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RESEARCH

Behavioral syndromes are associated with social plasticity and competence in a wild primate

Patrick J. Tkaczynski[1] · Liz A.D. Campbell[2] · Ann MacLarnon[3] · Bonaventura Majolo[4] · Caroline Ross[5] · Julia Lehmann[5]

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Abstract

The ability to optimize social behavior to varying socioecological circumstances has been termed "social competence" and relies on behavioral plasticity. Behavioral syndromes, i.e. consistent individual differences in intraindividual correlations among behavioral traits, appear to be a constraint on social competence, yet studies exploring this have largely been limited to experimental laboratory settings. Here, we tested the importance of behavioral syndromes to social competence in wild Barbary macaques (*Macaca sylvanus*), an endangered primate with established links between positive social relationships and survival. We studied two groups ($n = 27$ individuals) in which behavioral syndrome phenotypes were established in a previous study. Individuals with lower scores for the "excitable" phenotype (roughly equivalent to the "shy-bold" axis in other studies) showed greater plasticity compared to more "excitable" (i.e., "bolder") individuals in affiliative responses to the immediate social environment, being more likely to initiate grooming with larger numbers of conspecific bystanders present. Less excitable individuals increased their grooming social network connectivity to a greater degree compared to more excitable individuals in periods of higher anthropogenic pressure. During colder weather, less excitable individuals concentrated their grooming network into fewer ties, whereas more excitable individuals slightly increased their number of connections. Any changes in network connectivity in relation to socioecology were small, reflecting the fact that stability in social network position is a common phenomenon in various taxa. Overall, we show that behavioral syndrome phenotypes influence plasticity in affiliative behavior and thus may be a key factor in individual responses to the rapidly changing socioecologies of the Anthropocene.

Significance statement

Climate change and other anthropogenic factors are anticipated to increase the instability of the social and ecological environments of all group living animals, including humans. Positive social relationships are key for survival in many species, therefore, there is a growing interest in the flexibility of individuals in managing their social relationships against a rapidly fluctuating socioecological setting. Here we show that in wild Barbary macaques (*Macaca sylvanus*), a species that relies on social ties to survive in an extreme mountainous environment, behavioral syndromes (i.e., personality) predicted individual ability to change their levels of social engagement and network connectivity across various environmental gradients (i.e., changing numbers of social partners, human pressure, and shifts in temperature). This link between behavioral syndrome phenotypes and social plasticity has previously largely only been seen in laboratory settings. Therefore, our study is significant in that we show that this translates and is relevant in a wild setting and in a species with known links between its social behavior and its survival.

Keywords Personality · Plasticity · Sociality · Fitness · Networks

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Extended author information available on the last page of the article

Introduction

Among group-living animals, including humans, more social individuals tend to have improved fitness outcomes (Silk 2007; Cameron et al. 2009; Holt-Lunstad et al. 2010; Nuñez et al. 2015; Lehmann et al. 2016). Despite the benefits of being social, time and energy are limited resources for all animals (Dunbar et al. 2009; Korstjens et al. 2010; Grove 2012). Therefore, individuals often face choices about when to allocate resources to social interactions at the expense of other vital behaviors such as resting, foraging, parental care, travelling or vigilance (Dunbar 1992; Lehmann et al. 2007; Dunbar et al. 2009). Furthermore, to maximize the benefits of these social behaviors, individuals must also choose appropriate social partners to avoid social rejection or antagonism (Taborsky and Oliveira 2012; Mielke et al. 2018).

The social environment is vulnerable to fluctuation arising from changes in group-level factors, such as group size (Lehmann et al. 2007), sex ratios (L'Italien et al. 2012), and the stability of dominance hierarchies (Flack et al. 2006). Social time investment strategies may also be influenced by ecological variation. For example, in periods of low food availability or high predation risk, individuals may prioritize behaviors more closely related to survival (e.g. foraging or vigilance) rather than social interactions (Lehmann et al. 2007; Foster et al. 2012; Marshall et al. 2016). Lastly, individuals need to adjust social choices based on variation in the immediate social environment, i.e., the availability of social partners and potential bystanders to that social interaction (Kaburu and Newton-Fisher 2016; Mielke et al. 2018). Therefore, it maybe adaptive for individuals to be flexible in their own social choices and strategies to ensure dedicating appropriate time to socializing with appropriate partners or with the appropriate numbers of partners to maximize fitness in different socioecological settings. An individual's ability to adjust social behavior to the socioecological environment has been termed "social competence" (Taborsky and Oliveira 2012). Given the potential adaptive benefits of optimizing social living, there is growing interest in understanding which traits facilitate or constrain social competence in fluctuating environments (Jolles et al. 2019).

Behavioral syndromes, i.e. consistent individual differences in intraindividual correlations among behavioral traits (Dall et al. 2004; Sih et al. 2004), are anticipated to influence social decision making and thus social relationships and network formation (Krause et al. 2010). Behavioral syndromes may influence social relationships through homophily, whereby individuals of a particular behavioral phenotype occupy the same social niches as other individuals that behave in the same consistent fashion (Bergmüller and Taborsky 2010). Supporting this, social homophily based on behavioral phenotypes has been observed in humans and other animal taxa (Massen and Koski 2014; Aplin et al. 2015; Noë et al. 2016, 2018; Ebenau et al. 2019). Furthermore, studies across taxa reveal that individuals have relatively consistent social phenotypes that can persist over the course of the lifespan (Jacoby et al. 2014; Aplin et al. 2015; Fisher et al. 2016; Tkaczynski et al. 2020).

Behavioral syndromes may predict flexibility to fluctuations in the environment. In a number of fish studies, "bold" (consistently risk-prone and behaviorally proactive) individuals have been shown to have lower behavioral plasticity to changes in socioecological settings compared to "shy" (risk avoidant, reactive) individuals (Magnhagen and Bunnefeld 2009; Kurvers et al. 2010; Jolles et al. 2014, 2015, 2019; Kareklas et al. 2016; Ólafsdóttir and Magellan 2016). These results confirm assumptions of the "coping style" framework of behavioral syndromes, which distinguishes individuals as either behaviorally and physiologically "proactive" or "reactive" to stressful conditions (Koolhaas et al. 1999, 2010; Coppens et al. 2010). "Proactive" individuals tend to be more impulsive and risk taking and thus this phenotype tends to correlate with "boldness", whereas the "reactive" phenotype is similar to "shyness" (Koolhaas et al. 1999, 2010; Coppens et al. 2010). The coping style framework links these behavioral characteristics to physiology in that "proactive/bold" individuals are expected to have low levels of physiological stress activity and reactivity compared to reactive/shy individuals, meaning they are also expected to be less physiologically sensitive and behaviorally responsive to socioecological variation when compared reactive/shy individuals (Koolhaas et al. 1999, 2010; Coppens et al. 2010). These predicted relationships between behavioral syndromes and behavioral plasticity to the socioecological environment have typically been examined and confirmed through experimental manipulations in laboratory conditions (Kurvers et al. 2010; Jolles et al. 2014, 2015, 2019; Kareklas et al. 2016; Ólafsdóttir and Magellan 2016). However, whether behavioral syndromes affect social plasticity and social competence in natural settings, and in circumstances where social choices have established fitness consequences, merits further investigation.

In our study, we specifically test the relationship between behavioral syndromes and social plasticity and social competence in a wild primate, the Barbary macaque (*Macaca sylvanus*). Specifically, we examine (a) whether behavioral syndromes are associated with the degree to which individuals adjust social decision making in relation to changes in the immediate socioecological conditions (number of partners available, bystander composition, anthropogenic presence), and (b) whether behavioral syndromes are associated with the degree to which individuals adjust their social connectivity in relation to changes in the socioecology at a broader time scale (reproductive seasonality, anthropogenic presence, food availability, and temperature).

Barbary macaques are seasonal breeders (Fooden 2007; Young et al. 2013) and face extreme variation in climate with cold, snowy winters associated with peaks in mortality (Majolo et al. 2013b; McFarland and Majolo 2013). Furthermore, certain Barbary macaque groups occupy areas of varying anthropogenic activity and disturbance (Campbell 2019; Campbell et al. 2016, 2018a; Maréchal et al. 2011; Waterman et al. 2019). Importantly, in this species, individuals with strong social relationships, measured by social grooming interactions, have a reduced physiological stress response to colder weather (Young et al. 2014), while centrality in grooming social networks is associated with greater access to thermoregulatory huddles (Campbell et al. 2018b) and probability of survival during cold winters (Lehmann et al. 2016). Therefore, this species occupies a highly heterogeneous environment in which the cost-benefit ratio of social interactions, particularly grooming interactions, is likely to fluctuate, and in which social relationships are known to have fitness benefits.

Three behavioral syndromes have been quantified in Barbary macaques: Excitability, Sociability and Tactility (Tkaczynski et al. 2019a). On a behavioral level, Excitability is structurally similar to the "bold-shy" axis commonly studied in the behavioral syndrome literature (Sih et al. 2004; Tkaczynski et al. 2019a), with more "excitable" individuals behaviorally similar to bold individuals, and less "excitable" individuals behaviorally similar to shy individuals. Specifically, individuals with high "excitable" scores had higher frequencies of short-term (i.e., non-grooming) affiliative behaviors, namely embraces (both dyadic and triadic) and touches, as well as higher frequencies of facial displays (open mouths), contact aggressions, and tree shakes (a species specific behavior that may be related to frustration or displacement as often occurs after being aggressed). Conversely, individuals with low "excitable" scores would infrequently perform any of these behaviors (Tkaczynski et al. 2019a).

The similarity between "excitable" in Barbary macaques and the "bold-shy" phenotype in other species also appears to be physiological. In male Barbary macaques, more "excitable" individuals also have lower hypothalamic pituitary adrenal axis activity compared to less "excitable" individuals (Tkaczynski et al. 2019a), matching physiological predictions regarding the aforementioned "bold-shy/proactive-reactive" framework (Koolhaas et al. 1999). For the present study, only the Excitability syndrome was considered. Although the Sociability (characterized by time in proximity with other individuals and in spatially central positions within the group) and Tactility (characterized by rates of self- and allogrooming) behavioral syndromes identified in Barbary macaques may influence social plasticity in this species, they are not readily comparable to those more common in behavioral syndrome literature (Tkaczynski et al. 2019b). Furthermore, for Tactility, the analysis may result in issues of circularity when examining how grooming decisions vary in different circumstances. Therefore, we focus on Excitability and refer to this behavioral syndrome as Excitability/Boldness in the current study to be consistent with former research on this species yet make the results relevant and comparable to the broader behavioral syndrome literature.

Using detailed behavioral data from one autumn and two winter periods, we examined whether Excitability/Boldness is associated with plasticity in grooming social decision making and social connectivity (grooming social network centrality). We predicted that more challenging conditions (e.g., breeding vs. non-breeding season, greater anthropogenic presence in the form of higher numbers of tourists, lower availability of high-quality food, lower temperatures, greater numbers of bystanders or higher-ranking bystanders) would require energy to be reallocated to appropriately cope with said conditions (e.g., increase foraging activity), which in turn would inhibit social engagement, reduce the probability to engage in grooming, and lead to reductions in grooming social network centrality. We also predicted that less "excitable" macaques will demonstrate greater plasticity in social behavior compared to more "excitable" individuals based on studies of the bold-shy axis conducted in laboratory fish studies (Magnhagen and Bunnefeld 2009; Jolles et al. 2014, 2019; Ólafsdóttir and Magellan 2016) and predictions regarding plasticity based on the aforementioned "bold-shy/proactive-reactive" framework for behavioral syndromes (Koolhaas et al. 1999, 2010; Coppens et al. 2010).

Methods

NOTE: It was not possible to record data blind because our study involved focal animals in the field.

Study site and subjects

We collected data from two groups of wild Barbary macaques located in Ifrane National Park, Morocco (33° 24'N, 05° 12'W; elevation 1,500-2,000 m above sea level). Both groups were habituated to human researchers and were observed from approximately 7 m, with all subjects individually recognized. The subjects of this study were the adult males and females of each group ($n = 12$ [5 males] in the Blue group; $n = 15$ [6 males] in the Green group). Adults were defined as sexually mature individuals, which was based on body size in both sexes, the presence of anogenital swellings during mating season for females, and descended testicles and large canines for males (Fooden 2007).

Behavioral data collection

Behavioral data were collected to quantify behavioral syndromes, determine dominance hierarchies, analyze variation in behavioral time allocation and construct social networks. We used a combination of focal, scan, and *ad libitum* sampling (Altmann 1974), collected between October 2013 and March 2014, and between February 2015 and April 2015. Behavioral data were collected from near-dawn to near-dusk. Focal observational samples lasted 30 min and the order of subjects was pseudorandomized, with no individual sampled more than once on the same day.

During focal observations, the duration of state behaviors (foraging, feeding, resting, traveling, vigilance, play and grooming) were recorded continuously (Tkaczynski 2016), while the frequency of contact, proximity, agonistic, dominance and solitary behaviors, as well as facial displays (open mouth, bearing teeth) and vocalizations, (grunts, barks, screams, teeth chatters) were recorded as point events (Fischer and Hammerschmidt 2002; Tkaczynski 2016). For feeding behavior, we also noted what the individuals were eating, first at a broad categorical level (leaves/grass; insects; mushrooms; fruit/nuts; human-produced), then specific species noted if they were possible to identify (e.g., acorns from *Quercus ilex* and *Quercus faginea* oaks). At the start and end of the focal samples, proximity scans were conducted to record the number of conspecific group members, as well as humans (specifically tourists and vendors at eco-tourism sites) within 0–1 m, 1–5 m and 5–10 m of the subject of the focal sample. Observers also visually assessed whether subjects were central or peripheral within the group in terms of spatial position; individuals were considered peripheral if they were the outermost individual at the front, rear, or side of the group, and otherwise were considered to be central. The proximity and spatial data were incorporated into the behavioral syndrome quantification; the numbers of humans in proximity were used as a predictor variable in our models (see below). Additional aggression and dominance interactions were collected *ad libitum*; these aggression and dominance data were used in the dominance interactions and to assess whether focal individuals had received aggression on a given day prior to focal sampling.

All observation data was collected by a team including PJT, LADC and six research assistants. The data were collected using a Psion handheld computer and The Observer XT software version 8.0 (Noldus Information Technology 2008). Inter-observer reliability tests using intra-class coefficients (ICC; (Shrout and Fleiss 1979) were conducted for all researchers: researchers collected behavioral data only once they had recorded two consecutive tests where the frequency and duration of variables recorded were significantly reliable compared to those recorded by PJT (ICC >0.95; $p<0.05$).

Socioecological variables

To account for **seasonality**, we differentiated between mating and non-mating seasons. The dates of the mating seasons were determined by the first and last observed copulation with ejaculation within each group (Young et al. 2013): mating season 1 (Blue group: 11-Oct-2013:20-Jan-2014; Green group: 9-Oct-2013:9-Jan-2014), non-mating season 1 (Blue group: 21-Jan-2014:5-Mar-2014; Green group: 10-Jan-2014:6-Mar-2014) and non-mating season 2 (4-Feb-2015:18-Apr-2015 for both groups).

To quantify **anthropogenic presence**, at the start of each focal observation we estimated the number of humans (excluding researchers doing the observations) present within the radius of the group spread of the study group. We recorded the number of humans using a logarithmic index: 0 (no humans), 1 (between 1 and 10 humans), 2 (between 11 and 100 humans), and 3 (above 101 humans) humans present (Price et al. 2014). Using this index allowed for rapid and thus practical assessments of anthropogenic presence concurrent to behavioral data collection (Price et al. 2014). In addition, during the proximity scans at the start and end of focal samples, we recorded the number of humans within 10 m of the focal subject.

To quantify **high quality food in diet**, we calculated the proportion of high quality food items in the diet of subjects (Thompson and Wrangham 2008). Barbary macaques are dietary generalists that occupy a typically nutrient poor habitat and rely predominantly on herbaceous plants, shrubs, and grasses (Ménard 2002). However, during autumn and winter seasons, they preferentially feed on more nutrient-rich items, namely the acorns of oak trees (*Quercus ilex* and *Quercus faginea*), and the berries of hawthorn bushes (*Crataegus* spp) (Ménard 2002; Waterman et al. 2019). Therefore, for each day, we recorded the proportion of the total time spent feeding that was spent feeding on either acorns or hawthorn berries.

As **daily minimum temperature** increases physiological stress (Young et al. 2014) and the likelihood of the macaques to form larger thermoregulatory huddles (Campbell et al. 2018b), we used this measure as our temperature variable in our analyses. During 2013 and 2014, air temperature was recorded hourly when in the presence of subjects using a 3500 Kestrel Pocket Weather Station. In 2015, due to a change in protocol relating to associated projects, air temperature was recorded only when the subjects left or entered sleeping trees in the morning and evening, respectively. In all time periods, temperatures were recorded in the shade and with the device 1.5 m above the ground. In total, temperature recordings were made on 111 days during the entire study period, an average (±standard deviation) of 13.75 (±6.43) daily temperature recordings per study month.

Statistical analysis

All data preparation, analysis, and visualization were performed in R 3.6.3 (R Core Team 2020) using the RStudio interface (RStudio Team 2021). For data cleaning, preparation, and the generation of Figs, we used a combination of base R functions and the *tidyverse* suite of packages (Wickham et al. 2019).

Dominance rank calculations

Dyadic interactions of aggression (contact and non-contact) and submission were used for rank calculations. We used a likelihood-based adaptation of the Elo rating approach (Neumann et al. 2011; Foerster et al. 2016; Mielke et al. 2018). Elo ratings reflect the probability of an individual to 'win' in a dominance interaction with another individual, with traditional approaches applying a fixed starting value, k, to all individuals (Neumann et al. 2011). The likelihood modification uses a maximum-likelihood estimation to optimize the starting k for all individuals, such that all individuals enter the hierarchy with individual k values (Foerster et al. 2016; Mielke et al. 2018). We assigned continuous Elo ratings to subjects for each day of observation; each score was standardized between 0 (lowest rank) and 1 (highest rank) within each group.

Behavioral syndrome quantification

In a previous study (Tkaczynski 2016; Tkaczynski et al. 2019b), three independent, non-correlated and consistently expressed behavioral syndromes have been identified in our study subjects: Excitability, Sociability and Tactility. In brief, behavioral syndrome quantification involved two stages: (i) testing the repeatability of behavioral variables across the three seasons; (ii) identifying correlations among the repeatable behavioral variables. The repeatability of behavioral variables was estimated using the *rptr* package (Stoffel et al. 2018); factor analyses using the *psych* package (Revelle 2018) identified correlations among repeatable behaviors. The sums of the mean values of the behavioral variables that loaded onto a particular factor were used to create individual (subject-specific) scores for a particular behavioral syndrome. One score per behavioral syndrome per season was allocated to each subject, with higher scores indicating greater expression of the syndrome (Tkaczynski et al. 2019b). For the reason outlined above, for the present study, only scores for the Excitability syndrome were considered.

Social plasticity in decision making in relation to current social environment

In total, we collected 1,236 h of behavioral data, a mean ± SD of 46 ± 2 h per subject.

To determine individual choices about social grooming in relation to the current social environment, we first merged the activities in our focal data into two categories: grooming (included the former variables of giving grooming and of simultaneous grooming) and other activities (co-feed, feed, foraging, foraging-feeding, rest, self-groom, receiving grooming, travel, vigilance). Note, we included "receiving grooming" as separate from our "grooming" category, as we wanted to characterize variation in proactive social decisions about social time allocation from the perspective of the focal animal, i.e., an individual can be resting, approached by another individual and groomed, without making effort to participate in that social interaction.

We then converted the first 15 min of each focal sample into a single datapoint, recording whether or not the subject groomed an adult partner during this interval. We focused on adult grooming partners as relationships among adults have established fitness outcomes in this population (Campbell et al. 2018b; Lehmann et al. 2016; Young et al. 2014). The first 15 min was chosen as the duration of the interval, as this allowed us to use the proximity scan at the start of the focal to calculate, and thus include in our models the potential social partners and bystanders within 10 m of the subject, while allowing sufficient time for the subject to make a social decision to groom another individual or not. We excluded all intervals where the subject was out-of-sight for more than 1 min and any focal sample in which the focal subject was already engaged in grooming at the start of the focal. We further excluded all datapoints for which we were missing data on our main predictors of variation in social time allocation.

To test variation in social plasticity to the current social environment, we used a generalized linear mixed effect model (model 1) with a Bernoulli error structure and a logit link function; the dependent variable was each interval/choice and whether grooming with an adult partner occurred during that interval.

Our main predictors were the Excitability/Boldness score for each individual in interaction with the following socio-ecological variables:

- anthropogenic presence (number of humans within 10 m),
- number of conspecific bystanders within 10 m of subject, and.
- maximum rank difference (Elo score difference on day of observation) between the focal and the highest-ranking conspecific within 10 m of the subject.

We included control variables of the dominance rank (Elo score of subject on day of focal sample) and sex of the focal subject, the time of day of the interval (calculated as proportion of day, e.g. 12:00 = 0.50; including as a linear and a quadratic term to account for potential peaks in activity around dawn and dusk), the minimum temperature (°C) recorded that day, and group membership (Blue or Green) of the individual.

The random effect of individual identity was included in the model, as well as random slopes for anthropogenic presence, number of conspecifics within 10 m, maximum rank difference, dominance rank, time of day (liner and quadratic terms) and the minimum temperature within individual identity. These time allocation models also included a random effect (random intercept) of day of sampling to account for potential autocorrelation or non-independence of response, predictor, or control variables.

Plasticity in social connectivity in relation to fluctuating socioecology

Network construction and metrics For the network analyses, for each group, directed and weighted social networks based on dyadic grooming data were constructed, here focusing on all grooming bouts between adult partners. We aimed to generate grooming networks spanning short enough periods to determine potential short-term adjustments in social connectivity to fluctuations in socioecology. However, we also wanted to generate networks with sufficient observation time that individuals had the opportunity to interact with social partners. To determine the most appropriate temporal aggregation of our grooming data, we used the *netTS* R package (Bonnell and Vilette 2021). This package uses a "moving window" and bootstrapping approach to assess the robustness of networks aggregated at different length timespans.

On average (± standard deviation), each individual was observed at least once every 2.29 (± 0.07) days; the maximum interval between two focal samples for an individual within each field season was 17 days. Therefore, we specified our grooming data to be aggregated at 15-, 25-, and 40-day timespans, with a 5-day moving window. Using the 'check.windowsize' function of *netTS*, we performed 1,000 bootstrap comparisons between node degree (the number edges connected to the node) calculated in observed and bootstrapped networks for each of the three timespans. This function calculates the cosine similarity between the observed and bootstrapped metrics. The sensitivity to missing edges was assessed by bootstrapping from either 100, 80 or 70% of the original data.

The results of this procedure were visually assessed and are presented in Figs S1 and S2 of the supplementary materials. The 25-day aggregation was clearly preferable to the 15-day aggregations, with no marked improvement with a 40-day aggregation. Therefore, for the network analyses, we split the observational data into nine, 25-day time windows. This equated to roughly one month of data collection and guaranteed each individual was observed at least once, even in time windows with fewer observation days due to field conditions (extreme weather, difficulty finding groups). Subjects were observed for mean ± SD of 5.69 ± 1.05 h per time window (Table S3).

For each group and for each time window, we used Bayesian inference to quantify edge weights (grooming given and received) between dyads, and then construct social networks (Hart et al. 2021; Redhead et al. 2021). This approach allowed us to incorporate and measure uncertainty in the edge weights, which may be susceptible to variable sampling effort or measurement errors in observing each individual within the dyad, or interactions between particular dyads (Hart et al. 2021).

For each group and each time window, we fitted a mixed-effect binomial model (i.e., 9 models per group). In each model, the response variable was how many focal observations individuals within a dyad groomed one another given the opportunity (i.e., the total number of focal observations each individual was observed in) within a given time window. We included actor and recipient identities as a random effect, with this identity incorporating the direction of the grooming interaction. For example, if individual A was grooming individual B, the dyad identity for that interaction was "A-B"; if B was grooming A, the identity would be "B-A".

From these models (one for each group), we used the posterior draws ($n = 3{,}000$; see Model Fitting and Validation below) for the dyad identities to calculate the median edge weights for each dyad in each time window, i.e., the proportion of time individuals within a particular dyad either gave or received grooming given the opportunity to groom one another within a particular time window. Using the median edge weights of the posterior distribution, which are equivalent to the "simple ratio index" (Whitehead 2008; Hart et al. 2021), we constructed directed and weighted social networks. Figs S4-S21 in the supplementary materials illustrate each network within each time window ($n = 9$) for the

Blue and Green groups, as well as the uncertainty of edge estimates.

For each individual in each of the networks generated from the posterior draws, we calculated two metrics: (a) *out-degree*, the number of edges connected to the node (scaled between 0 and 1 to account for differences in group sizes), i.e. the number of partners to which the individual directed grooming; and (b) *out-strength*, the sum of all edge weights connected to the node, i.e. the total grooming rate per individual to all partners (Farine and Whitehead 2015). We chose these particular metrics as they have been related to fitness outcomes in this species and population previously (Lehmann et al. 2016; Campbell et al. 2018b). As these metrics were derived from the median posterior edge weights between each node, they represent the most probable out-degree or out-strength value for each individual based on sampling effort and potential measurement error for each individual in the study (Hart et al. 2021).

Social networks were constructed and illustrated, as well metrics calculated, using the *igraph* R package (Csardi and Nepusz 2006).

Social connectivity models For each time window of each group, we calculated the mean anthropogenic presence index, mean daily proportion of high-quality food in the diet, and mean daily minimum temperature (°C) during this observation period. Additionally, each network of each group was demarked as occurring during either in a mating or non-mating season.

During time window 4, the Blue group transitioned from a mating season to a non-mating season (55.85% of observations occurred during the non-mating period), therefore, we did not include the metrics derived from this network in the analysis.

For both social connectivity models ((a) out-degree, (b) out-strength), individuals social network metrics (out-degree or out-strength) were the dependent variables and our main predictors were the interactions between Excitability/Boldness score and mean anthropogenic presence index, mean daily proportion of high-quality food in the diet, and mean daily minimum temperature (°C), and seasonality (mating or non-mating) during each time window. The interactions were fit to measure plasticity (rate of change) in social connectivity given the socioecological gradients for different behavioral syndrome phenotypes. We included the sex and mean rank (Elo score) of each individual for each network as a control variable. The random effect of individual identity was included in the model, as well as random slopes for each of our socioecological predictors within individual identity.

Both the degree (model 2) and strength (model 3) models were fitted with Beta error structure and a logit link function.

Social network metrics are inherently non-independent variables and, therefore, do not meet the assumptions of responses in most frequentist statistical approaches, especially using null hypothesis testing (Croft et al. 2011; Franks et al. 2021). Using Bayesian inference rather than null hypothesis testing, the probability of a value occurring is determined not by its observed frequency alone, and we can calculate the uncertainty about any such probability (Brent et al. 2017).

Model fitting and validation

For our analyses we employed a Bayesian approach with all models fitted and estimated using Hamiltonian Monte Carlo methods and Stan software (Stan Development Team 2021) with the *brms* package (Bürkner 2018) within R.

Prior to model fitting, any potential issues of covariation or collinearity between our fixed effects were inspected via pairwise plots, pairwise correlations, and variance inflation factors (VIFs). Pairwise plots and correlation coefficients were generated using the 'covees' function of the *GGally* package (Schloerke et al. 2020); VIFs were generated using the 'VIF' function of the *car* package in R (Fox and Weisberg 2011). In the final presented models, there were no issues with collinearity or covariance among the variables (maximum VIF <4.5; maximum rho <0.7; Table S22 and Figs S23-24 in the supplementary materials). In the social connectivity models, mean anthropogenic presence was collinear with group identity (VIF >10.0); therefore, we included only the mean anthropogenic presence variable in those models.

For all models, numeric variables were standardized as z-scores. We fit models with weakly regularizing priors for the fixed effects ($\beta \sim \text{Normal}(0,1)$). For the priors for the components of the random effects, we used the default priors provided by the get*_prior* function of brms, namely a weakly regularizing half student-t prior ($df=3$, scale parameter $=10$) for the random intercepts, and a uniform LKJ Cholesky prior ($\eta=1$) for covariance matrices of the random slopes.

For all models, we specified three chains of 5000 iterations, 2000 of which were devoted to the warm-up. Sampling diagnostics (Rhat <1.01) and trace plots confirmed chain convergence for all models. Effective sample sizes confirmed no issues with autocorrelation of sampling for all models (Tables S25-27 list all effective samples sizes and Rhat values for the main models presented).

To interpret the strength and uncertainty of the associations between our predictor variables and outcomes, we report the model estimate, 90% credible intervals and the proportion of posterior (p+or p−) supporting the direction (positive or negative) of the model estimate of the associations (McShane et al. 2019; McElreath 2020; Martin et al. 2020). We considered effects whose direction was supported by more than 95% of the posterior distribution to be well supported, and those whose direction was supported by more than 90% of the posterior distribution to be weakly supported.

All models were validated using posterior predictive checks (see Figs S28-32 in the supplementary materials for plots of these checks).

Results

Model 1: plasticity in social decision making in relation to current social environment

A total of 1,467 datapoints from 27 subjects were included into the social decision-making analysis. Overall, subjects engaged in grooming in 164 (11.179%) of these samples.

Table 1 details the results of Model 1. The probability for subjects to initiate grooming with another adult partner increased with the number of conspecifics within proximity of the subject, and less “excitable” individuals (those with lower Excitability/Boldness scores) clearly responded more strongly to the number of conspecifics within proximity compared to more “excitable” individuals (those with higher Excitability/Boldness scores) (p- = 0.982; Fig. 1). Using the median values across all draws from the posterior distribution, more “excitable” individuals saw a 10.865% increase (from 0.054 to 0.060) in their probability to initiate grooming when going from having 0 to 5 conspecifics within proximity, whereas for less “excitable” individuals, the probability to groom increased by 55.168% (from 0.078 to 0.138).

The model also found that the probability for subjects to interact socially was lower for higher ranking individuals (p- = 0.908), males were less likely to initiate grooming (p- = 0.963), while across all individuals, the probability to initiate peaked in the middle of day (p- = 0.998; Fig. S30 in supplementary materials).

To check our results were not driven by the length of social choice window interval, we also re-ran this analysis using a shorter interval length of 5 min, or using the whole focal observation of 30 min (i.e. the whole focal sample length). Tables S33 and S34 in the supplementary materials provide the model estimates from these models; Fig. S35 in the supplementary materials shows the posterior predictive checks for both models. For both models, the direction of

Table 1 Fixed and random effect/slope estimates from “Plasticity in social decision making in relation to current social environment” model. Estimates reflect conditional probabilities of focal individual initiating grooming with another adult. Fixed effect estimates supported by more than 95% of the posterior are highlighted in bold; fixed effect estimates supported by more than 90% of the posterior are highlighted in italics. For categorical variables, the reference level is in parentheses

Coefficient	Estimate	Est.Error	Q5	Q95
Intercept	−1.910	0.343	−2.504	−1.375
Excitability/Boldness	0.230	0.198	−0.095	0.560
Number of humans within 10 m	*−0.204*	*0.242*	*−0.665*	*0.100*
Number of conspecifics within 10 m	0.163	0.128	−0.042	0.371
Maximum rank difference with bystander	0.145	0.156	−0.108	0.410
Daily minimum temperature	0.098	0.118	−0.094	0.288
Individual rank	*−0.286*	*0.219*	*−0.649*	*0.071*
Time of day	**−0.347**	**0.122**	**−0.553**	**−0.152**
Time of day2	**−0.364**	**0.140**	**−0.611**	**−0.155**
Sex (female)	**−0.912**	**0.513**	**−1.737**	**−0.070**
Group (Blue)	0.105	0.360	−0.478	0.705
Excitability/Boldness : Number of humans within 10 m	−0.001	0.163	−0.271	0.255
Excitability/Boldness : Number of conspecifics within 10 m	**−0.228**	**0.118**	**−0.428**	**−0.046**
Excitability/Boldness : Maximum rank difference with bystander	0.023	0.126	−0.192	0.224
Random effects and slopes				
Day of observation: Intercept	0.305	0.178	0.034	0.613
Individual identity: Intercept	0.612	0.231	0.227	1.003
Individual identity: Slope for Number of humans within 10 m	0.323	0.279	0.023	0.864
Individual identity: Slope for Number of conspecifics within 10 m	0.268	0.165	0.030	0.562
Individual identity: Slope for Maximum rank difference with bystander	0.399	0.200	0.072	0.733
Individual identity: Slope for Daily minimum temperature	0.289	0.162	0.040	0.571
Individual identity: Slope for Individual rank	0.252	0.195	0.020	0.620
Individual identity: Slope for Time of day	0.181	0.137	0.014	0.444
Individual identity: Slope for Time of day2	0.274	0.159	0.037	0.548

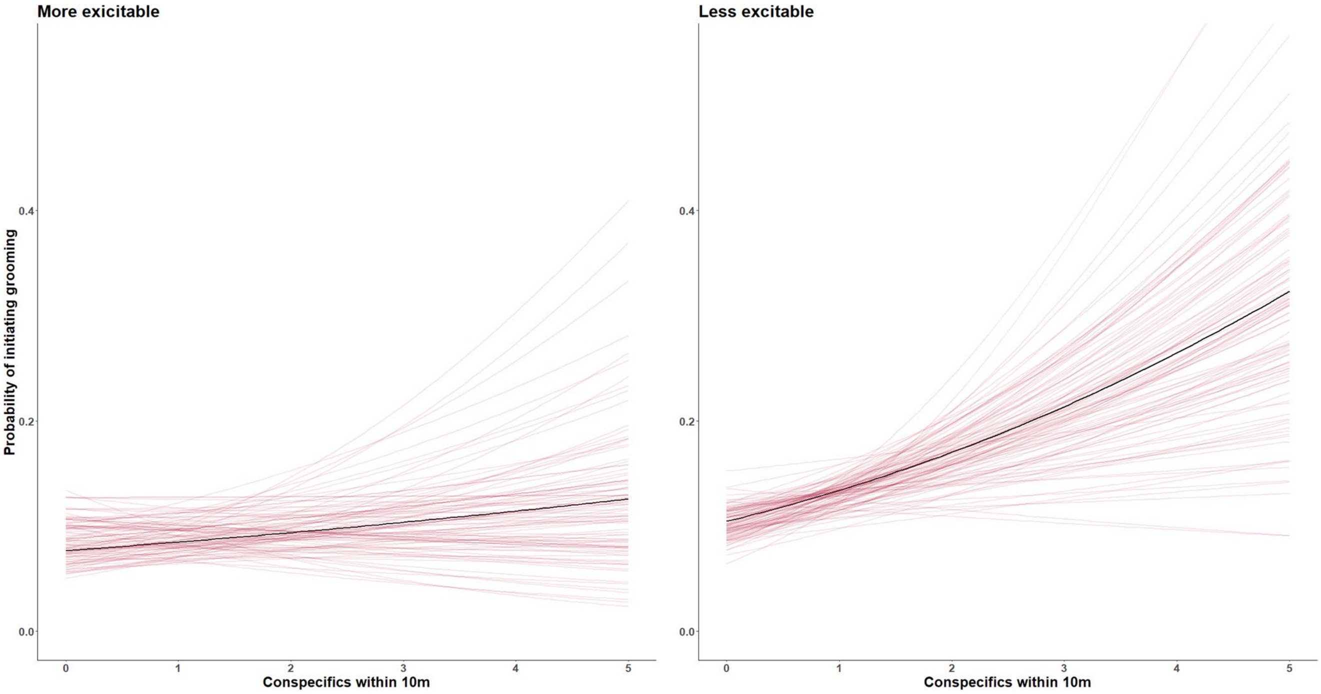

Fig. 1 Predicted probability of individuals initiating grooming contingent on behavioral syndrome score and the number of conspecifics within 10 m of the focal subject. The interaction between behavioral syndrome score and conspecifics in proximity was modelled using continuous variables; the categorization of "More excitable" and "Less excitable" is for illustrative purposes only. For this plot, subjects were classified as "More excitable" if they had an Excitability/Boldness score greater than the population mean and as "Less excitable" if they had an Excitability/Boldness score less than or equal to the population mean. Colored lines represent posterior draws ($n=100$), the solid black line represents the means of all posterior draws ($n=4{,}500$)

the estimate for the interaction between Excitability/Boldness score and the number of conspecifics within 10 m was the same as in our main model; for the 5-minute interval model the direction of the estimate had weaker support than our main model (p- = 0.934), whereas the direction of the estimate had stronger support in the 30-minute interval model (p- = 0.992).

Models 2 and 3: plasticity in social connectivity

Out-degree

A total of 231 network metrics from 27 subjects were included into model 2, examining changes in network out-degree in response to socioecological predictors.

Table 2a details the results of "Model 2: Plasticity in social connectivity – out-degree". "More excitable" and "less excitable" individuals (those with higher and lower Excitability/Boldness scores respectively) showed slightly different responses to changes in anthropogenic presence and mean minimum temperatures (Fig. 2a, b).

"Less excitable" individuals in general had slightly higher network out-degrees compared to "more excitable" individuals, while both "more" and "less excitable" individuals showed slight increases in network connectivity with increasing levels of anthropogenic presence (p+=0.966). Using median values from posterior draws, "more excitable" individuals had network out-degrees 9.115% higher in time windows of high anthropogenic presence (i.e., above the mean anthropogenic index across the study period) compared to time windows with low anthropogenic presence (i.e., below the mean). "Less excitable" individuals had network out-degrees 21.396% higher across the same gradient.

Although associated with some uncertainty (p- = 0.932), the interaction between Excitability/Boldness and mean minimum temperature within a time window showed that "more" and "less excitable" individuals differed in the direction of their response to this gradient. When comparing network out-degrees in time windows with lower temperatures (below the mean minimum temperature across the study period) to higher temperatures (above the mean), "more excitable" individuals decreased their network out-degrees by 14.337%, whereas "less excitable" individuals increased their network out-degrees by 5.401%. It is worth noting that for all individuals these changes in network out-degree were small in magnitude (changes of 0.022 and 0.013 for "more" or "less excitable" individuals respectively).

In model 2, we also observed that across all individuals, network out-degree was lower in non-mating seasons (p- = 0.998) and in males (p- = 0.963).

Table 2 Fixed and random effect/slope estimates from models exploring “Plasticity in social connectivity”. Part (a) shows the estimates from the model with out-degree as the response, (b) the estimates with strength as the response. Fixed effect estimates supported by more than 95% of the posterior are highlighted in bold; fixed effect estimates supported by more than 90% of the posterior are highlighted in italics. For categorical variables, the reference level is in parentheses

Coefficient	Estimate	Est.Error	Q5	Q95
(a) Out-degree				
Intercept	−0.875	0.205	−1.213	−0.532
Excitability/Boldness	0.060	0.148	−0.187	0.307
Season (mating)	**−0.616**	**0.188**	**−0.920**	**−0.310**
Mean anthropogenic index	−0.021	0.146	−0.262	0.218
Food availability	0.011	0.106	−0.161	0.187
Mean minimum temperature	−0.020	0.068	−0.131	0.090
Rank	−0.127	0.122	−0.320	0.074
Sex (female)	**−0.626**	**0.356**	**−1.225**	**−0.056**
Excitability/Boldness : Season (mating)	−0.048	0.173	−0.330	0.245
Excitability/Boldness : Mean anthropogenic index	**0.241**	**0.138**	**0.020**	**0.472**
Excitability/Boldness : Food availability	0.078	0.115	−0.112	0.265
Excitability/Boldness : Mean minimum temperature	*−0.098*	*0.068*	*−0.210*	*0.007*
Random effects and slopes	**Estimate**	**Est.Error**	**Q5**	**Q95**
Individual identity: Intercept	0.530	0.148	0.301	0.784
Individual identity: Slope for Season (mating)	0.528	0.213	0.151	0.877
Individual identity: Slope for Mean anthropogenic index	0.257	0.165	0.028	0.547
Individual identity: Slope for Food availability	0.166	0.118	0.015	0.387
Individual identity: Slope for Mean minimum temperature	0.179	0.091	0.032	0.336
(b) Strength				
Intercept	−1.360	0.135	−1.584	−1.141
Excitability/Boldness	−0.006	0.101	−0.169	0.163
Season (mating)	**−0.616**	**0.126**	**−0.825**	**−0.407**
Mean anthropogenic index	−0.062	0.064	−0.169	0.045
Food availability	−0.004	0.063	−0.111	0.097
Mean minimum temperature	**0.080**	**0.034**	**0.025**	**0.135**
Rank	−0.033	0.067	−0.143	0.076
Sex (female)	*−0.274*	*0.175*	*−0.558*	*0.014*
Excitability/Boldness : Season (mating)	0.063	0.104	−0.106	0.237
Excitability/Boldness : Mean anthropogenic index	0.058	0.057	−0.036	0.154
Excitability/Boldness : Food availability	0.004	0.061	−0.097	0.104
Excitability/Boldness : Mean minimum temperature	0.011	0.032	−0.041	0.062
Random effects and slopes				
Individual identity: Intercept	0.509	0.089	0.375	0.662
Individual identity: Slope for Season (mating)	0.449	0.085	0.319	0.595
Individual identity: Slope for Mean anthropogenic index	0.064	0.050	0.005	0.163
Individual identity: Slope for Food availability	0.104	0.066	0.012	0.222
Individual identity: Slope for Mean minimum temperature	0.110	0.035	0.058	0.170

Out-strength

Again, a total of 231 network metrics from 27 subjects were included into model 3, examining changes in network strength in response to socioecological predictors.

Table 2b details the results of “Model 3: Plasticity in social connectivity – strength”. In this model, we found no meaningful differences in the responses between “more” and “less excitable” individuals. However, across all individuals, network strength was lower in non-mating seasons (p- = 1.000) and in males (p-= 0.943) but increased in time windows with warmer minimum temperatures (p+=0.991).

Discussion

Studies of the links between behavioral syndromes, social plasticity, and social competence in the wild are rare (Couchoux et al. 2021); our study addresses this gap in the literature and validates findings previously found in the laboratory in a more ecologically valid and natural setting. Furthermore, the social traits we have studied in Barbary macaques have established links with fitness outcomes in this species (Lehmann et al. 2016; Campbell et al. 2018b). As all wild animals (and indeed humans) are living in rapidly changing environments (Otto 2018), our study lends

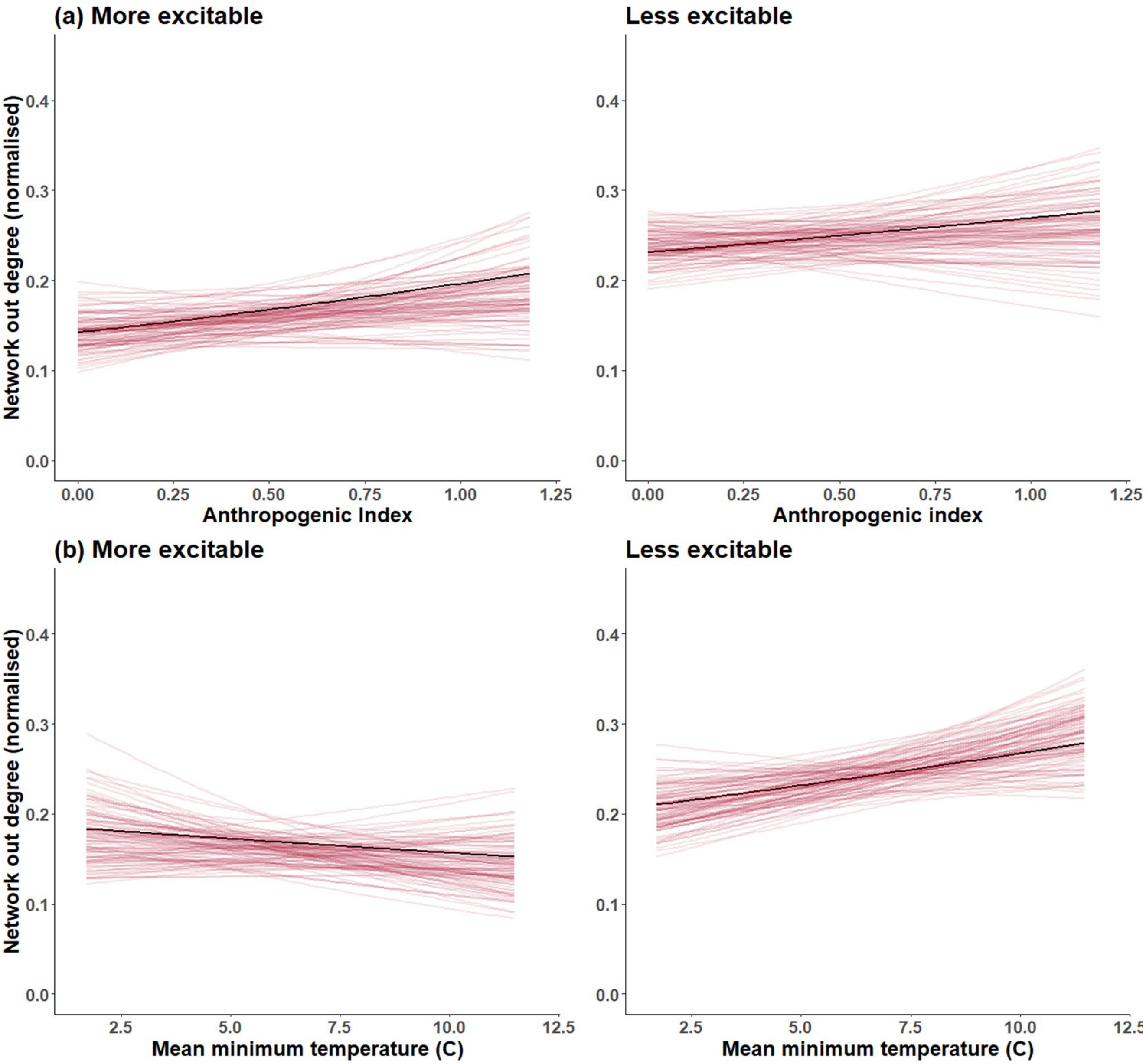

Fig. 2 Associations between grooming network out-degree and the interaction between (**a**) Excitability/Boldness score and mean anthropogenic index within a time window, and (**b**) mean minimum temperature (°C) within a time window. The interactions were modelled using continuous variables; the categorization of "More" and "Less excitable" is for illustrative purposes only. For this plot, subjects were classified as "More excitable" if they had an Excitability/Boldness score greater than the population mean and as "Less excitable" if they had an Excitability/Boldness score less than or equal to the population mean. Colored lines represent posterior draws (*n* = 100), the solid black line represents the means of all posterior draws (*n* = 4,500)

weight to the significance of behavioral syndromes in mediating individual ability or motivation to adjust behaviors to shifting social and ecological settings.

In our study, Barbary macaques adjusted their social decision making based on the number of bystanders and showed marginal changes in their social connectivity across different socioecological gradients. The extent to which individuals adjusted either their social decision making or connectivity was in part related to their behavioral syndrome phenotypes. In Barbary macaques, individuals were more likely to initiate grooming when in the presence of a larger number of bystanders, with "less excitable" individuals far more responsive to changes in bystander composition compared to "more excitable" individuals. Given the behavioral and physiological parallels between the bold-shy/proactive-reactive axes and the Excitability phenotype found in Barbary macaques (Tkaczynski et al. 2019a, b), our study lends further support to the "coping style" framework and replicates the aforementioned laboratory findings in other taxa (Magnhagen and Bunnefeld 2009; Jolles et al. 2014, 2019; Ólafsdóttir and Magellan 2016).

In the short-term, animals should adjust their decisions to engage in social interactions based on immediate social and ecological circumstances in order to optimize the cost-benefit ratio of any social engagement (Bshary et al. 2001; Mielke et al. 2018). In our study, Barbary macaques were generally more likely to initiate an affiliative grooming bout when there were more partners available, with "less excitable" individuals more sensitive to partner availability, i.e., these individuals were more likely to initiate grooming in larger aggregations compared to "more excitable" individuals when presented with the same social conditions. Both the rank differentials and degree of social bonds with bystanders are predictors of grooming initiation and interventions (interrupting grooming bouts of others) in several primate species (Kaburu and Newton-Fisher 2016; Mielke et al. 2018, 2021), including Barbary macaques (McFarland and Majolo 2012; Roubová et al. 2015). In our study, we did not have long-term affiliative data with which to calculate bonds; however, it is notable that we did not observe any sensitivity to the rank of bystanders (although higher ranking individuals were generally less likely to initiate grooming). Barbary macaques are considered to have a relatively egalitarian social system, which may mean rank is less influential in partner choice compared to more despotic species (Balasubramaniam et al. 2018; Moor et al. 2025). Meanwhile, our observed effect of grooming being more likely the higher the number of available social partners might reflect larger bystander sizes increasing the probability of bond partners being part of the available social cohort. It is interesting that "less excitable" individuals were more motivated to initiate grooming in larger aggregations as this might leave them vulnerable to interventions, something we might expect them to want to avoid. However, grooming interventions have not been specifically studied in this species; it may be strategically better to receive an intervention than outright aggression if not involved in a grooming bout. Future work in this species can hopefully incorporate longer-term affiliative data and more specific data collection on motivations to groom and intervene in grooming to address this gap in our study.

Adjusting social behavior to changes in the socio-ecological environment has been termed "social competence"(Taborsky and Oliveira 2012). "Less excitable" Barbary macaques are more responsive to changes in bystander composition, yet whether this is a fitness-enhancing or strategic adjustment remains unclear. "Less excitable" individuals may be taking more opportunities to reinforce bonds with key social partners when these opportunities present themselves. Similarly, in larger aggregations of individuals, these individuals may be more likely to initiate grooming to offset increased risks of agonism. In our study, aggressions were rare prior to observations meaning probabilities to initiate grooming are unlikely to have been driven by post-conflict dynamics (McFarland and Majolo 2011). As such, it remains unclear what advantage (if any), "less excitable" individuals gain from their sensitivity and plasticity compared to "more bold" individuals.

In contrast, for our measures of social connectivity we can make more potential predictions about the fitness benefits of behavioral syndrome-mediated adjustments in the face of changing socioecological settings. For Barbary macaques, anthropogenic pressures increases anxiety and stress (Maréchal et al. 2011), while grooming (both giving and receiving) is associated with reduced physiological stress levels (Shutt et al. 2007; Sonnweber et al. 2015), although not necessarily reduced anxiety (Semple et al. 2013), in this species. Unsurprisingly then, in our study, individuals increased the number of grooming ties in periods with higher amounts of anthropogenic presence, with "less excitable" individuals showing marginally more sensitivity to this gradient. As in our social decision-making analysis, we again see some suggestion of "less excitable" individuals showing greater social plasticity (or social competence), although the differences between the behavioral syndrome phenotypes were much less marked here. If "less excitable" individuals need more ties to buffer increased stress from human proximity, in the long-term, these individuals may be the most vulnerable to declining population sizes and higher levels of anthropogenic disturbance.

For Barbary macaques, cold and wet winters in their high-altitude environment are challenging and are associated with high mortality risks (Majolo et al. 2013a; McFarland and Majolo 2013). Individuals with more grooming social ties have access to larger thermoregulatory huddles (Campbell et al. 2018b) and are more likely to survive the winter (McFarland and Majolo 2013; Lehmann et al. 2016). All individuals tended to decrease their grooming network strength in cold weather. This likely reflects reduced grooming effort overall in poorer weather conditions when energy may be redirected to survival, i.e., increased foraging or energy conservation through increased resting. However, "less excitable" individuals showed a tendency to concentrate grooming effort into fewer ties, whereas "more excitable" individuals had marginally more ties in colder months. Both strategies may be adaptive: for "less excitable" individuals, building ties in warmer and more favorable weather may be a good long-term strategy to ensure key partners in winter, while for "more excitable" individuals (which overall had lower network out-degree compared to "less excitable" individuals), investing in more ties only when essential (i.e., winter) may be an efficient social tactic.

Indeed, these divergent but potentially equally adaptive strategies may explain how diversity in behavioral syndromes can be maintained within a population (Wolf and Weissing 2010). That said, in our study, the changes in network connectivity in relation to socioecological gradients observed, with the exception of between mating and non-mating season, were very small (i.e., less than 10% change across different temperatures or anthropogenic pressures), reflecting the fact that individual stability in social network position is a relatively common phenomenon in various taxa (Krause et al. 2010; Blumstein et al. 2013; Aplin et al. 2015; Fisher et al. 2016; Finger et al. 2017).

For all animals, including humans, social and ecological environments are becoming increasingly less stable (Otto 2018; Testard et al. 2021; Blumstein et al. 2022). Therefore, there is an urgent need to understand whether and to what extent individuals adjust to these fluctuations (Jolles et al. 2019). Our study supports a growing body of laboratory-based work that shows that behavioral syndrome phenotype is a trait influencing both short- and long-term social plasticity, and thus social competence. We also found that different behavioral syndromes show divergent social responses to certain environmental gradients (here changes in temperature): this suggests that maintaining behavioral syndrome diversity may be a key factor for species and population resilience and sustainability in the Anthropocene.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-025-03670-9.

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Data availability All data and code used to produce this manuscript are available from the following repository: [https://github.com/ptkaczynski/Social/_comp/_behav/_syn](https://github.com/ptkaczynski/Social_comp_behav_syn).

Declarations

Ethics approval All data collection was conducted following ethical approval by University of 854 Roehampton and the receipt of research permits from Haut-Commissariat 855 aux Eaux et Forêts et à la Lutte Contre la Désertification, Royaume du Maroc. 856 In this study, the use of animals was non-invasive and adheres to the 857 guidelines set forth by the Association for the Study of Animal Behaviour.

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Patrick J. Tkaczynski[1] · Liz A.D. Campbell[2] · Ann MacLarnon[3] · Bonaventura Majolo[4] · Caroline Ross[5] · Julia Lehmann[5]

✉ Patrick J. Tkaczynski
pjtresearchltd@gmail.com

[1] Research Centre for Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool L3 3AF, UK

[2] Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Oxford OX13 5QL, UK

[3] Department of Anthropology, Durham University, Dawson Building, South Road, Durham DH1 3LE, UK

[4] School of Psychology, University of Lincoln, Lincoln, UK

[5] University of Roehampton, Holybourne Avenue, London SW15 4JD, UK