

## Correspondences

# Father–daughter inbreeding avoidance in a wild primate population

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The most common way by which social animals avoid breeding with relatives is for members of one or both sexes to disperse before reproducing [1]. In capuchin monkeys — as in most primates — males disperse while females benefit from lifelong relationships with maternal kin within the group [2]. If  $\alpha$ -males — who sire most offspring in a given group — retain their rank for longer than 6 years, the age at which females reach sexual maturity, father–daughter inbreeding could occur. Here, we combine data from long-term observations and DNA analyses and present extensive genetic evidence for effective avoidance of father–daughter inbreeding without dispersal in wild primates.

Three wild groups of white-faced capuchin monkeys

habituated to observation were studied for up to 14 years in and near the Lomas Barbudal Biological Reserve in Costa Rica. Groups contained 2–11 adult males and 4–10 adult females. Male dominance ranks were determined by quantifying the number of times males cowered to or avoided one another in dyadic social contexts. There was always a clear  $\alpha$ -male in each group, whereas the dominance relationships among subordinate males could not be consistently ascertained. The  $\alpha$ -male of one group is estimated to have had a minimum tenure of 7 years and for the other two groups, two males, who continue to hold  $\alpha$  ranks, have held their positions for at least 12 and 13 years, respectively. However, to be conservative, the results presented here are based exclusively upon analysis of conceptions during the time periods for which dominance ranks are based upon behavioral observations.

We genotyped 172 monkeys using 18 microsatellite loci and determined the fathers of 41 surviving offspring conceived during these long tenures (see Supplemental Data published with this article online). The percentage of each group's offspring sired by  $\alpha$ -males ranged from 38% to 80% (Figure 1A), and each  $\alpha$  male sired more offspring than did any subordinate male in

their group. Combining the data sets on the three long-term  $\alpha$ -males, we found that they sired 49% of all offspring conceived during the observed periods of their tenures. To the extent that ranks could be unambiguously determined below the  $\alpha$ -rank, there was no obvious correspondence between rank and reproductive success among subordinate males. For example, the clear  $\beta$  male of the 'FF' group fathered no offspring, while lower-ranking males fathered three and one offspring, respectively.

We then checked whether the reproductive success of  $\alpha$ -males varied according to whether the reproducing female was his daughter or not.  $\alpha$ -males sired the clear majority (79%) of offspring produced by females other than their daughters. In contrast,  $\alpha$ -males sired only 6% (1 of 17) of the offspring produced by their daughters (Figure 1B), a highly significant difference (Fisher's exact  $p < 0.0001$ ,  $n = 41$ ). This shows that there is a strongly reduced incidence of  $\alpha$ -males siring offspring with their daughters.

Several processes that do not rely on kin recognition plausibly could have reduced the incidence of breeding by father–daughter pairs. First, female reproductive synchrony has been shown theoretically and empirically to reduce male reproductive skew in primates [3–5]. Thus, subordinate males may have sired offspring while multiple females were simultaneously fertile. However, of the 17 offspring of known birthdates that were sired by subordinate males during the tenures of the long-term  $\alpha$ -males, only four were born within 10 days of another infant's birthdate. Moreover, two subordinate males in one group experienced periods of 24 and 41 days, respectively, during which they each sired three offspring, while no other male sired any offspring.

A second possible explanation of our results is that father–daughter matings were rare because  $\alpha$ -males discriminated against nulliparous females generally rather than specifically against their

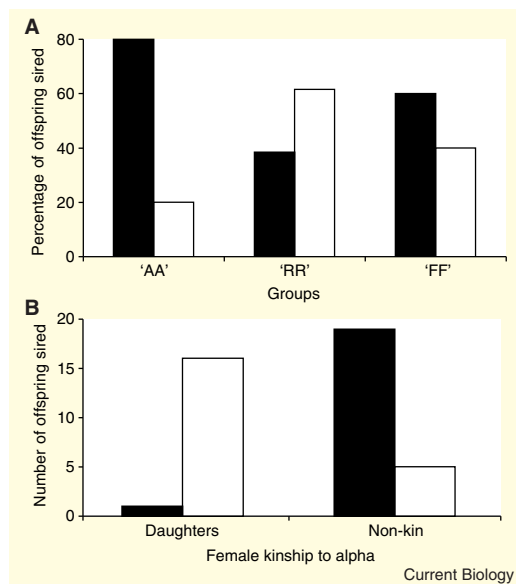


Figure 1. Inbreeding avoidance in wild capuchin monkeys.

(A) Distribution of male reproduction during observed periods of long  $\alpha$ -male tenures in three free-living groups ('AA', 'RR' and 'FF') of white-faced capuchin monkeys. Alpha-males (black); subordinates (white). (B) Distribution of male reproduction as a function of the offspring's mother's kinship (Daughter versus non-kin) to the  $\alpha$ -male.  $\alpha$ -males (black); subordinates (white).

daughters. However, our finding that  $\alpha$ -males sired their daughters' offspring less frequently than non-daughters' offspring remains highly significant when the analysis is restricted to the 34 offspring known to have been born to non-first time mothers (Fisher's exact  $p = 0.0003$ ).

A third alternative explanation for our findings is that father-daughter matings are not avoided, but when they occur they result in early fetal loss. This phenomenon would result in longer interbirth intervals for the daughters of resident  $\alpha$ -males, compared with other females. However, known interbirth intervals of these two classes of females were indistinguishable: for non-daughters ( $n = 11$ ) they were 23 months and for daughters ( $n = 7$ ) 22.5 months (Mann-Whitney  $U = 32.0$ ,  $p = 0.55$ ).

Thus, the most parsimonious explanation of our results is that father-daughter pairs of white-faced capuchin monkeys actively avoid mating. Female primates are generally more averse to inbreeding than males [6]. However, because courtship and copulations involving fertile females are rarely observed in this species [7], it cannot yet be determined whether it is the male, the female, or both, that avoid inbreeding. Individuals may avoid inbreeding by recognizing kin through long-term co-membership in the same group. The Westermarck effect, in which individuals develop sexual aversion to close childhood companions, is well supported in nonhuman primates [6,8]. In our data set, eight offspring that were produced by seven different females (including the single case of father-daughter inbreeding) were nonetheless sired by males who had been co-resident with the female during her infancy. However, white-faced capuchin infants generally spend substantially more time in proximity to the  $\alpha$ -male than to subordinate males, so we cannot rule out a role for social familiarity in producing inbreeding avoidance. Several recent studies also support a role for phenotype

matching in mediating recognition of paternal kin in primates [9–11], suggesting that closely related male–female pairs would be predicted to avoid mating even in the absence of close familiarity early in life.

#### Supplemental data

Supplemental data including Experimental Procedures and Acknowledgements are available at <http://www.current-biology.com/cgi/content/full/16/5/R156/DC1/>

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## Prey conspicuousness can explain apparent prey selectivity

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To study prey selection, ecologists compare the abundance of food resources with the actual prey spectrum [1,2]; selectivity is inferred when some prey are markedly overrepresented in an animal's diet [3]. However, the capabilities of an animal's sensory systems and the cues provided by potential prey both constrain its foraging behavior and access to food [4–9]. Here we report evidence from a study of the greater mouse-eared bat (*Myotis myotis*) which supports the hypothesis that selectivity patterns can be explained in part by the specific conspicuousness of the prey to the foragers' sensory systems ('passive prey selection'). Active prey selection might come into play as a second step within the food spectrum accessible to the bats' sensory systems. We conclude that considering sensory ecology is vital for understanding mechanisms of food selection in animals.

Greater mouse-eared bats are an ideal model system for investigating the role of sensory ecology in prey selection, because their foraging behavior and their sensory basis of prey detection are both well known. These bats, which each weigh about 30 g, occur in central and southern Europe and forage for ground-dwelling, surface-running (epigaeic) arthropods [1,10–12], which they glean from open, accessible ground [12–15]. As the echoes of an arthropod sitting on a textured substrate are masked by echoes from substrate, mouse-eared bats do not use echolocation to find prey, but rely on listening for rustling noises produced by