OFFSPRING PROTECTION BY MALE MANDRILLS, *MANDRILLUS SPHINX*

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Abstract

Most mammals are characterized by a lack of parental care by the male sex. This is particularly true in highly polygynous, sexually selected species and species in which fathers remain only weakly associated with their offspring. Here we report observations suggesting the existence of male parental care in the mandrill (*Mandrillus sphinx*, Primates: Cercopithecinae), one of the most sexually dimorphic mammal species known and a species in which, in the wild, males reside in social groups solely for the breeding season. Adult males in three captive groups exhibited aggressive, protective behavior when definite or likely offspring became involved in agonistic confrontations with individuals outside of the group. Males were observed to abandon feeding opportunities, sexual consorts, and allogrooming sessions to intervene on behalf of their threatened offspring. In one of the three groups, the male was occasionally removed, leaving only his mate and their two juvenile offspring; during these periods (when support from their father was unavailable) each of the juveniles initiated significantly fewer extra-group agonistic disputes. A fourth group was studied in which the male was unrelated to the two juveniles, and in this group the male failed to protect the juveniles from outside threats. Although these observations of paternal care were detected across varying social and ecological conditions, it is unclear to what extent they apply in the wild.

Introduction

In cases where parents remain in association with their offspring the opportunity arises for adaptive molding of parental care by natural selection (Wilson, 1975). Forms of care will be selectively favored when they contribute to increased survival and reproduction of progeny while minimally decreasing a parent's ability to invest in future offspring (Trivers, 1972). For example, parents could provide assistance to offspring engaged in agonistic conflicts, thereby protecting their vulnerable progeny from outside threats. In sexually dimorphic species the cost to a parent of providing such agonistic support would be lower for the larger, competitively superior sex, translating to a greater net benefit if the larger sex performs this type of parental care. In theory, however, the larger, competitively superior sex will generally be less inclined to provide parental care: this sex's dimorphism is likely a product of strong sexual selection for maximizing opportunities for progeny production rather than progeny care (Clutton-Brock, 1991).

An extreme sexual dimorphism is known to exist in mandrills (*Mandrillus sphinx*), Old World monkeys endemic to equatorial West Africa. Adult males of this

species are three times heavier than the average female (Wickings and Dixson, 1992), exhibit especially well-developed canines, and display the brightest coloration of any mammal (Darwin, 1871). A male mandrill's coloration (particularly its redness) appears to function as an intrasexual signal, communicating information about the male's current rank and resource holding potential (Setchell and Dixson, 2001). A strong history of sexual selection thus appears to have characterized mandrill evolution (Setchell et al., 2005a). Recent field observations of wild mandrills have further revealed that adult males remain only seasonally present in groups, becoming social exclusively while females are in estrous and otherwise living solitarily (Abernethy et al., 2002). The existence of paternal care (such as offspring protection by fathers) might therefore seem unlikely in mandrills, especially given adult males' weak association with groups (and hence with their progeny). As Abernethy et al. (2002, p. 136) conclude: "As most males are absent from the horde during half the year, it seems highly unlikely that they play any role in horde cohesion, protection or leadership."

We report on a series of captive studies suggesting that male mandrills may perform a valuable protective role within groups by intervening on behalf of offspring involved in extra-group agonistic encounters. We further show that this paternal protective behavior manifests itself across varying socio-ecological conditions and also in contexts where other fitness-enhancing behaviors are opportune alternatives for fathers.

Methods

Observations focused on four captive mandrill groups containing one or more adult males along with immature conspecifics. The immatures within the groups represented either offspring or non-offspring of the adult males and included juveniles and infants of both sexes. Two of the study groups were housed in zoos in NY, USA. The Syracuse group (at the Rosamond Gifford Zoo) consisted of an adult male, an adult female, and their two juvenile female offspring. The Buffalo group (at the Buffalo Zoological Gardens) consisted of an adult male, an adult female, and two juvenile females sired by a different male. Two other study groups were housed in larger, semi-free ranging colonies at the Centre International de Recherches Médicales in Franceville, Gabon. The 'Enclosure 3' group consisted of 2 adult males, 10 adult females, 5 juvenile males, 3 juvenile females, 2 infant males, and 3 infant females. The 'Enclosure 2' group consisted of 4 adult males, 10 adult females, 9 subadult males, 6 sub-adult females, 10 juvenile males, 12 juvenile females, 4 infant males, and 7 infant females. The observation period spanned January 2002 – May 2005 and details on enclosure habitat, feeding regimen, observation hours and sampling regimes for each group are provided in Table 1 in Laidre (2008).

The Syracuse group was the first group we studied and our general approach in this investigation was to use the behavior of the Syracuse adult male as a hypothesis for how males in other groups might behave if male mandrills protect their offspring. The groups we studied had varying housing environments and/or social compositions, allowing us to evaluate the generality of paternal protective behaviors across different conditions. If paternal protective behavior is a species-specific phenomena

in mandrills then it should occur (i) across different ecological conditions (ranging from small, indoor zoo enclosures to large, outdoor naturalistic enclosures), (ii) across different social conditions (ranging from single-male harem groups to multi-male, multi-female groups), and (iii) only in groups in which males are housed with definite or likely offspring. [DNA analyses have shown that paternity is strongly positively correlated with dominance rank in mandrills and that alpha males sire the great majority (80-100 %) of offspring (Dixson et al., 1993). Accordingly, we assumed that the dominant males in the Enclosure 2 and 3 groups were the likely fathers of the majority of the immatures within their groups, since they had been alphas for several years (E.J. Wickings, pers. comm.)]. Predictions (i) and (ii) were tested by comparing the Syracuse male's behavior with that of the dominant males in the Enclosure 2 and 3 groups (the latter of whom were housed in large, outdoor naturalistic enclosures and within multi-male, multi-female groups). Prediction (iii) was tested by comparing the Syracuse male's behavior with that of the Buffalo male (the latter of whom was also housed in a zoo enclosure but with unrelated immatures).

To assay possible paternal protective behavior we focused on extra-group agonistic interactions that involved immatures, determining if males ever intervened in these interactions on behalf of their offspring. In the zoo groups, extra-group agonistic interactions began when an immature slapped the glass wall that separated the enclosure and visitor viewing area. The glass was slapped directly at one or more visitors who had approached too closely, and the performance of a glass slap appeared hostile, frequently causing the visitors to jump back (Exemplars of this behavior were filmed and have been stored in the Visual Media Collections of the Cornell Laboratory of Ornithology's Macaulay Library. These video clips can be viewed though the Laboratory's website). In the two semi-free ranging groups, extra-group agonistic interactions occurred along the chain-link fence bordering the groups' enclosures, which were adjacent. Along the border individuals frequently became involved in altercations with non-group mates, screaming when the altercation became too rough. Such screaming appeared to be the vocal equivalent of glass slapping, and both behaviors were readily detectable by other group members, providing a means of attracting agonistic aid.

In addition to evaluating behavioral changes in adult males during such extra-group agonistic interactions, we also evaluated changes in the immatures' behavior during periods when their father was unavailable to provide protection. This was possible because the adult male in the Syracuse group was occasionally separated and housed off-exhibit. If agonistic protection provided by a mandrill father is beneficial to his offspring, then when a father is absent his offspring should be less successful in extra-group agonistic confrontations, thus initiating fewer confrontations. We tested this prediction by evaluating how often the juveniles in the Syracuse group performed glass slaps when their father was present versus absent.

Finally, we also report the amount of other forms of male care that we observed in mandrills, to compare the relative level of affiliative versus aggressive, protective care by fathers. Two additional groups (see Laidre, 2008) are included in the report of this data. (These groups were not included in our analysis of extra-group agonism since extra-group interactions were not observed to occur at these zoos.) The Tampa group from the Lowry Park Zoo (FL, USA) contained 1 adult male, 1 sub-adult male,

2 adult females, 3 juvenile males, 1 juvenile female, and 1 infant female (the adult male being the father of all the immatures). And the Paignton group from the Paignton Zoo Environmental Park (UK) contained 1 adult male, 1 adult female, and an unrelated infant male.

Results

The behavior of the adult male in the Syracuse group changed dramatically in response to the performance of glass slaps by his juvenile daughters (Fig. 1). In the period after either offspring's glass slap compared to the period before their glass slap the male significantly increased how often he charged the visitors, paced alongside the length of the glass, slapped the glass, and directed threat displays at the visitors (for each behavior: Two-tailed, paired t-test, $t > 5$, $df = 118$, $p < 0.0001$). The male's behavior frequently caused the visitors to jump back from their original location.

The Syracuse male remained vigilant of his offspring's welfare even after moving out of sight into the off-exhibit enclosure. If one of his daughters performed a glass slap after the male had moved off-exhibit (and if the door between the two enclosures had been left open), the male would immediately rush into the exhibit enclosure. The male would do so even if it required (a) abandoning food (which was provided in bulk only in the off-exhibit enclosure), (b) abandoning his estrous consort (a lone female who was kept in a separate cage in the off-exhibit enclosure), and (c) terminating an allogrooming session (with either his mate or the other, lone female). The male would not rush into the exhibit enclosure, however, when visitors pounded on the glass wall, confirming that his protective response was solely motivated by his offspring.
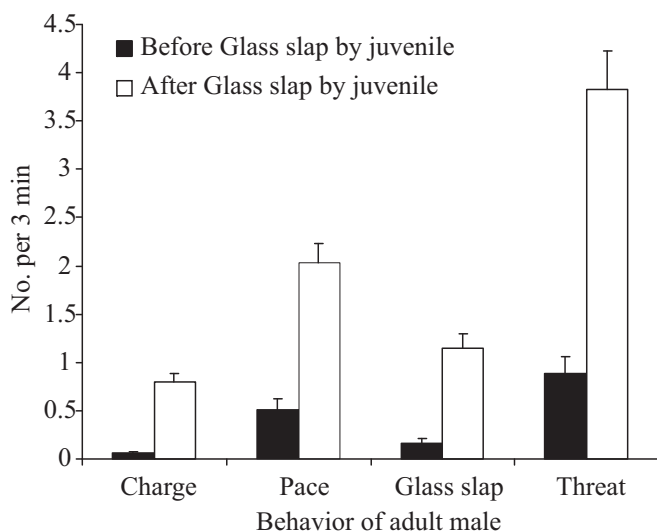

Fig. 1: Mean + SE of the number of times different aggressive behaviors were directed at visitors by the adult male in the Syracuse group 3 min before and after either of his juvenile daughters slapped the glass at the visitors. Included in the analysis are N=119 glass slaps by these juveniles. To ensure that the 3 min periods associated with different glass slaps did not overlap, glass slaps that occurred within 6 min of an earlier glass slap were not included in the analysis.

On one or more days each month, the male in the Syracuse group was removed from the rest of the group and locked in the off-exhibit enclosure for the entire day.

On days when the adult male was absent, both his juvenile daughters directed significantly fewer glass slaps toward the visitors: the younger juvenile averaged 0.67 glass slaps when her father was absent and 18.6 glass slaps when he was present (Two-tailed t-test, $t = 3.71$, $df = 18$, $p < 0.005$); the older juvenile averaged 0.67 glass slaps when her father was absent and 3.9 glass slaps when he was present (Two-tailed t-test, $t = 2.82$, $df = 18$, $p < 0.05$). These differences in the average number of glass slaps were not attributable to the number of visitors, which averaged 1596 on days when the male was present and 1539 on days when he was absent (Two-tailed t-test, $t = 0.30$, $df = 18$, $p = 0.77$).

Within the Enclosure 2 and 3 groups each dominant male consistently exhibited protective behavior when immatures from its group screamed during an extra-group agonistic confrontation. In the Enclosure 3 group, the only other adult male (the subordinate) never exhibited protective behavior, and in the Enclosure 2 group, only one of the subordinate adult males ever exhibited protective behavior. We were unable to record protective behaviors in as much detail as the Syracuse group (because the fence bordering the two Franceville enclosures faced away from our only observation point); however, on over thirty occasions across over 2 months of daily observation we observed the dominant males in each group charge the fence immediately after one of their immatures screamed. The only other context in which either of these males locomoted so rapidly was to drive off rivals (Laidre, 2005) within their group or to access newly discovered food (Laidre, 2006). Like the Syracuse male, the dominant males in each Franceville group were also observed to abandon feeding opportunities and allogrooming sessions to intervene on behalf of immatures.

In the Buffalo group (where the immatures were unrelated to the male) there was no significant increase in any form of aggressive, protective behavior by the male following a glass slap by one of the immatures. This male, however, showed a similar tendency to the Syracuse male to generally aggress against visitors, directing on average just over 7 threat displays per h at the visitors.

Across all study groups, representing over 1000 h observation (>700 for M.E.L. and > 500 for J.L.Y.), we never observed affiliative paternal care (such as carrying, holding, retrieving, embracing, or playing). In fact, virtually no non-aggressive tactile contact took place between adult males and immatures and on only one occasion (lasting under 10 sec) did we observe grooming of an immature by an adult male.

Discussion

Aside from monogamous and polyandrous species, paternal care within primates has also been reported in several Old World monkey species with a multi-male, multi-female group structure, including baboons and macaques (reviewed in Taub and Redican, 1984). Itani (1959), who first reported on paternal care in nonhuman primates, showed that male Japanese macaques safeguard infants, both by providing affiliative care (including carrying, hugging, grooming, playing, and food-access privileges) and by providing aggressive protection. This latter form of male care has been rarely reported in multi-male primate groups. As Borries et al. (1999, p. 351) note "only a few hints on protector males living in multimale groups are to be found in the primatological literature."

In this study, we found that adult male mandrills in captivity provided essentially no affiliative paternal care but were vigilant of possible threats to their offspring, exhibiting aggressive, protective behavior when offspring became involved in agonistic encounters. In some instances, a male's protective behavior even took priority over other, fitness-enhancing activities (like consorts with an estrous female, food consumption, or allogrooming), suggesting that the behavior fulfills an important function. There was also indirect evidence that offspring benefited from their father's protection, since they decreased their involvement in agonistic encounters when their father was absent. Lastly, the protective paternal care was (i) detected under varying ecological conditions (including small, indoor zoo enclosures to large, outdoor naturalistic enclosures), (ii) detected under varying social conditions (including single-male harem groups and multi-male, multi-female groups), and (iii) absent when a male was not the father of the immatures (Buffalo group) or performed rarely when a male was unlikely to have fathered the immatures (subordinates in Enclosure 2 and 3 groups). Altogether, these results suggest that male mandrills can provide beneficial paternal care by attacking potential sources of danger to their offspring (see also Yorzinski and Vehrencamp, 2008).

One explanation for these results is that male care is an artifact of captivity: fathers are forced to remain in continuous association with their offspring whereas in the wild they are only semi-permanent members of social groups. Wild male mandrills, however, could still potentially benefit from performing such care, since offspring that were protected would presumably be more likely to survive to reproductive age, thus enhancing a male's lifetime reproductive success. Also, even if a substantial portion of a male's time and energy budget is devoted to mate guarding (which has recently been shown to correlate with paternity in mandrills (Setchell et al., 2005b)), this need not preclude offspring protection: attempting to sire more offspring and caring for existing offspring are not mutually exclusive strategies (Parker and Schwagmeyer, 2005). Males could employ a 'mixed' strategy, pursuing and guarding fertile females some portion of the time while at other times (particularly when offspring are in danger) providing paternal care. The existence of such a mixed strategy would be plausible physiologically since the hypothesized form of paternal care (attacking threats to one's offspring) is hormonally compatible with aggressive mating competition, requiring no drop in a dominant male's elevated plasma testosterone level (Wickings and Dixson, 1992). Although extrapolations from captivity to the wild are necessarily tentative, our observations from zoos and semi-free ranging groups suggest the following prediction: if free ranging male mandrills tend to return to groups in which they were reproductively successful in the past, then protective care by fathers may also be detectable in wild mandrills. Detailed tests of this and other hypotheses about wild mandrill behavior will require overcoming the obstacles associated with field studies of this species (Abernethy et al., 2002).

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