True paternal care in a multi-male primate society

Jason C. Buchan[1], Susan C. Alberts[1,2], Joan B. Silk[3] & Jeanne Altmann[2,4,5]

[1]*Department of Biology, Duke University, Box 90338, Durham, North Carolina 27708, USA*
[2]*Institute of Primate Research, National Museums of Kenya, Nairobi, Kenya*
[3]*Department of Anthropology, UCLA, Los Angeles, California 90095, USA*
[4]*Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544, USA*
[5]*Department of Conservation Biology, Brookfield Zoo, Brookfield, Illinois 60513, USA*

Although male parental care is rare among mammals[1], adult males of many cercopithecine primate species provide care for infants and juveniles. This care is often in the form of grooming, carrying, support in agonistic interactions, and protection against infanticide[2,3]. For these behaviours to be interpreted as true parental care, males must selectively direct care towards their own offspring and this care must result in fitness benefits[4]. With the exception of males defending probable offspring from infanticide[5], male primates living in multi-male, multi-female social groups have not been shown to selectively direct care towards their own offspring[6,7]. We determined paternity for 75 juveniles in a population of wild savannah baboons (*Papio cynocephalus*) and collected data on interventions in agonistic disputes by adult males on behalf of juveniles as a form of male care. Here we show that adult males differentiate their offspring from unrelated juveniles and selectively support their offspring in agonistic disputes. As support in agonistic disputes is likely to contribute to rank acquisition and protect juveniles from injury and stress[2,3,5], this can be considered true parental care.

The subjects of the study were members of five wild savannah baboon groups in Amboseli, Kenya, and adjacent areas at the foot of Mount Kilimanjaro; the study population has been under continuous observation since 1971 (ref. 8). We collected data on interventions in agonistic disputes between July 1999 and July 2002. We also unambiguously identified the fathers for 75 of the 102 juveniles present during this period by analysing six microsatellite loci. The scope and extent of paternal care in baboons could be limited by the fact that males regularly transfer between social groups, so that fathers may leave a group before or shortly after the birth of infants they have sired. However, half of the 75 juveniles in our study still had their fathers present in their social group when the juveniles were 3 years of age, indicating that many males had the opportunity to provide paternal care.

Males helped their own genetic offspring significantly more often than they helped juveniles to whom they were not related (Fig. 1a; Wilcoxon matched-pairs signed-ranks test, $T = 8.5$, $P < 0.01$, $n = 15$ males that had both genetic offspring and unrelated juveniles present). All but 3 of the 15 males who had the opportunity to help genetic offspring and unrelated juveniles provided more care to their own offspring than to unrelated juveniles (Fig. 1a). This pattern of biased care towards offspring will arise if males can distinguish their own offspring from unrelated juveniles. However, it might also arise if males intervene at random in disputes that occur in their proximity, and they happen to be in proximity to their offspring more than expected by chance (if, for instance, they tend to be in proximity to females with whom they have mated in the past). If this 'random intervention' hypothesis for the biasing mechanism is correct, then males would intervene against their offspring as often as they intervene on behalf of their offspring. Our data do not support this 'random intervention' hypothesis. In 73 cases, the intervening male was known to be the father of one participant and unrelated to the other. Males intervened on behalf of their offspring in 69 of these interventions, and against their offspring in only 4 (Wilcoxon matched-pairs signed-ranks test, $T = 3$, $P < 0.008$, $n = 13$ males). The observed pattern of care might also occur if males biased care in favour of juveniles and this bias results in males providing more care to their own offspring by chance. However, if this 'age biased' hypothesis is correct, then males would intervene on behalf of their offspring as often as they intervene on behalf of unrelated juveniles when interactions are

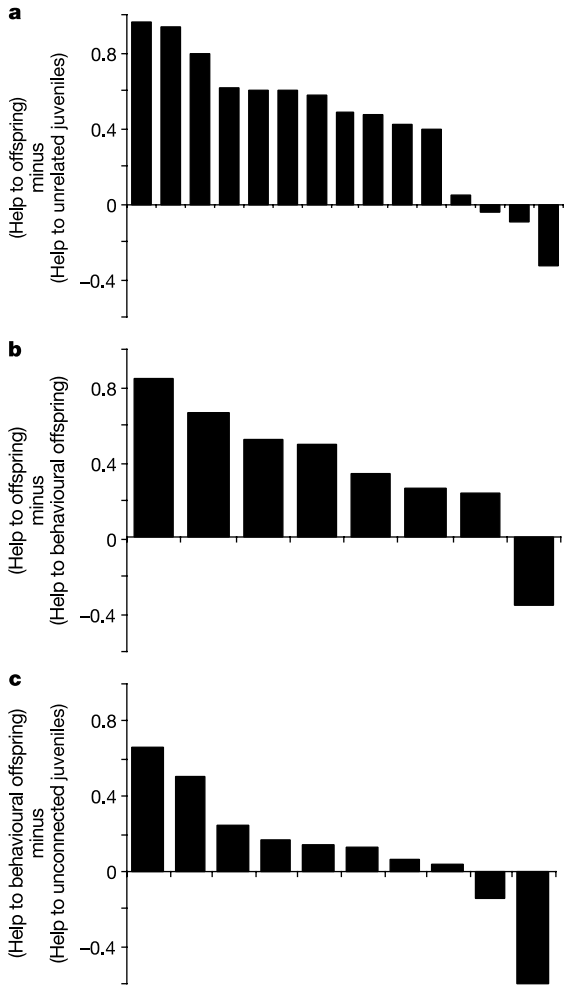

Figure 1 We counted all instances of help that each juvenile received from adult males. We measured the fraction of that help that each male gave to each juvenile, restricting the analysis in each case to the time period in which the male was present in the group. Two-tailed Wilcoxon matched-pairs signed-ranks tests were used to compare the amount of help males provided to juveniles in two different categories. Each bar represents the difference, for one male, between the fraction of help given to juveniles of each type. **a**, Difference, for each male, between the fraction of help he gave to his genetic offspring and to unrelated juveniles (Wilcoxon matched-pairs signed-ranks test, $P < 0.01$). Bars above the expected value of zero represent males that helped genetic offspring more than unrelated juveniles. **b**, Difference, for each male, between the fraction of help he gave to his genetic offspring and to his non-genetic 'behavioural' offspring ($P = 0.05$). Bars above the expected value of zero represent males that helped genetic offspring more than non-genetic behavioural offspring. **c**, Difference, for each male, between the fraction of help he gave to non-genetic behavioural offspring and to 'unconnected' juveniles ($P > 0.1$). Bars above the expected value of zero represent males that helped non-genetic behavioural offspring more than unconnected juveniles.

limited to those between juveniles. We considered the 28 cases in which both participants were juveniles, and the intervening male was known to be the father of one participant and unrelated to the other. Males intervened on behalf of their offspring in 24 of these interventions and against their offspring in only 4 (Wilcoxon matched-pairs signed-ranks test, $T = 4$, $P < 0.009$, $n = 12$ males).

Males were evidently able to distinguish their own offspring from unrelated juveniles. There are two types of mechanism of identification: direct discrimination of kin by using a process such as phenotype matching[9,10], or the use of behavioural rules-of-thumb based, for example, on sexual access to fertile females. To address the mechanisms underlying our results, we identified three non-overlapping classes of juveniles for each male. The first class comprised his genetic offspring. The second comprised his non-genetic 'behavioural' offspring: those juveniles for which the male consorted with the mother during the days of most likely conception for that juvenile, but for which he was not the genetic father (see Methods for a description of female sexual cycles and days of likely conception). The final class comprised unrelated juveniles that were neither genetic nor behavioural offspring (apparently 'unconnected' juveniles).

If males use phenotype matching, then we expect males to give more help to genetic than to non-genetic behavioural offspring, and not to differentiate between non-genetic behavioural offspring and unconnected juveniles. In contrast, if males use a simple rule-of-thumb based on whether or not they consorted with the mother when she was likely to conceive, males will not differentiate between genetic and non-genetic behavioural offspring, but will help non-genetic behavioural offspring more often than unconnected juveniles.

Most males supported genetic offspring more than non-genetic behavioural offspring (Wilcoxon matched-pairs signed-ranks test, $T = 4$, $P = 0.05$, $n = 8$ males with both genetic offspring and non-genetic behavioural offspring present; Fig. 1b). In contrast, there was no significant difference in the proportion of care provided to non-genetic behavioural offspring and unconnected juveniles (Wilcoxon matched-pairs signed-ranks test, $T = 13$, $P > 0.10$, $n = 10$ males with both non-genetic behavioural offspring and 'unconnected' juveniles present; Fig. 1c).

Although phenotype matching would explain this result, additional behavioural information, beyond simply whether or not they consorted with the mother during the days of likely conception, might shape males' paternal behaviour. For instance, males might respond to information about what proportion of the mother's 'available consort time' (total observed hours of mate guarding) they monopolized during the days of likely conception. This value was a strong predictor of paternity: the more of the female's consort time that a male monopolized during the days of likely conception, the more likely he was to father a given offspring (logistic regression, χ^2 approximation $= 11.52$, $P < 0.001$, $n = 63$). Hence this would serve well as a behavioural cue of paternity. Indeed, the probability that a male supported a juvenile at least once during the study was predicted by the proportion of its mother's consort time that he had monopolized during the days of likely conception (logistic regression, χ^2 approximation $= 6.57$, $P = 0.01$, $n = 43$). However, this relation between mating behaviour and paternal care does not allow us to differentiate between phenotype matching and mating information as the source of kin recognition cues. It only confirms that information about male mating behaviour relative to days of female fertility predicts paternity; males' use of this will be subject to constraints of memory and knowledge about female fertility. On the other hand, if phenotypic markers of relatedness are readily appropriated for kin recognition, then males may use these to differentiate offspring, and the observed relation between mating behaviour and paternal care would still be obtained. Studies in humans suggest a role for olfactory cues in signalling ovulation[11], in mate choice[12–14] and in providing cues of kin recognition[15]. Olfactory cues play well-documented roles in kin recognition in several other mammalian species as well[16]. There is also evidence that primates may use visual cues to recognize kin[17]. Hence, whether phenotype matching (for example, olfactory or visual cues) or behavioural cues (memory of mating behaviour combined with knowledge about female fertility) or their combined effects represent the more parsimonious explanation for our results is not clear.

A growing body of evidence indicates that primates can and do recognize paternal kin[5,18–21]. In several cases, evidence indicates that primates rely mainly on behavioural cues, such as age proximity, residence patterns or prior mating behaviour to identify paternal kin. Several of these studies, including two in the Amboseli study population[19,20], suggest that phenotype matching may complement behavioural cues in paternal kin recognition[18–20]. These findings concur with the current study but stand in stark contrast to several earlier studies, which failed to find evidence for paternal kin recognition in the laboratory (reviewed in ref. 22) and which led most researchers to conclude that primates do not recognize paternal kin. We suggest that the discrepancy between results obtained in the field and in the laboratory may result from the fact that animals in the wild rely on multiple cues, whereas laboratory experiments are designed to isolate single cues. In distinguishing offspring, males may use their own mating behaviour in combination with cues of female fertility, phenotype matching and even maternal behaviour towards potential fathers[23]. The fact that male baboons in Amboseli selectively support their own offspring indicates that even in species where females mate with multiple males, paternal care can and does evolve. □

Methods

Genetic analysis

Faecal (ref. 24) ($n = 172$ individuals) or blood (ref. 8) ($n = 22$ individuals) samples were collected from 194 baboons, including 79 infants, their mothers and putative fathers. Wherever possible, multiple faecal samples were collected for each individual. Faecal DNA extraction was done by using the QIAamp DNA Stool Mini Kit (QIAGEN GMBH) following the protocol for isolation of DNA from stool for human DNA analysis but with two modifications. We used 500 mg rather than 200 mg of wet faeces, and did not use InhibitEX tablets; instead, 1.2 ml of supernatant from step 3 was divided equally into two 2 ml microcentrifuge tubes containing 25 μl of Proteinase K as in step 9 of the QIAGEN protocol. Each tube was then carried through as per the protocol with the lysate from both tubes filtered through the same spin column. DNA samples were eluted in 200 μl of buffer AE. The amount of amplifiable DNA in all samples was quantified by using the 5′ nuclease assay as described in ref. 25. Four tetra-nucleotide (D4s243, D14s306, D10s611, D5s1457) and two di-nucleotide human microsatellite loci (D7s503, D13s159) were amplified for each sample. All microsatellites were analysed by using an ABI PRISM3700 DNA analyser and Genescan and Genotyper software. The number of replicates necessary to ensure the detection of allelic dropout was calculated based on the amount of DNA per reaction and the observed rates of allelic dropout[25,26].

Maternity for all offspring was known from observations of pregnancies and observations at or shortly after parturition. To ensure the correct identity of samples, mothers and offspring were checked for mendelian mismatches, and all putative fathers were genotyped from two separate faecal samples. If mismatches occurred, DNA was extracted from further faecal samples until the mismatch was resolved. All males that were at least four years of age and present during the conception of an infant were considered putative fathers, although males do not reach full adulthood until approximately 7.5 years (ref. 27).

Initially, duplicate polymerase chain reactions (PCRs) of all samples were done. If both PCRs produced identical heterozygotes, the genotype was considered to be correct. If, after two PCRs, an individual's genotype consisted of both a heterozygote and homozygote with a common allele, further replications were done until both alleles were observed at least twice. Individuals whose genotypes appeared to be homozygous were amplified seven times if samples contained less than 200 pg μl^{-1} and four times for samples with more than 200 pg μl^{-1} of DNA. Paternity was based on exclusion and further supported through the use of the likelihood-based paternity assignment program CERVUS 2.0 (ref. 28).

Behavioural data

Savannah baboons mate in the context of mate-guarding episodes that occur during the follicular phase of the female's cycle, when she has a prominent swelling of the sex skin[29]. Data on the identity of male and female partners in all mate-guarding episodes were collected as part of regular monitoring of study groups. We identified behavioural offspring as those offspring for which the male was observed to mate with the mother during the most likely days of conception for that juvenile, that is, during the last five days of the follicular phase of the sexual cycle[29]. The end of the follicular phase is signalled by deflation of the swollen sexual skin; the days of most likely conception are identified

retrospectively based on near-daily records of swelling size and state. Observers recorded all agonistic interactions and interventions on an *ad libitum* basis. In each case of agonism, observers recorded the identity of individuals involved in the aggressive encounter and its outcome[30]. When third parties intervened in disputes, observers recorded the identity of the individual who intervened (ally), the identity of the individual that received support, the identity of the individual against whom support was directed, and the type of support that was provided. Support took two forms. Allies either directed overt aggression towards one of the participants (designated the opponent), or established close proximity or affiliative physical contact with one of the participants (designated the beneficiary). See ref. 31 for more details of data collection; methods employed in that study were identical to those employed here.

Adult males supported juveniles in 193 disputes. In 93 of these events, both disputants were juveniles (less than 4 years old); in 36, the opponent was an adult female; in 49, a subadult male; and in 15, an adult male (see ref. 27 for definitions of subadult and adult males). The median age of juvenile recipients of adult male help was 2.25 yr; the interquartile range was 1.75 yr to 3.13 yr, and the youngest recipient was 4 months old.

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Correspondence and requests for materials should be addressed to S.C.A. (alberts@duke.edu).

Motion-induced spatial conflict

Derek H. Arnold & Alan Johnston

Department of Psychology and Institute of Cognitive Neuroscience, University College London, Gower Street, London WC1E 6BT, UK

Borders defined by small changes in brightness (luminance contrast) or by differences in colour (chromatic contrast) appear to move more slowly than those defined by strong luminance contrast[1–4]. As spatial coding is influenced by motion[5–7], if placed in close proximity, the different types of moving border might appear to drift apart[8]. Using this configuration, we show here that observers instead report a clear illusory spatial jitter of the low-luminance-contrast boundary. This visible interaction between motion and spatial-position coding occurred at a characteristic rate (~22.3 Hz), although the stimulus motion was continuous and invariant. The jitter rate did not vary with the speed of movement. The jitter was not due to small involuntary movements of the eyes, because it only occurred at a specific point within the stimulus, the low-luminance-contrast boundary. These findings show that the human visual system contains a neural mechanism that periodically resolves the spatial conflict created by adjacent moving borders that have the same physical but different perceptual speeds.

A bright red dot moving against a dark background provides a strong luminance-defined motion signal. A smaller equiluminant green dot superimposed on this target provides a weaker motion signal at the chromatic boundary. To the extent that motion influences spatial position[5–7], the green dot might be expected to lag progressively behind. This scheme has recently been suggested as an explanation for the classical 'fluttering hearts' illusion[8] (Fig. 1).

When we created this configuration (Fig. 2a), it was clear that the two parts of the stimulus did not appear to drift apart. However, a vivid perceptual illusion was immediately apparent. When fixation was maintained on a stationary target, the spatial position of the green dot appeared to jitter while moving. To examine this phenomenon, we constructed a stimulus consisting of four dots (Fig. 2a). A small green dot was superimposed on a larger red dot to form a bull's-eye configuration. Another green dot, of the same size, was shown against a dark background (isolated motion). All these dots rotated about a central static fixation point at a constant retinal velocity of $6.75^\circ\,s^{-1}$. During a run of trials, we systematically manipulated the luminance of the green dots. On each trial, observers were required to indicate whether the foreground green dot or, in different trial runs, the isolated green dot appeared to jitter while moving. Jitter was reported most often when there was little or no luminance contrast between the moving foreground and back-