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Three Sykes's Monkey *Cercopithecus mitis* × Vervet Monkey *Chlorocebus pygerythrus* Hybrids in Kenya

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Abstract: Hybridization in the wild between broadly sympatric species has been reported for 13 species of African primates. Three guenons, believed to be Sykes's monkey *Cercopithecus mitis* × vervet monkey *Chlorocebus pygerythrus* hybrids, are reported here; two at Diani on the south coast of Kenya and one at Ngong Forest Sanctuary, Nairobi. These are the first records of hybridization between these broadly sympatric species, as well as between these genera. Most of the phenotypic characters of these hybrids are intermediate between the parent species. This paper (1) describes these hybrids and the environments in which they live; (2) briefly reviews hybridization among Africa's primates; (3) describes scent-marking behavior by one of the hybrids; (4) briefly reviews scent-marking among Africa's monkeys; (5) discusses the environmental circumstances that may weaken genetic barriers and facilitate hybridization; and (6) suggests topics for research on the ecology, behavior, and evolutionary significance of these three hybrids.

Key Words: *Cercopithecus mitis, Chlorocebus pygerythrus*, hybrid, Kenya, scent-marking, Sykes's monkey, taxonomy, vervet monkey

Introduction

Natural hybridization is increasingly recognized as potentially playing an important function in the evolution of new taxa, including primates (Dutrillaux *et al*. 1988; Jolly *et al.* 1997; Allendorf *et al*. 2001; Barton 2001; Jolly 2001; Detwiler *et al.* 2005; Arnold and Meyer 2006). Among Africa's primates, natural hybridization appears to occur most often along the edges of the geographic ranges of parapatric subspecies of the same species, or of parapatric species of the same 'species group' (i.e., 'superspecies'). In some instances of 'allopatric hybridization' there is but occasional contact and hybrids are rare (Struhsaker 1970), while in others the 'hybrid zone' is extensive (Jolly 2001; Detwiler *et al*. 2005; De Jong and Butynski 2009; Zinner *et al*. 2009).

Cases of natural hybridization between well-differentiated, broadly sympatric species that are behaviorally and ecologically distinct are far less often reported than are cases of parapatric or allopatric hybridization. The primary examples given for 'sympatric hybridization' in the wild for African primates are Stuhlmann's blue monkey *Cercopithecus mitis stuhlmanni* × Schmidt's red-tailed monkey *Cercopithecus ascanius schmidti* hybrids in southwest Uganda (Struhsaker *et al*. 1988) and southwest Kenya (L. Tranter pers. comm.; D. Black pers. comm.), and Doggett's silver monkey *Cercopithecus mitis doggetti* × *C. a. schmidti* hybrids in northwest Tanzania (Detwiler 2002; Detwiler *et al*. 2005).

For African primates, we are aware of records for sympatric hybridization for only 11 other species (involving six species pair combinations). These are as follows: three probable gelada baboon *Theropithecus gelada* × olive baboon *Papio anubis* hybrids in the Bole Valley, Ethiopia (Dunbar and Dunbar 1974; Jolly *et al*. 1997); one presumed green monkey *Chlorocebus sabaeus* × western patas monkey *Erythrocebus patas patas* hybrid in Saloum Delta National Park, Senegal (Galat *et al*. 1993; Galat-Luong 1996); one probable mustached monkey *Cercopithecus cephus* × putty-nosed monkey *Cercopithecus nictitans* hybrid in Lopé Reserve, Gabon (Tutin 1999); two apparent Dent's monkey *Cercopithecus denti* × *C. m. doggetti* hybrids in Nyungwe National Park, southwest Rwanda (B. A. Kaplin pers. comm. in Detwiler *et al*. 2005); two mona monkey *Cercopithecus mona* × golden-bellied crowned monkey *Cercopithecus pogonias pogonias* hybrids at Indenau, Cameroon (Struhsaker 1970);

one *C. mona* × Gray's crowned monkey *Cercopithecus pogonias grayi* hybrid at Tinaso, Cameroon (Struhsaker 1970); and two apparent Sclater's monkey *Cercopithecus sclateri* × red-bellied monkey *Cercopithecus erythrogaster* hybrids in the Niger Delta, Nigeria (Oates and Baker in press; J. F. Oates pers. comm.).

This paper describes three new cases of natural hybridization between broadly sympatric genera/species in Kenya, some of the circumstances under which these hybridizations occurred, and some of the behaviors of these hybrids. Finally, this paper suggests topics for research on the ecology, behavior, and evolutionary significance of these hybrids.

Cercopithecus mitis albogularis × *Chlorocebus pygerythrus hilgerti* Hybrids at Diani, Kenya

Six primate species occur in and around Diani on the south coast of Kenya; Zanzibar Sykes's monkey *Cercopithecus mitis albogularis*, Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti,* Ibean yellow baboon *Papio cynocephalus ibeanus*, Peter's Angola colobus *Colobus angolensis palliatus*, white-tailed small-eared galago *Otolemur garnettii lasiotis*, and Kenya coast galago *Galagoides cocos*. On 14 December 2008, De Jong observed and photographed a free-ranging adult male guenon on the grounds of the Leopard Beach Hotel, Diani (04.2848°S; 39.5913°E; Fig. 1). Despite brief daily searches, De Jong encountered the hybrid only this once during four days (14–17 December).

Based on the intermediate phenotypic characters of this adult male guenon (Table 1), and the fact that only two species of guenon occur in the eastern half of Kenya (Kingdon 1971, 1997; De Jong and Butynski 2009), we believe that this individual is a Sykes's monkey × vervet monkey hybrid (Fig. 2). Given the locality, and following the taxonomy of Grubb *et al*. (2003) for *C. mitis* and of Groves (2001) for *C. pygerythrus* (see below), this is a *Cercopithecus mitis albogularis* × *Chlorocebus pygerythrus hilgerti* hybrid.

On 7 October 2009, we visited Diani for 3 days to observe (7.5 h) and photograph the 'Diani hybrid', and to search (12.5 h) for other hybrids on and around the extensive grounds of Leopard Beach Hotel, Leisure Lodge Hotel, Leisure Lodge Beach and Golf Course, and The Sands at Nomad.

As best as we can determine, the Diani hybrid represents the first record of hybridization (either in captivity or in the wild) between these two broadly sympatric species, and only the fifth record among African primates of a wild intergeneric hybrid (see above).

Table 1 presents a detailed comparison of the phenotypic characters of the Diani hybrid, adult male *C. m. albogularis* (Fig. 3), and adult male *C. p. hilgerti* (Fig. 4) at Diani. The phenotypic characters of the Diani hybrid are intermediate to the parent species in most respects, although the color of the face, neck collar, dorsum, back of the legs, sides, and tail appears to be slightly more like *C. mitis*, while body shape, and color of the iris, eyelids, shoulders, and ventrum appear to be slightly more like *C. pygerythrus*. The scrotum of the Diani hybrid is intermediate in size and color between *C. mitis* and *C. pygerythrus*. The muzzle of the Diani hybrid seems to be longer and more pointed than the muzzle of either *C. mitis* or *C. pygerythrus*. Interestingly, unlike either parent species, the Diani hybrid has a faint nose spot (recalling *C. nictitans* and members of the '*Cercopithecus cephus* species-group').

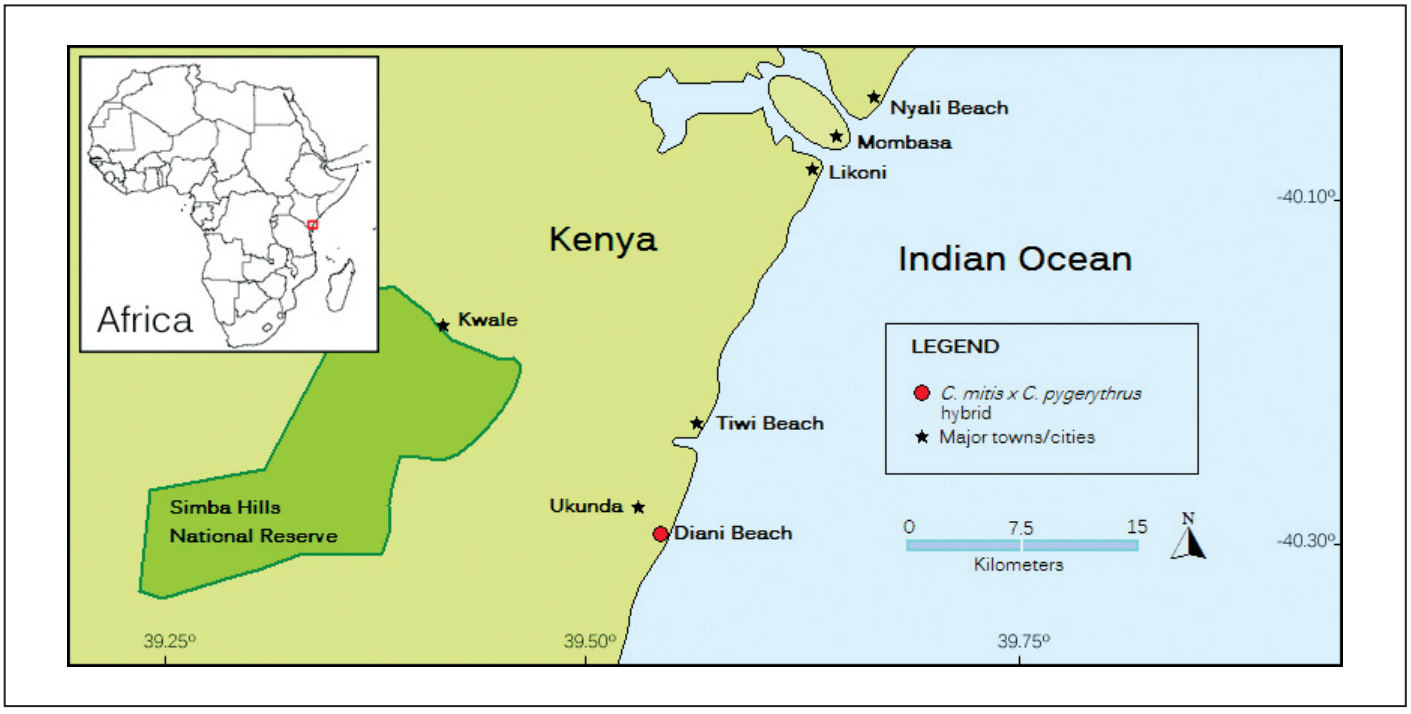

Figure 1. Location of Diani, south coast of Kenya, locality of the Zanzibar Sykes's monkey *Cercopithecus mitis albogularis* × Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid.

Table 1. Comparison of the phenotypic characters of the adult male Diani hybrid with adult males of *Cercopithecus mitis albogularis* and *Chlorocebus pygerythrus hilgerti* at Diani, Kenya.

Body part	Diani hybrid	*Cercopithecus mitis albogularis*	*Chlorocebus pygerythrus hilgerti*
Nose	Sooty-grey with pale grey nose spot.	Sooty-grey.	Jet black.
Naked skin of face	Triangle-shaped, sooty-grey skin around eyes and muzzle.	Sooty-grey skin around eyes and muzzle.	Egg-shaped. Jet black skin around eyes and muzzle.
Whiskers	Short to medium length, heavily grizzled pale grey.	Long and dense, forming a ruff. Heavily grizzled grey and pale olive-yellow.	Not grizzled. White, long, sparse, sweeping upwards and backwards to cover base of ears.
Lips	Sparse, short, pale grey hairs on upper and lower lips.	Short, pale grey, hairs on upper and lower lips.	Without hairs.
Iris	Mahogany brown.	Amber.	Mahogany brown.
Eyelids	Pinkish-grey.	Pale yellow.	Pale grey.
Skin around eyes	Pinkish-grey.	Pinkish-grey.	Black.
Front of ears	Skin blackish. Lightly-furred, pale grey.	Skin dark grey. Moderately-furred, off-white.	Skin jet black. Lightly furred, white.
Ear fringe	Narrow. Very pale grey.	Narrow. Off-white.	None.
Brow-band	Straight and narrow. Distinct but not well-demarcated. Hair of moderate length, projecting slightly upwards and forwards. Same color as whiskers (i.e., grizzled grey and pale grey), but slightly lighter.	Shallow triangle in shape, narrower distally. Indistinct and poorly-demarcated. Hair of moderate length, projecting forward but longer at the distal edges of brow-band where they project laterally. Same color as whiskers (i.e., heavily grizzled grey and pale olive-yellow), but slightly paler.	Curves downwards at sides. Distinct and well-demarcated. Hairs short, projecting slightly upwards and forwards. White.
Crown	Grizzled olive-grey. Color increasingly intense towards top of crown.	Grizzled dark olive-grey with faint rufus wash.	Grizzled olive-grey. Color increasingly intense towards front of crown.
Throat	Off-white.	White.	Off-white.
Neck collar	Present but not well demarcated. Around front *c.* 50% of neck. Front off-white. Sides mouse grey, increasingly grizzled dorsally.	Distinct but not well demarcated. Around front *c.* 60% of neck. Front white. Sides grizzled light grey.	Absent.
Shoulders	Heavily grizzled olive-grey.	Grizzled dark grey and blackish.	Heavily grizzled pale olive-grey.
Dorsum	Grizzled pale olive-grey. Color extends onto base of upper tail.	Grizzled rufus-grey. Color extends onto base of upper tail.	Grizzled olive-grey. Color extends onto base of upper tail.
Upper outer arms	Grizzled grey with olive wash.	Blackish with grey flecking.	Grizzled olive-grey.
Upper inner arms	Light grey.	Grey.	Off-white.
Lower outer arms	Blackish with grey flecking.	Black.	Grizzled grey.
Lower inner arms	Blackish with grey flecking.	Black.	Off-white.
Upper outer legs	Grizzled grey with olive wash.	Grizzled charcoal.	Grizzled olive-grey.
Upper inner legs	Light grey.	Grey.	Off-white.
Lower outer legs	Grizzled grey.	Grizzled charcoal.	Grizzled grey.
Lower inner legs	Grizzled grey with olive wash.	Grizzled grey.	Off-white.
Hands and feet	Blackish.	Blackish.	Black.
Back of legs	Hair moderately long. Cream to pale grey.	Hair long. Cream.	Hair short. Off-white to pale grey.
Ventrum	Pale grey.	Grey, paler towards center.	Off-white.
Sides	Like dorsum but paler and less grizzled.	Like dorsum but paler and less grizzled.	Like dorsum but brighter. Narrow off-white lateral stripe.
Upper side of tail	Grizzled pale olive-grey over proximal *c.* 10% grading into dark grey then blackish over distal *c.* 30%.	Grizzled rufus-grey over proximal *c.* 10% grading into black.	Grizzled olive-grey over proximal *c.* 10% grading into grizzled mouse grey with *c.* distal 10% blackish.
Subcaudal patch	Poorly developed. Pale russet.	Russet.	Bright red.
Scrotum	Medium-size. Skin blue. Readily observed from behind.	Small. Skin dark grey. Lightly covered with white hair. Difficult to observe from behind.	Large. Skin turquoise. Readily observed from behind.
Penis	Medium pink.	Pale pink.	Dark pink.
Overall	Grey animal with little contrast. Body shape most resembles *C. p. hilgerti*. Generally intermediate in color between *C. m. albogularis* and *C. p. hilgerti*.	Phenotypically like other populations of *C. m. albogularis.*	Phenotypically like other populations of *C. p. hilgerti*.

Additional photographs of the Diani hybrid, and of *C. m. albogularis* and *C. p. hilgerti* at Diani, can be viewed on the hybrid photographic map at: <www.wildsolutions.nl> (De Jong and Butynski 2010a).

In December 2008, the Diani hybrid was in association with two adult *C. mitis*, at least one of which was a male. The three animals moved over the grounds of the Leopard Beach Hotel feeding on human foods (including sugar in a rubbish bin) and indigenous and exotic plant parts. In October 2009, the Diani hybrid was encountered with a group of at least 20 *C. mitis* on the grounds of the Leopard Beach Hotel and the neighboring Leisure Lodge. The group was feeding on indigenous and exotic plant parts. In December 2008, the Diani hybrid exhibited no injuries or noticeable scars. In October 2009, however, he had a fresh, deep, about 10-cm-long wound in his left thigh, a slightly older cut on his right elbow, and new scars on his face and chest (Fig. 2). The two recent wounds caused him to limp on his left hind leg and right arm. During our observations the Diani hybrid frequently approached the group's resident adult male who always responded antagonistically. The resident male had a large fresh wound on the back of his right thigh (Fig. 3). It is likely that the wounds on the Diani hybrid and on the group's resident male were caused during fights between them.

Figure 2. Adult male Zanzibar Sykes's monkey *Cercopithecus mitis albogularis* × Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid at Diani, south coast of Kenya. Note the pale grey nose spot, the deep gash in the left thigh, and the blue scrotum. Photographs by Y. de Jong and T. Butynski.

Once, during our 7.5 h of observations, an adult female *C. mitis* presented herself to the Diani hybrid. Once, the Diani hybrid mounted an adult female but did not copulate. On at least three occasions, the Diani hybrid, while on the ground, actively 'scent-marked' by rubbing his chin, throat and chest in long strokes against tree branches (see below). The Diani hybrid once gave a 'pyow' loud call which was followed immediately by two 'ka-train' loud calls. These were presumably in response to a 'pyow' call produced by the group's resident adult male *c*. 20 m away. The 'pyow' is an intragroup rallying call and the 'ka-train' is an alarm call. On at least one occasion, the Diani hybrid produced a 'boom', a loud call given in response to various kinds of disturbance (for example, presence of other adult males), sudden loud noise (for example, falling trees or thunder claps), a female 'strained grunt-chorus', and sometimes for no discernable reason (Lawes *et al*. in press; T. Butynski pers. obs.). That the Diani hybrid produced 'pyow', 'ka-train' and 'boom' loud calls is interesting since, among the primate species present in eastern Kenya, these load calls are only given by adult male *C. mitis*; none of these three calls is part of the vocal repertoire of *C. pygerythrus* (Gautier 1988; Gautier *et al.* 2002; T. Butynski pers. obs.).

There is a second apparent *C. m. albogularis* × *C. p. hilgerti* hybrid at Diani. A photograph (Fig. 5.) of this individual was presented by A. Hayes in a blog (6 August 2009, <colobus.wildlifedirect.org>) of The Colobus Trust (which has its headquarters in Diani). The hybrid in the photograph is a subadult (probably a female). We searched for this hybrid in October 2009 but did not find it. Based on the photograph, and the opinions of the staff of the Colobus Trust, this individual is similar in appearance to the adult male Diani hybrid. That is, it is phenotypically intermediate between *C. m. albogularis* and *C. p. hilgerti*.

In December 2010, The Colobus Trust conducted a primate survey at Diani. The adult male hybrid was encountered on the grounds of Leisure Lodge. He appeared to be alone and in good health. No other hybrids were found (A. Donaldson pers. comm.).

Cercopithecus mitis kolbi × *Chlorocebus pygerythrus hilgerti* Hybrid at Nairobi, Kenya

Ngong Forest Sanctuary (hereafter referred to as 'Ngong Forest'; 01.3171°S; 36.7452°E, 1800 m a.s.l.; Fig. 6) is a 7-km² lower montane dry forest southwest of Nairobi city. Ngong Forest is connected in the southeast to Nairobi National Park.

Five primate species occur in and near Ngong Forest; Kolb's monkey *Cercopithecus mitis kolbi*, *C. p. hilgerti, P. anubis*, Kikuyu small-eared galago *Otolemur garnettii kikuyuensis*, and Kenya lesser galago *Galago senegalensis braccatus*.

Kenya Wildlife Service rangers at Ngong Forest reported a 'different looking' guenon that they believed to be a *C. mitis* × *C. pygerythrus* hybrid. In August 2009, P. Kahumbu informed us about this suspected hybrid and provided a photograph of the individual. On 2 November 2009, we visited Ngong Forest and encountered a female hybrid ('Ngong hybrid') near the southeast entrance (Fig. 7). The hybrid was travelling in a group of *C. mitis*. The rangers are familiar with this semi-habituated group of *C. mitis* as it spends much time foraging, resting and sleeping in the vicinity of the ranger's camp. The rangers said that an adult male *C. pygerythrus*

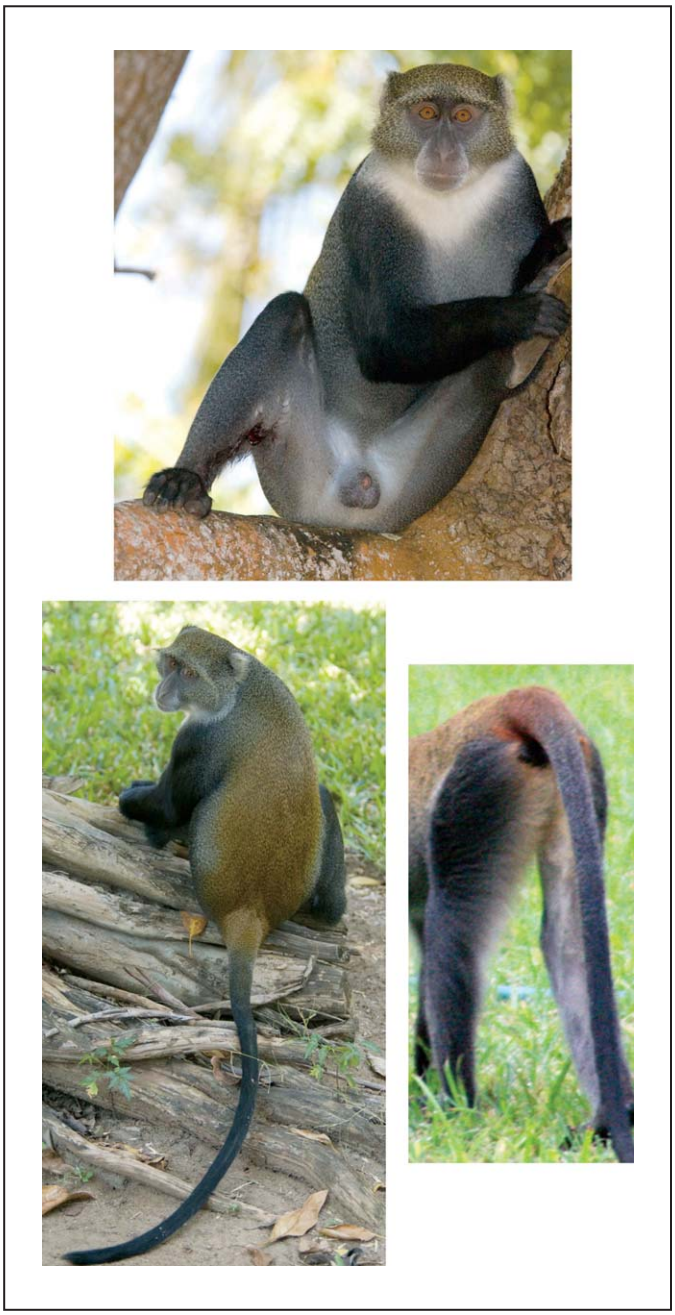

Figure 3. Adult male Zanzibar Sykes's monkey *Cercopithecus mitis albogularis* at Diani, south coast of Kenya. Note the absence of a greyish nose spot, the wound on the right thigh, and that the scrotum is small, dark grey, and not readily visible from behind. Photographs by Y. de Jong and T. Butynski.

Figure 4. Adult male Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* at Diani, south coast of Kenya. Note the black nose and the large, turquoise scrotum. Photographs by Y. de Jong and T. Butynski.

Figure 5. Subadult Zanzibar Sykes's monkey *Cercopithecus mitis albogularis* × Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid, south coast of Kenya. This is the second *C. m. albogularis* × *C. p. hilgerti* hybrid observed in Diani. Note the resemblance to the adult male Diani hybrid. Photograph by A. Hayes.

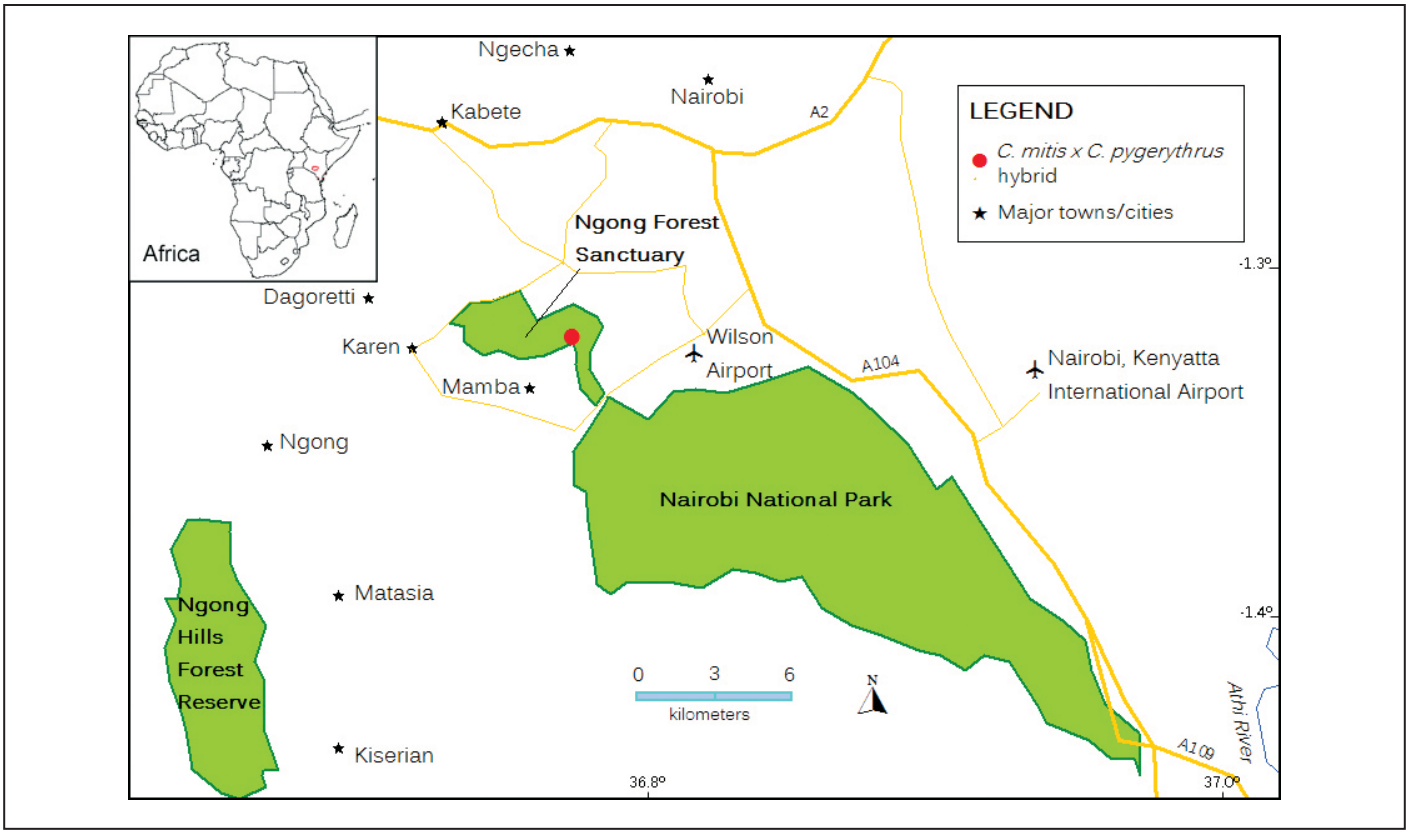

Figure 6. Location of Ngong Forest Sanctuary, Nairobi, Kenya, locality of the Kolb's monkey *Cercopithecus mitis kolbi* × Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid.

Figure 7. Subadult female Kolb's monkey *Cercopithecus mitis kolbi* × Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid at Ngong Forest Sanctuary, Nairobi, Kenya. Note the pale grey nose spot. Photographs by Y. de Jong and T. Butynski.

Figure 8. Adult male (top) Kolb's monkey *Cercopithecus mitis kolbi* at Langata, Nairobi, and adult female *C. m. kolbi* at Nanyuki, Mount Kenya (00.0334°S; 37.1320°E, 2110 m a.s.l.). Photographs by Y. de Jong and T. Butynski.

Table 2. Preliminary comparison of the phenotypic characters of the subadult female 'Ngong hybrid' with adult females of *Cercopithecus mitis kolbi* and *Chlorocebus pygerythrus hilgerti.*

Body part	Ngong hybrid	*Cercopithecus mitis kolbi*	*Chlorocebus pygerythrus hilgerti*
Nose	Sooty-grey with pale grey nose spot.	Sooty-grey.	Jet black.
Naked skin of face	Sooty-grey skin around eyes and muzzle.	Sooty-grey skin around eyes and muzzle.	Egg-shaped, jet black skin around eyes and muzzle.
Whiskers	Long and dense, forming a full ruff. Heavily grizzled pale grey.	Long and dense, forming a full ruff. Heavily grizzled dark grey with a pale olive-yellow wash.	Not grizzled. White, long, sparse, sweeping upwards and backwards to cover base of ears.
Lips	Whitish hairs on upper and lower lips.	Whitish hairs on upper and lower lips.	Without hairs.
Iris	Amber.	Amber.	Mahogany brown.
Skin around eyes	Pinkish-grey above eyes.	Sooty-grey.	Black.
Ears	Skin sooty-grey. Lightly furred, white.	Skin dark grey. Heavily furred tuft, white.	Skin jet black. Lightly furred, white.
Brow-band	Curves downwards at sides. Distinct and well-demarcated. Hairs medium long, projecting slightly upwards and forwards. Heavily grizzled pale grey.	Same color as whiskers (i.e., heavily grizzled dark grey with a pale olive-yellow wash). Hairs long, projecting slightly upwards and forwards.	Curves downwards at sides. Distinct and well-demarcated. Hairs short, projecting slightly upwards and forwards. White.
Crown	Grizzled grey with faint olive wash. Color increasingly intense towards front of crown.	Grizzled dark olive-grey with faint rufus wash.	Grizzled olive-grey. Color increasingly intense towards front of crown.
Throat	Off-white with pinkish wash.	Bright white, heavily furred.	Off-white.
Neck collar	Absent.	Distinct, bright white, long hairs and well demarcated. Around front *c.* 90% of neck.	Absent.
Shoulders	Grizzled grey.	Covered by long bright white hairs of neck collar.	Heavily grizzled pale olive-grey.
Dorsum	Grizzled grey.	Grizzled rufus-grey that extends onto base of upper tail.	Grizzled olive-grey.
Outer arms	Grizzled grey, increasingly dark towards the hands.	Blackish with grey flecking, black towards the hands.	Grizzled olive-grey.
Inner arms	Off-white.	Blackish with grey flecking, black towards the hands.	Off-white.
Outer legs	Grizzled grey.	Grizzled dark grey.	Grizzled grey with olive-grey wash on upper outer legs.
Inner legs	Off-white.	Pale grey.	Off-white.
Hands and feet	Dark grey.	Hands black. Feet dark grey.	Dark grey.
Ventrum	Off-white with pinkish wash.	Chest with long off-white to grey hairs. Lower part of ventrum dark grey.	Off-white.
Sides	Like dorsum.	Grizzled grey, long hairs.	Like dorsum but brighter. Narrow off-white lateral stripe.
Tail dorsum	Dark grey, grading into blackish or black.	Grizzled rufus-grey over proximal *c.* 10% grading into black.	Grizzled olive-grey over proximal *c.* 10% grading into grizzled mouse grey with *c.* distal 10% dark grey.
Tail ventrum	Pale grey.	Dark grey over proximal *c.* 10% grading into black.	Grizzled mouse grey.
Overall	Grey animal with little contrast. Body shape most resembles *C. m. kolbi*. Generally intermediate.	Phenotypically like other populations of *C. m. kolbi.*	Phenotypically like other populations of *C. p. hilgerti*.

joined this *C. mitis* group about 3 years ago and that he is probably the father of the Ngong hybrid. The rangers observed the Ngong hybrid mating with a *C. mitis* male in September 2009 (S. Kamotho pers. comm.).

Based on the intermediate phenotypic characters of the Ngong hybrid (Table 2), the observations of the rangers, and the fact that there are only two species of guenon present in this region (Kingdon 1971, 1997; Y. de Jong and T. Butynski pers. obs.), we believe that this individual is a *Cercopithecus mitis kolbi* × *Chlorocebus pygerythrus hilgerti* hybrid (Fig. 7). To the best of our knowledge, this is the first record of hybridization between these sympatric subspecies, and only the seventh record among Africa's primates of a wild intergeneric hybrid (see above).

Table 2 compares the phenotypic characters of the Ngong hybrid with those of *C. m. kolbi* (Fig. 8), and *C. p. hilgerti* (Fig. 4). The phenotypic characters of the Ngong hybrid are intermediate to the parent species in most respects, although the color of the nose, lips and eyes, the naked skin of the face, and body shape seem slightly closer to *C. m. kolbi*, while the absence of a neck collar, and the color of the brow-band, shoulders, ventrum, and inner limbs seem slightly more like *C. p. hilgerti*. Additional photographs of the Ngong hybrid, *C. m. kolbi* and *C. p. hilgerti* can be viewed on the hybrid photographic map at: <www.wildsolutions.nl> (De Jong and Butynski 2010a).

Current Taxonomy of *Cercopithecus mitis* and *Chlorocebus*

Here we have described three apparent instances of 'natural' hybridization between two broadly sympatric species that belong to different genera; two *Cercopithecus mitis albogularis* × *Chlorocebus pygerythrus hilgerti* hybrids at Diani, south coast of Kenya, and one *Cercopithecus mitis kolbi* × *Chlorocebus pygerythrus hilgerti* hybrid at Ngong Forest Sanctuary, Nairobi. Both parent species have a complicated and much debated taxonomy (Dandelot 1959; Lernould 1988; Groves 2000, 2001, 2005; Grubb 2001; Butynski 2002; Grubb *et al*. 2003; Groves and Kingdon in press; Kingdon in press).

The 'gentle monkey *Cercopithecus mitis/albogularis* subgroup' of the '*Cercopithecus nictitans* species group' (diploid chromosome number = 72; Dutrillaux *et al*. 1988; Romagno 2001) is extremely polytypic with all recent authorities recognizing no fewer than 16 subspecies (for example, Kingdon 1997, in press; Groves 2001, 2005; Grubb 2001; Grubb *et al.* 2003; Lawes *et al*. in press). In East Africa, west of the Eastern (Gregory) Rift Valley, *C. mitis* is most commonly referred to as 'blue monkey'. To the east of the Eastern Rift Valley the vernacular 'Sykes's monkey' is most frequently used. For *C. mitis* we apply the taxonomy of Grubb *et al*. (2003) and of De Jong and Butynski (2010b), both of which recognize *C. m. albogularis* as the subspecies that occurs along the south coast of Kenya, and *C. m. kolbi* as the subspecies that occupies the 'Highlands' east of the Eastern Rift Valley, including the Nairobi area.

The vervet monkey has most often been placed in the genus *Cercopithecus* (for example, Dandelot 1959; Kingdon 1971, 1997; Dandelot and Prévost 1972; Grubb *et al*. 2003). Molecular findings, however, indicate that the vervet and the Sykes's monkey belong to different phylogenetic clades; the vervet in the 'terrestrial guenon clade' (with *E. patas*, Preuss's monkey *Allochrocebus preussi*, l'Hoest's monkey *Allochrocebus lhoesti*, and sun-tailed monkey *Allochrocebus solatus*), and Sykes's monkey in the 'arboreal guenon clade' (with all of the other *Cercopithecus* spp.; Dutrillaux *et al*. 1988; Tosi *et al*. 2003, 2005; Xing 2007). This two-clade arrangement receives some support from craniodental (Martin and MacLarnon 1988; Groves 2000, 2001), vocal (Gautier 1988), protein (Sarich 1970; Ruvolo 1988), and ecological and behavioral studies (Gautier-Hion *et al.* 1988; Glenn and Cords 2002; Erhart *et al.* 2005). Furthermore, molecular data place the time of separation of these two clades at *c.* 8.1 mya (Tosi *et al.* 2005). Some of Africa's most widely recognized genera of primate are estimated to have split from their common ancestor <6 mya (e.g., *Homo* and *Pan*), and some as recently as 3–4 mya (e.g., *Cercocebus* and *Mandrillus; Papio, Lophocebus* and *Theropithecus*; Jolly *et al*. 1997; Goodman *et al.* 1998; Groves 2001; Toshi 2003). As such, here we apply the taxonomy of Groves (2000, 2001, 2005; Groves and Kingdon in press) in which the vervet is removed from *Cercopithecus* and placed in the resurrected genus *Chlorocebus*. *Chlorocebus pygerythrus* is, together with five other species, a member of the 'aethiops monkey *Chlorocebus aethiops* species group' (diploid chromosome number = 60; Dutrillaux *et al*. 1988; Romagno 2001). Monkeys in this group are often referred to as 'savanna monkeys'.

Natural *Cercopithecus mitis* Hybrids

Cercopithecus mitis is known to hybridize with (broadly sympatric) *C. a. schmidti* at three widely spaced sites in southwest Uganda (Budongo Forest Reserve, Itwara Forest Reserve, and Kibale National Park; Struhsaker *et al*. 1988), in northwest Tanzania (Gombe National Park; Detwiler 2002; Detwiler *et al*. 2005), and in southwest Kenya (Masai Mara National Reserve; L. Tranter pers. comm.; D. Black pers. comm.). While these hybrids are rare at the three Uganda sites (Struhsaker *et al*. 1988) and in the Masai Mara, they are common at Gombe, comprising *c.* 18% of the combined population of *C. mitis* and *C. ascanius* (Detwiler 2002; Detwiler *et al*. 2005). The only other species reported to hybridize with *C. mitis* is *C. denti* in Nyungwe National Park, southwest Rwanda (B. A. Kaplin pers. comm. in Detwiler *et al*. 2005).

Are the 'Blond Monkeys' of Cape Vidal, South Africa, Hybrids?

Mike L. Lawes (pers. comm.) observed no fewer than four 'blond monkeys' living in at least three groups of samango monkeys *Cercopithecus mitis erythrarchus* at Cape Vidal, east South Africa (28.0667°S; 32.5333°E; Fig. 9). These four monkeys appear to be *C. m. erythrarchus* in all respects except for their coloration; the pelage of the dorsum is sandy-yellow

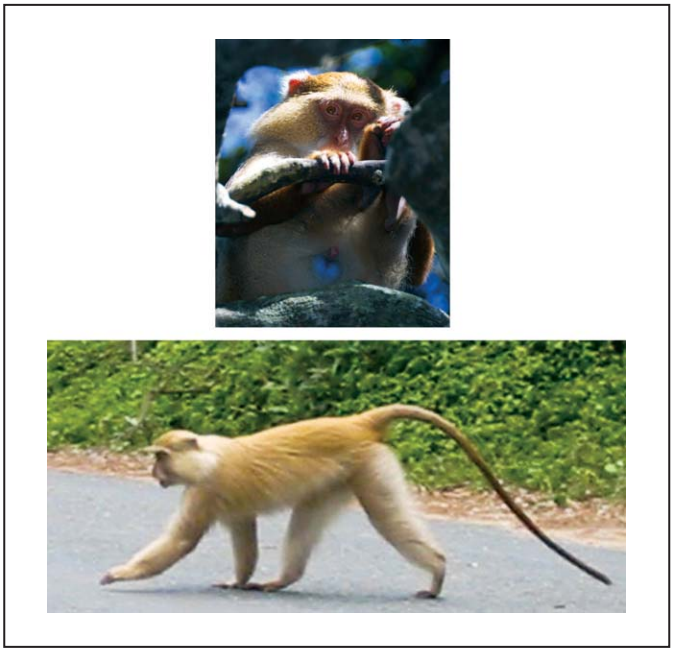

Figure 9. Adult male 'blond monkeys' at Cape Vidal, South Africa, that some suggest are samango monkey *Cercopithecus mitis erythrarchus* × southern vervet monkey *Chlorocebus pygerythrus pygerythrus* hybrids but which are probably erythristic or partial albino *C. m. erythrarchus*. Note the blue, small, scrotum in the top photograph. Photographs provided by C. Lehn (top) and M. Lawes. Photographers not known.

to blond, the skin is pinkish (as seen where the skin is bare, for example around the eyes and mouth, bridge of the muzzle, chin and digits), and the scrotum is blue and small. *Cercopithecus m. erythrarchus* and the southern vervet *Chlorocebus pygerythrus pygerythrus* are the only two species of guenon in southern Africa and both are common at Cape Vital. As such, and perhaps mostly because these blond monkeys have a blue scrotum, there has been some suggestion that they are hybrids. Overall, however, these blond monkeys look very different from the three apparent *C. mitis* × *C. pygerythrus* hybrids that we observed at Diani and Nairobi. If these blond monkeys are *C. mitis* × *C. pygerythrus* hybrids, it is expected that the scrotum would be intermediate in size. Instead, the scrotum is small, as for *C. mitis*. We, therefore, suggest that these blond monkeys represent erythristic or partial albino *C. mitis,* and that the blue scrotum is one effect of erythrism or partial albinism in this species.

Natural *Chlorocebus pygerythrus* Hybrids

The only previously reported cases of *C. pygerythrus* hybrids in the wild are with other members of the *C. aethiops* species group. *Chlorocebus pygerythrus* commonly hybridizes with (parapatric) *C. aethiops* over much of the southern one-third of Ethiopia (Dandelot 1959; Dandelot and Prévost 1972; Lernould 1988; Butynski and Kingdon in press) and with (parapatric) tantalus monkeys *Chlorocebus tantalus* over the southern half of Uganda (Kingdon 1971).

Captive-bred *Cercopithecus mitis* and *Chlorocebus pygerythrus* Hybrids

Captive-bred hybrids are reported between *C. mitis* and *C. mona*, lesser spot-nosed monkey *Cercopithecus petaurista*, DeBrazza's monkey *Cercopithecus neglectus*, *C. sabaeus*, *C. aethiops*, *C. ascanius*, and red-capped mangabey *Cercocebus torquatus* (Gray 1972; Lernould 1988; Erhart *et al.* 2005; Y. de Jong and T. Butynski pers. obs.). Erhart *et al.* (2005) report on two captive-bred *C. mitis* × *C. pygerythrus* hybrids, but these are probably *C. mitis* × *C. tantalus* hybrids (T. Rowell pers. comm.).

Chlorocebus pygerythrus is known to produce hybrids in captivity with *C. sabaeus*, *C. aethiops*, toque macaque *Macaca sinica*, bonnet macaque *Macaca radiata*, and crab-eating macaque *Macaca fascicularis* (Gray 1972; Lernould 1988).

Intergeneric Sympatric Hybridization

With the discovery of the *Cercopithecus mitis* × *Chlorocebus pygerythrus* hybrids in Kenya, three of the seven species pair combinations for sympatric hybridization among primates in Africa are intergeneric (see above). This is unexpected and its significance remains to be explored.

A number of cases of sympatric hybridization are known for the edges of the range of one or both of the parental species and may reflect a shortage of conspecific mates for one or both of the species (Jolly *et al.* 1997; Jolly 2001; Detwiler 2002; Detwiler *et al*. 2005). In these cases, hybridization is seen as increasing the options to reproduce when conspecific mates are scarce or absent. This appears to be the situation for the *C. mitis* × *C. ascanius* hybrids at Ngogo, Kibale Forest National Park (Struhsaker *et al*. 1988), where *C. mitis* is at the edge of its range, at very low density, adult females are uncommon, and solitary adult males are relatively abundant (Butynski 1990). This is not, however, the situation at Diani or Nairobi, where *C. mitis* and *C. pygerythrus* are both common. Our data from Diani are too few for calculating densities, but we would be surprised if either species were present at a density of <60 individuals/km². There are no data on the density of *C. mitis* or *C. pygerythrus* in the Ngong Forest area, but both species are common; *C. mitis* in the forest and *C. pygerythrus* in the residential areas around the forest and in the contiguous Nairobi National Park.

Cercopithecus mitis and *C. pygerythrus* occur throughout the extensive forest-woodland mosaic (that is one of the predominant vegetation types) of East Africa (Kingdon 1971, 1997; De Jong and Butynski 2009, 2010b). *Cercopithecus mitis* is a species of forests and dense woodlands, whereas *C. pygerythrus* is a species of forest edge, woodlands and lightly-wooded habitats. These two species are narrowly sympatric at the forest-woodland ecotone. The fact that the forest-woodland ecotone is a common 'habitat type' over this vast mosaic means that these two species meet frequently. Nonetheless, while *C. mitis* and *C. pygerythrus* 'associate' at common food sources along the ecotone (for example, large fig trees *Ficus* spp. with ripe fruit), these associations are usually localized, brief, and appear to be by chance. Groups of *C. mitis* and *C. pygerythrus* have not been observed to move together over long-distances as is often the case among species of forest-living monkeys. What does occur, however, is that young juvenile *C. pygerythrus* sometimes become well-integrated into *C. mitis* groups and probably grow up in them. In about 2001, L. A. Depew (pers. comm.) observed an apparent orphan *C. pygerythrus* (*c.* 6 months of age) in a *C. mitis* group at Bamburi (south coast of Kenya). This individual was in the *C. mitis* group for at least 5 months, at which time Depew moved from the area and observations ceased. It may be that such constant, long-term interspecific contact, especially for immature individuals, serves to reduce the behavioral barriers to interspecific mating.

The forest-woodland ecotone in East Africa has become considerably expanded and blurred during historic times through human activities that cause extensive habitat change and fragmentation, notably through farming, logging, establishment of settlements, construction of roads, and tourism (Anderson *et al*. 2007). As such, the forest-woodland 'ecotone' is much broader and more extensive today than in the past. This means that the area of habitat that *C. mitis* and *C. pygerythrus* share has increased greatly in historic times. In addition, *C. mitis* and *C. pygerythrus* come together particularly frequently at human residences and tourist facilities

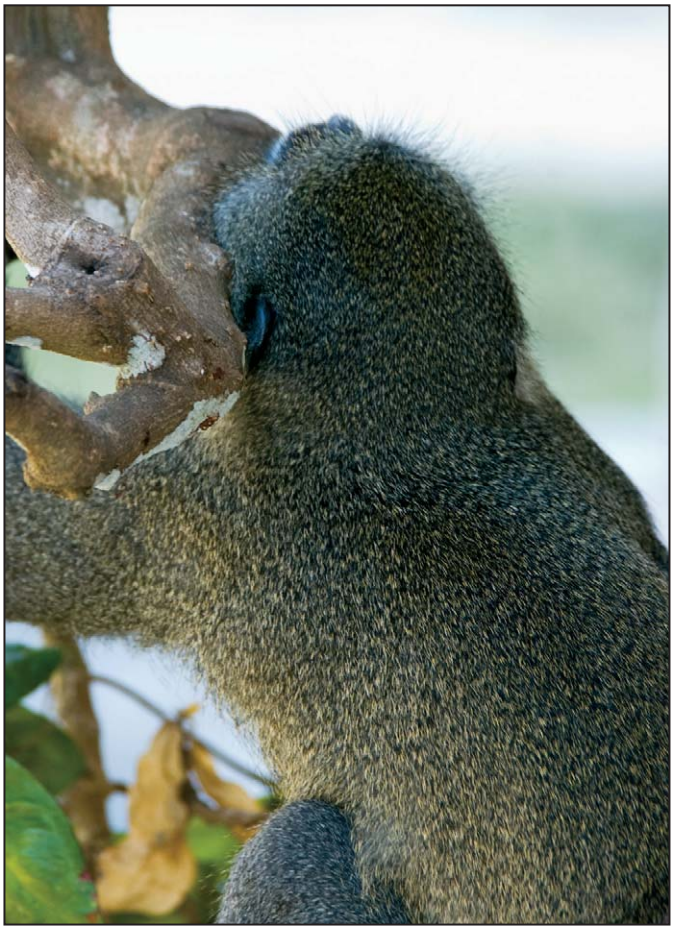

Figure 10. Adult male Zanzibar Sykes's monkey *Cercopithecus mitis albogularis* x Hilgert's vervet monkey *Chlorocebus pygerythrus hilgerti* hybrid scent-marking a tree at Diani, south coast of Kenya. Photograph by Y. de Jong and T. Butynski.

(for example, lodges, hotels, beaches, and picnic areas) where food is often relatively abundant at all times of the year (for example, on shrubs and trees on well-watered compounds, on tables, in garbage bins and pits, and around lights that attract insects at night). Here there is also often water to drink, large trees in which to sleep, few predators, and relatively little harassment by people. Under these circumstances, *C. mitis* and *C. pygerythrus* may drastically change their foraging behavior as they 'hang around' in a relatively safe anthropogenic habitat that they both can effectively exploit. In this new habitat, *C. mitis* and *C. pygerythrus* probably spend much more time in close proximity than when in their natural habitats, become more 'familiar', and likely have more time for interspecific social and reproductive activities. One result may be that the usual barriers to gene flow between *C. mitis* and *C. pygerythrus* have weakened due to anthropogenic environmental modifications and, in the cases of the Diani hybrids and Ngong hybrid, broken.

Scent-marking Behaviour in the Diani Hybrid and Other Guenons

During our 7.5 h of observation, the Diani hybrid was seen to scent-mark three times (Fig. 10). During each of the three bouts of scent-marking he rubbed his chin, throat and chest against tree branches in long, gentle strokes for about 30–60 seconds.

Active scent-marking is rarely reported in *C. pygerythrus* (see Loireau and Gautier-Hion 1988). Gartlan and Brain (1968) observed scent-marking by *C. pygerythrus* on Lolui Island, Uganda, and described it as territorial behavior. Lynne Isbell (pers. comm.), P. Lee (pers. comm.), and T. T. Struhsaker (pers. comm.) all conducted long-term research on *C. pygerythrus* in Kenya and never observed scent-marking in this species. Scent-marking was also not observed in *C. m. stuhlmanni* by T. Butynski (pers. obs.) during >3,000 h of observations in Uganda. In short, the only record of scent-marking by *C. pygerythrus* is that of Gartlan and Brain (1968) and there are no records of scent-marking by *C. mitis*.

The only other guenons for which active scent-marking has been reported are *C. neglectus*, owl-faced monkey *Cercopithecus hamlyni* (captive), *C. sabaeus,* and Allen's swamp monkey *Allenopithecus nigroviridis* (Gautier and Gautier 1977; Gautier-Hion and Gautier 1978; Loireau and Gautier-Hion 1988; Kingdon 1997; Gautier-Hion *et al.* 1999; Gautier *et al*. 2002; Hart *et al*. in press). All of these are semi-terrestrial species.

Loireau and Gautier-Hion (1988) speculated that in *C. neglectus* olfactory marking is associated with a number of traits; (1) low development of visual and vocal signaling, (2) small group size, (3) cryptic behavior, and (4) small home ranges. None of these traits applies to *C. pygerythrus*. Loireau and Gautier-Hion (1988) conclude that 'no consistent socio-ecological correlates can be found among species which display olfactory markings'.

Diani Hybrid Attempting to Assume the Resident Adult Male Position

In guenons, males are the dispersing sex and they sometimes form all-male associations after they leave their natal group (Cords 1987). During our first encounter with the Diani hybrid in December 2008, he was in association with two adult *C. mitis*, of which at least one was a male. At that time the Diani hybrid was a subadult or young adult. When observed in October 2009, the Diani hybrid was fully adult and in a heterosexual group of *C. mitis*. At that time he was attempting to usurp the group's resident male. The behaviors observed were the same as those observed at other sites where a non-resident adult male *Cercopithecus* is attempting to replace the resident adult male of a heterosexual group (Butynski 1982; Macleod *et al*. 2002). The Diani hybrid was (1) constantly following the resident male and in close proximity to him; (2) the resident male aggressively threatened and chased the Diani hybrid; (3) the Diani hybrid mounted an adult female;

and (4) both males showed fresh (severe) wounds and scars of recent wounds (suggesting that they had been in fights over a period of at least some weeks). What was atypical about the Diani hybrid at this time is that he (1) scent-marked and (2) produced 'pyow' and 'boom' calls—two vocalizations that (among Kenya's primate species) are given only by adult male *C. mitis* (T. Butynski pers. obs.).

Many (perhaps most) hybrids of parents that are not of the same species-group suffer from outbreeding depression and are aborted, stillborn, or die within hours, days, or weeks after birth (Gray 1972). This applies to both interspecific and intergeneric primate hybrids (Jolly 2001; Detwiler *et al*. 2005; Arnold and Meyer 2006). Those that survive to adulthood are often partially or completely infertile. According to Haldane's Rule (Haldane 1922; Barton 2001), this is especially the case for the heterogametic sex. The Diani hybrid gave every behavioral indication that he is 'interested' in assuming the resident male position and in breeding with *C. mitis* females. Whether he is genetically capable of siring viable offspring is, however, questionable.

Hybrids and the Common Ancestor to *Cercopithecus* and *Chlorocebus*

Might hybrids provide clues as to the appearance, behavior, ecology and environment of the common ancestor, both at the species and genus levels? It is interesting, if not insightful, that the adult male hybrid at Diani exhibits some phenotypic characters (for example, pale grey nose spot) and behaviors (for example, active scent-marking), which are absent or rare in both parent species and in one of the parent genera. Might these be traits exhibited by the common (*c*. 8.1 mya) ancestor to *Cercopithecus* and *Chlorocebus*? Did that common ancestor have a grey or white nose-spot, as is present today in several *Cercopithecus* species and in the terrestrial eastern patas monkey *Erythrocebus patas pyrrhonotus* but absent in *Chlorocebus*? Did that common ancestor practice active scent-marking, as is present today in several semi-terrestrial species of guenon but in none of the arboreal species?

That the Diani hybrid has the capacity to utter 'boom' and 'pyow' calls is surprising, given that these two loud calls likely play roles in group cohesion and reproductive isolation (Struhsaker 1970; Gautier 1988). Both the 'boom' and the 'pyow' involve complex, highly stereotyped behaviors and require morphologically distinct, large, extralaryngeal annexes (Gautier 1971, 1988). The 'pyow' call is of particular interest in that this call is, otherwise, confined to the two species in the *Cercopithecus nictitans* species group (*C. nictitans* and *C. mitis*) and, hence, likely has important phylogenetic implications. It is, therefore, of interest that an intergeneric hybrid has the ability to utter a loud call that is believed to have evolved to prevent interspecific hybridization between broadly sympatric species. The significance of this remains to be determined, but this might suggest that both the 'boom' and the 'pyow' are primitive calls that were present in the vocal repertoire of the common ancestor to *Cercopithecus* and *Chlorocebus*.

Research Questions and Recommendations

The three cases of intergeneric hybrids described here raise many questions related to hybridization. What are the conditions under which the usual mechanisms for reproductive isolation break down and allow hybridization? Is hybridization a viable reproductive strategy under some circumstances? What are the advantages and disadvantages of hybridization to the parents of the hybrid? What is the role of hybridization in evolution, especially in speciation (Barton 2001)? What can the study of hybrids tell us about phylogenetic affinities, and about the appearance, behavior, ecology and habitat of the common ancestor? How do anthropogenic environments affect rates of hybridization? What are the implications of 'anthropogenic hybridization' for the conservation of primate diversity (Allendorf *et al*. 2001; Jolly 2001; Detwiler *et al*. 2005)? The presence of these three apparent intergeneric hybrids also leads to questions related to cercopithecin taxonomy and phylogeny. Some light on a few of the above questions would be shed by comparative research on these three hybrids and their parental species. As such, here are a few recommendations for future research:

1. Produce a detailed description of the phenotypic characters of the Ngong hybrid, its behavior and its ecology.
2. Examine the molecular biology of the Diani and Ngong hybrids and of the parental species. Are these 'really' *C. mitis* × *C. pygerythrus* hybrids? Which is the maternal species? What is their karyotype?
3. Determine whether the Diani and Ngong hybrids are capable of successful reproduction? Do they copulate? Are there animals in the population of *C. mitis* and *C. pygerythrus* at both Diani and Ngong Forest that appear to be backcrosses?
4. Undertake surveys to determine if there are other *C. mitis* × *C. pygerythrus* hybrids in Kenya (or anywhere else). If so, what are the circumstances under which hybridization has occurred?
5. How does the behavior and ecology of these three hybrids differ from that of the parental species? How does their diet differ from that of *C. mitis* and *C. pygerythrus* at the same site? Is there evidence that the behavior and ecology of these hybrids make them better adapted than either of the parental species to exploiting the resources of the 'forest-woodland ecotone habitat'? Does hybridization expand the 'food niche' beyond that of the parental species?

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