

Title Drills and mandrills

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Abstract

Drills (*Mandrillus leucophaeus*) and mandrills (*Mandrillus sphinx*) are the only two extant species in the genus *Mandrillus*. They are large, highly sexually dimorphic and extremely colorful. They live in very large groups in the rainforests of west central Africa. Very little is known about the ecology or social organization of drills, although mandrills are somewhat better-studied. Drills face a very high, and mandrills a high, risk of extinction in the wild.

Main Text

Drills (*Mandrillus leucophaeus*) and mandrills (*Mandrillus sphinx*) are the only two extant species in the genus *Mandrillus*. They are most closely related to *Cercocebus mangabeys*, although they were previously thought to be forest baboons. They are highly sexually dimorphic and extremely colorful, suggesting strong sexual selection.

Drills and mandrills are the largest Old World monkeys and have short tails. Drills have a dark grey/brown pelage; mandrills have olive-green agouti pelage. Both species have a white ventrum. Both species have a crest, mane and beard. Drills have a white beard; mandrills a yellow beard. Both species have a long muzzle and bony paranasal swellings. Drills have a black face and smooth paranasal swellings. In adult males the black is shiny and clearly demarcated with contrasting white skin and pelage. Adult male drills also have a red stripe under the lower lip. Adult male mandrills have a red stripe down the middle of the muzzle and red around the nostrils, framed by blue, ridged, paranasal swellings. Female facial color ranges from black to bright pink and blue. Juveniles have dark faces. Adult males of both species have lilac genitals and red on the penis and above the groin, which extends to the inner thigh in drills. Fully developed adult males have a fat, blue, violet and pink rump. In drills the perianal skin is black; in mandrills it is red. Very unusually for Old World monkeys, both species possess a sternal scent-gland, which is more developed in adult males than in females.

Adult male mandrills are 3.4 the mass of adult females (asymptotic values 31.2 vs. 9.1kg). Adult male drills weigh 32.3kg; adult females 11.7kg (median values). This dimorphism arises from a

combination of sex differences in length of the growth period and growth rate. Males are heavily armed: full-sized male canine teeth have a mean height of 44mm in male mandrills, vs. 10mm in adult females.

Drills and mandrills are found in limited distribution ranges in western central Africa. Drills occur north of the Sanaga River (Cameroon), in Cameroon, Nigeria and on Bioko island. Mandrills occur south of the Sanaga River, in Cameroon, mainland Equatorial Guinea, much of Gabon and in the south-west of the Republic of Congo. Drills and mandrills inhabit tropical rainforests. They are diurnal, semi-terrestrial, digitigrade quadrupeds. They are omnivorous, eating fruit, seeds, leaves, pith, flowers, invertebrates and vertebrates including juvenile bay duiker. They sleep in trees. Likely predators include leopards, crowned eagles, rock pythons and Gabon vipers. Both species are commonly found in association with other primate species. Telemetry studies show that mandrills have a very large home range which they use unevenly. Drill home ranges are unknown.

Rainforest conditions make it very difficult to study the social system of wild drills and mandrills. Early studies suggested that drills and mandrills lived in one-male, multi-female units that aggregated into larger groups. However, both semi-free-ranging and wild studies contradict this, showing that mandrills live in large multi-male, multi-female groups. Films of wild groups crossing forest gaps or roads yield mean group sizes of 620 (Abernethy et al. 2002). These large groups are described as permanent, although they may also split into temporary subgroups. Comparisons of direct group counts with those obtained from film suggest that direct counts considerably underestimate group size. Direct counts of drill groups range 5–400 (Wild et al. 2005).

Mandrill society is primarily female-bonded. Females form stable matrilineal units and female dominance rank is stable over years, with daughters taking up a rank position below their mother but above older sisters. Male group membership is more variable. Adolescent male mandrills become peripheral and then solitary at 7-9 yr. Solitary males occur in both species. Among juveniles, the closest social relationships are mother-offspring and maternal half-siblings. However, juveniles also associate more with paternal half-siblings than with non-kin and father-offspring dyads are more closely associated than non-kin dyads, suggesting paternal kin discrimination despite their polygynandrous mating system (Charpentier et al. 2007).

Few data are published concerning drill reproduction. Females in both species show sexual swellings that are largest around the time of ovulation in mandrills. Median menstrual cycle length is 38 days in mandrills and breeding is moderately seasonal. Long-term data for semi-free-ranging mandrills in Gabon show that 63% of periovulatory periods fell in July-September (the dry season), with a corresponding birth peak in January-March, following a gestation of 175 days. Observations of female sexual swellings in the wild suggest a similar mating season. Both species are born with a white natal coat and a black cap. Females provide the great majority of parental care with alloparenting by female kin.

Under semi-free-ranging, provisioned conditions, mandrill interbirth intervals are just over a year (mean 405 days). Mandrills are polygynandrous and reproductive careers follow the predictions of sexual selection theory (Setchell et al. 2005): Males begin to reproduce later than females (mean 11.6 yr vs. 4.2yr) and are far more likely to die without reproducing. Male lifespan is shorter than females. High-ranking males attempt to monopolise access to periovulatory females via mate-guarding. Variance in male reproductive success is high under semi-free-ranging conditions: the top-ranking male sires 70-100% offspring born during a birth season. In the wild, the number of adult males in the group increases with the number of tumescent females.

Male-male competition is intense in both drills and mandrills. Adult male coloration increases with rank in both species and acts as a badge of status. Gaining top rank results in increased red coloration, testosterone levels, testicular volume, and sternal gland activity in mandrills; losing rank results in decreased expression of secondary sexual traits. In mandrills, more aggression occurs between similarly colored males than between differently colored males.

Dominance rank also influences female reproductive success in mandrills. Higher-ranking females benefit from an earlier age at first reproduction and shorter interbirth intervals. Higher-ranking females also have larger offspring who mature faster than those of lower-ranking females and are more likely to reach adulthood.

Female drills and both sexes of mandrill show mate choice for high rank. Male mandrills also prefer parous females, while females prefer colorful males independent of male rank. There is no evidence that female drills find male color attractive (Marty et al. 2009).

Affiliative behaviours include grooming. The mandrill's "grin" or silent, bared-teeth face is often interpreted as aggressive, but is actually an appeasement behavior. Aggression increases in severity from a stare, to a headbob, slapping the ground, lunging, rushing at, and then chasing another animal. Mandrills submit by presenting their rump, avoiding or fleeing.

The International Union for the Conservation of Nature (IUCN) lists drills as Endangered and mandrills as Vulnerable.

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