International Journal of Primatology, Vol. 26, No. 3, June 2005 (© 2005)
DOI: 10.1007/s10764-005-4372-0

Conservation Implications of Hybridization in African Cercopithecine Monkeys

Kate M. Detwiler,[1,2] **Andrew S. Burrell,**[1] **and Clifford J. Jolly**[1]

Received August 21, 2003; revision January 29, 2004; accepted February 29, 2004

Numerous field reports of hybrid monkeys and documented cases of persistent hybrid zones suggest that natural hybridization is common among African cercopithecines. Both theoretical considerations and a review of cases lead us to conclude that parapatric hybridization among closely related allotaxa is a widespread, usually natural process whose incidence may be modified by human influence. Sympatric hybridization, between species ecologically distinct enough to have overlapping ranges, is rarer, and in monkeys tends to occur in settings where natural or anthropogenic habitat edges restrict migration and hence access to unrelated conspecific mates. Although sympatric hybridization occurs in the absence of human disturbance, and may even have been a creative force in cercopithecine evolution, anthropogenic habitat fragmentation may increase its incidence. Hybridization with a more abundant form may increase the level of threat faced by a species whose numbers and range have been severely restricted, either naturally or artificially.

KEY WORDS: natural hybridization; natural hybrids; *Papio; Cercopithecus*; primate conservation.

INTRODUCTION

Hybridization, in the context of evolutionary theory, is defined as the interbreeding of members of genetically differentiated populations (Barton and Hewitt, 1985; Rhymer and Simberloff, 1996). Cercopithecine monkeys

---

[1] Department of Anthropology, New York University and New York Consortium in Evolutionary Primatology (NYCEP).
[2] To whom correspondence should be addressed at Department of Anthropology, New York University, 25 Waverly Place, New York, NY 10003; e-mail: kmd231@nyu.edu.

comprise a relatively recent adaptive radiation, and many taxa retain the ability to interbreed (Jolly, 2001). As in many extant taxa, 2 modes of natural hybridization can be distinguished. The more frequent parapatric hybridization (*sensu* Woodruff, 1973) involves natural hybridization at interfaces between differentiated, parapatric populations assigned to the same, or very closely related, species (allotaxa; Grubb, 1999). It typically occurs at an ecotone, or at the headwaters of a river basin (Colyn and Deleporte, 2002; Groves, 1993), and often generates a narrow hybrid zone that can be relatively stable through time. In most cases, the patchwork distribution of allotaxa that are physically distinct but not reproductively isolated can be attributed to a history of repeated contractions and expansions of geographical range, with subpopulations becoming isolated, differentiating, and then meeting again and secondarily hybridizing at their margins (Hewitt, 2001). A second, rarer, mode of natural hybridization occurs between ecologically distinct species with broadly overlapping ranges: sympatric hybridization (*sensu* Woodruff, 1973). In monkeys it is usually sporadic and ephemeral, and often occurs under unusual environmental circumstances.

Writers of the New Synthesis era tended to regard hybridization, especially between entities regarded as good species, as counter-adaptive, ephemeral, and of evolutionary importance mainly as a context in which interspecific reproductive barriers were reinforced. Recently however, biological, especially zoological, thinking has shifted towards an attitude that has always been more prevalent among botanists, namely, that natural hybridization probably has played a significant role as a creative evolutionary force (Arnold, 1997; Barton, 2001; Dowling and Secor, 1997). Viable and fertile hybrid progeny that mate among themselves and backcross with one or both parental taxa may serve as conduits for gene exchange among existing lineages, and may even lead to the formation of new, recombinant taxa (Barton, 2001; Grant and Grant, 1998). The development of molecular markers has greatly increased our awareness of hybridization by documenting cryptic introgression in many plant and animal taxa that show little morphological evidence of such a history. Stray foreign alleles may be the only evidence of the spread of one species at the expense of another, with minimal hybridization (Arntzen and Wallis, 1991); leakage of neutral alleles from one sympatric species to another may document hybridization that is not apparent in characters constrained by selection (Clarke *et al.*, 1998). In many cases, mitochondrial or sex-chromosomal markers document sex-specific introgression (Goodman *et al.*, 1999; Lehman *et al.*, 1991) that may be extensive enough to produce complete fixation of a foreign marker in an otherwise unremarkable population of the host species (Tosi *et al.*, 2002). The notion that hybridization can give rise to new species has long been accepted by botanists (Rieseberg, 1997), but apparent cases in biparental vertebrates are also documented (Salzburger *et al.*, 2002). In light of such cases, conservationists increasingly recognize that taxa resulting from introgression and hybridization can be considered natural products of evolution (Dowling and Secor, 1997; Arnold, 1997; Grant and Grant, 1992) and, when setting conservation policy, should be valued as highly as populations that are (supposedly) genetically pure (Allendorf *et al.*, 2001; Federal Register, 1996).

Conversely, the preservation of hybrids and hybrid zones may in some circumstances conflict with the primary conservation goal of ensuring the survival of endangered taxa. Hybridization can result in loss of a distinctive but rare and local taxon by genetic swamping from a more abundant neighbor, and the dismantling of co-adapted gene complexes, leading to outbreeding depression (Allendorf *et al.*, 2001; Arnold, 1997; Avise, 1994; Rhymer and Simberloff, 1996). Hybridization can threaten the existence of a rare taxon, even if its genome survives piecemeal, dispersed among its hybrid offspring. It has long been recognized that anthropogenic factors, such as local and regional habitat modification, can increase the incidence of hybridization (Rhymer and Simberloff, 1996). A distinction is thus drawn by some conservationists between natural hybridization, which can be tolerated or even preserved, and anthropogenic hybridization, which is regarded as undesirable and something to be eliminated if possible. The task then is to determine whether a particular case of hybridization is natural or anthropogenic (Allendorf *et al.*, 2001), which can be problematic.

The need to determine the implications of hybridization for the conservation of African cercopithecines is made all the more urgent by the rapid, anthropogenic habitat modification currently occurring in Africa. To address this question, we review reported cases of hybridization in African cercopithecines and then examine the potential causal factors and evolutionary consequences of their hybridization. An understanding of the likely factors that contribute to hybridization, and its possible outcomes, provides a baseline for exploring the relevance of hybridization to the conservation of African monkeys.

CASE STUDIES

Table I is a list of all records of hybridization among wild African cercopithecines known to us from the literature, personal observation, or personal communication with the observer. In all cases, hybrid individuals were identified by external phenotype, usually pelage, on the assumption that an individual with a phenotype intermediate between those of sympatric or parapatric taxa, occurring in the zone where they meet or overlap, is likely to be a hybrid. Following current hybrid zone theorists, we define an animal

Table I. Reports of natural hybridization in African cercopithecines

T	Hybridizing taxa	Location	Coordinates	Prot. Area	Dates Obs	Notes	Reference
P	*Cercocebus atys atys* × *C. a. lunulatus*	b/w Nzo and Sassandra Rs, Cote d'Ivoire	07-00N, 07-00W				19
P	*Lophocebus albigena osmani* × *L. a. albigena*	Dja Reserve, Cameroon	03-08N, 13-07E	Dja Reserve			17
P	*Cercopithecus ascanius ascanius* × *C. a. atrinasus*	S and E of the Wamba R headwaters, Angola	09-00S, 18-00E			multiple hybrids	17, 20, 24, 26
P	*Cercopithecus a. katangae* × *C. a. atrinasus*	near Cuilo R, Angola	08-00S, 19-40E			multiple hybrids	20, 26
P	*Cercopithecus a. ascanius* × *C. a. katangae*	north-central Angola	08-00S, 18-30E			1 hybrid	24, 25, 26
P	*Cercopithecus a. katangae* × *C. a. whitesidei*	b/w the Sankuru and Lomami Rs, DRC	05-00S, 24-00E				17
P	*Cercopithecus aethiops tantalus* × *C. a. pygerythrus*	from E DRC through SW Uganda to L. Victoria	00-00S, 30-00E		1950s	hybrid zone	12, 20, 24
P	*Cercopithecus a. aethiops* × *C. a. pygerythrus*	western shores of Lake Abaya, Ethiopia	06-00S, 38-00E		1968	multiple hybrids	13, 20, 24
P	*Cercopithecus a. aethiops/tantalus* × *C. a. pygerythrus*	SW Uganda to western Ethiopia	large region		1970s-present	zone of intergradation	23, 30
P	*Cercopithecus campbelli campbelli* × *C. c. lowei*	b/w Nzo/Sassandra and Cavally Rs, Cote d'Ivoire	05-30N, 07-00W	Tai NP	early 1950s	multiple hybrids	4, 7, 31
P	*Cercopithecus mitis albogularis* × *C. m. stuhlmanni*	Ngorongoro and Lake Manyara, Tanzania	03-30S, 36-00E	L Manyara NP	1968-present	persistent hybrid zone	6, 20
P	*Cercopithecus m. kolbi* × *C. m. stuhlmanni*	southwest of L. Naivasha, Kenya	01-00S, 36-30E				22
P	*Cercopithecus m. kandti* × *C. m. doggetti*	Mgahinga Gorilla NP, Uganda	01-23S, 29-35E	Mgahinga NP			22, 41
P	*Cercopithecus petaurista petaurista* × *C. p. buettikoferi*	b/w Nzo/Sassandra and Cavally Rs, Cote d'Ivoire	06-30N, 07-33W	Tai NP, Sapo NP	1956	1 hybrid	5, 20, 31

P	*Cercopithecus pogonias pogonias* × *C. p. grayi/nigripes*	b/w Sanaga R& Ogoue R, Atlantic to Congo/Gabon border	large region	Dja Reserve		zone of intergradation	11, 17
P	*Cercopithecus sclateri* × *C. erythrogaster pococki*	lower course of the Niger R, Nigeria	04-59N, 06-23E		present	1 wild born captive hybrid	3, 39
P	*Cercopithecus erythrotis camerunensis* × *C. cephus cephus*	left bank of Sanaga R below Edea, Cameroon	03-34N, 09-53E		1968	7 hybrids	11, 16, 17, 37
P	*Papio hamadryas* × *P. anubis*	near Seru, Wabi-Shebeli R, Ethiopia	07-45N, 40-16E		1989	2 hybrid troops	28
P	*Papio hamadryas* × *P. anubis*	near Chisa, Wabi-Shebeli R, Ethiopia	07-25N, 39-15E		1989	hybrid zone	28
P	*Papio hamadryas* × *P. anubis*	Awash R, b/w Metahara and Awash, Ethiopia	08-51N, 40-00E	Awash NP	1960s-present	persistent hybrid zone	8, 29, 33, 34
P	*Papio hamadryas* × *P. anubis*	east and northeast of Barentu, Eritrea	15-08N, 38-00E		1997-present	persistent hybrid zone	42
P	*Papio anubis* × *P. cynocephalus*	area of Ithumba, Kiboko, and Simba, Kenya	02-10S, 37-36E			hybrid troop	27
P	*Papio anubis* × *P. cynocephalus*	Kora NP, Kenya	00-20S, 38-30E	Kora NP	1970s	hybrid zone	10
P	*Papio anubis* × *P. cynocephalus*	near Amboseli NP, Kenya/Tanzania border	02-44S, 36-58E	nr Amboseli NP	1980s-present	persistent hybrid zone	1, 35
S	*Cercopithecus mona* × *C. pogonias pogonias*	Indenau, Cameroon	04-15N, 09-00E		1967, 1968	2 hybrids	16, 37
S	*Cercopithecus mona* × *C. pogonias grayi*	Tinaso, Cameroon	03-37N, 09-57E		1968	1 hybrid	16, 37
S	*Cercopithecus ascanius schmidti* × *C. mitis stuhlmanni*	Budongo FR, Uganda	02-00N, 31-00E	Budongo FR	1968	2 hybrids	2
S	*Cercopithecus a. schmidti* × *C. m. stuhlmanni*	Ngogo, Kibale NP, Uganda	00-27N, 30-25E	Kibale NP	1975-1986	9 hybrids	38
S	*Cercopithecus a. schmidti* × *C. m. stuhlmanni*	Kanyawara, Kibale NP, Uganda	00-27N, 30-25E	Kibale NP	1983	1 hybrid	38

Table I. Continued

T	Hybridizing taxa	Location	Coordinates	Prot. Area	Dates Obs	Notes	Reference
S	*Cercopithecus a. schmidti* × *C. m. stuhlmanni*	Itwara FR, Uganda	01-00N, 30-30E	Itwara FR	1971	2-3 hybrids	32
S	*Cercopithecus a. schmidti* × *C. mitis doggetti*	Gombe NP, Tanzania	04-40S, 29-38E	Gombe NP	1960-present	persistent hybrid zone	9, 14, 18, 36
S	*Cercopithecus cephus cephodes* × *C. nictitans nictitans*	Lopé Reserve, Gabon	00-00S, 11-30E	Lopé Reserve	c. 1993-1995	1 hybrid	40
S	*Cercopithecus mitis doggetti* × *C. wolfi denti*	Nyungwe NP, Rwanda	02-35S, 29-17E	Nyungwe NP	1990-1992	2 hybrids	21
S	*Theropithecus gelada* × *P. anubis*	Bole valley, Ethiopia	10-00N, 38-00E		early 1970s	3 hybrids	15

Note. T = type of hybridization: P = parapatric, S = sympatric. (1) Alberts and Altmann, 2001; (2) Aldrich-Blake, 1968; (3) Baker and Tooze, 2003; (4) Booth, 1955; (5) 1956; (6)1968; (7) Bourlière *et al.*, 1970; (8) Brett *et al.*, 1977; (9) Clutton-Brock, 1972; (10) Coe, 1985; (11) Colyn and Deleporte, 2002; (12) Dandelot, 1959; (13) Dandelot and Prevost, 1972; (14) Detwiler, 2002; (15) Dunbar and Dunbar, 1974; (16) Gartlan and Struhsaker, 1972; (17) Gautier-Hion *et al.*, 1999; (18) Goodall, 1986; (19) Groves, 1978; (20) 2001; (21) Kaplin, pers. com.; (22) Kingdon, 1971; (23) 1997; (24) Lernould, 1988; (25) Machado, 1965; (26) 1969; (27) Maples and McKern, 1967; (28) Mori and Belay, 1990; (29) Nagel, 1973; (30) Napier, 1981; (31) Oates, 1988; (32) pers. com.; (33) Phillips-Conroy and Jolly, 1986; (34) Phillips-Conroy *et al.*, 1991; (35) Samuels and Altmann, 1986; (36) Stanford, 1998; (37) Struhsaker, 1970; (38) Struhsaker *et al.*, 1988; (39) Tooze, pers. com.; (40) Tutin, 1999; (41) Twinomugisha *et al.*, 2003; (42) Zinner *et al.*, 2003.

of mixed ancestry as a hybrid, regardless of the conventional taxonomic status of the parental populations. This usage recognizes that the specific level is necessarily an arbitrarily privileged (and not always consistently defined) point on a continuum of probabilities of interpopulational gene-flow (zygostructure) and physical distinctiveness (phenostructure) (Jolly, 1993). In Table I, for ease of reference, we follow a recent review of the taxonomy of the group (Grubb *et al.*, 2003).

Hybridization among African cercopithecines occurs across a wide spectrum of conventionally recognized taxonomic levels (Table I). It is relatively common among differentiated, parapatric populations assigned to the same, or closely related, species, and in many of these cases persistent hybrid zones have formed in the contact areas. By contrast, hybridization is less common between sympatric, ecologically differentiated species, and where it occurs, sympatric hybridization apparently rarely leads to the formation of a persistent hybrid zone. We found only one example of long-term, extensive hybridization between sympatric species: the guenon hybrid zone at Gombe National Park, Tanzania. Hybridization in the wild between species allocated to different genera, if it occurs at all, is even rarer, but Dunbar and Dunbar (1974) reported 3 suspected hybrids between *Theropithecus gelada* and *Papio anubis* among a gelada group in the Bole Valley, Ethiopia.

The data in Table I have gaps and deficiencies. Field sightings and museum collections of hybrids are not always reported or are briefly mentioned in papers dedicated to other topics. Descriptions of hybrids are often vague and lack detailed information regarding the location, date, and ecological context of the hybrid sighting or collection. The most completely documented cases concern baboons (*Papio*) and guenons (*Cercopithecus*), and we review some of them in more detail as model cases from which to discuss the causes, evolutionary consequences, and conservation implications of hybridization among African cercopithecines.

Parapatric Hybridization in Baboons

Common baboons (*Papio* spp.) consist of phenotypically distinct, nonoverlapping, parapatric populations, or allotaxa (*sensu* Grubb, 1999). Hybrid zones recorded in the literature are all in eastern Africa (Table I; Fig. 1), though anecdotal and unpublished evidence suggest that hybridization occurs wherever baboon allotaxa meet in the wild. Wherever detailed surveys of the border have been made, anubis x yellow (Coe, 1985; Maples and McKern, 1967; Samuels and Altmann, 1986) or anubis × hamadryas (Mori and Belay, 1990; Nagel, 1973; Zinner *et al.*, 2004) hybrids have been found.

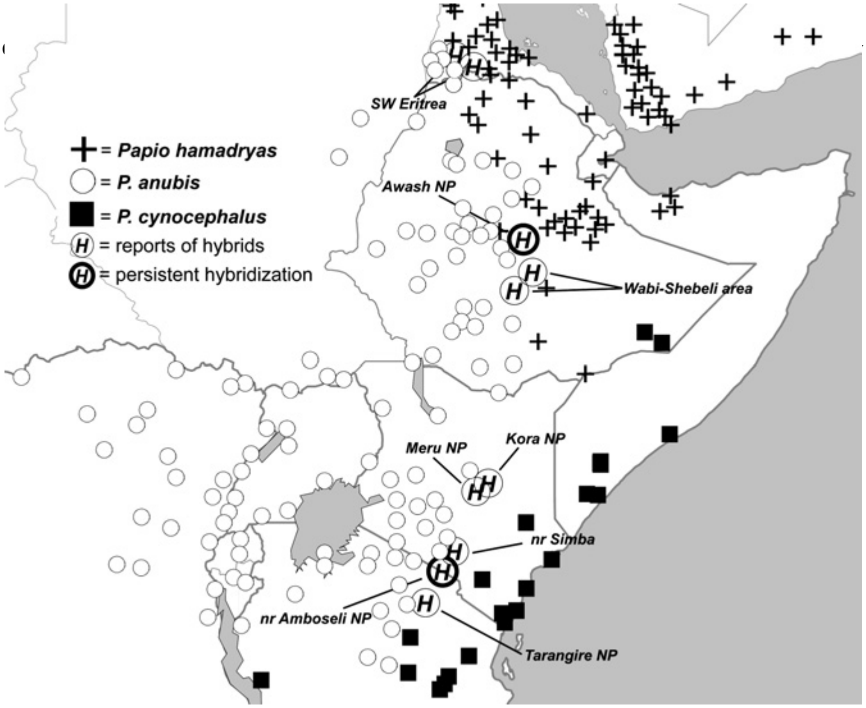

Fig. 1. An example of parapatric hybridization. Distributions of *Papio hamadryas*, *P. anubis*, *P. cynocephalus* in East Africa (Jolly and Burrell, in prep; Napier, 1981; Zinner *et al.*, 2003), showing areas where researchers have detected hybrid individuals (Table I).

From one border area—around the Awash National Park in Ethiopia—we have the most information about the dynamics of hybridization between 2 closely related primate allotaxa. The site is at the apex of a salient gallery forest along the Awash River that juts out into the thornscrub and semidesert environment inhabited by hamadryas baboons. At the tip of the salient, groups made of anubis in the east are replaced in a clinal fashion by a series of groups composed of individuals with increasingly hamadryas-like phenotypes. The sharply defined intertaxonal border, and narrow hybrid zone suggests that it is the result of secondary contact, rather than selection *in situ* for specific environments. The zone's existence has been documented for nearly 50 years, but its actual age is unknown.

Nagel (1973) has argued that the location of the hybrid zone is the result of behavioral adaptations in hamadryas baboons for exploiting dry thornscrub and semidesert environments. The hybrid zone is associated with 2 ecological phenomena: it lies within a steep ecological gradient between moister, midaltitude savanna and drier, lowland thornscrub, and occurs close to the location where the Awash River flows into a narrow gorge that severely constricts the gallery forest. Anubis baboons, which generally forage as coherent groups, make extensive use of the larger food-patches afforded by gallery forest trees, and may be less able to compete with hamadryas baboons in drier areas where resources are distributed in smaller, highly dispersed clumps. Ecological factors may determine the general area of contact between hamadryas and anubis baboons, but the exact position, size, and structure of the hybrid zone are more likely determined by complex interactions between climate, geography, and the behavioral ecology of the 2 forms (Phillips-Conroy and Jolly, 1986).

Hybridization is dependent, of course, upon the ability of heterospecifics to meet and to recognize each other as potential mates. Data from the Awash hybrid zone suggest that contact between male and female heterospecifics occurs in several different contexts, including the abduction of female anubis baboons by male hamadryas and their incorporation into hamadryas groups (Nagel, 1973); the fusion of anubis and hamadryas groups (Beyene, 1998; Newman, 1997), and, most importantly, the dispersal of anubis and hamadryas males into neighboring hybrid or heterospecific groups (Newman, 1997; Phillips-Conroy *et al.*, 1991; Woolley-Barker, 1999). Almost all baboons in the zone are hybrids of one degree or another.

The structure of the Awash hybrid zone and its location in an area of low ecological productivity and population density, suggest that it may be a tension zone (Barton and Hewitt, 1985), an area of hybridization confined in width by the conflicting effects of immigration from neighboring parental populations and selection against hybrids. It is not obvious, however, that hybrids in Awash are relatively unfit in the zone itself. There is no evidence for assortative mating (Phillips-Conroy *et al.*, 1991) or of lowered fertility or survivorship among hybrids (Bergman, 2000). If gene-flow out of the hybrid zone is restricted by intrinsic factors, the cause is likely to be difficulties experienced by hybrids in dispersing into, and breeding in, social groups of the parental species bordering the zone.

Hybridization has resulted in limited gene flow that extends well beyond the zone inhabited by obvious hybrids. Individuals showing some subtle phenotypic evidence of hybridization occur at least $\geq$40 km away from the center of the hybrid zone (Phillips-Conroy and Jolly, 1986). Genetic surveys of the area have shown different levels of introgression among several genetic systems. Mitochondrial haplotypes form a very steep cline across the hybrid zone (Newman, 1997). Nuclear genes form a series of less-steep clines across the hybrid zone, though some heterospecific microsatellite and allozyme alleles occur well outside the apparent hybrid zone (Shotake, 1982; Woolley-Barker, 1999).

Documented hybrid zones occur along the extensive contact between anubis (*Papio anubis*) and yellow baboons (*P. cynocephalus*) running from western Tanzania through to central Kenya (Fig. 1). As at Awash, hybridization is presumably the result of secondary contact between populations that differentiated in isolation some time during the Pleistocene. Hybrids were first reported near Simba Springs (Maples and McKern, 1967), and have since been documented at several other localities (Jolly and Burrell, in prep.). Yellow baboons with wavy rather than straight pelage—"ibean yellow baboons"—occur from northern Tanzania to Somalia, having perhaps acquired this trait by ancient gene flow from an anubis or anubis-like population.

Alberts and Altmann (2001) document recent changes in the hybrid zone, in and around Amboseli NP. The number of hybrid individuals in their study population has increased substantially over the past 2 decades, perhaps because intensification of cultivation on Kilimanjaro has displaced resident anubis baboons into yellow baboon range. Thus, while yellow-anubis hybridization in general is presumably natural, its occurrence in Amboseli may be at least in part anthropogenic.

Sympatric Hybridization in Guenons

Nineteen of the 23 guenon species (Cercopithecini) are members of the genus *Cercopithecus* (Butynski, 2002), of which all but one are rain forest specialists. Current taxonomy has *Cercopithecus* spp. into 9 species-groups (Butynski, 2002). Members of different species-groups often have broadly overlapping distributions, while those of the same species-group behave as allotaxa, with geographically distinct, non-overlapping, parapatric or allopatric distributions. In the one known exception, *Cercopithecus mona* overlaps with other members of the *mona* species-group: *C. pogonias* in Cameroon, and *C. campbelli* in a small area in Ghana (Oates, 1988). As with baboons, natural, parapatric hybridization occurs between many guenon allotaxa where their ranges meet (Table I). The genus also includes a few documented cases of sympatric hybridization between members of different species-groups. These cases suggest the circumstances that give rise to this rare but potentially important phenomenon.

Guenons are well known (Gautier-Hion, 1988) for forming frequent and persistent mixed-species associations, within which the species (almost always members of different species-groups) are easily distinguished by color and pattern of the face and body pelage, and male vocalizations. These distinctive features have been suggested to function in mate recognition, and thus to act as prezygotic isolating mechanisms defending the gene pool of each species (Gautier, 1988; Kingdon, 1980, 1988; Struhsaker, 1970). However, aside from theoretical questions about the validity of the concept of prezygotic isolating mechanisms (Paterson, 1985), it is clear that there are rare circumstances under which prezygotic barriers can be overcome (Table I).

Sympatric hybridization among biparental vertebrates, including primates (Bernstein, 1966; Struhsaker *et al.*, 1988), canids (Lehman *et al.*, 1991) and birds (Randler, 2002) often occurs in the context of local scarcity of conspecific mates for one or both species. This can occur in a variety of situations, including on the edge of a species' range, in a fragmented habitat, or where a species is relatively rare because of interspecific competition, poor habitat quality, a recent disease episode, or predation.

In guenons, males are the dispersing sex, and solitary males, or small all-male groups, are a natural component of populations (Cords, 2000). In an isolated, low density or peripheral population, an emigrant male will find few conspecific mates, and might therefore try to mate with any heterospecific females with which he shared enough of his mate recognition system. Likewise, females may seek, or at least tolerate, copulations with heterospecifics when few or no conspecific mates are available. As the following cases illustrate, such conditions can often be identified at sites where sympatric hybridization is occurring between guenon species that rarely or never interbreed elsewhere in their extensively overlapping distributions.

Cercopithecus cephus × *C. nictitans: Lopé Reserve, Gabon*

A recent study of guenons in the Lopé Reserve, Gabon (Tutin, 1999) exemplifies interspecific hybridization between sympatric guenons in a naturally fragmented habitat. In the northern part of the reserve, continuous rain forest gives way to a savanna zone with many natural forest fragments, including narrow riverine strips, forest corridors and small isolates completely surrounded by grassland (Tutin *et al.*, 1997). *Cercopithecus nictitans* and *C. cephus* co-occur in the continuous rain forest, and both are also permanent residents of some forest fragments as small as 5 ha (Tutin, 1999). No interspecific mating or obvious hybrid individuals have been reported from the main forest block. Both cross-specific mating and hybrid offspring occur in the forest fragments.

In one case (Tutin, 1999) a 9-ha forest block, isolated from the main forest by 100–200 m of grassland, was originally inhabited by one-male groups of *ca.* 13 *Cercopithecus cephus* and *ca.* 10 *Cercopithecus nictitans*. When the group of *Cercopithecus nictitans* vacated the fragment, a subadult male remained behind as a fully integrated member of the group of *C. cephus*. On $\geq$11 occasions, $\geq$3 different female *Cercopithecus cephus* (2 adults and 1 adolescent) presented to and copulated with him. Other adult or adolescent male *Cercopithecus nictitans* visited the fragment for short periods, but rarely approached, and never interacted with, members of the resident group *C. cephus*. Tutin (1999) suggested that such visitors may have been using the forest fragment to avoid encounters with conspecifics, before returning to the main forest and attempting to join or to form a mating group. No male *Cercopithecus cephus* visited the fragment.

No hybrid offspring was apparent, perhaps because the male *Cercopithecus nictitans* was immature (Tutin, pers. com.). However, in a second forest fragment, a phenotypically intermediate, presumably hybrid, individual was in a group of *Cercopithecus cephus*, suggesting that it resulted from a mating between a male *C. nictitans* and a female *C. cephus* (Tutin, 1999; pers. com.). These observations imply that mating between *Cercopithecus cephus* and *C. nictitans* is generally avoided by both sexes of both species, but becomes an option when prospects for conspecific mating are limited (Tutin, 1999).

Such mating may carry a fitness penalty in the form of infertility of male offspring. A 4-ha, naturally forested enclosure at the CIRMF Primate Research Center in Gabon originally housed males and females of both *Cercopithecus cephus* and *C. nictitans*. Four (1 male, 3 female) hybrids currently (mid-2003) survive. At least one F1 female hybrid produced viable offspring, but no female hybrid has given birth since the loss of the adult male *Cercopithecus nictitans*, suggesting that the remaining male hybrid may be sterile (J. Wickings, pers. com.).

Cercopithecus mitis × *C. ascanius: Kibale and Budongo Forests, Uganda*

Most reported cases of sympatric hybridization in guenons involve *Cercopithecus mitis* and *C. ascanius* in East Africa (Table I; Fig. 2). Despite the multiple reports, hybridization between these species at most sites is rare and sporadic, with phenotypically recognizable hybrids disappearing within a generation or 2 (Aldrich-Blake, 1968, 1970; Detwiler, 2002; Struhsaker *et al.*, 1988). Two case studies provide clues to local conditions favoring sporadic hybridization.

In the Budongo Forest Reserve, Uganda, Aldrich-Blake (1968, 1970) observed a female hybrid and her infant living in a group of *Cercopithecus mitis*. He suggested that the mother was the F1 offspring of a cross between a female *Cercopithecus mitis* and a male *C. ascanius*, and that the infant resulted from a back-cross to a male *C. mitis*. Population densities of the 2 species were high, stable, and approximately equal in this part of the forest (*C. ascanius* 71.4 ind/km^2; *C. mitis* 86.9 ind/km^2; Suzuki, 1979; Plumptre and Reynolds, 1994). However, local features (open grasslands and a road) might have restricted contact between the affected group of *Cercopithecus mitis* and its neighbors, limiting conspecific mating opportunities for resident females, while co-resident male *C. ascanius* provided a source of potential heterospecific mates. Continued research on

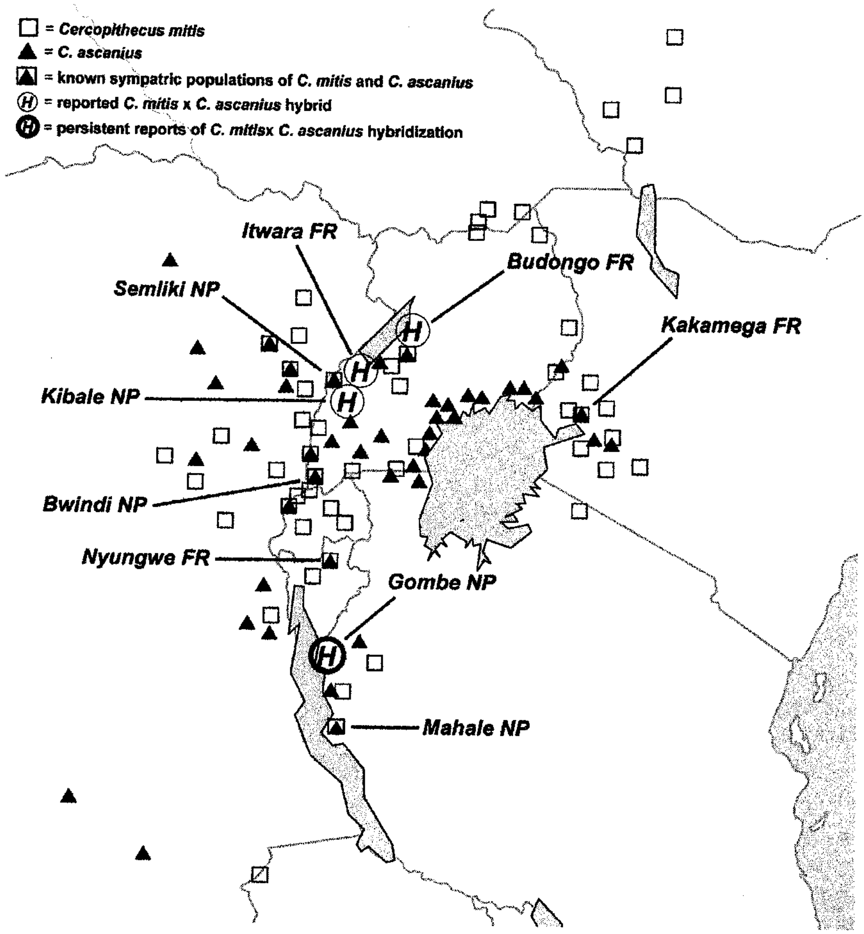

Fig. 2. An example of sympatric hybridization. Distributions of *Cercopithecus mitis* and *C. ascanius* in East Africa (Kingdon, 1971; Napier, 1981; Rahm, 1970), showing areas where researchers have detected hybrid individuals (Table I).

populations of *Cercopithecus mitis* and *C. ascanius* (Fairgrieve and Muhumuza, 2003; Plumptre, 2000; Sheppard, 2000; Tweheyo and Obua, 2001) has documented no further hybridization in Budongo.

In Kibale National Park, Uganda, Struhsaker and colleagues (1988) observed 2 female and 1 male, presumably F1, *mitis-ascanius* hybrids, and their offspring, over several years at the Ngogo study area. When first observed, all F1s were subadults and lived in different social groups of *Cercopithecus ascanius*, suggesting that they resulted from the cross between male *C. mitis* and female *C. ascanius*. The male hybrid successfully emigrated from his natal group into a neighboring group of *Cercopithecus ascanius* and mated with adult female *C. ascanius*, but no hybrid offspring appeared. By contrast, both females bred successfully and reared viable infants to maturity in their respective, natal, social groups of *Cercopithecus ascanius*. All 4 offspring of one female were *Cercopithecus ascanius*-like and presumably fathered by male *C. ascanius*. The other female's 3 offspring were all *mitis*-like and presumably fathered by an immigrant *Cercopithecus mitis*, who mated exclusively with her over his 6-yr residence.

The population of *Cercopithecus mitis* were 10–20 times less dense than *C. ascanius* in the Ngogo study area (Struhsaker *et al.*, 1988), and included a high proportion of solitary males (Butynski, 1990). The one resident group of *Cercopithecus mitis* experienced short male tenures and several cases of infanticide at turnover, suggesting intense male-male competition for conspecific mating opportunities, which perhaps made heterospecific mating a more attractive option (Struhsaker *et al.*, 1988). Nevertheless, as at Budongo, hybridization apparently died out at Ngogo (Detwiler, 2002; T. Windfelder, pers. com.), though *Cercopithecus mitis* continued to be rare there and elsewhere in the central-southern region of Kibale (Chapman and Chapman, 2000).

Cercopithecus mitis × *C. wolfi: Nyungwe Forest National Park, Rwanda*

B. A. Kaplin (pers. com.) observed hybrids between *Cercopithecus mitis doggetti* and *C. wolfi denti* in the Nyungwe Forest, a montane forest ranging in elevation between *ca.* 1600 m and 3000 m. *Cercopithecus m. doggetti* is a montane form of the *mitis-nictitans* species-group, and is one of the most common primate species in the Nyungwe Forest (Plumptre *et al.*, 2002). *Cercopithecus wolfi denti* is a Congo basin representative of the *mona* species-group, with a range extending marginally into Uganda and Rwanda (Kaplin, 1998 and pers. com.; Kingdon, 1971; Rahm, 1970). At Nyungwe, it occurs in low density (Plumptre *et al.*, 2002) and at lower elevations (Kaplin pers. com.). From 1990–1992, at *ca.* 2500 m elevation, Kaplin and colleagues frequently observed a group of *Cercopithecus m. doggetti* that included an adult *C. w. denti* and an immature monkey identified as a hybrid between them. They observed a second *mitis-wolfi* hybrid in a different group of *Cercopithecus m. doggetti* at *ca.* 1700 m elevation.

Kaplin's observations document an example of sympatric hybridization at the very edge of a species' range. The population of *Cercopithecus w. denti* at Nyungwe is marginal, both geographically and in terms of elevation. A male emigrating from its natal group is likely to find few conspecific groups to enter, and thus may attempt to join a breeding group of the more abundant species, *Cercopithecus m. doggetti.* Kaplin's observations support this explanation, because both hybrid individuals, presumably F1s, lived in social groups of *Cercopithecus m. doggetti* suggesting that they were the result of cross-mating between resident female *C. m. doggetti* and immigrant male *C. w. denti.*

Cercopithecus mitis × *C. ascanius: Gombe National Park, Tanzania*

Unlike the cases described, hybridization between *Cercopithecus mitis* and *C. ascanius* in Gombe National Park is much more frequent and persistent. Hybrids have been reported, and have probably been continuously present, for >30 yr. In 1969–70, Clutton-Brock (1972) noted ≥1 phenotypic hybrid in the majority of groups of *C. ascanius* visiting his study area, but none in groups of *C. mitis. Cercopithecus ascanius* were 6 times more common than *C. mitis* there (Clutton-Brock, 1972). These observations suggest that the initial heterospecific matings occurred in groups of *Cercopithecus ascanius* between resident females and immigrant male *C. mitis*. However, the wide variety of hybrid phenotypes, suggests that the initial hybridization occurred well before 1969, and by that time hybrids had themselves crossed successfully with both parental species, and possibly with other hybrids. Twenty years later (1991–95), Stanford (1998) observed hybrids in nearly every group of *Cercopithecus ascanius* that he encountered in an area that overlapped with Clutton-Brock's study site, and where population densities of *C. mitis* and *C. ascanius* were *ca.* 8 and 34 ind/km^2, respectively.

In 1996, Detwiler (2002) found both parental species and hybrids in all valleys in the northern two-thirds of the park. At least 44 hybrids of various age-sex classes and phenotypes (intermediate, *mitis*-like, and *ascanius*-like), occurred in apparently unmixed groups of *Cercopithecus ascanius* and *C. mitis*, in mixed-species groups, and in groups with predominantly hybrid membership. Of 10 complete copulations, only 5 were between conspecifics; one was between heterospecifics, and the other 4 involved ≥1 hybrid. The presence of female hybrids with suckling infants directly documented their fertility.

Gombe clearly differs from the other sites of sympatric hybridization in guenons in that hybrids comprise a large and perennial part of the breeding population. A high rate of primary hybridization might have arisen initially from the unusual topography of Gombe, which accentuates the edge effects and fragmentation associated with hybridization at other sites. At Gombe, steep slopes restrict much of the guenon habitat to narrow, blind-ended valleys separated by open grassland. Because guenon social groups in this environment have few conspecific neighbors, stochastic factors alone will frequently generate the local sex-ratio biases and shortages of conspecific mates that, as at other sites, are conducive to primary hybridization and production of F1s (Detwiler, 2002). The abundance and visible mating success of hybrids at Gombe suggests a further, intriguing possibility: that behavioral inhibitions to mating with individuals of atypical or heterospecific phenotype may have weakened, as the behavior, and perhaps even the gene-pools, of the guenons have evolved in response to the high frequency of primary hybridization and to the prevalence of hybrid individuals as available mates (Detwiler, 2002). The forest guenons of Gombe currently occupy an ecological island surrounded by cultivation (Pintea *et al.*, 2002), which will presumably tend to enhance the homogenization of the Gombe guenons and their divergence from other *Cercopithecus mitis* and *C. ascanius*, by preventing immigration from nonhybridizing populations (Detwiler, 2002). The unusually high levels of primary hybridization that may have set this feedback cycle occurred while Gombe was still part of a widespread forest-mosaic ecosystem with little obvious anthropogenic modification.

DISCUSSION

Any discussion of the conservation implications of hybridization in African monkeys, especially forest species, must be set against the backdrop of the current ecological disaster. Whatever the hazard posed by hybridization, it is minimal compared to the current threat of logging, hunting, and the displacement of primate habitats by hostile, anthropogenic environments (Oates, 1996, 1999). For many species, habitats that are clearly modified by human activities and populations that may be considered genetically suboptimal may be all that is left to conserve. It would be perverse in the extreme to withhold conservation effort from a relatively flourishing primate population with good prospects for survival, on the grounds that its ancestry might be mixed, and its present gene-pool influenced by anthropogenic hybridization. In fact, if scientific interest is weighed along with the usual concerns of conservation, then ecosystems containing hybrids, whether of natural or anthropogenic origin, would merit high priority as natural laboratories of speciation.

Hybridization is Both Natural and Anthropogenic

Hybridization between marginal populations of physically distinct allotaxa, exemplified by the baboons, is widespread among primates, as in other taxa (Table I). The baboons and savanna monkeys of the vervet-grivet group also exemplify the somewhat ambiguous taxonomic status of many of the hybridizing allotaxa. According to an author's concept of a species, they might be classified as subspecies (or other divisions of a species), as semispecies of a superspecies, or as full species. Grubb *et al.* (2003) concluded that all members of the vervet-grivet group should be allocated to a single species (*Cercopithecus aethiops*), while *Papio* baboons, which have very comparable phenostructure and zygostructure (*sensu* Jolly, 1993) comprise 5 full species. Such cases emphasize the natural continuity between infra- and interspecific variation, 2003), and hence the fallacy of making the nominal specific level a critical foundation of conservation policy.

The range expansions and contractions that generate allotaxa have been frequent, rapid, and extensive, especially in the past 2 million years, driven by climatic cycles related to the alternation of glacial and interglacial conditions (Hewitt, 1996, 2001). Therefore, it is clear that parapatric hybridization as a phenomenon (like the extinction of some allotaxa) would have occurred frequently in African cercopithecines, even in the absence of human activity. In baboons, as in macaques (Tosi *et al.*, 2003) genetic evidence is beginning to document a complex history of introgression and gene-pool fusion among allotaxa that long antedates the introduction of domesticated species and extensive anthropogenic modification of the habitat.

To recognize that parapatric hybridization is a common and natural phenomenon is not to minimize the fact that recent human activities have undoubtedly influenced its occurrence. An example is the hybridization (Dandelot, 1959) between 2 savanna guenon allotaxa, *Cercopithecus aethiops pygerythrus* and *C. aethiops tantalus*, west of Lake Victoria, in Uganda. Once separated by a block of rain forest, they now meet in the anthropogenic farming bush of this densely populated area (Chapman and Chapman, 1996; Kingdon, 1971).

Contrary to received wisdom, we suspect that humans have eliminated at least as many zones of parapatric hybridization as they have created. Theory (Barton and Hewitt, 1985; Barton, 2001) predicts that if hybrids are at some intrinsic disadvantage compared to the parental forms, a hybrid zone will tend to locate and stabilize in an ecologically unfavorable area of low population density, and hybrid zones between ecologically different forms will tend to settle near an ecotone. Other things being equal, such populations will be more vulnerable to extinction by humans than the core parental populations, and once gone they leave no overt sign of their existence, beyond, perhaps, some scattered, foreign genetic markers in the parental populations. By contrast, a human-made parapatric hybrid zone is easily recognized by a hybrid swarm of phenotypic intermediates in the anthropogenically modified habitat.

In many cases, the role of human activities in the formation of a nonhuman primate hybrid zone is impossible to disentangle from the effects of natural climatic and vegetational fluctuations. For instance, in recent decades the dynamics of the Awash National Park anubis-hamadryas hybrid zone have been affected not only by short-term climatic fluctuation (Phillips-Conroy and Jolly, 1986) but also by destruction of neighboring riverine forest for irrigated agriculture. In previous millennia there was not only a succession of Holocene climatic fluctuations but also the introduction of subsistence horticulture to the Awash valley, its replacement by transhumant pastoralism, and then the establishment of a relatively depopulated buffer zone between warring pastoralist peoples, which eventually became the Awash National Park. Each development undoubtedly influenced baboon-human interactions and the dynamics of the anubis-hamadryas contact zone. But these comparatively long-term trends themselves represent only the latest chapter in baboon-hominin coexistence that extends back for $\geq$4 million years, long antedating the appearance of the extant species.

In any case, if the intent is to duplicate the natural condition as far as possible, parapatric hybridization may represent a situation to be restored rather than prevented. The genetic effects of parapatric hybridization are, by definition, most pronounced at the allotaxon border itself, and become exponentially less influential as one proceeds away from it. In allotaxa with wide distributions, the proportion of individuals who actually have the opportunity to hybridize, and therefore may be selected to avoid it, is miniscule. In theory, however, parapatric hybridization allows advantageous alleles to flow from one population to the other, while filtering out foreign genes disadvantageous to the recipient population (Barton, 2001). By eliminating this contact, anthropogenic range reduction and fragmentation may reduce the efficiency of hybridization as a disseminator of advantageous variation across a cluster of allotaxa.

Many of the same considerations apply to sympatric hybridization. Sporadic hybridization between related, sympatric species is associated with situations in which animals are faced with a scarcity of conspecific mates, but potential heterospecific mates are present. In cercopithecine monkeys, a mate shortage is most likely to occur at a habitat edge, where opportunities for a male to migrate into a group of unrelated conspecifics are limited. Many such edges will occur at the altitudinal or geographical limit of species' ranges (as at Nyungwe), and where the habitat is physically fragmented (as at Lopé), but others may be caused by purely local barriers to dispersal (as at Budongo), or by slight habitat transitions within continuous ecosystems. It seems obvious that edges, on a regional and local scale, have always occurred in any region of diverse topography or mosaic habitat patches, whether or not the habitat has been anthropogenically modified.

Sporadic occurrences of sympatric hybridization are therefore probably as old as the species themselves, and as in the case of parapatric hybridization, provide a channel by which intraspecific genetic diversity is supplemented with already-tested genetic material (Jolly *et al.*, 1997).

Situations such as we hypothesize at Gombe represent an extreme case of sympatric hybridization where the frequency of hybrids may have reached a critical threshold, such that selection has begun to favor relaxation of barriers to hybridization, and, given time, a new stabilized hybrid species might emerge. Though necessarily much rarer, there seems no reason to doubt that Gombe-like situations must also have occurred in the absence of human influence, as forest isolates expanded and contracted, driven by Pleistocene climatic change. Almost by definition, they are confined to small, isolated enclaves.

Thus, sympatric hybridization, like parapatric hybridization, can and almost certainly did occur without human intervention. However, anthropogenic modification of the habitat of a species can artificially increase its incidence. If a specific range is reduced and fragmented, the proportion of edge to middle becomes greater, and the chances of sympatric hybridization correspondingly increased. Even so, only in rare cases of extreme habitat fragmentation (where fragments are <3 territories wide) will a substantial proportion of social groups be situated actually on an edge, and thus be under direct pressure to hybridize. Like the populations of the main forest block at Lopé, most of them will continue to be surrounded by enough conspecific groups that hybridization offers no advantage.

Finally, there may be some specific, usually anthropogenic, situations wherein hybridization could well be associated with a threat to the global survival of a species, and intervention might be justified to prevent it. For example, if habitat destruction or persecution has reduced the range of a species to a few, very small habitat patches, shared with a more widespread species with which it also shares a mate recognition system, genetic swamping by the more numerous population would be a risk. For instance, Kingdon (1997) suggested that hybridization with the widespread and adaptable grivet, *Cercopithecus aethiops aethiops*, is a real threat facing the endangered Bale monkey, *Cercopithecus djamdjamensis*. Other examples might be guenon species now confined to very small forest patches in farming areas of Nigeria, such as *Cercopithecus sclateri* (Baker and Tooze, 2003; Oates *et al.*, 1992; Tooze, 1995). However, even here the root cause of the crisis is the population and habitat reduction of the rare species, not its ability to hybridize *per se*.

Hybridization, of both modes, is intrinsically neither good or bad, and, at least in the African context, the anthropogenic component in its causation is hard to isolate. It is best treated as one of many natural evolutionary processes that have played an important role in shaping the biodiversity that conservation aims to protect, and will continue to do so as long as a variety of population structures and zones of contact and overlap are allowed to exist. As so often in conservation, direct intervention to manipulate a wild population, in this case by preventing or promoting hybridization in a particular local situation, must be regarded as a strategy of last resort, that in no way substitutes for enforcement of existing protective legislation or for effective, large-scale, planned conservation efforts. If implemented, region-wide conservation plans such as the proposal for the Guinean-Congolian Forest and Freshwater Region (WWF, 2003), would preserve a setting in which hybridization would continue to occur, and its role as a natural evolutionary process be available for further study.

ACKNOWLEDGMENTS

We thank Lindsay Magnuson and Mary Glenn for inviting Detwiler to participate in the ASP symposium "Conservation of African Monkeys" on which this paper is based. We are grateful to B. A. Kaplin, C. E. G. Tutin, and E. J. Wickings for sharing unpublished data on guenon hybrids.

REFERENCES

Alberts, S. C., and Altmann, J. (2001). Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. *Am. J. Primatol.* 53: 139–154.

Aldrich-Blake, F. P. G. (1968). A fertile hybrid between two *Cercopithecus* species in the Budongo Forest, Uganda. *Folia Primatol.* 9: 15–21.

Aldrich-Blake, F. P. G. (1970). *The Ecology and Behaviour of the Blue Monkey*, Ph.D. Thesis, University of Bristol, Bristol.

Allendorf, F. W., Leary, R. F., Spruell, P., and Wenburg, J. K. (2001). The problems with hybrids: setting conservation guidelines. *Trends Ecol. Evol.* 16(11): 613–622.

Arnold, M. L. (1997). *Natural Hybridization and Evolution*, Oxford University Press, Oxford.

Arntzen, J. W., and Wallis, G. P. (1991). Restricted gene flow in a moving hybrid zone of the newts *Triturus cristatus* and *T. marmoratus* in western France. *Evolution* 45(4): 805–826.

Avise, J. C. (1994). *Molecular Markers, Natural History and Evolution*. Kluwer Academic, London.

Baker, L. R., and Tooze, Z. J. (2003). Status of the Sclater's guenon (*Cercopithecus sclateri*) in southeastern Nigeria. *Am. J. Primatol.* 60: 88–89.

Barton, N. H. (2001). The role of hybridization in evolution. *Mol. Ecol.* 10: 551–568.

Barton, N. H., and Hewitt, G. M. (1985). Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16: 113–148.

Bergman, T. J. (2000). *Mating Behavior and Reproductive Success of Hybrid Male Baboons* (Papio hamadryas hamadryas *x* Papio hamadryas anubis), Ph.D. Thesis, Washington University, Missouri.

Bernstein, I. S. (1966). Naturally occurring primate hybrid. *Science* 154: 1559–1560.

Beyene, S. G. (1998). *The Role of Female Mating Behavior in Hybridization Between Anubis and Hamadryas Baboons in Awash, Ethiopia*, Ph.D. Thesis, Washington University, Missouri.

Booth, A. (1955). Speciation in the Mona monkeys. *J. Mammol.* 36: 434–449.

Booth, A. (1956). The Cercopithecidae of the Gold and Ivory Coasts: Geographic and systematic observations. *Ann. Mag. Nat. Hist.* 12(9): 476–480.

Booth, C. (1968). Taxonomic studies of *Cercopithecus mitis* Wolf (East Africa). *Nat. Geogr. Soc. Res. Reports* (1963 projects): 37–51.

Bourlière, F., Hunkeler, C., and Bertrand, M. (1970). Ecology and behavior of Lowe's guenon (*Cercopithecus campbelli lowei*) in the Ivory Coast. In Napier, J. R., and Napier, P. H. (eds.), *Old World Monkeys*, Academic Press, New York, pp. 297–350.

Brett, F., Jolly, C. J., Socha, W., and Wiener, A. S. (1977). Human-like ABO blood groups in wild Ethiopian baboons. *Yrbk. Phys. Anth.* 20: 276–289.

Butynski, T. M. (1990). Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol. Monogr.* 60: 1–26.

Butynski, T. M. (2002). The guenons: an overview of diversity and taxonomy. In Glenn, M. E., and Cords, M. (eds.), *The Guenons: Diversity and Adaptation in African Monkeys*, Kluwer Academic/Plenum, New York, pp. 3–13.

Chapman, C. A., and Chapman, L. J. (1996). Mid-elevation forests: a history of disturbance and regeneration. In McClanahan, T. R., and Young, T. P. (eds.), *East African Ecosystems and Their Conservation*, Oxford University Press, Oxford, pp. 385–400.

Chapman, C. A., and Chapman, L. J. (2000). Interdemic variation in mixed-species association patterns: common diurnal primates of Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* 47: 129–139.

Clarke, B., Johnson, M. S., and Murray, J. (1998). How 'molecular leakage' can mislead us about island speciation. In Grant P. R. (ed.), *Evolution on Islands*, Oxford University Press, Oxford, pp. 181–195.

Clutton-Brock, T. H. (1972). *Feeding and Ranging Behavior in the Red Colobus*. Ph.D. Thesis, Cambridge University, Cambridge.

Coe, M. (1985*). Islands in the Bush: A Natural History of the Kora National Reserve, Kenya*, George Phillip, New York.

Colyn, M., and Deleporte, P. (2002). Biogeographic analysis of central African forest guenons. In Glenn, M. E., and Cords, M. (eds.), *The Guenons: Diversity and Adaptation in African Monkeys*, Kluwer Academic/Plenum, New York, pp. 61–78.

Cords, M. (2000). The number of males in guenon groups. In Kappeler, P. (ed.), *Primate Males*, Cambridge University Press, Cambridge, pp. 84–96.

Dandelot, P. (1959). Note sur la classification des cercopitheques du groupe *aethiops*. *Mammalia* 23: 357–368.

Dandelot, P., and Prevost, J. (1972). Contribution a l'etude des primates d'Ethiopie (Simiens). *Mammalia* 36: 607–633.

Detwiler, K. M. (2002). Hybridization between red-tailed monkeys (*Cercopithecus ascanius*) and blue monkeys (*C. mitis*) in East African forests. In Glenn, M. E., and Cords, M. (eds.), *The Guenons: Diversity and Adaptation in African Monkeys*, Kluwer Academic/Plenum, New York, pp. 79–97.

Dowling, T. E., and Secor, C. L. (1997). The role of hybridization and introgression in the diversification of animals. *Annu. Rev. Ecol. Syst.* 28: 593–619.

Dunbar, R. I. M., and Dunbar, P. (1974). On hybridization between *Theropithecus gelada* and *Papio anubis* in the wild. *J. Hum. Evol.* 3: 187–192.

Fairgrieve, C., and Muhumuza, G. (2003). Feeding ecology and dietary differences between blue monkey (*Cercopithecus mitis stuhlmanni Matschie*) groups in logged and unlogged forest, Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 41: 141–149.

Federal Register (1996). Endangered and threatened wildlife and plants; proposed policy and proposed rule on the treatment of intercrosses and intercross progeny (the issue of 'hybridization'); Request for public comment. Federal Register 61(26): 4710–4713.

Gartlan, J. S., and Struhsaker, T. T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *J. Zool.* 168: 221–266.

Gautier, J. P. (1988). Interspecific affinities among guenons as deduced from vocalizations. In Gautier-Hion, A., Bourliere, F., Gautier, J.-P., and Kingdon, J. (eds.) *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge, pp. 194–226.

Gautier-Hion, A. (1988). Polyspecific associations among forest guenons: ecological, behavioural and evolutionary aspects. In Gautier-Hion, A., Bourliere, F., Gautier, J.-P., and Kingdon, J. (eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge, pp. 452–476.

Gautier-Hion, A., Colyn, M., and Gautier, J.-P. (1999). *Histoire Naturelle des Primates d'Afrique Centrale*, ECOFAC, Libreville.

Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*, Harvard University Press, Cambridge.

Goodman, S. J., Barton, N. H., Swanson, G., Abernethy, K., and Pemberton, J. M. (1999). Introgression through rare hybridization: a genetic study of a hybrid zone between red and sika deer (genus *Cervus*) in Argyll, Scotland. *Genetics* 152: 355–371.

Grant, B. R., and Grant, P. R. (1998). Hybridization and speciation in Darwin's finches. In Howard, D. J., and Berlocher, S. H. (eds.), *Endless Forms: Species and Speciation*, Oxford University Press, Oxford, pp. 404–422.

Grant, P. R., and Grant, B. R. (1992). Hybridization of bird species. *Science* 256: 193–197.

Groves, C. P. (1978). Phylogenetic and population systematics of the mangabeys (Primates: Cercopithecoidea). *Primates* 19(1): 1–34.

Groves, C. P. (1993). Speciation in living hominoid primates. In W. H. Kimbel, and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*, Plenum Press, New York, pp. 109–121.

Groves, C. P. (2001*). Primate Taxonomy*. Smithsonian Institution Press, Washington, DC.

Grubb, P. (1999). Evolutionary processes implicit in distribution patterns of modern African mammals. In T. G. Bromage, and F. Schrenk (eds.), *African Biogeography, Climate Change, and Human Evolution*, Oxford University Press, New York, pp. 150–164.

Grubb, P., Butynski, T. M., Oates, J. F., Bearder, S. K., Disotell, T. R., Groves, C. P., and Struhsaker, T. T. (2003). An assessment of the diversity of African primates. *Int. J. Primatol.* 24: 1301–1357.

Hewitt, G. M. (1996). Some genetic consequences of ice age, and their role in divergence and speciation. *Biol. J. Linn. Soc.* 58: 247–276.

Hewitt, G. M. (2001). Speciation, hybrid zones and phylogeography – or seeing genes in space and time. *Mol. Ecol.* 10: 537–549.

Jolly, C. J., Woolley-Barker, T., Beyene, S., Disotell, T. R., Phillips-Conroy, J. E. (1997). Intergeneric hybrid baboons. *Int. J. Primatol.* 18: 597–627.

Jolly, C. J. (1993). Species, subspecies, and baboon systematics. In W. H. Kimbel, and L. B. Martin (eds.), *Species, Species Concepts, and Primate Evolution*, Plenum Press, New York, pp. 67–107.

Jolly, C. J. (2001). A proper study for mankind: analogies from the papionin monkeys and their implications for human evolution. *Yrbk. Phys. Anth.* 44: 177–204.

Kaplin, B. A. (1998). *Ecology of Two African Forest Monkeys: Temporal and Spatial Patterns of Habitat Use, Foraging Behavior, and Seed Dispersal*, Ph.D. Thesis, The University of Wisconsin, Madison.

Kingdon, J. (1971). *East African Mammals: An Atlas of Evolution in Africa*, Academic Press, New York.

Kingdon, J. (1980). The role of visual signals and face patterns in African forest monkeys (guenons) of the genus *Cercopithecus*. *Trans. Zool. Soc. Lond.* 35: 425–475.

Kingdon, J. (1988). What are face patterns and do they contribute to reproductive isolation in guenons? In Gautier-Hion, A., Bourliere, F., Gautier, J.-P., and Kingdon, J. (eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge, pp. 227–245.

Kingdon, J. (1997). *The Kingdon Field Guide to African Mammals*, Academic Press, New York.

Lehman, N., Eisenhawer, A., Hansen, K., Mech, L. D., Peterson, R. O., Gogan, P. J., and Wayne, R. K. (1991). Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution* 45(1): 104–119.

Lernould, J.-M. (1988). Classification and geographical distribution of guenons: A review. In Gautier-Hion, A., Bourliere, F., Gautier, J.-P., and Kingdon, J. (eds). *A Primate*

Radiation: Evolutionary Biology of the African Guenons, Cambridge University Press, Cambridge, pp. 54–78.

Machado, A. B. (1965). Acerca do achado em Angola de uma forma racial inedita do *Cercopithecus ascanius* (Audebert, 1799) (Primates, Cercopithecidae). *Boletim da Academia das Ciencias de Lisboa*. 37: 182–198.

Machado, A. B. (1969). Subsidios para o estudo da biologia na lunda. Mamiferos de Angola ainda nao citados ou pouco conhecidos. *Publicacoes Culturais da Companhia de Diamantes Angola*. 46: 93–231.

Maples, W. R., and McKern, T. W. (1967). A preliminary report on the classification of the Kenya baboon. In Vagtborg, H. (ed.), *The Baboon in Medical Research. Vol. 2*, University of Texas Press, Austin, pp. 13–22.

Mori, A., and Belay, G. (1990). The distribution of baboon species and a new population of gelada baboons along the Wabi-Shebeli River, Ethiopia. *Primates* 31: 495–508.

Nagel, U. (1973). A comparison of anubis baboons, hamadryas baboons, and their hybrids at a species border in Ethiopia. *Folia Primatol.* 19: 104–165.

Napier, P. H. (1981). *Catalogue of Primates in the British Museum (Natural History). Part II: Family Cercopithecidae, Subfamily Cercopithecinae*, British Museum (Natural History), London.

Newman, T. K. (1997). *Mitochondrial DNA Analysis of Intraspecific Hybridization in* Papio hamadryas anubis *and* Papio hamadryas hamadryas *and Their Hybrids in the Awash National Park, Ethiopia*. Ph.D. Thesis, New York University, New York.

Oates, J. F. (1988). The distribution of *Cercopithecus* monkeys in West African forests. In Gautier-Hion, A., Bourliere, F., Gautier, J.-P., and Kingdon, J. (eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge, pp. 79–103.

Oates, J. F., Anadu, P. A., Gadsby, E. L., and Werre, J. L. (1992). Sclater's guenon-a rare Nigerian monkey threatened by deforestation. *National Geographic Research and Exploration* 8(4): 476–491.

Oates, J. F. (1996). *African Primates: Status Survey and Conservation Action Plan*, Revised Edition. IUCN/SSC Primate Specialist Group, IUCN, Gland, Switzerland.

Oates, J. F. (1999). *Myth and Reality in the Rain Forest: How Conservation Strategies are Failing in West Africa.* University of California Press, Berkeley.

Paterson, H. E. H. (1985). The recognition concept of species. In Vrba, E. S. (ed.), *Species and Speciation*, Transvaal Museum Monograph No. 4 Transvaal Museum, Pretoria, pp. 21–29.

Phillips-Conroy, J., and Jolly, C. J. (1986). Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. *Am. J. Phys. Anth.* 71: 337–350.

Phillips-Conroy, J., Jolly, C. J., and Brett, F. L. (1991). Characteristics of Hamadryas-like male baboons living in Anubis baboon troops in the Awash hybrid zone, Ethiopia. *Am. J. Phys. Anth.* 86: 353–368.

Pintea, L., Bauer, M. E., Bolstad, P. V., and Pusey, A. (2002). Matching multiscale remote sensing data to interdisciplinary conservation needs: the case of chimpanzees in western Tanzania. In Morain, S., and Budge, A. (eds.), *Pecora 15/Land Satellite Information IV/ISPRS Commission I/FIEOS 2002 Conference Proceedings: Integrated Remote Sensing at the Global, Regional and Local Scale*.

Plumptre, A. J. (2000). Monitoring mammal populations with line transect techniques in African forests. *J. Appl. Ecol.* 37: 356–368.

Plumptre, A. J., and Reynolds, V. (1994). The effect of selective logging on the primate populations in the Budongo Forest Reserve, Uganda. *J. Appl. Ecol.* 31: 631–641.

Plumptre, A. J., Masozera, M., Fashing, P. J., McNeilage, A., Ewango, C., Kaplin, B., and Liengola, I. (2002). Biodiversity surveys of the Nyungwe Forest Reserve in S. W. Rwanda. WCS Working Papers No. 18.

Rahm, U. H. (1970). Ecology, zoogeography, and systematics of some African forest monkeys. In Napier, J. R., and Napier, P. H. (eds.), *Old World Monkeys*, Academic Press, New York, pp. 589–626.

Randler, C. (2002). Avian hybridization, mixed pairing and female choice. *Anim. Behav.* 63: 103–119.

Rhymer, J. M., and Simberloff, D. (1996). Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27: 83–109.

Rieseberg, L. H. (1997). Hybrid origins of plant species. *Annu. Rev. Ecol. Syst.* 28: 359–389.

Salzburger, W., Baric, S., and Sturmbauer, C. (2002). Speciation via introgressive hybridization in East African cichlids? *Mol. Ecol.* 11: 619–625.

Samuels, A., and Altmann, J. (1986). Immigration of a *Papio anubis* male into a group of cynocephalus baboons and evidence for a anubis-cynocephalus hybrid zone in Amboseli, Kenya. *Int. J. Primatol.* 7: 131–138.

Sheppard, D. J. (2000). *Ecology of the Budongo Forest Redtail: Patterns of Habitat Use and Population Density in Primary and Regenerating Forest Sites*, M.Sc. Thesis, The University of Calgary, Calgary.

Shotake, T. (1982). Population genetical study of natural hybridization between *Papio anubis* and *Papio hamadryas*. *Primates* 23: 285–308.

Stanford, C. (1998). *Chimpanzee and Red Colobus: the Ecology of Predator and Prey*, Harvard University Press, Cambridge.

Struhsaker, T. T. (1970). Phylogenetic implications of some vocalizations of *Cercopithecus* monkeys. In Napier, J. R., and Napier, P. H. (eds.), *Old World Monkeys,* Academic Press, New York, pp. 365–444.

Struhsaker, T. T., Butynski, T. M., and Lwanga, J. S. (1988). Hybridization between redtail (*Cercopithecus ascanius schmidti*) and blue (*C. mitis stuhlmanni*) monkeys in the Kibale Forest, Uganda. In Gautier-Hion, A., Bourliere, F., Gautier, J. -P., Kingdon, J. (eds.), *A Primate Radiation: Evolutionary Biology of the African Guenons*, Cambridge University Press, Cambridge, pp. 477–497.

Suzuki, A. (1979). The variation and adaptation of social groups of chimpanzees and black and white colobus monkeys. In Bernstein, I. S., and Smith, E. O. (eds.), *Primate Ecology and Human Origins*, Garland STPM Press, New York, pp. 153–174.

Tooze, Z. (1995). Update on Sclater's guenon *Cercopithecus sclateri* in southern Nigeria. *African Primates* 1(2): 38–42.

Tosi, A. J., Morales, J. C., and Melnick, D. J. (2002). Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. *Int. J. Primatol.* 23: 161–178.

Tosi, A. J., Morales, J. C., and Melnick, D. J. (2003). Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution* 57(6): 1419–1435.

Tutin, C. E. G. (1999). Fragmented living: behavioral ecology of primates in a forest fragment in the Lopé Reserve, Gabon. *Primates* 40(1): 249–265.

Tutin, C. E. G., White, L. J. T., and Mackanga-Missandzou, A. (1997). The use by rain forest mammals of natural forest fragments in an equatorial African savanna. *Cons. Biol.* 11(5): 1190–1203.

Tweheyo, M., and Obua, J. (2001). Feeding habits of chimpanzees (*Pan troglodytes*), redtail monkeys (*Cercopithecus ascanius schmidti*) and blue monkeys (*Cercopithecus mitis stuhlmanni*) on figs in Budongo Forest Reserve, Uganda. *Afr. J. Ecol.* 39: 133–139.

Twinomugisha, D., Basuta, G. I., and Chapman, C. A. (2003). Status and ecology of the golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda. *Afr. J. Ecol.* 41: 47–55.

Woodruff, D. S. (1973). Natural hybridization and hybrid zones. *Syst. Zool.* 22: 213–217.

Woolley-Barker, T. (1999). *Social Organization and Genetic Structure in a Baboon Hybrid Zone,* Ph.D. Thesis, New York University, New York.

WWF. (2003). *Biological Priorities for Conservation in the Guinean-Congolian Forest and Freshwater Region*. WWF-US/CARPO, Washington, DC.

Zinner, D., Peláez, P., Torkler, F., and Berhane, D. (2003). Primates of Eritrea – current distribution and habitat. *African Primates* 5: 7–17.