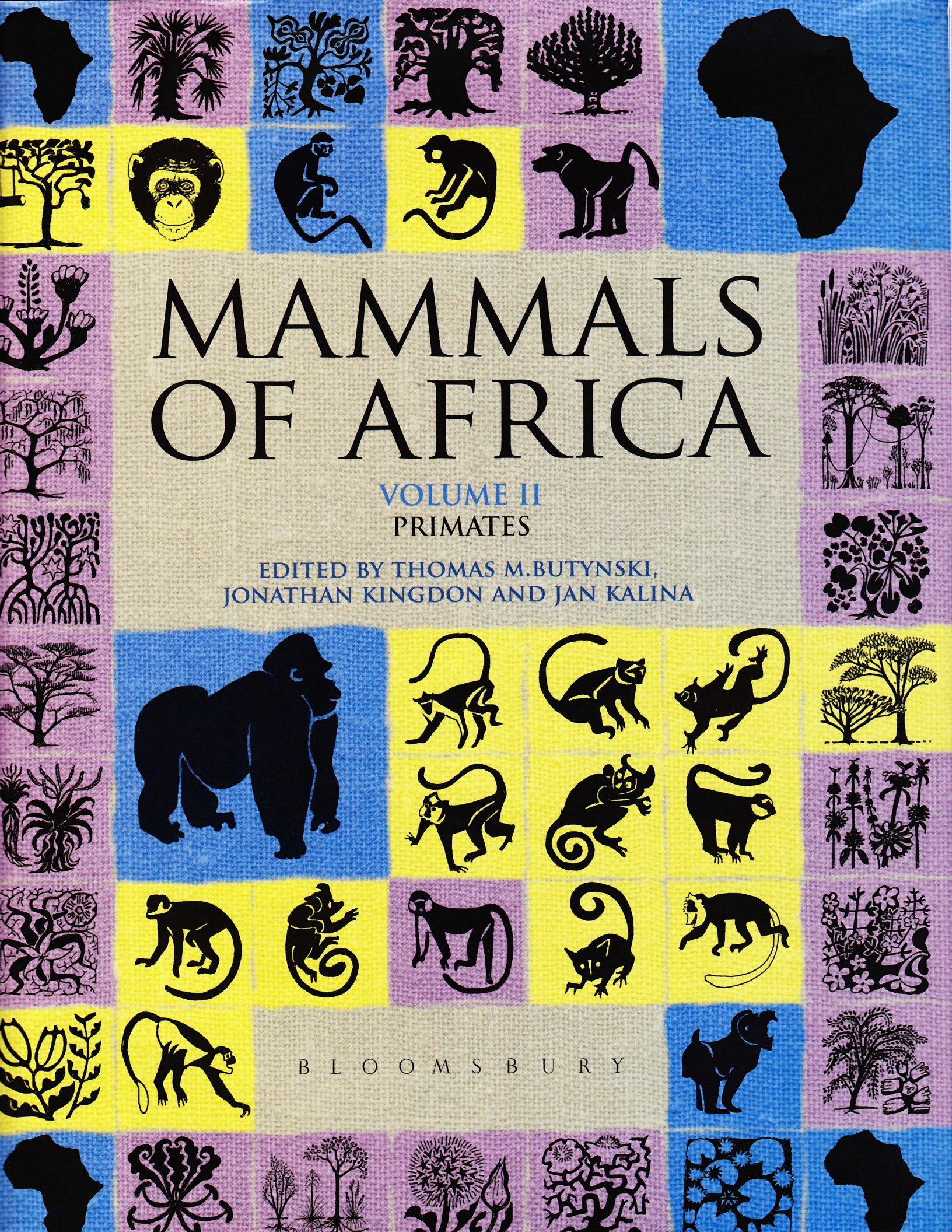


MAMMALS OF AFRICA

VOLUME II
PRIMATES

EDITED BY THOMAS M. BUTYNSKI,
JONATHAN KINGDON AND JAN KALINA

BLOOMSBURY

(6% of the population, 10% for adults, 4% for immatures), Galat-Luong *et al.* (1994b) showed the importance of differing strategies in the choice of sexual partners for the transmission of SIV (multiple partners among Green Monkeys and single-male groups among Patas). Transmission of Green Monkey's SIVagm to Patas in the wild occurs (Bibollet-Ruche *et al.* 1996, Galat-Luong *et al.* 1996). Infection with SIV or STLV-I (Simian T-cell Lymphotropic Virus) increases the risk for a second retroviral infection (Durand *et al.* 1995).

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Only some populations are threatened, such as at Île à Morfil, Senegal, where an 85% reduction of the *A. nilotica* forest resulted in the disappearance of 83% of the Green Monkeys. Here the number of ♀♀ per ♂ dropped from 3.0 in 1975 and 2.5 in 1976 (wet season data) to 1.4 in 1988 as a result of increased mortality among adult ♀♀. Likewise, the number of young per adult, which was 0.96 in 1975 and 0.76 in 1976, declined to 0.67 in 1988 (Galat-Luong & Galat 1994).

Measurements

Chlorocebus sabaeus
HB (♂♂): 540 (470–650) mm, n = 7
HB (♀♀): 420, 460 mm, n = 2
T: n. d.
HF: n. d.
E: n. d.
WT (♂♂): 6.3 (4.7–7.5) kg, n = 17
WT (♀♀): 4.4 (3.4–5.9) kg, n = 20
Body measurements: HB: Senegal and Côte d'Ivoire (A. Galat-Luong pers. obs.)
WT: Senegal (Galat-Luong *et al.* 1996)

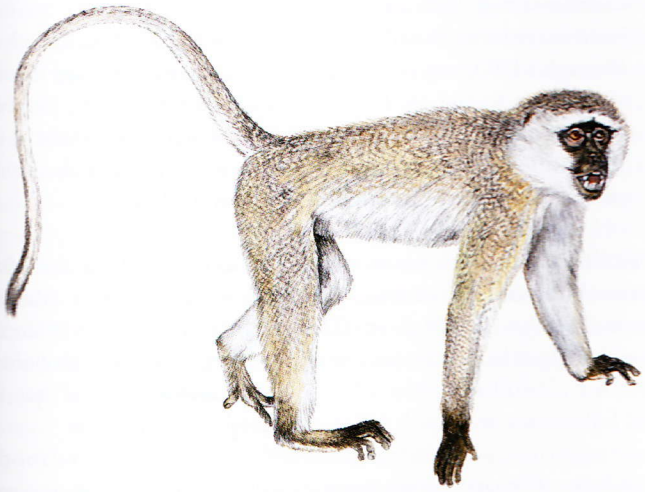
Key References Galat 1983; Galat & Galat-Luong 1976, 1977; Harrison 1982; Oates 2011.

Gérard Galat & Anh Galat-Luong

Chlorocebus pygerythrus Vervet Monkey

Fr. Vervet; Ger. Südliche Grünmeerkatze

Chlorocebus pygerythrus (F. Cuvier, 1821). Histoire Naturelle Mammifères, pl. 139, pt. 24: 2. 'Africa'.



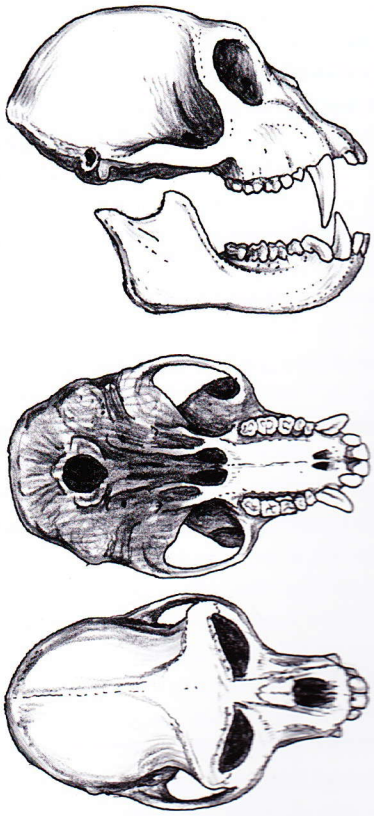
Vervet Monkey *Chlorocebus pygerythrus* adult male.

Taxonomy Polytypic species. Dorst & Dandelot (1969), Kingdon (1971), Haltenorth & Diller (1977), Napier (1981) and Grubb *et al.* (2003) considered the Vervet to be a subspecies (*Cercopithecus aethiops pygerythrus*) within the *C.* (*aethiops*) Group. Hill (1966), Dandelot (1974) and Kingdon (1997) treated *C. pygerythrus* as a distinct species with 13, 14 and 6 subspecies, respectively. Groves (2001, 2005c) also viewed the Vervet as a full species (with five subspecies), but places this taxon within the genus *Chlorocebus*. Here we adopt the taxonomy of Groves (2001, 2005c), but with reservations over the use of the genus name '*Chlorocebus*' as we believe current evidence supports '*Cercopithecus*' as the more appropriate genus for the *C.* (*aethiops*) Group (see our comments in the *Chlorocebus* genus profile). Only cases of hybridization in the wild are of one Zanzibar Sykes's Monkey *Cercopithecus mitis albogularis* × *C. pygerythrus* hybrid at Diani, SE Kenya, and of one Kolb's White-collared Monkey *Cercopithecus mitis kolbi* at Nairobi, SC Kenya (De Jong & Butynski 2010b). Synonyms: *arenaria*, *callida*, *centralis*, *?circumcinctus*, *cloetei*, *contigua*, *ellenbecki*, *erythropyga*, *excubutor*, *flavidus*, *rubellus*, *rufoniger*, *rufoviridis*, *glaucus*, *helvescens*, *hilgerti*, *johnstoni*, *lalandii*, *luteus*, *marjoriae*, *nesiotes*, *ngamiensis*, *pembae*, *pusillus*, *silaceus*, *tumbili*, *voeltzkowi*, *whytei*. Chromosome number: 2n = 60 (Sineo *et al.* 1986).

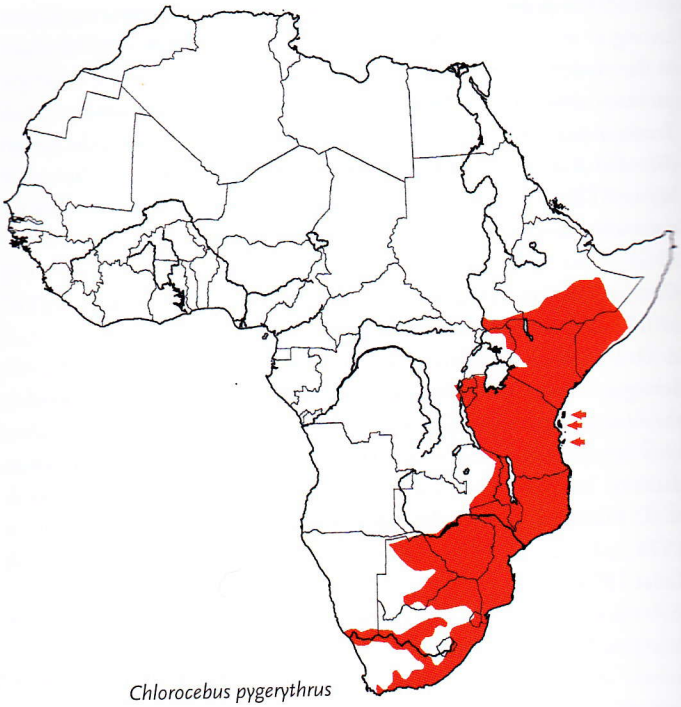
Description Medium-sized, semi-terrestrial, long-tailed monkey with grizzled light brown, greyish-brown, tawny, olive-brown, olive-green or brownish-yellow dorsum and sides. Adult ♀ weighs about 70% as much as adult ♂. Adult ♂ and adult ♀ similar except for colouration over anogenital region. Face black with white cheek-whiskers and brow forming ring around face. Eyes and ears black. Ventrum white or off-white. Limbs greyish-brown to grey outside, white inside. Feet and hands black. Tail light to dark brown dorsally, light brown ventrally, with tip dark brown to black. Ischial callosities grey. Adult ♂: scrotum turquoise blue surrounded by white hairs. Adult ♂ with patch of red hairs under base of tail, perianal skin and penis red, perineal stripe white. Adult ♀: perineum pink, clitoris red, vulvar area blue, no perineal stripe. Infants: face pink, pelage black or dark brown. By the third month, the face is black, the brow white and the cheek-hairs obvious. By six months, the back has acquired adult colouration (Struhsaker 1971b). Photographs of *C. pygerythrus* from many sites in Kenya and Tanzania available at: www.wildsolutions.nl

Geographic Variation Five subspecies recognized:

C. p. excubitor Manda Vervet Monkey. Manda I. and Patta I., north coast of Kenya. Pale brownish-yellow; smaller than *C. p. hilgerti*.



Lateral, palatal and dorsal views of skull of Vervet Monkey *Chlorocebus pygerythrus* adult male.



Chlorocebus pygerythrus

C. p. hilgerti Hilgert's Vervet Monkey. E Uganda through Kenya to S Ethiopia east of the Rift Valley, S Somalia and N Tanzania. Similar to *C. p. excubitor* but larger.

C. p. nesiotes Pemba Vervet Monkey. Pemba I. and Mafia I., Tanzania. Brownish-fawn; whiskers long, speckled; ventrum often reddish; smaller than *C. p. rufoviridis*.

C. p. pygerythrus Southern Vervet Monkey. South of Zambesi R. in Botswana, Zimbabwe, Mozambique and South Africa. Grey or olive-green; greyer in west, greener in east.

C. p. rufoviridis Reddish-green Vervet Monkey. S Uganda west of L. Victoria, through Tanzania, south to Zambesi R. east of Luangwa R., Zambia. Similar to *C. p. nesiotes* but larger.

Similar Species

Chlorocebus aethiops. East of White Nile R. and south of Khartoum, Sudan, to C Eritrea, C Ethiopia into Djibouti. Hybridizes with *C. p. hilgerti* at Omo R., Ethiopia. Cheek-hair long and fluffy; face often with white moustache; back yellower; feet and hands pale grey; base of tail with tufts of white hair to either side; tail tip whitish; scrotum sky blue.

Chlorocebus djamdjamensis. Parapatric on the Bali Massif, SC Ethiopia. Only in bamboo forest above 2400 m. Temples black. Brow-band absent or narrow. Thin white moustache. Tail short. No red patch under base of tail in adult ♂.

Chlorocebus tantalus. Nigeria to S Sudan, N and C Uganda and NW Kenya. Hybridizes with *C. p. rufoviridis* along northern and western shores of L. Victoria, Uganda. Cheek-hair long and yellow with short black tips; white facial ring broken by black line from eyes to temples; white above eyes more sinuous than rounded; back and crown gold to greenish; base of tail with tufts of white hair to either side; tail tip whitish; perineal area orange; scrotum sometimes with light covering of orange hairs.

Chlorocebus cynosuros. Distribution relative to *C. pygerythrus* is unclear. Through S DR Congo and Angola to N Namibia, eastward to west of Luangwa R. and southwards to north of Zambezi R., Zambia, and L. Kariba, Zimbabwe. Face pinkish, blotched. Dorsum olive-buff to olive-grey. Bare skin of palms and soles pinkish. Ischial callosities rose-pink. Scrotum slate blue to violet.

Distribution Endemic to eastern and southern Africa. Somalia–Masai Bushland, Zambezian Woodland, Coastal Forest Mosaic, South-West Arid and Highveld BZs. Occurs in S Somalia, S Ethiopia, E and S Uganda, Kenya (including Manda I.), Tanzania (including Pemba I., Zanzibar I., Mafia I.), Malawi, Zambia, Mozambique, N and E Botswana and South Africa. See Geographic Variation.

Habitat Primarily along water-courses, swamps, lakeshores, and the coast of the Indian Ocean in savanna-woodlands. In Amboseli N. P., S Kenya, until the 1990s when groves of *Acacia xanthophloea* declined, Vervets live in habitats dominated by *A. xanthophloea* near water and *Acacia tortilis* away from water. On the Laikipia Plateau, C Kenya, Vervets feed and sleep along rivers dominated by *A. xanthophloea*, and also feed in non-riverine habitat dominated by *Acacia drepanolobium* (Isbell *et al.* 1998b). In Samburu-Isiolo National Reserves, Kenya, Vervet habitats along the Ewaso Nyiro R. are dominated by *Acacia elatior*, *Hyphaene coriacea* and *A. tortilis* farther away from the river (Whitten 1983, 1988). On Lolui I., L. Victoria, Uganda, Vervets live in areas dominated by *Alchornea cordifolia* and *Antiaris schweinfurthii* (Hall & Gartlan 1965, Gartlan & Brain 1968). At Windy Ridge Game Park, Natal Province, South Africa, they are found in mixed *Acacia* woodland (Baldellou & Henzi 1992). In the Karkloof area of Natal, Vervets live in mature montane forest

edged with Black Wattle *Acacia mearnsii* commercial plantations and cultivated crops, e.g. yams *Dioscorea* sp. (Bruorton *et al.* 1991). Near L. Sibayi, KwaZulu Province, South Africa, they live in strips of dune forest that include *Celtis africana*, *Acacia karroo* and *Acacia kraussiana* (Van der Zee & Skinner 1977). In Ndumu G. R., NE South Africa, Vervets live along the Usutu R. and Pongola R. where *A. xanthophloea* and *Ficus sycomorus* dominate. Some groups here range mainly in habitats dominated by thickets of *Acacia burkei*, *Acacia nigrescens* and *Dicrostachys cinerea* (De Moor & Steffens 1972). Along the Milk R., Klein Karoo Region of Western Cape Province, South Africa, Vervets are found with *A. karroo*, *Rhus lancea* and *Schinus molle* (McDougall 2011).

Mean annual rainfall in eastern Africa ranges from 330 mm (Amboseli) to 1524 mm (Lolui I.), but tends to be low. At four Vervet sites in Kenya, annual rainfall ranges from ca. 200–400 mm (Kimana), 350–400 mm (Samburu), 400–600 mm (Mosiro) and >600 mm (Naivasha) (Whitten & Turner 2004). Annual rainfall in southern Africa is more extreme. In Klein Karroo, mean annual rainfall is 300 mm (McDougall *et al.* 2010), but near Windy Ridge, just nine months spanning 1987–88 (excluding Jul–Sep 1988) yielded 9920 mm (490 mm in Dec 1987 to 2000 mm in Mar 1988) (Baldellou & Adan 1998). Rainfall patterns are variable, with two distinct wet seasons (Nov–Dec and Mar–Apr) in Amboseli (Cheney *et al.* 1988), two wet seasons (Apr–Jun and Oct–Nov) at Segera (Isbell *et al.* 2009), and year-round rainfall on Lolui I. (Gartlan 1969). At Ndumu there is one wet season (Nov–Apr; De Moor & Steffens 1972). Minimum and maximum daily temperatures are ca. 9 and ca. 32 °C, respectively, in Amboseli (Struhsaker 1967c). Annual mean monthly minimum and maximum temperatures from Jan 1993 to Feb 2002 were 11.3 and 29.6 °C, respectively, at Segera (L. A. Isbell pers. obs.). Near Windy Ridge, mean monthly minimum temperatures for Oct 1987 to Jun 1988 ranged from 13.3 °C in Jun to 22.6 °C in Mar, while mean monthly maximum temperatures ranged from 21.9 °C in Jun to 29.3 °C in Feb (Baldellou & Adan 1998). Altitudinal limits are from sea level in coastal areas (e.g. coastal East Africa) to >2000 m at Naivasha (Whitten & Turner 2004; T. Butynski & Y. de Jong pers. comm.), to >2000 m at Mt Hanang, N Tanzania (Y. de Jong & T. Butynski pers. comm.), to 1900 m in the Udzungwa Mts, SC Tanzania (Rovero *et al.* 2009).

Abundance Widespread but patchy and prone to local extinction. Densities 9–>104 ind/km^2. In Amboseli the density of Vervets in the Kitirua/Ol Lengia area declined from 79–104/km^2 in 1977 to 29–56/km^2 in 1983, continuing a decline that began in the early 1970s (Struhsaker 1973, 1976, Cheney *et al.* 1988). By 1988, six groups became so small that they joined other groups (Hauser *et al.* 1986, Isbell *et al.* 1991). This population decline is attributed to a die-off of *A. xanthophloea*, exacerbated by a period of heavy predation (Cheney *et al.* 1988, Isbell 1990). Vervet densities on Segera also declined, from 80/km^2 in 1992 to 9/km^2 by 2002 (L. A. Isbell pers. obs.). This decline is attributed to poor recruitment of ♀♀ and heavy predation (Isbell & Enstam 2002, Isbell *et al.* 2009). The density of Vervets on Lolui I. is ca. 50–88/km^2 (Hall & Gartlan 1965, Gartlan & Brain 1968) and in Samburu, 39/km^2 along the river and 1.6/km^2 in the Reserve as a whole (Whitten 1982). At Burman Bush Nature Reserve, South Africa, where Vervets are provisioned by humans, the density is 59–89/km^2 (Henzi & Lucas 1980).

Adaptations Diurnal and semi-terrestrial. Compared to the sympatric, more arboreal, Gentle Monkeys *Cercopithecus mitis*, Vervets possess more traits associated with terrestrial locomotion, i.e. shorter trunk length relative to body weight, shorter humerus relative to the femur, and higher brachial (i.e. longer forearm relative to arm) and crural (i.e. longer crus relative to thigh) indices (Anapol *et al.* 2005). Vervets also have traits that are associated with arboreal locomotion, including wider humeral and talar heads, a shorter tibia, a longer ischium and a longer tail than expected of terrestrial primates (Taylor 1976, Rodman 1979, Anapol *et al.* 2005). In Amboseli, Vervets spend equal amounts of daytime on the ground and in trees overall but there is considerable variation among groups (Cheney & Seyfarth 1990, L. A. Isbell pers. obs.). Similarly, at Segera, one group of Vervets spent more time on the ground than another (L. A. Isbell pers. obs.). At Segera, when Vervets are not in *A. xanthophloea*, ca. 60% of their time is spent on the ground (Enstam & Isbell 2002). Vervets at Segera climb nearly four times as often as sympatric Patas *Erythrocebus patas*, reflecting their greater use of tall trees, but they do not leap more often (Isbell *et al.* 1998a). At Naivasha, where Vervets are terrestrial only 20% of the time, leaping constitutes 10% of their locomotion (McGraw 2002). At Ngezi Forest, some groups of Vervets live well within the forest where they are strictly arboreal. No other guenon is present on Pemba I. That Vervets live within forest at Ngezi, and are arboreal, is probably attributable to 'competitive release' (T. Butynski & Y. de Jong pers. comm.).

Foraging and Food Omnivorous. Vervets forage both arboreally and terrestrially, typically beginning the day by feeding within their sleeping trees. By mid-morning they descend to forage on shrubs and herbaceous plants. After a mid-day rest, Vervets continue foraging, either on the ground or in trees, until dusk when they climb back into sleeping trees. At Segera seven adult ♀♀ in one group maintained a mean 6.6 m from their nearest neighbour. This is close to the mean of 6.1 m between feeding sites (Isbell & Enstam 2002). In Amboseli, individuals in six groups spent 30–40% of their time feeding and 15–20% of their time moving (Isbell & Young 1993b). Two groups with mean group sizes of 17.2 and 16.4 in Amboseli travelled a mean 950 m and 1440 m/day, respectively (135–2558, n = 114 days; Struhsaker 1967c). Daily travel distances of two groups at Segera were 1025 m (n = 44 days) for a group averaging eight members and 1632 m (n = 144 days) for a group averaging 27 members (based on straight-line distances of the groups during 30-minute periods; Isbell *et al.* 1999b, Enstam & Isbell 2007). Larger groups and groups in poorer habitats travel farther per day than smaller groups and groups in higher-quality habitats (Struhsaker 1967c, Isbell *et al.* 1999b).

Vervets use hand-to-mouth movements to eat leaves, flowers, fruits, seeds and arthropods, but apply the mouth directly to scrape gum off trees. They rely heavily on *Acacia* spp. In Amboseli, flowers, gums, leaves and pods of *A. xanthophloea* and *A. tortilis* account for ca. 50% of total time spent feeding (Lee & Hauser 1998). At Segera, *A. drepanolobium* and *A. xanthophloea* account for ca. 35% and ca. 22% of the diet, respectively (Pruetz & Isbell 2000). In Samburu, *A. tortilis* and *A. elatior* account for >60% of total time spent feeding (Whitten 1988). Other important food species are the woody shrubs *Azima tetracantha* and *Salvadora persica*, the herbs *Abutilon mauritianum* and *Lycium europaeum*, and the grasses *Pennisetum mezianum*, *Cynodon*

dactylon and *Cynodon plectostachyus* in Amboseli (Struhsaker 1967c, Lee & Hauser 1998), *Acacia gerrardii*, *Acacia seyal*, *Commelina* spp., *L. europaeum* and *Euclea divinorum* at Segera (Pruetz & Isbell 2000), and *H. coriacea*, *Boerhavia erecta*, *Abutilon hirtum*, *F. sycamorus* and *Aphania senegalensis* in Samburu (Whitten 1983).

With the exception of gums, which are available year-round, foods are eaten as they come into season. Flowers are preferred over other foods in Amboseli and Samburu. In Amboseli, *A. tortilis* flowers are most abundant in Jan–Mar, Oct–Dec (Wrangham & Waterman 1981, Isbell 1995, Lee & Hauser 1998). In Samburu Vervets spend 43% of their feeding time eating flowers (Whitten 1988). At Segera, which has no *A. tortilis*, gums are eaten more frequently (37%) than flowers (8%). Other foods eaten at Segera are fruits (10%), seeds and grasses (8% each), and leaves and swollen thorns (2% each). Small, unidentified items account for 23% of the diet; most of these are probably arthropods (L. A. Isbell pers. comm.), e.g. termites, beetles, moths, butterflies, grasshoppers, spiders and army worms *Spodoptera exempta*. Though percentages are not available for the diet of Vervets in the southern part of their range, foods of Vervets in the dune forests near L. Sibayi include floral parts of *C. africana*, fruits of *Mimusops caffra*, *Ziziphus mucronata*, *Sideroxylon inerme*, *Ficus natalensis*, *Grewia* sp. and *Cucumis* sp., seeds of *A. karroo*, *A. kraussiana* and *Albizia adiantifolia*, and leaves of *C. africana*, *A. karroo*, *A. kraussiana*, *Vepris undulata* and *A. adiantifolia* (Van der Zee & Skinner 1977). Although omnivorous, Vervets in southern Africa eat leaves less often than Samango Monkeys *Cercopithecus mitis labiatus* and have gastrointestinal tracts that are less specialized for digesting foliage (Bruorton *et al.* 1991). Vervets sometimes eat the eggs and young of birds (Struhsaker 1967c, Skinner & Skinner 1974, Lee & Hauser 1998), and they drink regularly when water is available (Wrangham 1981). In Amboseli, Vervets visited waterholes, on average, about once every two days, and drank most often in the early afternoon (n = 53 in 1677 h) (Struhsaker 1967c). At Segera, Vervets are no longer able to drink throughout the year because irrigation practices upstream have caused the Mutara R. to dry up entirely from Mar–Jul in recent years, e.g. 1999 and 2000 (L. A. Isbell pers. obs.). Young Vervets acquire adult food habits as they mature. During their first two months infants feed asynchronously with their mothers. At three months, infants begin to feed synchronously with their mothers on the same food items (Hauser 1993). Adult ♂♂ and adult ♀♀ eat the same foods (L. A. Isbell pers. obs.).

Vervets live in home-ranges of 5–103 ha (n = 27) (Struhsaker 1967d, De Moor & Steffens 1972, Whitten 1982, Cheney & Seyfarth 1987, Isbell *et al.* 1990, 2002, Lee & Hauser 1998). Large group size, low density of food trees and absence of neighbouring groups all increase home-range size (Struhsaker 1967d, De Moor & Steffens 1972, Isbell *et al.* 1990, L. A. Isbell pers. obs.). Vervets use all parts of their home-range throughout the year, and invariably defend the boundaries of their home-ranges against incursions by neighbouring groups (Struhsaker 1967d, Gartlan & Brain 1968, De Moor & Steffens 1972, Cheney 1981, L. A. Isbell pers. obs.). Home-range overlap in Amboseli was 11–33% in 1963–64, 26–42% in 1977–80 and 4–57% in 1986–88 (n = 15) (Cheney 1987, Isbell *et al.* 1990). The wider range of overlap in the latter time period occurred because some neighbouring groups ceased to exist and larger groups expanded into the home-ranges of smaller groups.

Vervets prefer to sleep in trees that are tall and large. In Amboseli, Vervets prefer *A. xanthophloea* over *A. tortilis* (Struhsaker 1967c), and prefer groves rather than isolated trees (Struhsaker 1967c, L. A. Isbell pers. obs.). The same few sleeping sites are repeatedly used (De Moor & Steffens 1972, L. A. Isbell pers. obs.). Small groups often share the same sleeping tree. Larger groups may split into subgroups and spread out to sleep within a small number of trees. Individuals typically sleep on the highest branches and as far along the distal ends of branches as will bear their weight (Andelman *et al.* 1985, L. A. Isbell pers. obs.).

Social and Reproductive Behaviour Social. Vervets live in cohesive groups of 2–10 adult ♀♀ and their offspring, usually accompanied by multiple adult ♂♂ (Struhsaker 1967c, Whitten 1983, Young & Isbell 1994, Whitten & Turner 2004). In Amboseli, maximum group size declined over 30 years from 53 (n = 4) to 4 (n = 2) (Struhsaker 1967b, Cheney & Seyfarth 1987, L. A. Isbell pers. obs.). At Segera group sizes declined over ten years in two groups from 10 and 30 to one group of 9 (Isbell *et al.* 2009). On Lolui I., group sizes ranged from 6 to 21 (n = 46) (Gartlan & Brain 1968). In Samburu group sizes were 37 and 40 (n = 2) (Whitten 1983). In Mosi-Oa-Tunya N. P., Zambia, group sizes ranged from 23 to 47 (n = 4) (Tembo 1994). At Burman Bush Nature Reserve, where groups are provisioned by tourists, three groups ranged in size from 8 to 37 (Henzi & Lucas 1980). At Windy Ridge one group had a maximum of 23 individuals (Baldellou & Henzi 1992). At Nduma, South Africa, two groups comprised ca. 22 and 37 members (De Moor & Steffens 1972). Along the Milk R., two groups had 48 and 69 members (McDougall *et al.* 2011).

Females remain in their natal groups throughout life, except under unusual circumstances, e.g. group fusions. Males disperse from their natal groups around sexual maturity (ca. 5–6 years). Most dispersing natal ♂♂ do not become solitary but immediately join adjacent groups (Henzi & Lucas 1980, Cheney & Seyfarth 1983, Isbell *et al.* 2002). In Amboseli, over a five-year period, 22 of 23 (96%) natal ♂♂ in three groups dispersed to adjacent groups (Cheney & Seyfarth 1983). At Segera, over a ten-year period, five of six (83%) ♂♂ in two groups joined neighbouring groups and stayed an average of 16 months (Isbell *et al.* 2002). Males also disperse with siblings and join groups that former groupmates previously joined (Cheney & Seyfarth 1983, Isbell *et al.* 2002). The tendency of Vervets to live along narrow strips near rivers limits the number of adjacent groups to two in most areas. When this is coupled with the high risk of mortality that Vervets face while moving into unfamiliar areas (Isbell *et al.* 1990, 1993), dispersal options become more limited and, thus, likely result in shorter dispersal distances and greater relatedness among Vervet ♂♂ than among ♂♂ of other species of primates. Limited dispersal options may contribute to the social system of Vervets, which is unusual among the Cercopithecini in having a permanent multimale presence in most areas (Isbell *et al.* 2002). Vervets do form single-male multifemale groups in some areas, e.g. along L. Naivasha and in the dune forests near L. Sibayi (Van der Zee & Skinner 1977, Whitten & Turner 2004, T. R. Turner pers. comm.). Solitary ♂♂ must exist in such places but they have not been reported.

Adult ♂♂ and adult ♀♀ both have easily detectable, linear dominance hierarchies (Struhsaker 1967d, Whitten 1983, Isbell &

Pruetz 1998). Males assert their dominance over subordinate ♂♂ with vocalizations and displays, e.g. the red-white-and-blue display, in which the dominant ♂ holds his tail high while walking back and forth or circling the subordinate ♂, thereby exposing his red perianus, blue scrotum and white stripe of fur that connects the scrotum and perianus (Struhsaker 1967b). Female hierarchies are more stable than those of ♂♂, with daughters occupying ranks near their mothers (Cheney 1983, Lee 1983b). The female dominance hierarchy also influences grooming and coalitionary support during agonistic interactions (Seyfarth 1980).

Young Vervets begin interacting with group members other than their mothers within the first week of life, often through play with other immatures. Time spent playing increases during the first three months of life (Lee 1984), more so in ♂♂ than ♀♀ (Lee 1983c). Males become more socially peripheral as they mature, whereas ♀♀ remain active in social life, maintaining grooming bonds and handling infants of other ♀♀ (Lee 1983a). It is not always apparent that infant handlers are helpers. In most cases infants are handled gently when they are taken from the mother (Lee 1983a); rarely, infants are mistreated (e.g. bitten). Mothers continue to carry their infants for up to one year, but the frequency tapers off after one month (Struhsaker 1971b, Lee 1984). In their first three months infants are carried for 30–100% of the time mothers are moving. By the time infants are four months old they are carried only 1–20% of the time (Whitten 1982).

Vervets produce at least 33 acoustically distinct vocalizations (e.g. 'squeals', 'screams', 'grunts', 'chutters', 'wrrs', 'waas' and 'aarrs') (Struhsaker 1967a). Some (e.g. grunts and 'loud aarr' calls) convey information about the identities of group members and members of other groups (Cheney & Seyfarth 1980, 1982a, b, 1990). Vervets also give different alarm calls to mammalian predators, raptors, snakes and humans (Struhsaker 1967a, Seyfarth *et al.* 1980b). Alarms to Leopards *Panthera pardus* of adult and subadult ♂♂ differ from those of adult ♀♀ and juveniles (Struhsaker 1967a, Seyfarth *et al.* 1980b, Enstam & Isbell 2002). Because Vervets give alarm calls to some species but not others, they effectively categorize species into predators and non-predators. Adults are the most selective, and give alarm calls to their most dangerous predators (Seyfarth *et al.* 1980a). Though infants are able to distinguish between general classes of predators, they are more likely to direct alarm calls at inappropriate stimuli (Seyfarth & Cheney 1980).

Vervets respond differently to different alarm calls (Struhsaker 1967a, Seyfarth *et al.* 1980b). They respond to 'eagle alarms' primarily by looking up and to 'snake alarms' by looking down and approaching the snake (Struhsaker 1967a, Seyfarth *et al.* 1980b, Cheney & Seyfarth 1990, Enstam & Isbell 2002). In areas with tall trees, Vervets respond to 'leopard alarms' primarily by climbing or remaining in trees. In areas with shorter trees, Vervets respond by descending trees, running away and scanning while bipedal (Enstam & Isbell 2002). Vervets also attend to alarm calls of other animals, e.g. Superb Starling *Lamprotornis superbus*, Helmeted Guineafowl *Numida meleagris*, Crowned Lapwing *Vanellus coronatus*, Impala *Aepyceros melampus*, Plains Zebra *Equus quagga*, Common Warthog *Phacochoerus africanus* and Yellow Baboon *Papio cynocephalus* (Struhsaker 1967c, Cheney & Seyfarth 1990). They are mobbed by birds, e.g. Lilac-breasted Roller *Coracias caudata*, Fork-tailed Drongo *Dicrurus adsimilis*, Northern White-crowned Shrike *Eurocephalus rueppelli* and Hildebrandt's Starling *Lamprotornis hildebranti* (Struhsaker 1967c).

Vervet Monkey *Chlorocebus pygerythrus* adult female.

Vervet groups do not form polyspecific associations with other primate species, though occasionally they are found in proximity to baboons *Papio* spp., Sykes's Monkeys, Patas and Northern Lesser Galagos *Galago senegalensis*. One exception appears to occur in Ngezi Forest, where preliminary observations suggest that the Zanzibar Red Colobus *Procolobus kirkii* (an introduced species) is frequently, if not almost always, in association with Vervets (T. Butynski & Y. de Jong pers. comm.). Vervets react variably to Yellow Baboons, Olive Baboons *Papio anubis* and Patas, sometimes moving away and other times ignoring them. Juvenile Vervets sometimes play with juvenile Yellow Baboons and Patas (Struhsaker 1967c, L. A. Isbell pers. obs.). Individual Vervets may temporarily, at least, join groups of Yellow Baboons or Patas (Struhsaker 1967c, Enstam & Isbell 2007, L. A. Isbell pers. obs.).

Vervets have no elaborate courtship behaviour. Males and ♀♀ do not form consortships (Andelman 1987). Males are single-mount ejaculators (Struhsaker 1967b) and matings are brief. Female Vervets do not have obvious indicators of reproductive state, other than a willingness to copulate more during some months of the year than others. None the less, ♂♂ initiate copulations most frequently around the period of conception (Andelman 1987), suggesting that ♀♀ provide some cue(s). Vaginal secretions perhaps indicate reproductive state. Males frequently sniff the perineum of ♀♀, and may obtain information about reproductive state in this way. Chest-rubbing (i.e. apparent scent-marking) occurs but perhaps not in all populations (Gartlan & Brain 1968, De Jong & Butynski 2010b, Freeman *et al.* 2012).

Reproduction and Population Structure Vervets are seasonal breeders. In Amboseli ♀♀ copulate from Apr–Oct, but conceptions occur about two months after the onset of mating. Females normally conceive on the first ovulatory cycle of the year (Andelman 1987). Most births (87%) occur in Oct–Dec (n = 75; Cheney *et al.* 1988). In Samburu copulations occur in Mar–Jun (n = 22); most births (88%) occur in Nov–Dec (n = 16; Whitten 1983). Timing of matings and births in Amboseli and Samburu associated with seasonal abundance of flowers, especially those of

Acacia spp. (Whitten 1983, Butynski 1988). At Segera, copulations observed in all months except Jan, Mar and Apr, but most often in Jun–Oct (L. A. Isbell pers. obs.). Over a ten-year period, 30 of 40 births (75%) that could be assigned to a particular month occurred in Jan–Mar. The percentage of births that occurred outside these peak birth months was nearly double (25%) that of Amboseli (13%) (Cheney *et al.* 1988, L. A. Isbell pers. obs.). Segera's less distinct birth seasonality may be related to its less seasonal rainfall (Butynski 1988). Females also copulate during pregnancy (Gartlan 1969, Andelman 1987). Mean length of gestation in captivity is 163.2 days ± 6.2 S.D. (n = 38) (Johnson *et al.* 1973). In the wild, gestation length for one ♀, based on hormonal analyses of urine, was 156–161 days (Andelman *et al.* 1985).

Females give birth to one infant every 1–2 years, depending largely on habitat quality and the survival of preceding infants. In Amboseli, mean inter-birth intervals for ♀♀ in three groups ranged from 13.8 to 21.3 months, with the longer inter-birth interval occurring in a group without access to permanent water (Cheney *et al.* 1988). At birth, infants weigh 300–400 g (Smithers 1971, Nowak 1999). Weaning begins at around three months and is complete by around 18 months, or earlier if the mother reproduces the next year (Whitten 1983). Infants orphaned at six months can survive. The earliest age at first reproduction is ca. 3.5 years (Isbell *et al.* 2009). In Amboseli mean age at first reproduction was earlier (4.4 years) in a group with better access to food and water than in two groups with poorer access (5.1 and 5.7 years) (Cheney *et al.* 1988). At Segera, where water is no longer always available year-round, the mean age at first reproduction was 5.1 years (3.5–6.1) for the three ♀♀ born during the ten-year study that survived long enough to reproduce. The youngest ♀ to reproduce gave birth unusually during the mating season after an extraordinarily wet El Niño event. This female's two subsequent births were also six months off the peak birth season and well into the mating season (L. A. Isbell pers. obs.).

During the mating season ♀♀ mate with multiple ♂♂. High-ranking ♂♂ do not monopolize matings during the most probable week of conception. Females refuse most attempts by ♂♂ to copulate (Andelman 1987). Males can commit infanticide, but incidence appears to vary with habitat structure, costs of dispersal, and corresponding degree of relatedness between immigrants and members of the groups they join. Where Vervets are restricted to linear home-ranges along rivers (e.g. Segera), high costs of dispersal limit movement to one of two adjacent groups and increases genetic relatedness between immigrants and the groups they join. In such groups infanticide is rare, if it occurs at all. In nine years of observation no attempts at infanticide were observed at Segera (Isbell *et al.* 2002). In areas with more dispersal options (e.g. a greater number of adjacent groups in Amboseli), genetic relatedness between immigrants and members of non-natal groups declines, and infanticide is more common. In Amboseli, where each group shared home-range boundaries with up to five other groups, three infants were victims of immigrating ♂♂, at a rate of 0.03 infanticides/100 immigration events (Isbell *et al.* 2002). No data are available for Vervets at Naivasha where genetic relatedness between immigrant ♂♂ and non-natal groups must be lower because groups are limited to only one adult ♂. The rate of infanticide in Green Monkeys *Chlorocebus sabaeus* living in single-male groups in Barbados is 4.5/100 immigration events (Horrocks & Baulu 1988, Isbell *et al.* 2002). Infanticide is normally attributed to intense male–male competition for reproductive success, but there is no *a priori* reason to expect competition to be less intense in multimale groups unless ♂♂ are more closely related to each other.

Sex ratios at birth are biased toward ♂♂. In Amboseli the birth sex ratio of 41 (56%) ♂♂ and 32 (44%) ♀♀ was 1 : 0.8 (Cheney *et al.* 1988). Of 50 unambiguously sexed infants at Segera the birth sex ratio of 31 (62%) ♂♂ and 19 (38%) ♀♀ was 1 : 0.6 (L. A. Isbell pers. obs.). This is not an artefact of easier identification of ♂♂ in the first weeks of life; in fact, ♀♀ were initially sexed incorrectly more often than ♂♂. The sex ratio becomes more biased toward ♀♀ in adulthood. In Amboseli the adult sex ratio per group varied from 1 : 0.8 to 1 : 7.0 (n = 3) over five years (Melnick & Pearl 1987, Cheney *et al.* 1988). In Samburu the mean adult sex ratio for two groups was 1 : 1.0 (Melnick & Pearl 1987). On Lolui I. the adult sex ratio was 1 : 1.4 (Hall & Gartlan 1965). At Segera the mean monthly adult sex ratio of two groups was 1 : 1.2 (n = 101 months) and 1 : 1.5 (n = 73 months) (L. A. Isbell pers. obs.).

At Segera mean annual birth rate was 0.62 offspring/adult ♀ over ten years. Mean annual infant mortality rate for two groups over ten years was 48%; mean annual adult ♀♀ mortality rate over 11 years was 15% (Isbell *et al.* 2009). In Amboseli, 57% of individuals died during their first year, on average. Vervets can live to about 30 years in captivity (Nowak 1999) and to at least 18 years in the wild (Cheney & Seyfarth 1990).

Predators, Parasites and Diseases Predation accounted for at least 69% of all Vervet deaths and only 27% of ♀♀ survived to adulthood in Amboseli (Cheney *et al.* 1988). Such high losses to predators may account for the large percentage of time (30–40%) Vervets devote to scanning the environment (n = 54 individuals in six groups) (Isbell & Young 1993a). Similarly, at Segera, at least 7 of 15 adult ♀♀ (47%) died of suspected or confirmed predation (Isbell & Enstam 2002, Isbell *et al.* 2009). Only 16% (3/19) ♀♀ born during the study survived to adulthood (Isbell *et al.* 2009).

Confirmed predators of Vervets include Leopards, African Crowned Eagles *Stephanoaetus coronatus*, Martial Eagles *Polemaetus bellicosus*, Central African Rock Pythons *Python sebae*, Yellow Baboons and Domestic Dogs *Canis familiaris* (Struhsaker 1967c, Cheney *et al.* 1988, Baldellou & Henzi 1992, Isbell & Enstam 2002, T. Butynski pers. comm.). Potential predators include Lions *Panthera leo*, Spotted Hyaenas *Crocuta crocuta*, Cheetahs *Acinonyx jubatus* and Black-backed Jackals *Canis mesomelas*, based on alarm calls or greater vigilance of Vervets toward those animals. Though large enough to attack Vervets, African Hawk-eagles *Hieraaetus spilogaster*, Black-chested Snake Eagles *Circaetus pectoralis*, Tawny Eagles *Aquila rapax* and Giant Eagle-owls *Bubo lacteus* are not likely predators, based on their dietary preferences and the indifference of Vervets to those animals. Egyptian Cobras *Naja haje*, Black Mambas *Dendroaspis polylepis* and Puff Adders *Bitis arietans* are not predators but Vervets give alarm calls to them (Struhsaker 1967a, L. A. Isbell pers. obs.) and bites can, undoubtedly, be fatal. Estimated annual predation rates range from 6% in Samburu to 15% in Amboseli (Cheney & Wrangham 1987, Cheney *et al.* 1988). Predation rates occasionally spike. In Amboseli the estimated predation rate was at least 45% in 1987, largely from a brief period of intense predation by Leopards (Isbell 1990). Similarly, brief but intense Leopard

predation over a seven-month period at Segera resulted in the loss of 21 of 28 (75%) study animals (Isbell & Enstam 2002, Isbell *et al.* 2009). Predators depress Vervet populations periodically, even to the extent of decimating local populations. Evidence from carcasses, scratch marks on tree trunks and footprints indicates that Leopard predation often occurs at night while Vervets are in their sleeping trees, and that multiple Vervets can be killed in one night, especially when ♀ Leopards hunt with cubs (Isbell *et al.* 2009). Leopard predation is less likely to occur when humans are nearby (Isbell & Young 1993a).

Vervets sometimes develop an unidentified seasonal malady. In Amboseli, in at least two consecutive years during Nov–Jan, 16 of 51 (34%) adults and subadults, and four of 22 (18%) juveniles, lost hair on their abdomens, knees, elbows and/or inner thighs, and developed hyperpigmentation of the exposed skin. Males also developed scrotal hyperpigmentation (Isbell 1995). Hair loss occurs more rarely at Segera, in May–Jun (L. A. Isbell pers. obs.). In no case has this disease progressed to scrotal bleeding or bursting as observed in Amboseli (Struhsaker 1967c). At Segera, infants may have been more susceptible than adults to respiratory illnesses. Those that died within their first year (n = 17, excluding those dying of predation and after losing the mother) were, on average, born in significantly wetter months (mean 45 mm rainfall) than infants that survived their first year (mean 24 mm rainfall, n = 24) (Isbell *et al.* 2009).

Vervets harbour a variety of viruses, protozoa, bacteria and helminths. Viruses include HTLV-like STLV-1, Papillomavirus SA-12, Spumavirus Simian Foamy Virus, Lentivirus SIV agm, Alphavirus-SFV Complex Chikungunya and Polyomavirus SAV-12. Protozoa include *Babesia macaci* and *Babesia pitheci*. Bacteria include *Salmonella* sp., *Shigella* sp., *Borrelia harveyi*, *Chlamydia* sp., *Leptospira* sp. and *Rickettsia cornorii*. Helminths include *Schistosoma mattheei*, *Schistosoma mansoni*, *Cercopithifilaria verveti*, *Dirofilaria aethiops* and *Enterobius bipapillatus* (Nunn & Altizer 2005). Vervets are implicated, along with Olive Baboons, in Kenya's first recorded outbreak of Yellow Fever among humans in 1992–93 in the Kerio Valley (Reiter *et al.* 1998). The effects of parasites and diseases on Vervet populations are unknown.

Conservation IUCN Category (2012): Least Concern. CITES (2012): Appendix II.

Though Vervets are geographically widespread and can tolerate a wide range of habitats, they are none the less patchily distributed. In the two areas where Vervets were studied for at least ten years (Amboseli and Segera), the Vervet populations suffered severe declines (Cheney *et al.* 1988, Isbell *et al.* 2009). More limited surveys at Kasoje in the Mahale Mts, Tanzania (Uehara & Ihobe 1998) and L. Naivasha (L. A. Isbell pers. obs.) also suggest local declines. In the latter case the decline is likely the result of human encroachment and habitat destruction along the lake shore. Though it is difficult to determine overall population trends from a few studies of this widespread species, reported declines, combined with the absence of studies reporting increases in numbers of Vervets, suggest that Vervet populations are declining, particularly where habitat change (e.g. tree die-offs, river water depletion and human encroachment) is occurring. The tendency for Vervets to live in small, isolated populations probably makes them particularly susceptible to local extinction. Detailed surveys of the extent of isolation are needed throughout their range.

Measurements

Chlorocebus pygerythrus pygerythrus
HB (♂♂): 490 mm, n = 30
HB (♀♀): 446 mm, n = 30
T (♂♂): 652 (600–750) mm, n = 30
T (♀♀): 575 (485–653) mm, n = 30
HF (♂♂): 144 (133–170) mm, n = 30
HF (♀♀): 125 (115–137) mm, n = 30
E (♂♂): 38 (31–42) mm, n = 30
E (♀♀): 35 (30–40) mm, n = 30
WT (♂♂): 5.5 (3.9–8.0) kg, n = 29
WT (♀♀): 4.1 (3.4–5.3) kg, n = 30
N Botswana (Smithers 1971). Range for HB not given.

C. p. hilgerti
HB (♂♂): 492 (430–570) mm, n = 4
HB (♀♀): 451 (420–515) mm, n = 4
T (♂♂): 646 mm, n = 47
T (♀♀): 548 mm, n = 61
HF (♂♂): 140 mm, n = 35
HF (♀♀): 120 mm, n = 48
E (♂♂): 27, 33 mm, n = 2
E (♀♀): 30 (25–33) mm, n = 4
WT (♂♂): 4.2 kg, n = 48
WT (♀♀): 2.7 kg, n = 61
Various localities
T, HF, WT: Samburu, Mosiro and Kimana (Anapol *et al.* 2005); range not given.
HB and E: compiled by T. Butynski from Heller (1913) and Hill (1966)

Key References Cheney & Seyfarth 1990; Gartlan 1969; Isbell *et al.* 2002, 2009; Struhsaker 1967b, c.

Lynne A. Isbell & Karin L. Enstam Jaffe