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Research

Cite this article: Patterson SK, Strum SC, Silk JB. 2022 Early life adversity has long-term effects on sociality and interaction style in female baboons. *Proc. R. Soc. B* **289**: 20212244.
https://doi.org/10.1098/rspb.2021.2244

Received: 17 October 2021
Accepted: 4 January 2022

Subject Category:
Behaviour

Subject Areas:
behaviour, developmental biology, evolution

Keywords:
early life adversity, development, sociality, temperament, *Papio anubis*

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Electronic supplementary material is available online at rs.figshare.com.

THE ROYAL SOCIETY
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Early life adversity has long-term effects on sociality and interaction style in female baboons

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Social bonds enhance fitness in many group-living animals, generating interest in the processes that create individual variation in sociality. Previous work on female baboons shows that early life adversity and temperament both influence social connectedness in adulthood. Early life adversity might shape sociality by reducing ability to invest in social relationships or through effects on attractiveness as a social partner. We examine how females' early life adversity predicts sociality and temperament in wild olive baboons, and evaluate whether temperament mediates the relationship between early life adversity and sociality. We use behavioural data on 31 females to quantify sociality. We measure interaction style as the tendency to produce grunts (signals of benign intent) in contexts in which the vocalization does not produce immediate benefits to the actor. Early life adversity was negatively correlated with overall sociality, but was a stronger predictor of social behaviours received than behaviours initiated. Females who experienced less early life adversity had more benign interaction styles and benign interaction styles were associated with receiving more social behaviours. Interaction style may partially mediate the association between early life adversity and sociality. These analyses add to our growing understanding of the processes connecting early life experiences to adult sociality.

1. Introduction

A growing body of evidence demonstrates that sociability enhances individual fitness in a wide range of mammalian species [1]. For example, female bighorn sheep (*Ovis canadensis*) with greater social network centrality are more likely to survive and produce more offspring than other females [2], male killer whales (*Orcinus orca*) that are more socially integrated have lower mortality than other males [3], and gregariousness enhances the survival of female giraffes (*Giraffa camelopardalis*, [4]). This has prompted interest in identifying the factors that contribute to individual variation in sociability. These factors include individual traits, such as sex, age, and dominance rank [5–10]; characteristics of the social milieu, such as group size and kin composition [11–14]; and environmental factors that influence resource competition and shape activity budgets [15–17].

Developmental plasticity in response to early life experiences can also be an important contributor to variation in sociability [18]. Sensitive windows are developmental periods in which organisms are particularly susceptible to external cues and exhibit heightened phenotypic plasticity [19–21]. Phenotypic adjustments in response to early life adversity often lead to disadvantageous outcomes later in life, even if they provide an immediate benefit of increased survival chances during development ([22–24]; but see [25]). Early life adversity is linked to poor health, shortened lifespan, and reduced fitness in a range of taxa from insects to humans [26–29]. Adversity can also impact social network position. Experimental studies of rodents (order *Rodentia*) and correlational studies of humans generally show that early life adversity leads to less social connectedness [30], but wild studies of gregarious species have produced mixed results. Wild zebra finches (*Taeniopygia guttata*) that faced high competition as nestlings, forage in larger groups and have more central social network positions than finches that faced less competition [31]. Wild yellow baboons (*Papio cynocephalus*) that faced more forms of early life adversity are less socially connected than those that faced less early adversity [32,33].

Variation in individual temperament may also affect sociability [34]. The links between temperament (also called personality or behavioural style) and sociability are complicated by the fact that sociability is sometimes treated as an *element* of temperament and is sometimes treated as the *outcome* of temperament. For example, Réale *et al.* [35] identify sociability as one of five major categories of temperament traits, along with shyness/boldness, exploration/avoidance, activity, and aggressiveness. Individual variation in the sociability dimension has been reported in a wide variety of taxa, ranging from Asian elephants (*Elephas maximus*; [36]) to western mosquitofish (*Gambusia affinis*, [37]). However, there is also evidence that elements of individuals' temperaments can affect their sociability. For example, in cichlids (*Neolamprologus pulcher*), boldness and aggressiveness influence group composition, position in social networks, and the nature of social ties [38]. In Trinidadian guppies (*Poecilia reticulata*), shy fish have a larger number of connections and stronger connections than bolder fish, and the pattern of connections is linked to individual participation in cooperative predator inspection [39]. In humans, high scores on extraversion are associated with more central positions in friendship networks [40].

While much remains to be learned about the development of temperament, evidence indicates that temperament can be influenced by early life experiences. Developmental stress is often linked to increased anxiousness and aggression [30,41]. For example, young mice (*Mus musculus*) that are exposed to olfactory cues of potentially infanticidal males are more anxious and less exploratory as adults than control mice [42]. Pre-natal exposure to glucocorticoids is associated with heightened aggression in adult chickens (*Gallus gallus*) [43], but exposure to cues of competition are associated with reduced aggression in field crickets (*Gryllus integer*) [44]. Studies have yet to link all three variables: early life adversity, development of temperament, and later life sociability; but links drawn between each pair of variables suggests that exposure to early life adversity might shape temperament, which could then impact sociability.

Baboons are an ideal study system for examining links between early life adversity, temperament, and sociality. Yellow, chacma (*Papio ursinus*), and olive baboons (*Papio anubis*) live in large, multimale, multifemale groups [45,46]. Females typically remain in their natal groups throughout their lives [45,46] and develop strong, equitable, stable, supportive, and tolerant relationships with selected female partners, particularly close maternal kin and peers [47–51]. Baboon females that are more socially integrated or have stronger and more stable social ties experience fitness advantages in the form of higher offspring survivorship and longer lifespans [49,50,52–55]. Early life adversity has negative impacts on baboon longevity, hypothalamic-pituitary-adrenal (HPA)-axis function, fertility, maternal care, and offspring survival [32,33,56–59].

Both early life experience and temperament contribute to variation in sociability among baboons. Females that experience less early life adversity are more socially integrated as adults [32,33]. Seyfarth *et al.* [60] used exploratory factor analysis to identify animals' temperament, which revealed three dimensions that were labelled 'nice', 'loner', and 'aloof'. Females that scored higher on the 'nice' factor and lower on the 'loner' factor had stronger social bonds than other females [60].

Grunts play an important role in negotiating social interactions because they function as honest signals of benign intent [61,62]. Female baboons sometimes utter quiet, low frequency calls, called grunts, as they approach conspecifics [63–65]. These calls are effective in reconciling conflicts [63,66] and are associated with lower levels of aggression and higher levels of affiliative interactions [62,64,67]. Grunts seem to play an important role in reducing uncertainty about the likely outcome of interactions between individuals whose relationships are not predictably friendly [61,62,64].

In this paper, we evaluate the links between early life adversity, interaction styles, and female sociality in wild olive baboons. Building on previous work, we hypothesized that early life adversity influences females' interaction styles, and this, in turn, influences their ability to form strong social bonds. Following our hypothesis, we have three main predictions. First, as observed in yellow baboons [32,33], we predicted that higher levels of early life adversity will be associated with lower levels of female sociability. Second, following observations in chacma baboons [60], we predicted that females with more benign interaction styles will have higher levels of social connectedness. Third, we tested the novel prediction that females which experience more early life adversity will be less likely to develop benign interaction styles. The effects of interaction styles may partially mediate the effects of early life adversity on female sociability.

2. Methods

(a) Study site and population

We studied three groups of wild olive baboons (PHG, ENK, and YNT) that range in Laikipia, Kenya. These groups are monitored by the Uaso Ngiro Baboon Project (UNBP) [68,69]. Observers update demographic records (births, deaths, disappearances) daily. Maternal kinship relationships among natal females are known from genealogical records extending back to the 1970s. Data on grass biomass are collected monthly using the slanting pin intercept technique [70,71]. For more details about the study site, see the electronic supplementary material and: [51,72,73].

(b) Behavioural observations

We used a hand-held computer to conduct 15 min focal observations on all subadult and adult females in the study groups. Females are considered subadults when they begin having sexual swellings and are considered adults once they give birth. Observers recorded the focal females' activity state, social interactions, and vocalizations on a continuous basis. For social interactions and vocalizations, observers recorded the type of behaviour, the identity of the partner, and whether the behaviour was initiated by the focal, the partner, or jointly. The main behavioural dataset is based on 2615 h of observation of 31 females (mean ± s.d. = 81.73 ± 28 h per female).

(c) Assessment of dominance rank

We used the likelihood-based Elo-rating method to assess female dominance rank [74]. This method uses maximum likelihood fitting of individuals' initial Elo-scores when entering the hierarchy, and fits the constant k which, multiplied by the winning probability of the loser prior to the interaction, determines the increase in Elo-score for the winner and the decrease in Elo-score for the loser following the interaction. This generates scores for each individual on each day.

(d) Assessment of early life adversity

The early life adversity index is a modified version of the cumulative index used by the Amboseli Baboon Research Project [32,33,57,58], and is described in more detail elsewhere (electronic supplementary material; [59]). Briefly, we considered five measures of adversity: grassland biomass during the birth year as an indicator of environmental conditions, group size at birth as an indicator of within-group competition, early loss of mother, interbirth interval (IBI) as an indicator of mother's condition, and primiparity. We used continuous measures for all components of the index except primiparity. Continuous measures were normalized so values range from zero to one. Primiparity was scored as 1 for females who were first-borns, and 0 for females who were not first-borns. Pairwise correlations among the three continuous variables are all under 0.37. Only one female lost her mother during early development so tests of correlation were not performed for this variable. The only significant correlation between the continuous variables and primiparity is between IBI and primiparity (logistic regression: $p = 0.024$). All five scores were summed to create the cumulative index, which ranged from 0.33 to 3.4 (out of 5) with a mean and standard deviation of 1.72 ± 0.63.

The rationale for creating a cumulative adversity index is based on previous research which indicates that the accumulation of adversities is a better predictor of adult outcomes than any particular form of adversity [28,32]. However, because different forms of adversity might have different impacts in particular populations, we constructed parallel models with the cumulative index and with separate forms of adversity modeled separately.

(e) Assessment of composite sociality index values

To measure overall sociability, we created a composite sociality index (CSI) index using two forms of positively correlated affiliative behaviours: approaches and grooming [75]. For each focal in each year, we tabulated the rates of each behaviour with adult female partners. The CSI is calculated using the following formula:

$$\mathrm{CSI}_x = \frac{\sum_{i=1}^{d} f_{ix}/\overline{f_i}}{d},$$

where x represents an individual, d is the number of behaviours measured, f_i is the rate or frequency of behaviour i for individual x, and $\overline{f_i}$ is the mean rate or frequency of behaviour i. Because these measures varied across the study groups and across years, we computed separate means for each group in each year. The CSI can range from zero to infinity with an average value of 1. We computed a joint index for interactions initiated and received (CSI_joint), an index for only interactions initiated by the focal (CSI_initiated), and an index for interactions directed to the focal (CSI_received).

(f) Assessment of interaction style

To assess interaction styles, we focused on approaches to unrelated lower-ranking females without infants. We excluded approaches to females with young infants (under the age of 91 days) to exclude situations in which approaching females have an immediate strategic objective, i.e. infant handling [76–79]. We also excluded approaches to related females because females are less likely to grunt as they approach close kin than others [61,62]. Grunts to lower-ranking females that do not have young infants function to provide reassurance that the dominant actor's intentions are benign [61,62,64].

We recorded the time of all approaches and the time of all subsequent vocalizations and behaviours between the actor and recipient. Approaches were recorded as instantaneous events when one individual moves within 1 m proximity of another individual. We analysed a subset of approaches directed to unrelated lower-ranking females without young infants (n = 5190 approaches). We categorized sequences in which the first event was a grunt by the approaching female as 'vocal approaches' and all other sequences as 'silent approaches'. Approximately 90% of these vocalizations occurred within 10 s of the initial approach. For each female in each year, we tabulated the number of vocal approaches and the number of silent approaches. Females who are more likely to grunt in these contexts are considered to exhibit a more benign interaction style.

(g) Statistical models

We fitted models using the map2stan function in the 'rethinking' package (v.1.59) [80], which uses an efficient Hamiltonian Markov chain Monte Carlo, r-STAN v.2.18.2 [81], to fit Bayesian models in R v.3.3.2. [82]. All continuous predictors were transformed to a mean of 0 and a standard deviation of 1. We included varying intercepts for female identity and observation year. In the tables, larger posterior means indicate greater magnitude of effect, and smaller standard deviations indicate greater certainty in that effect. Generally, if the effect size is not zero and the error is smaller than the effect size, a relationship between the parameters might be gleaned. However, we focus on graphs of model predictions to assess results. We plot the posterior median, 89% credible intervals, and full posterior predictions over the raw data. These figures provide information regarding the relative magnitude and certainty of the effects of variables on the scale of the outcome variable. We ran models with the cumulative early life adversity index and with individual measures of adversity. The cumulative index produced a better fit than separate adversity measures for all models, so we present these results in the text below. The effects of each individual form of adversity are presented in the electronic supplementary material, tables S1–S3. The code and data used can be found here: https://github.com/skpatter/socialityXela [83].

(h) Sociality and early life adversity

To test the association between early life adversity and sociality, we constructed gamma models because CSI values cannot be negative. In these models, we controlled for female dominance rank (mean annual Elo score), number of maternal kin present, and group membership. We constructed parallel models for indexes based on behaviours given and received (CSI_joint), behaviours initiated by focal females (CSI_initiated), and behaviours directed towards focal females (CSI_received). We also evaluated the effects of early life adversity on the individual social behaviours (grooming and approaches) received and initiated. We constructed Poisson models with counts of behaviour as the output and the amount of time the focal female was observed as an offset.

(i) Interaction style and early life adversity

To test the prediction that early life adversity will influence females' interaction styles, we constructed aggregated binomial models. The outcome variable was the count of vocal approaches (approaches in which the approaching female grunted) and the number of trials was the total number of approaches. We controlled for dominance rank and group membership, but not kin

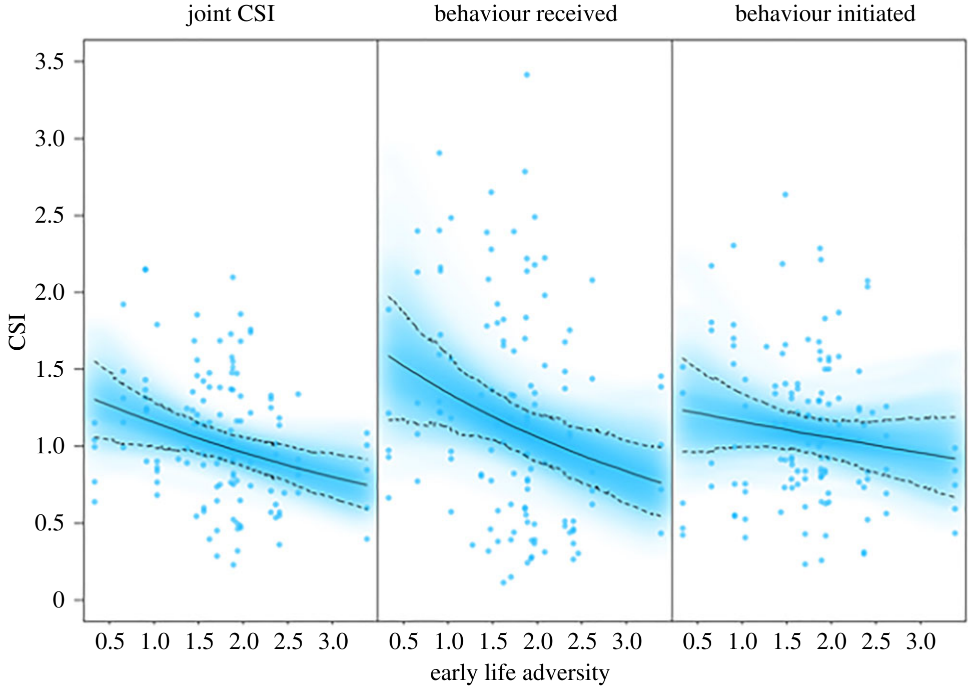

Figure 1. Female CSI as a function of early life adversity. Model posterior predictions for the influence of cumulative early life adversity on CSI scores (left), CSI scores based on behaviours received (middle), and CSI scores based on behaviours initiated (right). The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. Model sample sizes are as follows: 31 females and 124 data points in each panel. (Online version in colour.)

availability because the grunts metric was limited to approaches towards non-kin.

(j) Sociality and interaction style

To test the relationship between interaction style and sociability, we reran the joint CSI gamma models and added a measure for interaction style—the proportion of approaches in which a female grunted. Not all focal females each year had interaction style scores, so this analysis used a subset of the main dataset. We also ran this model without interaction style. By comparing results of the model with and without interaction style, we can learn more about these associations (see directed acyclic graphs in [80]).

3. Results

(a) Female sociality and early life adversity

Females who experienced more early life adversity had lower CSI values than females with less adversity (ß = −0.12 ± 0.05; figure 1; electronic supplementary material, table S1). This negative association was stronger for social behaviours the focal female received (ß = −0.16 ± 0.07) than behaviours she initiated towards others (ß = −0.06 ± 0.06; figure 1; electronic supplementary material, table S1). Females who experienced more early life adversity were the recipients of fewer grooming bouts (ß = −0.13 ± 0.16) and approaches (ß = −0.20 ± 0.09) than females with less adversity (electronic supplementary material, figure S1, table S4). There was a slight negative effect of early life adversity on grooming initiated, but there was substantial uncertainty in this relationship (ß = −0.06 ± 0.12). There was an effect size of zero for the relationship between early adversity and approaches initiated (ß = 0.00 ± 0.05; electronic supplementary material, figure S1, table S4). Higher-ranking females were more social than lower-ranking females overall (ß = 0.08 ± 0.05; electronic supplementary material, figure S2, table S1). Higher-ranking females received more grooming (ß = 0.10 ± 0.12) but groomed others less (ß = −0.12 ± 0.10) and were approached less (ß = −0.14 ± 0.05) but approached others more (ß = 0.13 ± 0.04) than lower-ranking females (electronic supplementary material, table S4). The number of maternal kin present was positively associated with all measures of sociality (overall CSI: ß = 0.09 ± 0.04; electronic supplementary material, figure S2, table S1, table S4). When modelled separately, the effects of different forms of adversity seem consistent with how we interpreted the measures. Effects of adversity on sociability seem primarily driven by grass biomass and primiparity (electronic supplementary material, table S2).

(b) Female interaction style and early life adversity

Females that experienced more early life adversity had less benign interaction styles. Females with more early life adversity were less likely to grunt when approaching unrelated, lower-ranking females without young infants than females with less adversity (ß = −0.22 ± 0.07; figure 2; electronic supplementary material, table S5). Rank had a positive association with interaction style (ß = 0.29 ± 0.07; electronic supplementary material, figure S3, table S5). When modelled separately, the different forms of adversity performed as predicted. Effects of adversity on interaction style seem primarily driven by group size, grass biomass, IBI, and maternal loss (electronic supplementary material, table S2).

(c) Relationship between female sociality, interaction style, and early life adversity

Females who were more likely to grunt (i.e. had more benign interaction styles) had higher CSI scores than females who were less likely to grunt (ß = 0.06 ± 0.04; figure 3; electronic

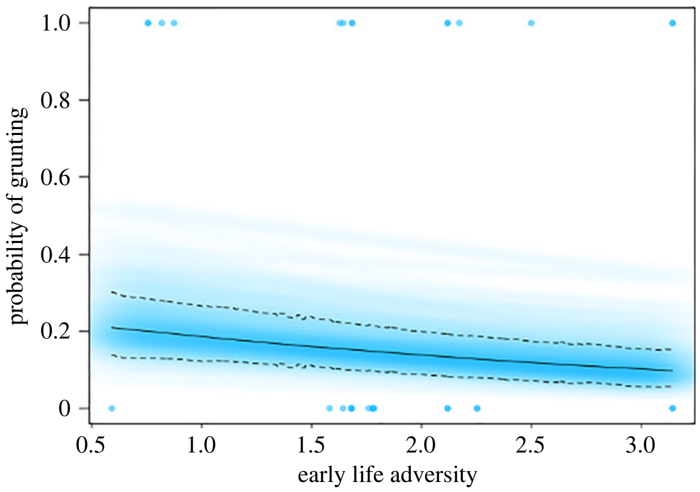

Figure 2. Benign interaction style and early life adversity. Model posterior predictions for the influence of cumulative early life adversity on the probability of grunting as approaching a lower-ranking, unrelated female without a young infant (i.e. benign interaction style). Model sample sizes are as follows: 27 females and 101 data points. (Online version in colour.)

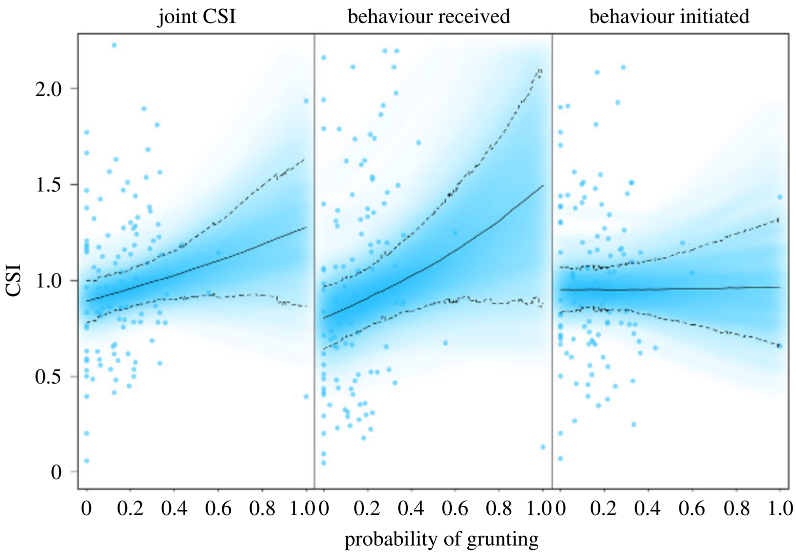

Figure 3. CSI scores and benign interaction style. Model posterior predictions for the influence of the probability of grunting (i.e. benign interaction style) on CSI (left panel), CSI based only on behaviours received from other females (middle panel), and CSI based only on behaviours initiated towards other females (right panel). Model sample sizes are as follows: 27 females and 111 data points. (Online version in colour.)

supplementary material, table S6). This association was primarily driven by how others behaved towards the focal female (ß = 0.10 ± 0.05) rather than how she behaved towards others (ß = 0.00 ± 0.04; figure 3, electronic supplementary material, table S6). Females who were more likely to grunt were approached and groomed by other females substantially more than females who were less likely to grunt (approach: ß = 0.14 ± 0.09; groom: ß = 0.18 ± 0.04; electronic supplementary material, figure S4, table S6). The effects on social behaviour initiated was modest in comparison to the effect on behaviours received. Females with more benign interaction styles approached others slightly more (ß = 0.04 ± 0.02) but groomed others slightly less (ß = −0.06 ± 0.05) than females with less benign interaction styles (electronic supplementary material, figure S4, table S6).

If interaction style fully mediated the effect of early life adversity on CSI, then including interaction style in the model would eliminate the effect of early life adversity on CSI [80]. The coefficients for the effects of early life adversity on sociality were slightly reduced when interaction style was included in the models (electronic supplementary material, figures S5 and S6, table S6), which indicates interaction style might partially mediate the association between early life adversity and sociality. Models for most sociality measures (CSI, behaviours received, grooming received, approaches received, and approaches initiated) that included interaction style fit better than models without interaction style (Watanabe-Akaike information criterion scores in the electronic supplementary material, table S6).

4. Discussion

Early life adversity influences interaction style and sociality in wild olive baboons. Females that experienced more early life adversity were less likely to develop benign interaction styles, and females that had less benign interaction styles were less sociable than other females. Females who experienced more early life adversity were less social overall than other females, a finding that is consistent with previous evidence from yellow baboons [32,33].

Early life adversity had a stronger effect on behaviours directed towards females than behaviours initiated by females. This difference provides insights about the proximate factors that shape the relationship between early life adversity and sociality. If early life adversity affects female sociality by influencing females' condition and ability to allocate time and energy towards socializing, then behaviours initiated by the focal should be affected. In support of this notion, females exposed to early life adversity initiated fewer social behaviours than others. However, early life adversity had a stronger effect on social behaviours received than behaviours initiated. Early life adversity seemed to make females less attractive partners. Together, these patterns suggest early life adversity impacts social connectedness via multiple pathways including effects on physical condition and social attractiveness.

Females who experienced more early life adversity may have been less attractive partners because adversity influenced their interaction style. Females who experienced more early life adversity had less benign interaction styles, as they were less likely to grunt in situations in which they did not have immediate instrumental objectives and there was some ambiguity about their intentions. Females that had more benign interaction styles were more social overall, and this was largely owing to how other females behaved towards them. This parallels the finding in chacma baboons that females who are 'nicer' form stronger social ties and are more likely to be approached by others than those who are less 'nice' [60,84]. While accounting for female interaction style reduces the effect of early life adversity on sociality slightly, it does not eliminate the effect. Our results indicate interaction style might partially mediate the relationship between early life adversity and sociality, but more data are needed to disentangle the pathways.

Links between sociality and fitness suggest that a less benign interaction style and lower sociability might be consequential. A less benign interaction style might arise because it was advantageous under early life conditions [85], or because the effects of sociability are conditional on early experiences, such that fitness benefits of sociability are reduced among those with early life adversity [86,87]. However, another possibility is that females exposed to early life adversity allocated fewer resources to socializing during sensitive windows, and this set them on a trajectory that led to their adult interaction style [22–24,85]. Empirical work suggests that early social interactions influence brain development and adult behaviour [88–90]. For example, mice raised in socially stimulating environments have increased levels of nerve growth factor and brain-derived neurotrophic factor [91]. As adults, these mice are more social and faster to conform to a dominance position than mice raised in less social environments [91]. In this population of olive baboons, infants who develop in harsher maternal and ecological conditions spend less time playing socially and are less behaviourally independent than infants developing in better conditions [92,93]. If females exposed to early life adversity are unable to invest in social development because they must prioritize maintenance, immune function, and growth to survive to maturity, then they might develop less advantageous interaction styles and form weaker social bonds in adulthood.

There are several mechanisms that might mediate and moderate the associations between early life experiences, developmental trajectories, and behavioural outcomes. Research has pointed to the inter-related effects of neurobiology, the HPA-axis, and epigenetics [1,22,28,85,94]. Exposure to adversity during development can have lasting effects on brain organization, which might then influence social behaviour [29,95]. Early life adversity seems to influence the development of neural networks associated with threat detection, reward processing, and cognitive control, although longitudinal studies and information about causal links are still needed [96]. The HPA-axis can become dysregulated in response to early life adversity in humans and other species such as rats, voles (*Microtus mandarinus*), and rhesus macaques (*Macaca mulatta*) [97–101]. Consistent with this pattern, female baboons who are exposed to early life adversity have elevated adult glucocorticoids, which puts them at a heightened risk of death [33,59,102]. In yellow baboons, the relationship between early life adversity and glucocorticoids is not mediated by social ties [33], but glucocorticoids might shape interaction styles, which in turn influences females' ability to form social bonds. Owing to a limited sample of hormones, we were unable to test these associations here. Epigenetic modifications in response to early life adversity shape physiology, brain development, behaviour, and temperament [24,103–109]. For example, European starlings (*Sturnus vulgaris*) deprived of food as nestlings exhibit accelerated telomere attrition and feeding behaviours typical of acutely hungry birds despite access to food [110]. In wild spotted hyenas (*Crocuta crocuta*), maternal care and social connectedness during early life predicted later life glucocorticoids and DNA methylation near genes involved in inflammation, immune response, and ageing [111].

Interaction style and sociality are also influenced by demographic factors and genes. As observed in yellow and chacma baboons, we found that female olive baboons with more kin were more sociable [47,50]. Female dominance rank is not consistently linked to sociality (e.g. [47]), but we found that higher-ranking females were more sociable than lower-ranking females. However, the effects of rank vary with the direction and type of behaviours measured. Higher-ranking females received more grooming but groomed others less, and were approached less but approached others more than lower-ranking females. In some cases, combining different behaviours into a composite index might not demonstrate an overall relationship between sociality and rank because the positive and negative patterns for each directed measure balance out. Higher-ranking females were also more likely than lower-ranking females to exhibit benign interaction styles. We are unable to consider the role of genetics in this study, but personality and interaction style are heritable traits ([112], e.g. great tits (*Parus major*): [113], squid (*Euprymna tasmanica*): [114], rhesus macaques: [115]), and genetic variations can contribute to vulnerability to early life adversity (e.g. [105,107,113]).

These analyses add to a growing body of work that connects early life adversity to disadvantageous adult outcomes. Female baboons that experience more early adversity develop less benign interaction styles, become less attractive social partners, develop weaker social bonds, reproduce less successfully, and die at earlier ages than females that experience more advantageous early life conditions [32,33,56–59,116]. In humans, both exposure to early life adversity and social isolation increase mortality risk and susceptibility to a variety of diseases [117–121]. The parallels make it important to understand the proximate mechanisms that underlie early life adversity, temperament, sociality and unravel the causal pathways that link early life adversity to fitness outcomes.

Ethics. The study conformed to U.S. and Kenyan regulations and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. The project was approved by the Arizona State University Institutional Care and Use Committee. All animal protocols followed the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014). This was a strictly observational study.

Data accessibility. Data and code used for this manuscript are uploaded on GitHub at the following link: https://github.com/skpatter/socialityXela [83].

Authors' contributions. S.K.P.: conceptualization, formal analysis, funding acquisition, writing—original draft, writing—review and editing; S.C.S.: project administration, resources, supervision, writing—review and editing; J.B.S.: conceptualization, funding acquisition, project administration, resources, supervision, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This research was funded by the National Science Foundation (BCS-1732172; GRFP-1841051; SMA-2105307), the Leakey Foundation and Arizona State University. The funders had no role in study design, data collection and analysis or preparation of the manuscript.

Acknowledgements. We thank the Office of the President of the Republic of Kenya, the Kenya Wildlife Service, the African Conservation Centre and the UNBP. We thank Kate Abderholden, Megan Best, Megan Cole, Moira Donovan, Alexandra Duchesneau, Jessica Gunson, James King'au, Jeremiah Lendira, Joshua Lendira, Molly McEntee, Frances Molo, David Muiruri, Laura Peña, Eila Roberts and Leah Worthington. We thank Robert Seyfarth, Robert Barton and three anonymous reviewers for comments on an earlier draft of this paper.

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