaction effect between video type and familiarity was found (*t* = -1.77, *P* = 0.08). Finally, the rank of the observer was also a significant predictor of attention (*t* = 5.38, *P* = 0.003), which increased as rank decreased (Fig. 3).

To assess any confound sex may have had on our results, we looked at the data with female stimuli removed. The model with only male stimuli was still a significant improvement from the null model (LRT: $X^2_3 = 12.484$, $P = 0.006$). Subjects attended to familiar males (mean = 50.10 s, SE ± 8.60) more than unfamiliar males (mean = 36.91 s, SE ± 4.36), and scratching males (mean = 35.99 s, SE ± 6.46) more than neutral males (mean = 45.36 s, SE ± 4.98). So when controlling for the sex composition of stimuli, we found very comparable patterns to the responses to the full, mixed-sex stimuli set. Therefore, the comparison between familiar and unfamiliar is not confounded by sex composition.

Our second model, which included the CSI and the rank difference between the actor and observer, was a significant improvement from the null model (LRT: $X^2_3 = 6.61$, $P < 0.037$). CSI was a significant predictor of attention, but only during the presentation of scratching videos (*t* = -2.59, *P* = 0.018), and not neutral videos (*t* = 0.413, *P* = 0.685). Here, subjects increased attention towards weak bonded group mates, as indicated by a lower CSI (Fig. 4). Rank difference had no significant influence on attention (t = -0.43, P = 0.672).

<H2>*Influence on orientation towards group mates*

Our first model, which included video type, familiarity and rank of the observer, was not a significant improvement from the null model (LRT: X^2_3 = 3.193, P = 0.561) indicating poor explanatory value of these predictors on the subjects' orientation towards the rest of the group.

Our second model, which included the CSI and the rank difference between the actor and observer, was also not a significant improvement from the null model (LRT: X^2_3, P = 0.610) again indicating poor explanatory value of these predictors on the subjects' orientation towards the rest of the group.

<H1>Discussion

When compared with neutral videos, videos of scratching conspecifics elicited a significant behavioural response in the Barbary macaques. This response was not the increase in self-scratching found in some other studies (Feneran et al., 2013; Nakayama, 2004), but instead was increased attention towards the stimuli, with subjects monitoring scratching for longer than neutral controls. The social relationship between the subject and scratcher also affected attention. The macaques were more attentive when they were presented with their group mates scratching, particularly those with whom they were weakly bonded. This increased attention of the observer towards scratching, and these modulating effects of social relationships, suggest that the macaques were perceiving these behaviours differently from neutral, uninformative postures. Although a social function of stress-associated self-directed behaviour has been suggested (Bradshaw, 1993; Maestripieri et al., 1992; Nakayama, 2004; Waller et al., 2014), these data may represent the first empirical evidence to support this idea.

The passive transmission of negative emotional states, through the contagion of associated behaviour such as scratching, has been proposed as an adaptive strategy (Nakayama, 2004). Being able to mirror the negative emotions of others, possibly via an empathetic type of response (Palagi et al. 2009), may enable an increase in awareness of the environment that can enhance an individual's ability to avoid danger (Feneran et al., 2013). In this study, however, we found no contagious effect of scratching. This could be reflective of our small sample size, which reduces statistical power and the likelihood of uncovering significant effects (Field, Miles, & Field, 2012), or alternatively, this response could be weaker or completely lacking in this species. We argue that a facultative response to stress behaviours, depending on both species and context, is a more adaptive strategy. Our subject species (the Barbary macaque), although very closely related, differs greatly in social style to the species previously used in scratch contagion research (rhesus macaque, Feneran et al. 2013; Japanese macaque, Nakayama 2004). The socially tolerant species, such as the Barbary macaque, are characterized by a much greater tendency for cooperation compared with their less tolerant counterparts such as the Japanese and rhesus macaque (Thierry & Aureli, 2006). It could be that instead of a passive transmission of negative emotions seen in the intolerant species, tolerant species may favour an active strategy in which negative emotions, such as stress, are provided as information rather than transferred passively, and where a decision can then be made about how exactly to respond.

Primates acquire and respond to information in ways that match the adaptive value of the information being acquired (Watson, Ghodasra, Furlong, & Platt, 2012). In macaques, we can find both a visual preference (Deaner, Khera, & Platt, 2005) and selective attention (Waitt, Gerald, Little, & Kraiselburd, 2006) towards communicative signals, with subjects choosing to view images of signals over nonsignals and directing their gaze towards these for longer periods of time. In our study, subjects systematically attended more towards scratching videos than neutral videos, suggesting the macaques were finding these videos more interesting and potentially more informative than those featuring animals free of any salient behaviour (Waitt et al., 2006; Winters, Dubuc, & Higham, 2015). Although our results cannot inform us exactly why monitoring the scratching of others would be adaptive (at least to the receiver), it could be that the animals are responding to the potential stress of the scratcher (Maestripieri et al., 1992). The ability to assess the emotional state and intentions of other individuals is extremely important for social animals to coordinate future interactions (Parr & Waller, 2006), which could explain why behavioural manifestations of stress are beneficial to produce and were therefore selected. Or, it could also be that these behaviours serve no signalling function at all. As information leaks out through behaviour, as animals attempt to cope with stress (Koolhaas et al., 1999), associations between coping behaviours and behavioural or emotional states could provide an advantage to receivers. This would not necessarily provide a benefit to the stressed individual from a communicative perspective, but instead this information could be exploited and lead to a cost for the producer.

If there is a social function to stress-related behaviours, we should also expect the relationship between subject and scratcher to play a key role in this shift in attention. Animals select specific opportunities to cooperate with friends and allies, whether that is responding to distress and alarm signals (macaques, Micheletta et al. 2012), cooperative foraging opportunities (ravens, *Corvus corax*, Massen et al. 2015; coral trout, Vail et al. 2014) or reconciling conflict (F Aureli, Cords, & van Schaik, 2002). Contrary to our predictions, the macaques, although more attentive to familiar individuals overall, were actually more attentive to their weakly bonded group mates. This suggests that there is another reason to monitor scratching than cooperation and social bonding opportunities. Primates redirect aggression to alleviate stress (Virgin & Sapolsky, 1997), and in some species, aggressors choose the victims of redirection systematically (Filippo Aureli, Cozzolino, Cordishi, & Scucchi, 1992). By paying close attention to the stress of weakly bonded group mates, this may provide a strategy to avoid becoming involved in unnecessary conflict by inferring future behaviour (Waller, Whitehouse, & Micheletta, 2016). Additionally, individuals may be looking for key opportunities to increase their competitive success, and by looking for weaknesses in opponents (including weakly bonded individuals), individuals could choose appropriate opportunities for competition (Byrne & Whiten, 1989). If such a shift in attention is competitively driven, it is difficult to interpret these responses as having a signal function. For such a signal to evolve there must be an advantage or benefit for both the sender and receiver; however, these results demonstrate that producing self-directed behaviours may actually provide a disadvantage to the sender. If the animals in this study were responding to stress, it could be that an exploitation of behaviours produced as a product of coping could be a more plausible interpretation here.

Here we found that subjects attended more to familiar individuals than unfamiliar individuals. Although further investigation is necessary, it could just be that subjects were more wary of staring at the unfamiliar individuals, as these could represent a potential threat or danger. Additionally, as rank decreased in our subjects, their attention towards all social stimuli presented increased. This phenomenon was not specific to scratching, however, but instead was found across all conditions. Lower ranking individuals can often be found on the periphery of the social group (Sosa, 2016; Sueur et al., 2011; Whitehouse, Micheletta, Powell, Bordier, & Waller, 2013) and are the most frequent targets of redirected aggression (Aureli et al., 1992). So, perhaps an increased sensitivity to social information, including information about the emotional states of group mates, could allow individuals to both reduce competition from others and capitalize on important social bonding opportunities.

These results not only increase our fundamental understanding of stress behaviours, but also highlight the necessity to address the adaptive function of emotional behaviours in animals through research. Too much focus on the internal state of the sender, and less focus on how this relates to the response of the receiver, restricts our understanding of behaviour and, ultimately, our understanding of why behaviour evolves. By approaching stress behaviours from the point of view of the receiver, this study suggests that they may not only be relevant as coping strategies, but also have the potential to directly impact the future behaviours of others by informing about the actors emotional state. How exactly these behaviours affect social interactions however, calls for further research, in which we should focus on social responses of the receiver as well as on how the composition of the audience affects production of these behaviours.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi

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Figure Legends.

Figure 1. Measuring attention. The video camera was placed above the monitor displaying experimental stimuli. Subjects were considered to be attentive to the videos when they directed their gaze at the screen. (a) Attention to the video and (b) no attention to the video.

Figure 2. Effects of video type and familiarity on attention. Attention of the subjects to familiar neutral videos (FN), familiar scratching videos (FSC), unfamiliar neutral videos (UFN) and unfamiliar scratching videos (UFSC). Boxes represent the interquartile range of the data, lines through the boxes represent the median data point, and the whiskers represent the full range of data. Each circle refers to data points within the analysis.

Figure 3. Effect of observer rank on attention towards all videos. Attention of the subjects to all videos is compared with their group ranking: 1 represents top ranking and 5 represents lowest ranking. Boxes represent the interquartile range of the data, lines through the boxes represent the median data point, and the whiskers represent the full range of data. Each circle refers to data points within the analysis.

Figure 4. Effects of CSI on attention to familiar videos. Attention to (a) familiar neutral and (b) familiar scratching videos in relation to the composite sociality index (CSI, were a higher CSI suggests a stronger social bond) between subject and individual in the video. Shapes represent different subjects, and lines represent the best fit through each subject's data points.