

Subtypes of aggression and their relation to anxiety in Barbary macaques

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Human aggression can be differentiated into reactive aggression (RA), displayed in face of a real or perceived threat and associated with high levels of anxiety, and proactive aggression (PA), displayed to achieve a certain goal and linked to lower anxiety levels. To study the origins of these aggression subtypes and their relation to anxiety, we tested if both subtypes can be distinguished in a nonhuman primate species, characterized their occurrence within the study group, and examined the link between aggression subtype and anxiety. Data were collected on 29 individuals of a semi-free ranging group of Barbary macaques (*Macaca sylvanus*) at Affenberg Salem, Germany, via focal animal (303 hr) and event sampling (1,222 agonistic events). Using *a priori* definitions, each aggressive event was classified as either reactive or proactive. We found both aggression types in our study population as well as individual differences in the proportion at which they occurred. The predominant use of one subtype of aggression was linked to the individual's dominance rank, age and sex, but not related to standard behavioral and physiological measures of anxiety. Our results suggest that reactive and proactive subtypes of aggression also exist in Barbary macaques, indicating a deeper evolutionary history of these aggression types observed in humans.

KEYWORDS

aggression, anxiety, fear, glucocorticoids, primates, proactive, reactive

1 | INTRODUCTION

Although aggression is an integral part of social life (de Waal, 1992), some of its ultimate outcomes are a major problem of human society. Aggressive behavior ranges from mild forms such as insults, gossiping, and threats (Björkqvist, 1994) to violent forms like robbery, rape, and homicide (Anderson & Bushman, 2002). Different types of violence are associated with different types of aggression (Brendgen, Vitaro, Tremblay, & Lavoie, 2001). Thus, the occurrence of violent forms of aggression may be reduced by prevention programs that focus on the nature of different types of aggression (Vitaro & Brendgen, 2005). Investigating aggression types is indispensable for understanding the origins, underlying mechanisms, and functions of this widespread behavior (Caprara, Barbaranelli, Pastorelli, & Perugini, 1994).

Aggression can be distinguished based on different criteria (Ramírez & Andreu, 2006), such as form (e.g., verbal), function (e.g., defensive), proximate mechanisms (e.g., hormones), or context (e.g., sexual aggression or aggression during feeding). Reactive and proactive aggression fall under the function category: Proactive aggression (PA) is displayed to obtain a certain goal. In contrast, reactive aggression (RA) is a response to a real or perceived threat, provocation, or frustration with the goal to end the threat. PA and RA can consequently be distinguished based on their ultimate goal using questionnaires (Raine et al., 2006).

RA and PA can also be distinguished physiologically. Measures of heart rate and skin conductance indicate that PA is characterized by low levels of arousal, whereas RA is often accompanied by high levels of arousal as well as anxiety (Vitiello & Stoff, 1997). Proactively

aggressive individuals may be less anxious and therefore less afraid of negative consequences, whereas reactively aggressive individuals may be more anxious, leading to impulsive aggression (Frick & Morris, 2004; van Goozen, 2005; Vitaro & Brendgen, 2005). As, to our knowledge, these aggression subtypes have not been studied systematically in primates other than humans, we tested whether RA and PA will be present in a nonhuman primate.

As in humans, aggression is ubiquitous in nonhuman primates, and displayed to maintain and defend status (Higley, Suomi, & Chaffin, 2011) and resources (Nelson & Trainor, 2007). Aggressive behavior is mostly classified by intensity (Aureli, 1997; Muller & Wrangham, 2004; Thierry, 1985) and can be distinguished into defensive and offensive aggression (Kalin, 1999), with the former being a response to an attack and the latter being impulsive and unprovoked. Although this resembles the distinction of RA and PA, those subtypes are not the same (Wrangham, 2017). For instance, defensive aggression only includes responses to real but not perceived threats, while RA includes both.

Recently there has been an attempt to investigate human and nonhuman RA and PA from an evolutionary perspective (Wrangham, 2017), yet systematic attempts differentiating nonhuman primate aggression into RA and PA are rare or missing, despite several hints to their existence. Redirection of received aggression by the victim toward non-involved bystanders, commonly observed in macaques and baboons (Aureli & van Schaik, 1991; Sapolsky & Ray, 1989; Thierry, 1985), may be classified as RA, as is counter-aggression, which is defined as immediately returned aggression toward the initial aggressor. Similarly, an increased probability of aggression in situations in which the individual "has to relinquish a seemingly desired object or contact, or is confronted with other presumably unwanted changes in its situation" as observed in chimpanzees (*Pan troglodytes*; de Waal & Hoekstra, 1980, p. 935) is consistent with RA. PA, on the contrary, is expressed, for example, during border patrols often leading to escalated between-group aggression or during infanticidal attacks by males (Wrangham, 2017).

In contrast to aggression types, anxiety has been intensively studied in nonhuman primates and can be noninvasively measured via self-directed behavior such as scratching as validated in pharmacological studies (Barros & Tomaz, 2002; Schino, Perretta, Taglioni, Monaco, & Troisi, 1996). Self-directed behavior is induced, for example, by close spatial proximity to a higher-ranking individual (Castles, Whiten, & Aureli, 1999; Maestriperieri, 1993), isolation from the group (Rowell & Hinde, 1963), uncertain dominance relationships (Schino, Maestriperieri, Scucchi, & Turillazzi, 1990), low dominance rank (Kaburu, Maclarnon, Majolo, Qarro, & Semple, 2012), following agonistic interactions (Aureli, 1997; Aureli, Cords, & van Schaik, 2002; Aureli & van Schaik, 1991; Schino, Rosati, Geminiani, & Aureli, 2007) and the elevated risk of aggression (Maestriperieri, 1993). The fearful reaction to the non-agonistic approach of a higher ranking individual ("fear index") constitutes another behavioral measure of anxiety (de Waal & Luttrell, 1989; Schino et al., 1996). Finally, glucocorticoid (GC) levels can be used as a physiological measure of anxiety (Majolo, Ventura, & Koyama, 2009), as administration of an

anxiogenic drug increased levels of cortisol in rhesus macaques (*Macaca mulatta*; Ninan, Insel, & Cohen, 1982). GC levels reflect the activity of the hypothalamic-pituitary-adrenocortical axis, which mobilizes energy supplies in response to stressors (Cheney & Seyfarth, 2009) and is often referred to as a physiological stress response.

Studies on nonhuman primates suggest an association between anxiety and aggression. Anxiogenic drug treatment of long-tailed macaques (*Macaca fascicularis*) not only increased the individual's rate of self-directed behavior, but also its aggression rate (Schino et al., 1996). Similarly, when confronted with an acoustic threat, Barbary macaque females showed more self-scratching, higher GC levels and aggressive behavior compared to a control experiment (Gustison, Maclarnon, Wiper, & Semple, 2012). However, these studies did not investigate whether subtypes of aggression are associated differentially with anxiety. We thus aimed to investigate the occurrence of RA and PA as well as its association with anxiety in Barbary macaques. In line with the human literature, we predicted a positive relationship between an individual's amount of RA used and measures of anxiety.

We chose Barbary macaques as our study species. They show a relatively "egalitarian" dominance style (Matsumura, 1999), where aggression is more frequent, less intense and sometimes bidirectional within a given dyad. Thus, counter-aggression in Barbary macaques is not as common as in "egalitarian" macaque species but not as rare as in "despotic" macaque species (Balasubramaniam et al., 2012). Compared to the latter, Barbary macaques may be a better model for modern egalitarian human societies (Boehm, 1999). They are the ancestral species of the genus (Morales & Melnick, 1998) making them a good starting point to investigate whether RA and PA already exist in macaques.

We provide a method to distinguish RA and PA that can be applied to adults across contexts. We used *a priori* definitions, based on the circumstances of the agonistic encounter (potential or actual threat present or not), to assign each aggressive encounter as being either RA or PA, under the assumption that close proximity to higher-ranking individuals is perceived as threatening. To substantiate this operationalization of a threat, we predicted that if close spatial proximity to higher-ranking individuals was perceived as threatening, then it should be evident in increased scratching rates compared to times when higher-ranking individuals were absent. Once categorized, we predicted that PA resulted more often in an immediate positive outcome (food, grooming, or infant handling) compared to RA, as it is displayed in order to achieve a certain goal. Examining the link between both subtypes of aggression and anxiety, we predicted a positive relationship between RA and behavioral as well as physiological measures of anxiety (i.e., fecal glucocorticoid concentrations), as more reactive aggressive individuals are thought to be more anxious. As our definitions of RA were based on differences in dominance rank, which in Barbary macaques is strongly linked to sex and also a function of age, we investigated the relationship between aggression subtypes and these three factors, predicting specifically more RA in lower-ranking, female and younger individuals.

2 | METHODS

2.1 | Ethical statement

This research was completely non-invasive, followed the Animal Behaviour Society's guidelines for the treatment of animals in behavioral research and teaching, and was approved by the Animal Welfare Body of the German Primate Center (No. E9-16).

2.2 | Study group

The study was conducted at Affenberg Salem, Germany (de Turkheim & Merz, 1984), a 20 ha enclosure inhabited by three semi-free ranging groups of Barbary macaques. Apart from foraging on natural vegetation, monkeys are provisioned daily with grains, fruits and vegetables, and have ad libitum access to monkey chow and water (Paul & Kuester, 1988). Data were collected from June to October 2014 on group C, consisting of 59 individuals (16 adult males, 6 subadult males, 20 adult females, 11 juveniles, 7 infants). All adult males (>6 years, $n = 16$) and females (>4 years) without dependent offspring ($n = 13$) were study subjects. Females with dependent offspring were excluded, as infant presence might influence their social behavior. One old focal female died during the study period.

2.3 | Behavioral observations

Data were collected using a combination of event sampling of aggressive interactions and continuous focal animal observation (Martin & Bateson, 2007). During the main feeding time (approx. between 8:00 and 11:00 am), when food competition was highest and conflicts were frequent, agonistic encounters were recorded using event sampling. A group of 2–6 foraging individuals was observed, remembering the shifts in spatial proximity, as well as aggressive and submissive behavior. When an individual (aggressor) displayed aggression toward another individual (victim), this was recorded as well as the following information retrospectively regarding the 30 s before the aggressive encounter: social behavior to and by the victim as well as other individuals, spatial proximity of the aggressor toward all other individuals within 10 m, and shifts in proximity. It was noted also whether the aggressor achieved a positive outcome within 10 s of the end of the aggression, which was defined as excluding others from the food patch, attaining food from the victim, infant handling and/or receiving grooming.

Before and after event sampling, focal animal protocols (Martin & Bateson, 2007) of 40 min duration were recorded in a randomized manner and balanced throughout the time of day. We recorded continuously close spatial proximity (<1.5 m) as well as social and self-directed behavior. For every occurrence of self-scratching, spatial proximity to other individuals within 10 m was noted. If possible, aggressive encounters during focal animal observations were recorded the same way as in the event sampling. Instantaneous sampling was used to record the spatial proximity of all adult individuals within 10 m distance to the focal animal each full minute using different categories

(body contact, within 1.5, 1.5–5, 5–10 m). Ad libitum data on the outcome of agonistic interactions were recorded to supplement focal animal data used to calculate the dominance hierarchy.

2.4 | Hierarchy computation

A dominance hierarchy was computed based on 4,742 decided dyadic interactions (without counter-aggression) where only one partner showed submissive behavior ("make room", "give ground", "flee" and "crouch") using DomiCalc (Schmid & de Vries, 2013). The optimal order was based on Combi1 indices from the I&SI-method with a linearity index of 0.72% and 20.4% of unknown relationships. All adult males except the oldest one outranked all adult females except the two top-ranking females (see Supplemental Material, Table S1). Two individuals had the same Combi1 index, thus shared one rank position.

2.5 | Data analyses

Based on focal animal data (303 hr, mean \pm SD: 10.45 ± 0.74 hr per individual), hourly rates of scratching were calculated per observation hour for each individual. To calculate individual scratching rates for certain conditions (only higher-ranking individuals present or only lower-ranking individuals present) the number of scratching events in this condition was divided by the total amount of time spent in this condition. For analysis, all occurrences of body contact were excluded, because those situations cannot be clearly interpreted as perceived threat or not (Molesti & Majolo, 2013).

In total, 1,222 agonistic encounters were recorded (mean \pm SD: 42.14 ± 4.87 encounters per individual). Each encounter was classified as either reactive or proactive aggressive. RA was defined as any agonistic behavior within 30 s following a real or perceived threat, that is, receiving aggression, a higher-ranking individual being in close spatial proximity (<5 m) of the later aggressor or continuously reducing its spatial proximity or approaching it in a fast or direct way (also >5 m). When RA is caused by aggression, it comprises either counter-aggression (when it is directed toward the former aggressor) or redirected aggression (when it is directed toward a third individual). All occurrences of counter- and redirected aggression are RA, but not all RA are counter- or redirected aggression. PA was defined as any agonistic interaction not classified as reactive aggressive. The proportion of RA was calculated for each individual as the number of RA events divided by the total number of aggressive events. As the top-ranking male only engaged in PA ($n = 35$), he was excluded from further analyses. The two individuals that occupied the same rank position were regarded as "higher-ranking" to each other for analysis of aggressive encounters.

A Fear Index (similar to "Fear Response Index"; Schino et al., 1996; "negative approach result"; de Waal & Luttrell 1989) based on focal animal data were computed as the percentage of non-aggressive approaches of a higher-ranking individual which resulted in submissive behavior, the display of "bared teeth", "present submission", or departing the higher-ranking individual within 10 s.

2.6 | Fecal glucocorticoid metabolite (fGCM) analysis

Fecal samples were collected opportunistically immediately after defecation and homogenized using disposable gloves ($n = 225$ samples; mean \pm SD per individual: 8.04 ± 1.15). Approximately 1–2 g fecal material was put in 20 ml polypropylene tubes. Samples were stored on ice in thermos flasks until the end of the field day (max. 10 hr) and later frozen at -20°C until transport to the Endocrinology Laboratory of the German Primate Centre for hormone analysis.

Fecal samples were analyzed for fGCM concentrations using validated methods described in detail in Heistermann, Ademmer, and Kaumanns (2004); Heistermann, Palme, and Ganswindt (2006). In brief, fecal samples were lyophilized, pulverized, and an aliquot representing 0.05–0.07 g of the resulting fecal powder (exact weight recorded) was extracted with 3 ml 80% watery methanol (Palme, Touma, Arias, Dominchin, & Lepschy, 2013). fGCM concentrations in fecal extracts were determined applying an enzyme immunoassay (EIA) for 11β -hydroxyetiocholanolone, a group-specific assay for the measurement of fecal cortisol metabolites (Ganswindt, Palme, Heistermann, Borrigan, & Hodges, 2003). The assay has been proven to reliably track changes in glucocorticoid output in primate species of all major taxa, including Barbary macaques (Heistermann et al., 2006; Young, Majolo, Heistermann, Schülke, & Ostner, 2014). The EIA was performed as described in detail in Heistermann et al. (2004, 2006). Sensitivity of the assay at 90% binding was 0.6 pg. Intra- and inter-assay coefficients of variation (CV) of high- and low-value quality controls were $<10\%$ and $<15\%$, respectively.

2.7 | Statistical analyses

Statistical analyses were carried out using R (Version 3.1.2; R Development Core Team, 2008). The influence of proximity of higher-ranking individuals on scratching rate was tested using paired t -tests comparing individual mean scratching rates for times when only higher-ranking individuals were within 10 m with times when only lower-ranking individuals were present, including all individuals that spent at least 20 min in both conditions ($n = 20$, mean time [min] spent in each condition \pm SD: higher-ranking 65 ± 32 , lower-ranking 107 ± 85). The effect of aggression type (RA or PA) on the positive outcome of aggression (yes/no, depending on whether at least one of the categories for a positive outcome (see above) was met or not, response variable) was tested using a generalized linear mixed model (GLMM) with binomial error structure (lmerTest package), fitted with maximum likelihood and logit link function, including z-transformed dominance rank, age, and sex as fixed, control factors and individual identity as random factor. Sex differences in the predominant use of either aggression type were assessed using Mann-Whitney- U -tests. Rank effects on the proportion of RA were assessed using spearman rank correlations (ppcor package). To test the effect of anxiety on the aggression subtype used we ran a binomial GLMM (lmerTest package) fitted with maximum likelihood, including z-transformed anxiety measures (scratching rate, Fear Index, mean fGCM) as predictors, the occurrence of RA as response, sex, z-transformed rank and age as

control variables and individual identity as random factor. For this model, variance inflation factors (car package) were larger than 4 for sex (4.1) and rank (4.4), indicating some collinearity between rank and sex. However, we decided to include both in the final model, as full models had a significantly better fit compared to reduced models excluding either of the two (model comparison using likelihood ratio test with the R function anova, setting the argument test to "Chisq," full model to model excluding rank: $\text{Chisq} = 13.71$, $p < .0003$, full model to model excluding sex: $\text{Chisq} = 6.77$, $p < .01$). For both GLMMs, we assessed leverage (df-betas and cooks distances) of individuals and single datapoints (influence.ME package) as well as variance inflation factors (car package), to assess model validity. None of the tests indicated violation of model assumptions except the hint to collinearity between sex and rank in the anxiety model.

3 | RESULTS

We tested whether proximity to higher-ranking individuals posed a threat to individuals lower in rank, indicated by increased scratching rates. Individuals scratched themselves significantly more often when only higher-ranking individuals were within 10 m compared to when only lower-ranking individuals were present (Figure 1; Paired t -test: $t [20] = 5.72$, $p < .0001$, 95% CI [17.3, 37.3]; mean number of scratches per hour \pm SD: only higher-ranking individuals = 52.77 ± 21.22 , only lower-ranking individuals = 25.49 ± 9.88). Based on this finding we

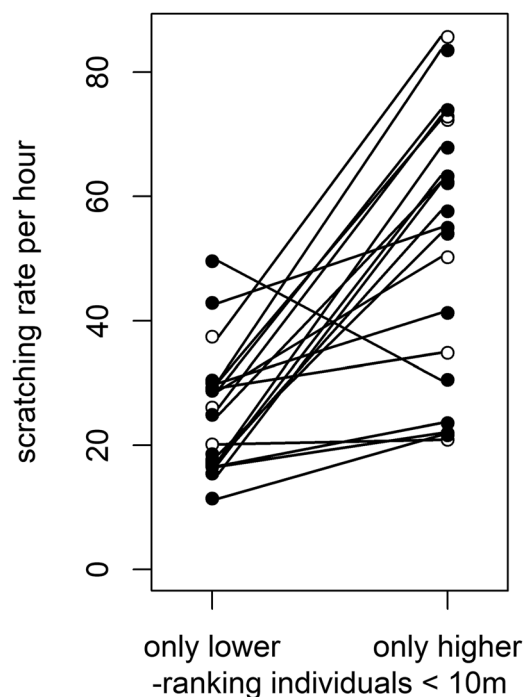


FIGURE 1 Pair-wise comparison of individual scratching rates per hour when only higher-ranking individuals or only lower-ranking individuals are present within 10 m. Only individuals that spent at least 20 min in each condition were considered ($n = 20$, full circles = females, open circles = males)

classified all conflicts into PA or RA depending on whether they occurred in response to such a perceived or real threat or not.

We predicted that PA will result more often than RA in a positive outcome of the conflict for the aggressor in the sense that the aggressor obtained access to space, food, or a social partner. 206 of 556 (37.1%) PA events led to a positive outcome compared to 50 of 631 (7.9%) RA events. Males achieved 169 of 256 (66.0%) positive outcomes, females 87 (34.0%). However, when looking at the positive outcomes of each aggression type separately by sex, PA resulted slightly more often in a positive outcome in females (51 out of 134 = 38.1%) than males (155 out of 422 = 36.7%). RA was also followed more often by a positive outcome in females (36 out of 417 = 8.6%) compared to males (14 out of 214 = 6.5%). A GLMM revealed a significant relationship between a positive outcome following an aggressive interaction and PA (Table 1). Female and higher-ranking individuals also achieved significantly more positive outcomes—although the effects were smaller (Table 1).

RA and PA occurred at similar frequencies across the study group and mainly consisted of threats (RA: 582/631; PA: 522/556). Only rarely aggression escalated into chases (RA: 11/631, PA: 6/556) or physical assaults (RA: 38/631, PA: 28/556). RA mostly resulted from situations with a perceived and not a real threat, that is, the mere presence of a higher-ranking individual was enough to elicit aggression toward a third individual. Only 84 RA events occurred after actual aggression. Thus, they comprised either counter- or redirected aggression.

Although all individuals expressed both subtypes of aggression, the majority used one subtype predominantly (Figure 2). Rank and the proportion of RA were positively correlated (Figure 3; Spearman rank correlation: $\rho = 0.82$, $n = 28$, $df = 26$, $p < .0001$). The higher-ranking an individual, the more likely it was to use PA. To account for the generally lower rank of females, we also tested both sexes separately; then the rank effect remained among males (Spearman rank correlation only males: $\rho = 0.68$, $n = 15$, $df = 13$, $p = .005$), but disappeared among females (Figure 3; only females: $\rho = 0.40$, $n = 13$, $df = 11$, $p = 0.17$). Also, females used significantly more often

TABLE 1 Effect of aggression type on the outcome of aggression

Predictors	Estimate	SE	Z value	95% CI
(Intercept)	-1.91421***	0.18432	-10.385	[-2.3, -1.6]
TypePA	1.78730***	0.19434	9.197	[1.4, 2.2]
z_rank	-0.66610***	0.13291	-5.012	[-0.9, -0.4]
sexm	-1.01576***	0.25565	-3.973	[-1.6, -0.5]
z_age	0.16695 [†]	0.09054	1.844	[>0, 0.4]

Best binomial GLMM ($r^2 = 0.55$, $vifs < 2.7$) explaining the effect of aggression type ($n = 1187$) on the positive outcome of aggression, controlling for the effects of rank, sex, and age (fixed factors) as well as individual identity (random factor). Predictor aggression type was levelled on proactive aggression (PA) and control variable sex was levelled on males (m). Rank and age were z-transformed and are thus displayed as z_age and z_rank.

[†] $p < 0.1$.

*** $p < .001$.

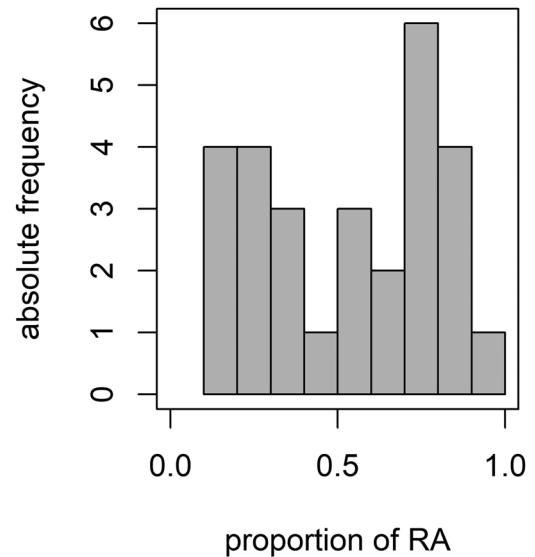


FIGURE 2 Absolute frequency of individual proportions of reactive aggression (RA) within the study group ($n = 28$). A proportion close to 0 indicates that individuals mainly used proactive aggression, whereas proportions close to 1 indicate individuals mainly used RA

RA (417 out of 551 interactions = 75.7%) than PA compared to males (214 out of 636 interactions = 33.6% RA; Figure 3; Mann-Whitney $U = 185$, $n(f) = 13$, $n(m) = 15$, $p < 0.0001$, mean \pm SD: for females 0.75 ± 0.13 , for males 0.35 ± 0.18).

None of the anxiety measures (scratching rates, Fear Index, fGCM levels) was significantly related to the subtype of aggression an individual used (Table 2, mean \pm SD: Fear Index: 0.18 ± 0.14 ; fGCM value: 349.86 ± 100.17 ; hourly scratching rate: 20.73 ± 5.25), but sex, age, and rank did with females, young, and low-ranking individuals engaging more often in RA (Table 2).

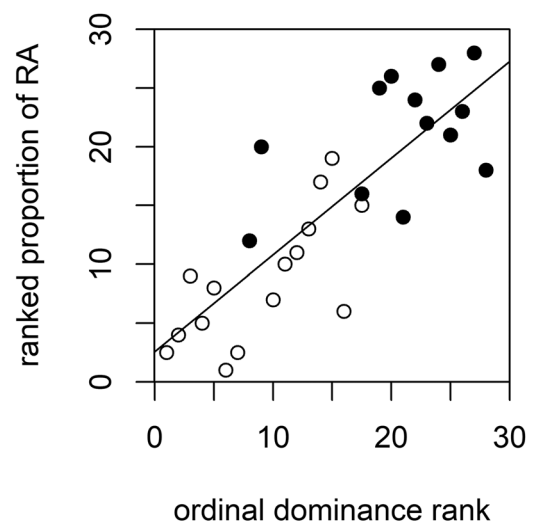


FIGURE 3 Ordinal dominance rank (1 = highest rank, 28 = lowest rank) of each individual ($n = 28$, full circles = females, open circles = males) in relation to his/her ranked proportion of reactive aggression (RA, 1 = lowest amount of RA, 28 = highest amount of RA)

TABLE 2 Effect of anxiety measures on the type of aggression used

Predictors	Estimate	SE	Z value	95% CI
(Intercept)	0.69077***	0.19573	3.529	[0.3, 1.1]
z_FearIndex	-0.11488	0.14544	-0.790	[-0.4, 0.2]
z_ScratchingRate	0.10314	0.11124	0.927	[-0.1, 0.3]
z_GC	0.02468	0.10998	0.224	[-0.2, 0.3]
z_rank	0.74960***	0.18292	4.098	[0.4, 1.1]
z_age	-0.51588***	0.12270	-4.205	[-0.8, -0.3]
sexm	-0.91878**	0.33010	-2.783	[-1.6, -0.2]

Best binomial GLMM ($r^2 = 0.60$, $vifs < 4.5$) explaining the effect of anxiety measures (Fear Index, scratching rate, and glucocorticoid [GC] levels) on the aggression subtype used ($n = 1,187$), leveled on RA, controlling for sex, rank, and age (fixed factors) as well as individual identity (random factor). Predictors with a "z_" had to be z-transformed in advance.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

4 | DISCUSSION

This study presents a method to distinguish RA and PA in Barbary macaques by using *a priori* definitions based on the presence or absence of real and perceived threats. Threats included receiving aggression and presence of higher-ranking individuals, a situation that elicited increased self-scratching behavior. The validity of our definitions was supported by our findings that PA was significantly associated with a positive outcome and thus seems to be more goal-oriented affecting the actor's ability to access resources. This does not necessarily imply that PA is in general more successful than RA. As suggested for humans (McGuire, 2008) an individual might reduce its tension due to a potential threat via attacking a third individual. Long-tailed macaques that redirected aggression (a form of RA) after a conflict showed lower scratching rates, indicating a reduction in anxiety and thus a faster attenuation of the stress response (Aureli & van Schaik, 1991). Consistent with this, male olive baboons (*Papio anubis*) that often redirected aggression had lower basal cortisol levels than males that did not (Sapolsky & Ray, 1989). Redirecting aggression could also reduce the risk of renewed aggression by diverting attention of the former aggressor toward another individual (Aureli & van Schaik, 1991). As we did not measure immediate changes in anxiety or risk of renewed aggression following RA, our study does not speak to the relative efficacy of PA or RA.

Individuals expressed a bias toward one or the other type of aggression. Across adults, the bias toward RA was negatively correlated with rank; the lower ranking an individual was, the higher was the bias toward using RA. As aggression in Barbary macaques is usually directed down the hierarchy (see Table S1), lower-ranking individuals might be confronted more often with a potentially threatening situation and, thus, use RA more often. Higher-ranking individuals might use PA more often as they have more potential victims and are themselves less often faced with a potential threat they might have to respond to with RA. In separate analyses for males and females, the dominance effect on RA bias was still observed among males. Among females alone, however, dominance rank could not explain individual variation in the use of aggression subtypes,

suggesting that variation in the use of aggression subtypes is not simply a consequence of variation in opportunity.

The effect of sex on the use of aggression subtypes is difficult to interpret because sex and rank were confounded in this study, with most females being lower-ranking than males. Female Barbary macaques inherit their rank position from their mother and rarely change it, whereas male dominance hierarchies are individualistic and less stable (Preuschoft, Paul, & Kuester, 1998) which may affect both the role of imminent and perceived threats and the function of RA for males. Studies on human sex differences in RA and PA report conflicting results, with comparable levels in men and women (Connor, Steingard, Anderson, & Melloni, 2003) and higher levels of PA in men (Miller & Lynam, 2006).

Apart from male and higher-ranking individuals, older individuals used PA relatively more often. Studies in humans also indicate different developmental patterns for RA and PA, with RA being more prevalent at a young age (Connor, Steingard, Cunningham, Anderson, & Melloni, 2004). Older Barbary macaques might have learned to actively avoid potentially threatening situations and thus reduce their need to use RA. In support of this, female rhesus macaques received lower rates of aggression with age, potentially leaving less opportunity for RA (Brent, Ruiz-Lambides, & Platt, 2017). Furthermore, age also has negative effects on the number of partners and time spent being groomed by others in female Barbary macaques suggesting that overall sociality declines with age (Almeling, Hammerschmidt, Sennhenn-Reulen, Freund, & Fischer, 2016).

Sex and rank also played a significant role in the outcome of an aggressive interaction, although aggression subtype (PA) explained most of the variance. Female and higher-ranking individuals achieved more often positive outcomes of aggression. High-ranking individuals might be more efficient in achieving this due to their position in the hierarchy, which gives them more potential victims and the opportunity to choose the one from whom they would be most likely to receive a certain benefit. The effect of sex on the outcome of aggression might be due to our definitions of a positive outcome, which did not include access to mating partners (which is more important to males than females).

None of our anxiety measures were significantly related to how reactively aggressive an individual was. Three non-mutually exclusive explanations may account for this. Firstly, the measures used may not accurately represent the important anxiety components in the study individuals. Instead of using an individual's average scratching rates or fGCM level, scratching rate during or fGCM levels following potentially threatening situations may have been more meaningful. The Fear Index captures anxious responses to an approach of a higher-ranking individual. However, an individual may already respond anxiously before this happens (as seen in the increased scratching rates when higher-ranking individuals are within 10 m) and increase distance to the higher-ranking individual—a factor the Fear Index does not capture.

Secondly, the association between aggression type and anxiety may not be as straightforward as predicted. In talapoin monkeys (*Miopithecus talapoin*) application of an anxiogenic drug increased, whereas treatment with an anxiolytic drug decreased, aggressive behavior, but only in dominant individuals (Vellucci, Herbert, & Keverne, 1986). This had an indirect effect on subordinate individuals receiving more aggression in the anxiogenic treatment, indicating that rank may be an important modulator of the effect of anxiety on aggression. Dominant individuals may use more RA additionally to PA when levels of anxiety increase, whereas in subordinate individuals levels of RA may already be near maximum, diminishing possible effects of increased anxiety.

Thirdly, anxiety is not the single key in understanding the mechanisms of RA and PA, as aggression in general is already the result of a complex interaction of several factors (Nelson & Trainor, 2007). For instance, impulsivity, defined as the tendency to act quickly and without regard to consequences, is known to be differentially associated with RA and PA (Derefinko, DeWall, Metze, Walsh, & Lynam, 2011). Unfortunately, behavioral measures of impulsivity in nonhuman primates (Fairbanks & Jorgensen, 2011) fail to separate different aspects of impulsivity as they do in humans (Miller, Flory, Lynam, & Leukefeld, 2003). Furthermore, in humans differences in the use of RA and PA are also influenced by other personality factors (Miller & Lynam, 2006). Indeed, in Barbary macaques, individuals showing high values in the personality factor "Confidence" were more aggressive and less anxious (named "fearful," Konečná, Weiss, Lhota, & Wallner, 2012). RA and PA are also related to differences at the cellular level, for example, the genetic setup of an individual. Genes like COMT and MAOA, which play a role in dopamine and serotonin turnover, have been associated with aggression in humans (Buckholtz & Meyer-Lindenberg, 2008; Qayyum et al., 2015) and nonhuman primates (Gutleb, Roos, Noll, Ostner, & Schülke, 2017; Newman et al., 2005). Both genes are linked to certain aggression types in humans, making them more prone to RA or PA (Buckholtz & Meyer-Lindenberg, 2008; Kolla, Attard, Craig, Blackwood, & Hodgins, 2014). Since behavior heavily relies on the brain, deficiencies in social information processing and cognitive functioning are also related to aggression subtypes (Kempes, Matthys, De Vries, & Van Engeland, 2005). Individuals ranking high on RA show below-average baseline activity in the frontal cortex (Nelson & Trainor, 2007). Transferring this finding to our study group, more reactively aggressive individuals might interpret situations as more threatening than they are,

and behave more aggressively according to this bias, resulting in higher levels of RA. Testing the cognitive predispositions of nonhuman primates and the severity of a perceived threat is a major methodological obstacle yet to be overcome.

This is to our knowledge the first study to systematically investigate the relative occurrence of RA and PA in a nonhuman primate. By studying both types of aggression and their link to anxiety we contribute to the understanding of why primates behave aggressively and add comparative data for testing the idea that human RA and PA have evolutionary origins within non-human primates (Wrangham, 2017). As distinct evolutionary pathways have been proposed for RA and PA (Wrangham, 2017) this further emphasizes the importance of distinguishing between aggression subtypes. Future studies incorporating genetic, cognitive, hormonal, developmental, and environmental factors will elucidate our understanding of their complex interplay in eliciting aggression. A better understanding of the origins and mechanisms of RA and PA may ultimately advance treatment programs for pathological levels of aggression.

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