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Cite this article: Pfefferle D, Ruiz-Lambides AV, Widdig A. 2014 Female rhesus macaques discriminate unfamiliar paternal sisters in playback experiments: support for acoustic phenotype matching. *Proc. R. Soc. B* **281**: 20131628.
<http://dx.doi.org/10.1098/rspb.2013.1628>

Received: 24 June 2013

Accepted: 17 October 2013

Subject Areas:

behaviour

Keywords:

kin discrimination, vocalization, mechanism, phenotype matching, paternal kin, playback experiment

Author for correspondence:

Dana Pfefferle

e-mail: dpfefferle@eva.mpg.de

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2013.1628> or via <http://rspb.royalsocietypublishing.org>.

Royal Society Publishing

Female rhesus macaques discriminate unfamiliar paternal sisters in playback experiments: support for acoustic phenotype matching

Dana Pfefferle^{1,2}, Angelina V. Ruiz-Lambides^{2,3} and Anja Widdig^{1,2}

¹Junior Research Group of Primate Kin Selection, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

²Behavioural Ecology Research Group, Institute of Biology, University of Leipzig, Germany

³Caribbean Primate Research Center-Cayo Santiago, University of Puerto Rico, Punta Santiago, USA

Widespread evidence exists that when relatives live together, kinship plays a central role in shaping the evolution of social behaviour. Previous studies showed that female rhesus macaques (*Macaca mulatta*) recognize familiar maternal kin using vocal cues. Recognizing paternal kin might, however, be more difficult as rhesus females mate promiscuously during the possible conception period, most probably concealing paternity. Behavioural observations indicate that semi free-ranging female rhesus macaques prefer to associate with their paternal half-sisters in comparison to unrelated females within the same group, particularly when born within the same age cohort. However, the cues and mechanism/s used in paternal kin discrimination remain under debate. Here, we investigated whether female rhesus macaques use the acoustic modality to discriminate between paternal half-sisters and non-kin, and tested familiarity and phenotype matching as the underlying mechanisms. We found that test females responded more often to calls of paternal half-sisters compared with calls of unrelated females, and that this discrimination ability was independent of the level of familiarity between callers and test females, which provides, to our knowledge, the first evidence for acoustic phenotype matching. Our study strengthens the evidence that female rhesus macaques can recognize their paternal kin, and that vocalizations are used as a cue.

1. Introduction

Kinship can play an essential role in the evolution of social behaviour. Favouring kin in social interactions is a taxonomically widespread phenomenon, being reported from insects to primates [1]. However, corresponding evidence is heavily biased towards maternal kin (e.g. house mice, *Mus domesticus* [2]; spotted hyena, *Crocuta crocuta* [3] and rhesus macaques, *Macaca mulatta* [4]), for which the degree of relatedness corresponds to the degree of familiarity being the highest among mother–offspring pairs [5]. Nevertheless, preference for paternal kin should be favoured by selection for similar reasons as preference of maternal kin, i.e. to minimize the risk of inbreeding, increase fitness by acting nepotistic and decrease the risk of infanticide [6]. In multi-male groups in which females typically mate with multiple partners during their possible conception period (leading to paternity uncertainty), and in which paternity is skewed, it is expected that recognizing paternal kin is more difficult than recognizing maternal kin. Today, there is evidence that, at least in some species, males can discriminate their own offspring as they preferentially defend or associate with them ([7–10], but see [11]). Mechanisms underlying father–offspring recognition suggest that males might assess their paternity probability from mating frequency [7,8,12] or that both, father and offspring, might use post-birth recognition mechanisms [7,9]. In species with a

promiscuous mating system, paternal half-siblings (born to different mothers but sired by the same male) can use only post-birth mechanisms to recognize each other. Given that in many species of mammals male reproduction is skewed towards a few sires, individuals sharing the same father are quite frequently found [6]. Indeed, evidence from field studies applying genetic analyses suggest that mammals, including primates, preferentially associate with paternal half-siblings (e.g. Belding's ground squirrels, *Spermophilus beldingi* [13,14]; golden hamsters, *Mesocricetus auratus* [15,16]; spotted hyena [3]; rhesus macaques [17]; savannah baboons, *Papio cynocephalus* [18,19] and mandrills, *Mandrillus sphinx* [20]). However, other studies that found no evidence for paternal kin discrimination (chimpanzee, *Pan troglodytes* [21] and white-faced capuchins, *Cebus capucinus* [22]) concluded that paternity cues might not be reliable for kin recognition, but see [5] for discussion.

To date, the mechanisms underlying paternal half-sibling discrimination (hereafter, paternal kin discrimination) are still not clear, but familiarity and phenotype matching are considered to be the most likely ones [6,23]. Kin discrimination by familiarity predicts that those conspecifics are recognized as kin with whom individuals are associated during a critical period during their lives [24]. Familiarity among paternal kin has been expected to occur to a much lower extent than among maternal kin [6,17,18]. However, owing to the high skew in male reproduction found in many species [5,25], paternal siblings tend to be born in the same age cohort [26]. As age mates go through the same life-history stages at the same time, they can be found to preferentially interact with each other [27,28]. Age proximity was therefore suggested (at least) as a primary mechanism for paternal kin recognition [17,18]. However, not only age proximity might trigger familiarity among paternal kin. Preferred associations among paternal siblings might additionally result from mothers or fathers mediating familiarity among them [6]. By contrast, under the phenotype matching hypothesis animals are expected to use either self or a known kin (the father or another known paternal relative) as a template to assess kinship to other (even unfamiliar) individuals [29,30]. Phenotype matching has also been inferred as the mechanism underlying paternal kin discrimination by several recent studies that controlled for the effect of age [17,18,31]. Studies aiming to control for familiarity by investigating the ability to recognize paternal kin in individuals that have been reared apart from their parents (i.e. no possible mediation through them) [32,33], however, failed to provide evidence for phenotype matching. Yet, these studies did not consider the possibility that the phenotypic template might not be innate but needs to be learned, which might be prevented when offspring are raised apart from their parents. This should especially apply to species in which complex social relationships are linked to learning, such as in primates (cf. [5]).

Up to now, no study was able to control for all possible sources of familiarity while ensuring that a template for paternal kin can develop under natural conditions; thus no direct evidence for phenotype matching exists. Hence, the aim of our study was to test the mechanisms of paternal kin discrimination by disentangling phenotype matching from familiarity under natural conditions. Direct evidence for phenotype matching would require detecting paternal kin bias while controlling for familiarity owing to age proximity and mediation through both mother and father.

Among primates, the most probable cues used to identify kin may be acoustical, olfactory and/or visual cues [6,24]. While most cues have rarely been tested among primates (e.g. olfactory [34], visual [35,36]), acoustical studies on kin discrimination are more common [37–39]. Vocal communication is especially important among primates as it may provide various types of information about the vocalizer, such as identity [40], sex [41], age [42], size [43], hormonal state [44,45] and very likely kinship [37,39,46,47]. The acoustic structure of 'coo' calls, a contact call uttered in pro-social context, in rhesus macaques suggest that it encodes information about maternal kinship [46]. 'Coo' calls presented to maternally related females elicited a stronger response than 'coo' calls uttered by more distant related or unrelated females [39]. Moreover, a recent study on grey mouse lemurs (*Microcebus murinus*) found that females responded differently towards the presentation of advertisement calls of their fathers versus unrelated males, suggesting that information about patrilineal membership is encoded in this call type [47]. However, these findings could alternatively be explained by the knowledge of individual call characteristics, as subjects were familiar with one another and could have linked the caller identity to relatedness information driven from other cues (e.g. odour, visual). This is in fact supported by data for Campbell monkeys (*Cercopithecus campbelli campbelli*) indicating that social bonding (expressed by grooming rate), but not genetic relatedness, explains similarities in the call structure [48].

The present study had two main aims: (i) to investigate if female rhesus macaques use the acoustic modality to discriminate between paternal half-sisters and unrelated females, and (ii) to identify the mechanism/s underlying this discrimination process. To disentangle the effects of relatedness and different sources of familiarity, we designed playback experiments allowing us to test for familiarity via age proximity, parent mediation and co-residence in the same group. Based on previous results [39], we predicted that if rhesus macaques are able to discriminate between paternal kin and non-kin, they should preferentially react towards paternal kin. We first tested the females' ability to discriminate paternal half-sisters from unrelated females under two conditions: (1) the test individual and both callers (kin and non-kin call donor) were born in the same birth cohort and group, and co-resident during the study (hereafter, 'familiar peers' condition); and (2) test individual and both callers were born in different birth cohorts within the same group, and co-resident during the study ('familiar non-peers'). If paternal kin can be discriminated only under condition (1), familiarity based on age proximity would be supported as underlying mechanism. However, if females show a preference for paternal kin under conditions (1) and (2), paternal kin might be recognized based on parent-mediated familiarity and/or phenotype matching. At this stage, no discrimination between the two mechanisms is possible. Given that male reproduction is skewed among rhesus macaques [49] and males do show multiple dispersals [50], a high proportion of paternal siblings are residential in the same group since birth (familiar), but likewise in different groups (unfamiliar), although in the latter unlikely to be born in the same cohort. This opens the possibility to test for phenotype matching among unfamiliar subjects while controlling for familiarity through age proximity and/or parent mediation. Our third test condition therefore comprised paternal kin and non-kin of different groups ('unfamiliar'), i.e. never co-resident in the same group. Under this test

condition, the recognition of paternal kin can only be based on phenotype matching.

2. Material and methods

(a) Study site and subjects

The study was carried out on the semi free-ranging rhesus macaque population on Cayo Santiago, a 15.2 ha island southeast of Puerto Rico [51], between June and December 2009/2011. From long-term observations of the Caribbean Primate Research Center (CPRC), demographic data on date of birth, natal group and duration of group membership were available for each individual of the study population. All animals were habituated to humans and could be recognized on an individual basis. During the data collection between 960 and 1200 individuals inhabited the island, belonging to six different naturally formed social groups, with group sizes ranging approximately from 100 to 300 individuals. A total of 72 sexually mature females (mean age in years = 7.96, range: 4.6–18.7) of all social groups participated in the study either as test subject, caller or both.

(b) Vocal recordings

We recorded 'coo' calls uttered in the same context (group progression [39]). Vocalizations could be obtained at close range (mean $\pm$ s.d.: 1.79 $\pm$ 1.05 m) ad libitum throughout the day using a Marantz PMD661 recorder (D&M Professional, Longford, UK) and a Sennheiser directional microphone (Sennheiser, Wedemark, Germany; ME66 with K6 power module with Rycote Modular Windshield System and a Rycote Windjammer, Rycote Ltd., Stroud, UK). We transferred recordings to a computer and saved them at 16 bit resolution and 44.1 kHz sampling rate. For playback, we selected high-quality recordings with no background noise. Using COOLEDT2000 (Syntrillium, Phoenix, USA), we standardized all playback stimuli to the same peak sound pressure level of 68 dB, measured at 5 m from the loudspeaker (Sound Level Meter: PeakTech5055, Ahrensburg, Germany).

(c) Female dominance hierarchy

Female rhesus macaques form a stable linear hierarchy, with daughters securing rank immediately below their mothers [52], structuring females in matrilineal lines consisting of closely ranked and maternally related individuals. Hierarchy information of adult females from all six groups was collected ad libitum as well as during focal observations, and based on the direction and outcome of agonistic interactions [53].

(d) Genetic parental assignment

We assigned parents based on long-term genetic data including biological samples (mainly blood) from animals that survived their first year of life and were born after, or had been still alive in, 1992. In order to increase power, over the last decade, we increased the number of short tandem repeat markers used to 43 currently, including one sex-linked marker [54]. Additionally, the protocols have been optimized to incorporate multiple tubes [55] and a multiplex approach [56,57]. At the time this study was conducted the database consisted of 3735 animals being genotyped on average at 34.18 $\pm$ 8.25 loci ($\pm$ s.d.). Excluding the sex-linked marker (DXS2506), there was no indication of the presence of null alleles at these loci and no sign of deviation from the Hardy–Weinberg equilibrium. The mean number of alleles was 8.42 $\pm$ 3.28 per locus, the mean observed heterozygosity across loci was 0.71 $\pm$ 0.14, the mean expected heterozygosity was 0.71 $\pm$ 0.14, and the mean polymorphism information content over all 43 loci was 0.66 $\pm$ 0.13 (values calculated with CERVUS v. 3.0; [58]). The overall

typing error rate for mother–offspring dyads with at least one mismatching locus was 0.02 (n = 3273 mother–offspring dyads).

From the 72 individuals that participated in this study, all mothers listed in the demographic database were genetically confirmed (n = 63, unique mothers, as some subjects shared the same mother). Subsequently, the maternal information was used in paternity analyses for which all males older than 1250 days and present on the island 200 days prior to the birth of a given individual [10,59] were considered as potential sires. The mean number of common loci typed for mother–sire–offspring trios was 26.4. Paternity was assigned using exclusion and likelihood method. We solved paternities for all 72 females (n = 35 unique sires). In all assigned cases, the sire had no mismatch with the assigned mother–offspring pair, and all other potential sires had been excluded by at least two loci.

We also aimed to assign the maternal and paternal grandparents. For the 63 unique dams, we were able to genetically determine 56 (88.8%) mothers, i.e. the maternal grandmother of the offspring, confirming the demographic information. Based on the assigned sires (n = 35), we could genetically confirm the paternal grandmothers in 88.6% of the cases. Owing to the low level of demographically misassigned mothers (2.47%) in the study population, we felt confident to use the demographic assigned grandmothers in cases where a genetic sample of the grandmother was not available. Based on the 63 unique dams, we could determine 54 (85.7%) maternal grandfathers, excluding in all but two cases, other potential grandfathers at two or more loci. In the remaining two cases, the assigned grandfather had no mismatch with the respective mother–offspring pair, but all other candidates could only be excluded at one locus. We supported these cases additionally at the 95% confidence level by the maximum-likelihood method calculated by CERVUS v. 3.0. Based on the 35 unique sires of our 72 females, we could genetically determine the paternal grandfathers in 88.6% of the cases. In all these cases, the assigned grandfather had no mismatch with the respective mother–offspring pair, and all other candidate grandfathers were excluded on at least two loci.

(e) Assignment of playback pairs

Based on the parental assignments, we established pedigrees up to the grandparent generation. Subsequently, we determined dyads of paternal half-sisters and unrelated individuals. Paternal half-sisters were defined as a pair of individuals that share the same father (and by definition the same paternal grandparents), but have different mothers and different maternal grandparents. We defined non-kin as a pair of individuals that have up to the grandparent generation, no ancestors in common. In cases where either the maternal or paternal grandfather of the test individual or caller was missing, we used two independent exclusion criteria to ensure that a given dyad was indeed unrelated: (i) checking if the assigned grandfather of individual A was excluded as grandfather of individual B by at least two mismatches, or (ii) the grandfather of individual A was too young (i.e. less than 1250 days at the time of offspring conception) to have sired the father or mother, respectively, of individual B.

We tested the females' ability to recognize paternal kin in the following three familiarity conditions: (1) familiar peers: test individual and both callers were born in the same birth cohort and group (i.e. they were peers), and co-resident during the study. We controlled for disparities in ranks of the callers by selecting the non-kin call donor accordingly to the rank of the kin call donor; (2) familiar non-peers: test individual and both callers were born in different birth cohorts within the same group (i.e. they were non-peers), and co-resident during the study. Again we controlled for disparities in ranks of the callers; and (3) unfamiliar: test individual and both callers were born in different social groups and never co-resident in the same group

(based on CPRC lifetime census data). We assumed that rank information is unavailable among subjects from different groups and hence unimportant for our test design. Therefore, rank difference did not play a role in the selection of callers. However, since on Cayo Santiago a hierarchy between groups exists, we aimed on selecting both callers from the same social group. This was possible in all but three cases, for which we selected callers relative to the rank of their groups (i.e. minimum disparity, based on own observations of group encounters). Furthermore, we aimed at choosing callers of similar age, although age proximity is unlikely to account among subjects resident in different groups.

(f) Playback experiment

Each test female was presented with two calls, one from the paternal half-sister ('kin' condition) and one from the unrelated female ('non-kin' condition). The order of call presentation was counterbalanced and separated by at least one day (mean days = 13.2, range: 2–58). The experimenters were blind with regard to the condition (kin versus non-kin). We conducted all playbacks using a DAVIDactive5001 loudspeaker (Visonik, Berlin, Germany) connected to a Marantz Flash Card Recorder. The behavioural response of the test subject towards the playback of calls was recorded using a digital video camera (Panasonic NV-GS330 or JVC HD Everio Memory Camcorder GZ-HM650, Japan). The general procedure of the playback experiment was the following: we first tracked down the test female and followed her to establish her level of activity pre-playback and to ensure that the female whose call was going to be presented was out of sight. The loudspeaker-person then concealed the speaker behind dense vegetation, 11.4 ± 1.9 m (mean $\pm$ s.d.) away and between 0° and $\pm 45^\circ$ behind the test subject (if 0° refers to the position straight behind her back). The camera-person positioned herself in front of the test female (about 5 m away) and started videotaping. When the test female was settled, awake but not engaged in grooming (except self-grooming) or feeding activity, not disturbed by any surrounding activity or noise, and if she was facing away from the loudspeaker, the playback was started. After the experiment, we drew a map noting down the position of the loudspeaker in relation to the test female. Experiments were conducted all times of the day, except when the group of the test subject was feeding. To prevent habituation to the experimental protocol, we aimed on conducting no more than three experiments per group and day (mean $\pm$ s.d.: 1.5 ± 0.7).

In total, we conducted 86 playback experiments (paired design: $n = 43$ kin, $n = 43$ non-kin; conditions: familiar peers $n = 30$ tests, familiar non-peers $n = 24$ tests, unfamiliar $n = 32$ tests), with a total of 32 females serving as both callers and test individual, 29 serving only as callers and 11 only as test individual. Callers served on average 1.4 times as call donor in different tests. In cases where callers were repeatedly used, different calls of that individual were presented. Each test female participated in only one of the three familiarity conditions (i.e. familiar peer, familiar non-peer or unfamiliar).

(g) Analysis of playback experiments

The analysis of the playback experiments was based on video recordings and done blind in regards to the test condition. Using iMOVIE (v. 9.0.4, Apple Inc., USA), we determined the exact frame of the call onset and subsequently defined the first 10 s as the potential response time (i.e. looking). A response to the playback was defined as a turn of the females' head over her shoulder so that her face entered the right angle towards the loudspeaker. This head movement had to occur within the first 10 s after the playback call was broadcasted. If these conditions were not fulfilled, no response was recorded. Standing up and moving towards the loudspeaker was rated as response

if it occurred within the 10 s after playback start, as each only happened once out of 86 trials. One person scored all video-clips, while a second person re-scored 65% of the trials to establish inter-observer reliability. The two observers were in good agreement (Cohen's Kappa: $K = 0.79$, $n = 56$, $p < 0.001$). We also aimed at measuring the total time spent looking towards the loudspeaker, as well as the latency of response. However, because only 32 females responded towards the playback, checks of modal stability revealed instability of statistical results. We therefore had to refrain from testing these response variables.

(h) Statistical analysis

We first tested whether paternal kinship (i.e. paternal half-sisters or non-kin females) and familiarity (i.e. familiar peers, familiar non-peers or unfamiliar) had an effect on the probability that the tested female reacted towards the presentation of the vocalization by running a generalized linear mixed model (GLMM; [60]) with binomial error structure and logit link-function. Since the ability to discriminate between paternal half-sisters and non-kin was suggested to depend on the level of familiarity, we also included the interaction between these two predictors into the model. In addition, we included the playback order (i.e. whether the kin or the non-kin call was presented first) as fixed effect and the ID of the test subject and caller as random effects. The model was fitted in R v. 2.14.1 [61] using the function 'lmer' of the R-package lme4 [62]. We checked for model stability by excluding data points one by one from the dataset and compared the estimates derived with those obtained for the full model; no indication of the existence of influential cases was found. As an overall test of the effect of kinship and familiarity [63] we used a likelihood ratio test [64] comparing the full model with the null model comprising only the intercept, the fixed effect of playback order and the random effects (R function 'anova' with argument test set to 'Chisq'). Having demonstrated significance of the full model, we checked for significance of the interaction term by comparing the fit of the current model with that of the reduced version using a likelihood ratio test. The same was done for the predictor familiarity. All statistical tests were two-tailed with the α -level set to 0.05.

3. Results

Across the three playback conditions 53.5% of the test females showed a response ($n = 21$ females looked, 1 stood up and looked in the direction of the loudspeaker, 1 stood up and walked towards the loudspeaker) when presented with a call of a paternal half-sister. By contrast, 21.0% of the test females ($n = 9$) did respond when presented with a call of an unrelated female. See electronic supplementary material, table S1 for a detailed description of test females' responses across familiarity conditions.

The overall test of the effect of kinship and familiarity (and its interaction) revealed that at least one of the predictors influenced the probability of the test females' response towards the playback (likelihood ratio test comparing the full with the null model: $\chi^2_5 = 11.9$, $p = 0.03$). However, the interaction between kinship and familiarity was not significant ($\chi^2_2 = 1.85$, $p = 0.39$). Additionally, the overall test of the influence of familiarity turned out to be non-significant ($\chi^2_2 = 2.13$, $p = 0.34$), however because we had a special interest in this predictor we kept it in the final model. After removing the interaction between kinship and familiarity, it appeared that the probability to respond towards the playback was smaller in the non-kin condition, compared with the kin condition (figure 1 and table 1). Familiarity did not

Figure 1. Probability of females to respond when presented with calls of a paternal kin (i.e. half-sister) versus non-kin. $*p < 0.01$.

have an effect on the probability of the test females' response (figure 2 and table 1). Playback order showed no significant effect on the probability of response (table 1).

4. Discussion

The results of our study show that female rhesus macaques are capable of discriminating 'coo' calls played back from a paternal half-sister and an unrelated female, suggesting that they can use the acoustic modality for paternal kin discrimination. This finding is in line with results in female grey mouse lemurs [47], providing evidence for acoustic kin discrimination on the father–daughter level. Our data adds on Kessler's result [47] by suggesting that information encoded in the call structure can be sufficient to discriminate paternal kin on an even lower relatedness level, i.e. paternal half-siblings. Since in our study, we found the ability to discriminate between paternal half-sisters and unrelated females to occur independent of the familiarity status (being a member of the same versus different cohort and/or same versus different group, factors Kessler and colleagues were unable to control) we provide direct support for acoustic phenotype matching as an underlying mechanism of paternal kin discrimination in primates.

Phenotype matching has been suggested as an underlying mechanism by most studies investigating paternal kin discrimination using the olfactory or visual modality [14,16,65–67]. In rodents, for instance, the recognition of odours from conspecifics varied linearly with the degree of relatedness, allowing estimates of kinship even among more distant and unfamiliar relatives [14,16]. A similar pattern emerged for the visual modality [66], with facial resemblance

Table 1. Results of the final GLMM testing the effect of kinship and familiarity on the probability that a female responded towards the playback. (The test subjects ID and the callers ID were included as random effects. The level of 'kin' for kinship and 'familiar peers' for familiarity condition are included in the intercept and serve as a reference for the remaining predictor levels. Since the interaction between kinship and familiarity condition was not significant, it is not included in the final model.)

	estimate	s.e.	z	p-value
intercept	1.864	0.867	2.15	0.032
kinship:				
non-kin	−1.414	0.506	−2.795	0.005
familiarity condition ^a :				
familiar	−0.716	0.637	−1.123	0.262
non-peers				
unfamiliar	−0.783	0.585	−1.338	0.181
playback order	−0.875	0.499	−1.753	0.079

^aoverall likelihood ratio test: $\chi^2_2 = 2.13$, $p = 0.345$.

being positively correlated with fathers' investment into offspring [65].

To support phenotype matching as an underlying mechanism of (paternal) kin discrimination, important aspects to consider are possible species-specific requirements for the development of a phenotypic kin template. Especially in species that form complex social bonds, such as the ones observed in primates, the development of a kin template is likely to rely on social learning, instead of solely being dependent on hormonal determinants of bonding (reviewed in [5]). This is supported by findings on non-human primates, which do not exhibit an innate social preference for their kin [68] or even of their own offspring immediately after birth [69], but learn to do so through experience and association [70–72]. Considering social learning as an important aspect for establishing a phenotypic kin template in species with complex social bonds may explain why studies on captive non-human primates investigating phenotype matching by separating test subjects from their mothers (and fathers) immediately after birth and raising them in peer groups, have failed to show a paternal kin bias [32,33]. By contrast, studies on non-human primates carried out under natural conditions in which animals had the opportunity to interact with conspecifics of different kin levels, found evidence for paternal kin bias through phenotype matching [17,18,31]; although in these studies, not all possible sources of familiarity were controlled for (see Introduction). By taking advantage of the secondary dispersal patterns in male rhesus macaques, we here aimed to control for familiarity and, at the same time, allowed individuals to establish a kin template under natural conditions. Taken together, our results and the above-mentioned findings indicate the importance of an interplay between familiarity (being a requisite to learn a paternal kin template) and phenotype matching (transfer of kin template to distant or even unfamiliar paternal kin), a process referred to as 'phenotype matching via indirect familiarity' [23] (*sensu* 'familiar imprinting' [73]).

Figure 2. Probability of females to respond when presented with calls of familiar peers, familiar non-peers or unfamiliar individuals.

If males reproduce in different groups, the possibility arises that during inter-group encounters subjects might gain knowledge about paternal sibship living in other social groups, e.g. via a mixture of facial and vocal cues. Consequently, despite the necessity to test phenotype matching under natural conditions (see above), familiarity owing to inter-group encounters may question the potential to control for all possible sources of familiarity. Despite a potential familiarity between social groups, rhesus macaques have been shown to discriminate between individuals of the same versus different group [74]. Altogether, our result represents the best possible indication for the involvement of phenotype matching in the process of paternal kin recognition, accounting for the necessity of social learning to establish a (paternal) kin template.

In general, either one's self or other related animals could be used as potential templates in phenotype matching [30]. In terms of the acoustic modality, using self (i.e. own adult voice) as a template is, however, rather unlikely. This is because the hearing of one's own voice is through a combination of bone and air conduction, leading to a perceived dominance of low frequencies [75]. Consequently, the perception of one's own voice is different from the perception of others making the comparison between one's own voice and potential kin difficult. By encouraging infants to associate with offspring's of females who conceived from the same male, mothers could potentially mediate familiarity between paternal siblings [6]. However, in rhesus macaques no preferred association between mothers of paternal siblings have been found [17], making this scenario rather unlikely. If present in the group after birth, the father of the offspring could have served as a template for paternal kin recognition during

individual development [6]. Recently, a study on rhesus macaques of our study population found that sires affiliate more with their offspring compared with unrelated offspring [10]. As male rhesus macaques produce more than one offspring [49], offspring potentially have the chance to associate with paternal siblings through their father. Consequently, the potential for establishing a (acoustic) template for paternal kin recognition is available in this species.

Finally, it is worth noting that although the association between maternal kin has been found to be much stronger than among paternal kin, for females the biological importance to recognize paternal sisters might emerge in cases in which maternal kin are absent. In such situations, female savannah baboons have been found to form stronger bonds with their paternal sisters [19].

It is important to note that the underlying mechanism/s as well as the cue used have to work within a species' social system and reflect its communicative channels. Hence, differences across species have to be expected [76]. It is therefore important to distinguish which stimuli signal kinship and which are indeed used to identify kin in a given species. With our study, we give support to the notion that the acoustic modality plays an important role in paternal kin discrimination in rhesus macaques and that phenotype matching is (one of) the underlying mechanisms. However, other cues such as the visual modality bear potential to be used in paternal kin discrimination too [36,67,77]. Kin discrimination is therefore very likely to be multimodal [24] as shown in sheep, which combine sound, vision and olfaction in mother–offspring recognition [78].

This study was approved by the CPRC and the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico (protocol no. 4060105).

Acknowledgement. We thank the CPRC, especially the census takers E. Davila, J. Resto, G. Caraballo-Cruz and N. Rivera-Barreto for their support, collecting demographic data and DNA samples, as well as E. Maldonado for data management. We are grateful to F. B. Bercovitch, M. J. Kessler, J. D. Berard, M. Krawczak, P. Nürnberg and J. Schmidtke for starting the genetic database of the Cayo Santiago population, and L. Vigilant for providing laboratory access. We acknowledge M. Krawczak and O. Junge for access to the genetic data management program FINDSIRE; L. Muniz and S. Bley for improving the genetic database; and the Max Planck Institute for Evolutionary Anthropology in Leipzig for logistic support. We are grateful to R. J. Sullivan, K. B. Duffy, N. Miosga, S. Winters, V. Du and S. Schunack for helping to conduct playback experiments; thanks a lot for your patience. Additionally, we thank D. Langos for support in the field. L. J. N. Brent and S. Larson kindly provided additional information of female hierarchy. Special credit goes to R. Mundry for statistical advice and R. R. Brockhausen for his help to construct pedigrees. We thank the two anonymous reviewers for their helpful comments on the manuscript. The content of the publication is solely the responsibility of the authors and does not necessarily represent the official views of NCRR or ORIP.

Data accessibility. Data file containing necessary data to perform GLMM analyses (see the electronic supplementary material, S2).

Funding statement. This project was founded by the German Research Foundation (DFG; grant nos. PF659/3-1, WI1808/3-1 and 1808/5-1 awarded to D.P. and A.W., respectively) and conducted within the Emmy-Noether Group of 'Primate Kin Selection' (awarded to A.W.). The population of Cayo Santiago is currently supported by the National Center for Research Resources (NCRR; grant no. 8P40OD012217 awarded to the CPRC) and the Office of Research Infrastructure Programs (ORIP) of the National Institute of Health.

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