

11 Behaviour and Ecology of Olive Colobus

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Introduction

The olive colobus monkey, *Procolobus verus* (van Beneden 1838) is a unique primate in many respects. It is monotypic and early studies showed it to be the smallest of the colobines; a drab-coloured, 'thicket-haunter' that often associates with guenon species, with the distinctive behaviour (among anthropoids) of mothers carrying infants in their mouths (Booth, 1956, 1957). Though these early observations were accurate, more recent research has revealed new information about the ecology, behaviour and social organization of this species. One of the most important features of olive colobus natural history is their habit of following and remaining in association with large groups of guenons (Oates and Whitesides 1990), which influences their behaviour and ranging significantly. Our objective is to review what is currently known about olive colobus behaviour, morphology and ecology to help stimulate further research on this fascinating species.

Morphological Features

The olive colobus is named for its relatively drab coloration, an olive-brown on the back and the tops of the limbs, with a lighter grey on the underside (Hill 1952). The flat face is black and there is a small crest of hair on the crown in both males and females. The tail is slender, untufted and olive-brown. Olive colobus are the smallest of the colobines, showing little sexual dimorphism, with males weighing an average of 4.6 kg ($n = 22$) and females weighing an average of 4.1 kg ($n = 17$) (Oates 1988a). Like all colobines, the thumbs are reduced to a tubercle and the back limbs are longer than the fore limbs (Hill 1952). The neonatal coat in olive colobus is not as pronounced as it is in most colobines, with infants being only slightly darker than their mother (Oates 1994).

Adult male olive colobus are notable for having relatively large testes to body size compared to other African colobus monkeys and for having horny spicules on the glans penis (Hill 1952). Sexual swellings occur several times in the life cycle of olive colobus monkeys. Newborn infants have been reported to have swelling of the perineal region. Females have perineal swellings that develop before sexual maturation and then fluctuate in tumescence with female reproductive cycles (Korstjens and Noë 2004). Oates (1994) reports female swellings to be pink or greyish-pink with a width of approximately 6 cm and length of about 5 cm. Relative to body

size, they are as large as those of *Piliocolobus badius* and larger than those of many other *Piliocolobus* species (e.g. *P. tephrosceles*; pers. obs.). Prior to attaining sexual maturity, juvenile males actually resemble females in having an undescended penis and testes, an imperforate depression where a female's vaginal opening would be, and a perineal swelling mimicking a female's (Hill 1952). These features suggest that young males may have been selected for female mimicry to allow them to potentially mate when young but avoid direct, aggressive competition with adult males (i.e. the female mimicry hypothesis, Rohwer et al. 1980). Alternatively, young males may be providing a reliable signal of their low status to older, larger males (i.e. the status-signalling hypothesis, Rohwer et al. 1983; Lyon and Montgomerie 1986).

The teeth of olive colobus show adaptations for folivory having the thinnest enamel and relatively the highest second-molar shearing cusps of any Old World anthropoid (Kay 1981). The lower third molar is notable for having six cusps (Napier and Napier 1985). Surprising given the small degree of sexual dimorphism in body size, olive colobus have the greatest sexual dimorphism in canine size (breadth and length) in the African colobines. However, in the other teeth, they show few sex differences in mean values (Hayes et al. 1996). Research has shown that body mass and canine size are under different selective pressures (Plavcan 2004) and that canine size dimorphism in the primates is strongly determined by the frequency and intensity of male-male competition (Plavcan and van Schaik 1992; Plavcan 2004). These results, along with large male testes size, the presence of penile spines and the occurrence of sexual swellings, suggest that sexual selection has played an important role in shaping the morphology of olive colobus.

As in other colobines, the digestive system is set up for foregut fermentation of leaves, allowing olive colobus monkeys to eat a high proportion of this hard to digest food source. The genus *Procolobus* shows a four chambered stomach, with the first two chambers acting as expanding fermenting chambers, the third chamber producing hydrochloric acid to break down the material coming in, before it moves to the fourth chamber, which functions like the stomach in other non-colobine primates (Ankel-Simons 2007). Another unique feature of olive colobus is that the fundus of the stomach and the rectum are sacculated (Hill 1952).

Virological Studies

Research has shown that, like most African primate species, olive colobus are naturally infected with Simian Immunodeficiency Viruses (SIV) (Courgnaud et al. 2003). The newly discovered SIV carried by olive colobus (SIV_{olc}) was found to be most closely related to, and derived from, the SIV carried by western red colobus (*Piliocolobus badius*) labelled SIV_{wrc} (Courgnaud et al. 2003; Liégeois et al. 2009). The SIVs of these two colobus monkeys are most closely related to those found in L'Hoest (*Cercopithecus l'hoesti*) and suntailed monkeys (*C. solatus*) based on full-length genome sequences (SIV_{lho/sun}, Liégeois et al. 2009).



Figure 11.1 Distribution of olive colobus monkeys in West Africa. Data from Rowe and Myers (2016)

Geographic Distribution and Habitat

Olive colobus are located in the Upper Guinea forest block of West Africa, extending from the coastal forests of Sierra Leone in the west all the way to Nigeria in the east, occurring just east of the Niger River (Figure 11.1; Oates 1981; Grubb et al. 1998). This species does not show any evidence of subspecific variation despite being distributed across both the Niger River and the Dahomey Gap, two important zoogeographic barriers (Menzies 1970; Oates 1981; Campbell et al. 2008). The distribution of olive colobus is now highly fragmented and the IUCN currently lists them as Vulnerable, with a decreasing population trend due mostly to habitat loss (Oates et al. 2020a). The species is thought to have declined more than 20% since 1980, especially in the eastern part of its range (Oates et al. 2008).

Olive colobus are diurnal and arboreal, inhabiting the middle and lower strata of the forest where there is dense vegetation (McGraw 1998a). They are commonly found in lowland moist forest along riverbanks and near swamps or in secondary forests (Booth, 1956, 1957; Galat and Galat-Luong 1985; Oates 1988a). They are reported to be most abundant in riverine forest but can also occur in gallery forest in the dry forest zone (Oates 1981). Olive colobus tend to use larger boughs to travel on but forage on fine branches and twigs (McGraw 1998a). In general, smaller branches are used by olive colobus compared to other larger colobus monkeys, due to their preferred strata of the canopy (McGraw 1998b).

Field Studies

There are no ongoing field studies of olive colobus monkeys, but three long-term studies have been conducted in the past and shorter observations of unhabituated

groups have been done. The earliest observations were unsystematic and were conducted on unhabituated groups (Booth, 1956, 1957; Kuhn 1964), yet Booth (1956, 1957) especially was able to record some accurate information on olive colobus natural history. In the late 1970s and early 1980s, Galat and Galat-Luong collected data on some primates found in Taï National Park, Ivory Coast, including olive colobus (Galat-Luong and Galat 1978; Galat-Luong 1983; Galat and Galat-Luong 1985).

The first long-term study conducted on a habituated group was carried out by John Oates at Tiwai, Sierra Leone over a total of 21 months spread between June 1982 and January 1987 (Oates, 1988a; 1994). Subsequently, Ronald Noë supervised various student MSc projects and AHK's PhD project in Taï National Park that monitored and collected data on four groups of olive colobus between 1994 and 1999 (Korstjens and Schippers 2003; Korstjens and Noë 2004; Korstjens et al. 2007a). Two habituated groups of olive colobus were again followed at Taï National Park from June 2001 to February 2002 by Jean-Claude Koffi Bene for his PhD dissertation (Bene et al. 2012). Unhabituated groups have also been followed for short periods at two sites in Benin, the continuous Lama Forest and forest fragments around the Community Forest of Domè, by research teams supervised by Brice Sinsin (Djogo-Djossou et al. 2018).

Social Organization and Dispersal Patterns

Olive colobus form relatively small groups that have one to three adult males and one to six adult females with immatures. At Tiwai, the average group size was 8.5 (range: 3–11, $n = 1$), while at Taï it was 7.1 individuals (range: 2–12, $n = 10$) (reviewed in Fashing 2011).

Monitoring of olive colobus groups at Taï over 5 years, showed that both sexes commonly disperse but that female dispersal is relatively more frequent than male dispersal (Korstjens and Schippers 2003). Their relatively high dispersal rates in comparison to other primates may be due to their associations with guenon species. An individual may not experience increased predation risk while transferring between olive colobus groups if it associates with guenons during this time (Korstjens and Schippers 2003). For instance, Korstjens and Schippers (2003) observed both solitary males and solitary females on occasion and these individuals were always associated with a partner Diana monkey group.

Females at Taï dispersed preferentially to smaller groups that had a single adult male (Korstjens and Schippers 2003), despite the observation that multi-male groups had better immature to female ratios, suggesting that male defence against predators and other groups is beneficial to infant survival (Korstjens and Noë 2004). Dispersal of a female with a young infant has been observed (Korstjens and Schippers 2003), implying that infanticide by males may not be a risk in olive colobus (Korstjens and Noë 2004). Females transferred between groups frequently without a sexual swelling but usually became sexually receptive and developed a swelling upon entering a new group.

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The occurrence of male dispersal was linked to a high male/female ratio in the group of origin and thus likely occurred to increase a male's access to mates (Korstjens and Schippers 2003). Males had several options upon dispersal, solitary males were observed attracting females to form a group, males could take over a group of females by ousting the previously resident male, or males could join an existing uni-male, multi-female group to form a multi-male, multi-female group (Korstjens and Schippers 2003).

Juvenile sex could not be determined but juveniles were five times more likely than adults to disappear or emigrate. Juvenile dispersal was not clearly linked with group size and occurred before sexual maturity, so did not seem to be explained by access to mates or avoidance of inbreeding. In terms of the timing of juvenile dispersal, Korstjens and Schippers (2003) note that in four cases, the juvenile's mother had given birth to a new offspring within a month of the dispersal event, suggesting the potential role of parent-offspring conflict or avoidance of competition with kin. Nonetheless, parallel dispersal was also observed frequently at Tai, where colobus transferred into nearby groups together or joined groups with familiar individuals (cf. van Hooff 2000) suggesting that animals may have been able to maintain some kin relationships despite frequent dispersal (Korstjens and Schippers 2003).

Diet

Olive colobus spend most of their feeding time in the middle canopy, dispersed in dense growth and liana tangles and are rarely observed high in emergent trees (Galat and Galat-Luong 1985; Oates 1988a). At both sites where long-term data have been collected, this species has been reported to eat primarily young leaves (Table 11.1). While Oates (1988a) reported that seeds were the second most common food item at Tiwai and were particularly important in the dry season (Davies et al. 1999), Korstjens and colleagues (2007a) did not see seed-eating at Tai and report that fruit was the second most common food item (Table 11.1). In Benin, young leaves were also eaten most often (51%) but dietary diversity was lower in forest fragments (25 species) compared to continuous forest (32 species) (Djogo-Djossou et al. 2018).

Olive colobus are reported to be highly selective feeders, ignoring most mature foliage and selecting young leaves. In Tiwai, they selected trees that were not very

Table 11.1. Plant parts (%) in the annual diet of olive colobus at two study sites

Site	Mature leaves	Young leaves	Leaves (unknown age)	Petioles	Fruit	Seeds	Flowers	Other	Source
Tiwai	2	59	4	9	5	14	7	0	^a
Tai	1	83	1	0	8	0	4	3	^b

^a Oates (1988).^b Korstjens et al. (2007).

common, whilst in Tai, the biomass of the preferred feeding trees was similar to the biomass of trees preferred by red and black-and-white colobus (Korstjens et al. 2007). The young leaves of lianas appear to be particularly important; these made up at least 13% of the diet at Tiwai (Oates, 1988a, 1994). This preference for young foliage likely allows olive colobus to avoid leaves high in secondary compounds (Oates 1988a). If other plant parts besides leaves are considered, lianas were found to make up about 27% of the diet of olive colobus in Tiwai, and 13% in Tai (Korstjens 2001, chapter 6). When fruit is eaten by olive colobus, it tends to be unripe with either dry flesh or very little flesh (Davies et al. 1999).

Activity Patterns and Behaviour

Olive colobus monkeys are notoriously difficult to observe; their coloration and behaviour has evolved for crypticity, they tend to disperse in the dense lower layer of the canopy, making few loud vocalizations, and they can be inactive for long periods (Oates 1988a). The activity patterns of this species appear to be greatly influenced by the guenon groups that they associate with (Oates and Whitesides 1990) and show much less resting and more moving than the typical colobine. At Tiwai and Tai (Oates and Korstjens 2013), activity budgets of 28% and 16% feeding, 39% and 50% resting, 26% and 30% moving, 7% and 4% social respectively are shown. Travel is primarily quadrupedal and olive colobus are noted to leap more than larger colobus monkeys (McGraw 1998a).

Female olive colobus show very little affiliation and coalition formation among females has never been observed (Korstjens et al. 2007a). Co-resident adult males are tolerant of one another and have been seen to form alliances, though only towards extra-group individuals. Co-resident males will jointly threaten and chase individuals from other groups during inter-group encounters (Korstjens and Noë 2004; McGraw and Zuberbühler 2008). Natal attraction and infant handling by individuals other than the mother in olive colobus has not been observed (Oates 1994; AHK, pers. obs.).

Association with Other Species

Olive colobus are notable for their adaptation of living in polyspecific associations with guenon species (Oates and Whitesides 1990). Early observations of this species showed that it is almost always in close proximity to some guenon species, including Campbell's mona monkeys (*Cercopithecus campbelli*), mona monkeys (*C. mona*), spot-nosed monkeys (*C. petaurista*), putty-nosed monkeys (*C. nictitans*) and Diana monkeys (*C. diana*) (Booth 1957; Rucks 1976; Galat-Luong and Galat 1978; Oates 1982). At the two sites where longer-duration studies on olive colobus have been conducted (Tiwai and Tai), Diana monkeys (*C. diana*) are the species most frequently associated with by the colobus, though other guenon species are present (Oates and Whitesides 1990; Korstjens 2001). Diana monkeys are excellent sentinels, often detecting predators before other primate species do (Bshary 2007). Although olive colobus have been observed to switch associations between guenon species in a

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single day, at Tiwai and Taï, certain olive colobus groups were associated with a partner Diana monkey group and these relationships were long-lasting. At Tiwai, Oates and Whitesides (1990) report that one olive colobus group associated with the same Diana monkey group for at least three years. Individuals from these groups were within 50 m of one another on at least 83% of scan samples and it was the olive colobus that appeared to be maintaining the association by following the Diana monkey group when it moved (Oates and Whitesides 1990). At Taï, olive colobus study groups spent 90%–100% of their time within 50 m of their partner Diana monkey group (Korstjens and Schippers 2003). Interactions between the species, both aggressive and affiliative, have been reported to occur rarely (Oates and Whitesides 1990), with play between juveniles being the most common interaction (Whitesides 1989). While in association with another species, it has been noted that olive colobus tend to adopt the behaviour of that species to some extent (i.e. being more conspicuous when with Diana monkeys but more cryptic when with spot-nosed monkeys) (Galat and Galat-Luong 1985; Oates and Whitesides 1990).

The polyspecific associations formed by olive colobus seem to be part of an evolved, predation avoidance strategy. Although this species lives in small groups and forages cryptically in the low-canopy, it can still gain the advantages of large group size, such as detection and dilution, by staying in close proximity to a guenon group (Oates and Whitesides 1990; Oates 1994). Olive colobus respond to the alarm calls of other species and forming associations with guenons allows them to largely avoid food competition due to differing diets while functionally increasing the size of groups (Oates and Whitesides 1990). In addition, Korstjens and Noë (2004) have argued that Diana monkeys are an important mate-finding resource for olive colobus in Taï, with solitary individuals following Diana groups and using them to find conspecifics and attract mates.

Infant-Carrying

Booth (1957) suggested that a combination of factors led to olive colobus being the only anthropoid to carry their infants in their mouths: the short adult coat, the absence of a thumb and the dense nature of the preferred low-canopy habitat. Early descriptions of this behaviour stated that only young infants were carried in the mouth and later these infants could cling to the mother's ventrum (Booth 1957) or around her neck (Galat-Luong and Galat 1978). Oates (1994) notes that in Tiwai, infants were only ever carried in the mouth. The mother would grasp the infants flank, tucking the belly of the infant into her neck and the infant's tail would wind around the mother's neck and upper back. Figure 11.2 provides a photo of this behaviour and a video is also available at: <https://talk.chimpandsee.org/#/subjects/ACP0004hm8>. Tiwai mothers were only seen to carry infants when the group moved and infants were put down whenever the mother was stationary. Infant-carrying got less frequent as infants aged, though Oates (1994) observed a large infant of about 10-months old being carried in the mouth.



Figure 11.2 An olive colobus monkey carrying an infant in its mouth. Photo courtesy of W. Scott McGraw

Reproductive Behaviour

The reproduction of olive colobus is moderately seasonal. Oates (1994) reports that most copulations at Tiwai were seen between March and August and the majority of swollen females were observed between April and August (though observations were not taken in the month of September). Young infants were only observed November through April, months that coincided with the dry season. Similarly, Korstjens and Noë (2004) report that at Tai, births occurred from October to April. The timing of mating and the subsequent appearance of infants suggests a typical colobine gestation time of six months (Oates 1994). Korstjens and Schippers (2003) report that at Tai, interbirth intervals showed a mean of 1.6 (± 0.3) years (range: 1.2–2 years, $n = 6$) and females nursed each infant for an average of 12 months.

About half of olive colobus groups contain more than one male and in multi-male groups, both males have been observed to mate, though the alpha male mates much more frequently than the subordinate (Oates 1994; Korstjens and Noë 2004). Females solicit copulations slightly more than males (Korstjens and Noë 2004). At Tiwai, males closely followed and appeared to form consortships with, females that had maximally tumescent swellings, mating with them many times over a few days. These consortships may be mate guarding, as the dispersed feeding pattern of olive colobus in dense vegetation make extra-group copulations likely (Oates 1994). Indeed, at Tai, Korstjens and Schippers (2003) report that adult females often visited neighbouring groups and solitary males while they had a swelling to engage in mating. Copulations and copulation attempts have also been observed during

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inter-group encounters (Korstjens and Noë 2004). These female strategies to confuse paternity likely contribute to the seeming lack of infanticide by males in olive colobus.

Oates (1994) observed copulations by both males in his Tiwai study group with a single female in close succession without any overt aggression between the males. This behaviour along with the large testes size, spicules on the glans penis (Hill 1952) and coagulating sperm (Korstjens and Noë 2004) are strongly suggestive of sperm competition in olive colobus (Møller 1988). Oates (1994) notes that on a day when the two males in his study group were mating with four different females, one male copulated at least 46 times and the other copulated at least eight times.

The vast majority of copulations that have been observed have been between males and females with a sexual swelling, though rarely, copulations by females with no swelling have been observed (Oates 1994; Korstjens and Noë 2004). At Taï, female sexual swellings last about 17 days (range: 14–20 days, $n = 6$ females) and the time between the onset of two consecutive swellings for two females was 27 and 29 days. Females experience two to eight cycles in their interbirth interval and data indicate that some swellings were non-conceptive because females gave birth not long after their last swelling. A median time of 3.8 months (range: 2.5–5.5 months, $n = 6$) was observed between the last swelling and birth (Korstjens and Noë 2004). Within the same group, females sometimes overlapped in receptivity, but more than one maximally swollen female at a time was not observed. Though males attempted to mate guard maximally swollen females (Oates 1994), the ability of males to monopolize females in olive colobus is greatly hampered by the long duration of female swellings (Korstjens and Noë 2004).

Range Size and Defence

At the two main study sites, the home ranges of olive colobus monkeys have been found to be large for a colobine of such small body and group size. This appears to be largely due to their habitual association with Diana monkey groups (Oates 1994) and perhaps their low population densities. At Tiwai, Oates and Whitesides (1990) reported a home range size of 28 ha for their study group. At Taï, Korstjens (2001) reported a mean home range of 56 ha for the two study groups, with an approximate overlap of 14% with other groups. Groups also had long daily paths for a colobine with a mean of 1212 m travelled per day (range: 482–2105 m). The home range of each olive colobus study group overlapped completely with the range of the Diana monkey group it was associated with (Korstjens and Noë 2004).

Vocalizations

In keeping with its cryptic nature, most calls used by olive colobus are soft and infrequent (Oates and Korstjens 2013). Males are reported to do the majority of vocalizing (Bene et al. 2012) and the most obvious call, which researchers have referred to as the loud call, is given in response to calls by other primate species and during inter-group encounters (Oates and Whitesides 1990). Hill and Booth (1957)

termed this a 'laughing call' and described it as rising in pitch to the penultimate syllable 'hoo hoo hoo hoo yow yow wee wee yow', dying away at the last syllable.

Bene et al. (2007) describe eight different call types made by olive colobus during four different contexts, alarm, conflict, peaceful and during inter-group encounters. Three of these call types are used most frequently, the 'Zih', 'Hoo' and 'Zuk', and five others are produced less often, the 'Tr', 'ZZ', 'Whi', 'Ha' and 'Thio'. Bene and colleagues (2012) report that these call types are combined in several ways into different contextual sequences. These authors were able to distinguish nine additional calls that consisted of combinations of the eight call types, showing that olive colobus have a very diverse and potentially powerful communication system.

Inter-group Interactions

Korstjens and Noë (2004) report that groups of olive colobus often exchange loud calls when they come into proximity (0–150 m) and that calls are certain to occur once the groups are within 50 m. Males are the primary vocalizers in these instances, though females will also emit shorter, quieter calls. About half of interactions between groups are reported to include threats (e.g. moving the head and shoulders side to side with an open mouth) and 8% of those recorded at Taï ($n = 50$) included chasing between groups. Though copulations may occur during inter-group encounters, the presence of swollen female(s) does not appear to influence the amount of aggression that occurs (Korstjens and Noë 2004).

Conclusions

As this summary of olive colobus natural history demonstrates, this monotypic species is unique in many respects. Though it is found in several protected areas, the threat of bushmeat hunting throughout its range is extreme. Renewed research effort with individual recognition is needed to expand our knowledge of this exceptional animal.

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