RESEARCH ARTICLE

Kinda Baboons (*Papio kindae*) and Grayfoot Chacma Baboons (*P. ursinus griseipes*) Hybridize in the Kafue River Valley, Zambia

C.J. JOLLY[1]*, A.S. BURRELL[1], J.E. PHILLIPS-CONROY[2], C. BERGEY[1], AND J. ROGERS[3]
[1]*New York University, Anthropology, New York, New York*
[2]*Washington University School of Medicine, Anatomy and Neurobiology, Missouri*
[3]*Baylor College of Medicine-Human Genome Sequencing Center, Houston, Texas*

The ranges of small kinda (*Papio kindae*) and much larger grayfooted chacma (*P. ursinus griseipes*) baboons adjoin in the Kafue National Park, Zambia. In a visual survey of baboons at 48 sites in the Kafue River drainage we found that, contrary to previous reports, groups at the species interface near the town of Ngoma are phenotypically diverse and presumably formed by multigenerational hybridization. Mitochondrial and/or Y-chromosome genetic markers from fecal samples ($N = 164$) collected at 29 sites support this conclusion. Groups with phenotypic signs of a history of hybridization also had taxon-specific mitochondria and Y-haplotypes from both parental species. Although the distribution of mitochondrial haplotypes largely mirrored that of external phenotypes, a significant proportion of male specimens from grayfoot as well as hybrid groups carried kinda Y-chromosomes, and kinda Y-chromosomes were involved in all observed cases of mitochondrial/Y-chromosome discordance. These observations are consistent with, though they do not prove, a population history in which the range of chacmas and the hybrid zone have advanced at the expense of the kinda range. They also suggest that, unexpectedly, kinda male × chacma female matings are much more common than the reciprocal cross in the ancestry of hybrids. We suggest that distinctive male kinda behavior and the ''juvenile'' appearance of kinda baboons of both sexes, perhaps combined with obstetric difficulties of a small kinda female carrying the large offspring of a chacma male, may account for this bias. Am. J. Primatol. 73:291–303, 2011.   © 2010 Wiley-Liss, Inc.

INTRODUCTION

Natural populations that are phenotypically distinct and, therefore, consistently diagnosable, yet are partially or fully interfertile and exchange genes under natural conditions, are of particular interest in the context of speciation theory [Harrison, 1990]. Examination of the behavioral and demographic processes, involved in this type of genetic exchange, informs our hypotheses regarding the process of speciation as well as the interpretation of diversity among fossil forms [Jolly, 2001]. Extant baboons of the genus *Papio* comprise a phenotypically diverse array of geographically replacing forms (allotaxa; [Grubb, 1999]) that hybridize naturally in the wild. Current taxonomic practice usually allocates *Papio* baboons to five (or more) phylogenetic species [Groves, 2001; Grubb, 1999; Kingdon, 1997] or to a single, polytypic, ''biological'' species [Delson et al., 2000; Frost et al., 2003]. The distinction in formal taxonomy is not relevant to our understanding of either the demographic processes at play or their long-term evolutionary consequences [Jolly, 1993]. Following the growing consensus, we accept full species status for the five ''major forms'' (Guinea or western,

anubis or olive, hamadryas or sacred, chacma, and yellow) as *P. papio*, *P. anubis*, *P. hamadryas*, *P. ursinus*, and *P. cynocephalus*, respectively. The kinda baboon (Fig. 1) (rhymes with ''Linda,'' named after its type locality in the Democratic Republic of Congo (DRC)) is generally considered a subspecies (*P. c. kindae*) of *P. cynocephalus* [Groves, 2001; Kingdon, 1997]. We recognize it as a full species (*Papio kindae*) because it is as distinctive as the five others, both morphologically [Frost et al., 2003] and genetically [Burrell, 2009; Zinner et al., 2009].

In the Kafue river drainage of central Zambia (Fig. 2), *P. kindae* (here called ''kinda'') coexists with
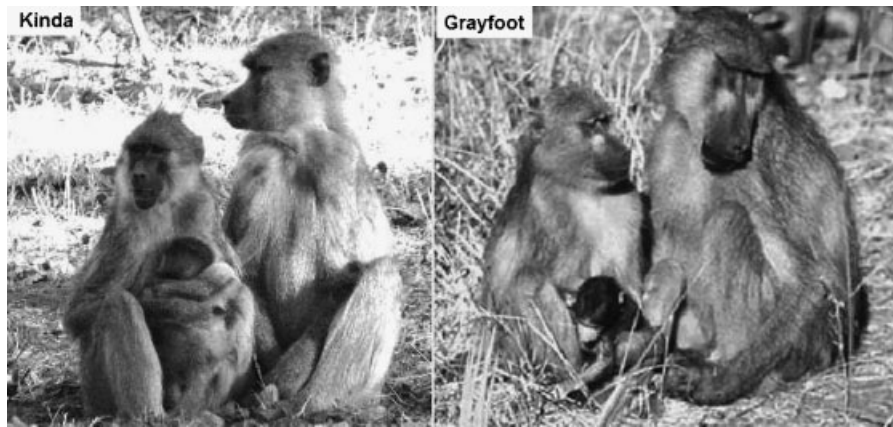
Fig. 1. Grayfoot chacma (R) and kinda (L) baboons. Adult female (with infant) and male.
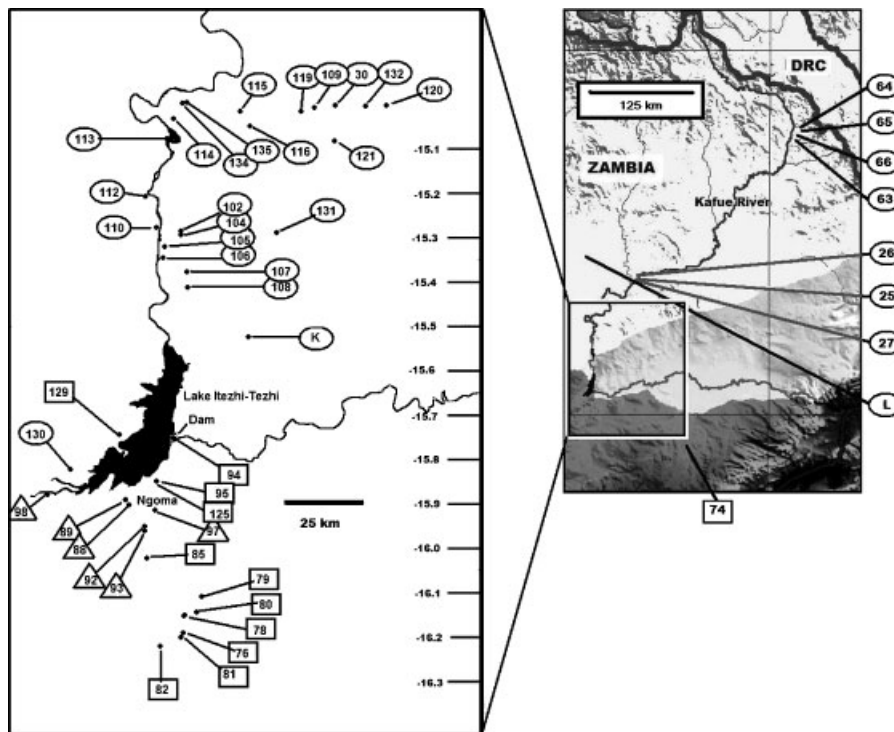

Fig. 2. Localities where baboons were observed in the Kafue River basin. Circles: sites with only kindas; squares: sites with only or mostly grayfoots; triangles: sites with mostly mixed phenotypes. Smaller scale map shows ranges of taxa, from this study and Ansell [1978]. Light shading: kinda range; dark shading: grayfoot range; intermediate shading: no records.

Papio ursinus griseipes (here called "grayfooted chacma" or "grayfoot"), a form that differs not only in pelage, but also in size and size-correlated features, including degree of sexual dimorphism (Table I, Fig. 1). Grayfooted chacmas are distributed from the Limpopo valley northwards through Zimbabwe, southern Mozambique, the Okavango region of Botswana, the Caprivi Strip, Namibia, and the lower Zambezi valley. In Zambia, most of its range lies within drier miombo woodland (<900 mm mean annual rainfall). The grayfoot is one of the largest extant baboons [Barrett & Henzi, 1997; Delson et al., 2000],

and its cranial morphology, size, and coloration ally it with other chacmas (*Papio ursinus*, sensu lato). Kindas have a more northerly distribution, mostly in miombo woodland with >1,000 mm mean annual rainfall [Ansell, 1978]. Their range extends from extreme southwest Tanzania and the Luangwa valley, Zambia, westwards through to the southern DRC and most of Angola. Kindas have the overall coloration characteristic of the yellow baboon group (*P. cynocephalus*, sensu lato) as well as some unique external features (Table I, Fig. 1). Their most distinctive features are a slender, long-limbed build and small overall size.

TABLE I. External Characteristics of Adult Kinda and Grayfoot Chacma Baboons

Character	Grayfoot Chacma Baboon	Kinda Baboon
Overall size	Large (adult male c30 kg est)	Small (adult male c16 kg)
Sexual size dimorphism	Greater: adult male average 2.0 × adult female (Okavango population)	Less: adult male 1.7 × adult female)
Body build	More robust	Very gracile, long limbed
Tail carriage	Usually ''broken'', with flatter arch	Usually high arch
Relative tail length	Longer, reaches calves	Shorter, reaches knee
Circumorbital skin	Dark (Except pregnant female)	Light pink ''spectacles'' surrounding eyes
Light muzzle hair patches	Present, conspicuous	Absent
Facial length (allometrically size correlated)	Relatively long, with flat, downwardly flexed muzzle profile	Relatively short, with profile of muzzle somewhat concave
Overall color of dorsal hair	Uniform, drab gray-brown	Yellow-brown
Color of ventral hair	Dark, such as back and limbs	Light, yellow
Color of cheek hair	Somewhat contrasting, lighter gray	Strongly contrasting, yellow
Nape hair (adult male)	Long, curled, black	Not prominent
Head hair	Even length or slight median crest	Often well-developed ''mohawk'' of black hair, contrasting with crown

Successful interbreeding between kinda and grayfoot baboons might be considered inherently unlikely because of their extreme size difference. Documented examples of hybridization in *Papio* [Alberts & Altmann, 2001; Phillips-Conroy & Jolly, 1986; Samuels & Altmann, 1986; Tung et al., 2008]; all involve hybridizing forms (*Papio anubis* and *P. cynocephalus*, and *P. anubis* and *P. hamadryas*, respectively) that are distinct in external phenotype, but very similar in body mass and degree of sexual dimorphism, and close to the median size for the genus. Crosses in both directions between kindas and grayfoots would involve an unusual size difference. On average, in a male chacma × female kinda mating, the female's mass would be 35% of the male's. This is comparable to the size differential in *Mandrillus*, the most sexually dimorphic of extant African papionins, in which mean female mass is 36% of mean male mass [Delson et al., 2000]. The reciprocal mating, between a male kinda and a female grayfoot chacma (averaging about 88% of his body mass), would bring together partners closer in size than in any extant African papionin species [Delson et al., 2000]. Either combination might be expected to face behavioral and mechanical, pre- and postzygotic obstacles to successful reproduction.

Opportunities for interbreeding and the behavioral dynamics involved are likely to be influenced by patterns of dispersal characteristic of the taxa concerned. Both kindas and grayfoots live in multi-male, multifemale troops. Most grayfoot males disperse from their natal troop and join another before breeding, whereas females almost invariably spend their lives in the troop of their birth [Henzi et al., 2000]. The dispersal regime of kindas has yet to be determined, but available genetic evidence [Burrell, 2009; and below] is consistent with male dispersal and female philopatry.

Evidence that the taxa might coexist without interbreeding was provided by the late W.F.H. Ansell [1960, 1978], who identified areas in the Kafue National Park where they apparently had marginally overlapping ranges. Other workers [Jolly, 1993] have speculated that the two populations might be reproductively isolated in the Kafue region, yet be linked by gene flow via intermediate-sized yellow baboons in eastern and Southeastern Zambia, thus forming a ring species [Mayr, 1942] Our research program in Zambia is designed to collect observational and genetic information from areas of contact and possible hybridization among all the Zambian baboons. This article describes findings on phenotypic and genetic variation in the region of the Kafue River drainage where kindas and grayfoots come into contact.

METHODS

All methods used in the field and the laboratory conformed to the rules and regulations of the National Parks of Zambia and adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates. None involved contact with, or disturbance of, any wild primates. We conducted short field surveys by road and on foot during the dry season (austral winter) of 1999, 2002, 2004, 2006, 2007, and 2008. Whenever baboons were encountered, we recorded the location as a GPS waypoint (WP), estimated the size of the group, and evaluated the animals' appearance, in most cases also recording it in photographs and videotape. We observed baboons at 48 locations in the Kafue drainage and at Choma (WP 74), in the adjoining Zambezi valley (Fig. 2). We compared individual animals against a list of diagnostic features (Table I), but did not attempt numerical phenotypic scoring [Nagel, 1973; Phillips-Conroy & Jolly, 1986]. In addition to the features listed—which are visible in adults, especially males, and to a lesser

extent in juveniles—we also noted the pelage color of infants. Infant grayfoot chacmas have the blackish natal coat typical of *Papio*, but a substantial proportion of infant kindas have natal coats that are all or mostly white.

After the baboons left the area, we collected fecal samples into a preservative solution (RNALater, Ambion). No sample could be attributed to a particular, observed individual. We collected samples from each group only once, and selected feces that were of similar freshness, and far enough apart to be confidently attributed to different individuals. For specimens collected in this way, genetic testing using microsatellite markers has positively excluded duplication in more than 90% of cases [Burrell, 2009]. Specimens were transported without refrigeration and stored in the lab at $+5°C$.

Samples ($N = 164$) from 29 locations were used for the genetic analyses presented here. All lab work was performed by workers with no prior knowledge of the phenotypic or taxonomic makeup of the baboon groups sampled. They extracted DNA from fecal samples using QIAamp DNA Stool Mini Kits [Qiagen, Valencia, CA] following the manufacturer's protocol. They then genotyped 148 specimens for the mitochondrial hypervariable region 1 (HV1), using the ''long-template'' PCR' approach [Burrell et al., 2009] followed by cycle-sequencing with primers listed in Hapke et al. [Hapke et al., 2001]. Extensive surveys of mitochondrial variation in baboons [Burrell, 2009] had previously identified clades of haplotypes closely associated with kinda and grayfoot phenotypes, respectively. Both of these taxon-associated clades fall into the ''southern'' major mitochondrial clade [Burrell, 2009; Zinner et al., 2009] but are widely separated within it. HV1 haplotypes identified in this study were clustered using a Bayesian approach as implemented in MRBAYES [Ronquist & Huelsenbeck, 2001]. Support for the mitochondrial clades was substantial (Grayfoot clade: Bayes Credibility Score = 1.00, Maximum Likelihood bootstrap score > 99%; kinda clade: Bayes Credibility Score = 1.00, Maximum Likelihood bootstrap score = 99%). All the mitochondrial haplotypes observed in the Kafue specimens could be unambiguously assigned to either the kinda or the grayfoot clade.

Most specimens ($N = 131$) could be assigned to sex by the method of DiFiore [Di Fiore, 2005]. Of those determined to be male ($N = 88$), 70 could be typed for taxon-specific Y-chromosome markers. Analysis [Burrell et al., 2010] of the Y-linked testis-specific protein locus (TSPY) [Tosi et al., 2003b] had found three consistent differences between kindas from Tanzania, Kafue, and other regions of Zambia ($N = 26$), and grayfoot and other chacmas from Zambia, South Africa, and Botswana ($N = 7$). At position 78, kindas have T, chacmas have C; at position 265, kindas have A, chacmas have C; and at position 1,434, kindas have G, chacmas have A.

Preliminary work on kindas and grayfoot chacmas ($N = 37$) from the Kafue and other sites (unpublished; see Table II) had also shown that shorter (< 281 bp) alleles of the Y-chromosomal microsatellite DYS576 [Erler et al., 2004] were always associated with the CCA (chacma) TSPY haplotype, whereas longer (> 281 bp) alleles always occurred with the TAG (kinda) haplotype (alleles with 281 bp were found in association with both haplotypes). This association allowed Y-chromosomes to be assigned to taxon in most of the 34 samples in which DYS576 was amplified, but TSPY was not.

Of the 70 males typed for Y-chromosome haplotype, 55 were also successfully assigned to a mitochondrial haplotype, allowing cases of discordance between the two sex-associated genetic systems to be identified.

RESULTS

Figure 2 shows the distribution of group phenotypes in the Kafue drainage. We observed few baboons outside protected hunting areas, private reserves, and the Kafue and Lower Zambezi National Parks. Although our findings are compatible with a clinal distribution of genetic variation across the survey area, for descriptive purposes we divide the survey area into three somewhat arbitrary ''zones.'' At sites in the upper Kafue valley and the northern part of the Kafue National Park, north of approximately $-15.5°$ latitude (the ''Kinda Zone''), all baboons clearly observed had typical kinda morphology. All 38 male specimens tested had kinda Y-chromosomes and all but 1 of the 54 specimens tested carried kinda mitochondria. The exception was a male specimen from WP 105, which combined its kinda Y-chromosome with a grayfoot mitochondrial haplotype. The only phenotypic indication of admixture in this zone came from brief, distant views of baboons at the southerly sites WP 108 and WP K, at both of which we observed that some animals appeared larger and grayer than typical kindas.

All groups found south of approximately $-16.0°$ latitude (WPs 76, 78, 79, 80, 81, 82, 74) and those at sites between Ngoma and the Itezhi-Tezhi dam (WPs 94, 95) (the ''Grayfoot Zone'') included a majority of animals of grayfoot phenotype (Fig. 3), but in some of them a few individuals showed phenotypic signs of kinda admixture. An adult female at WP 76 and a subadult male at WP 79 had more yellow and less gray pelage and lighter cheeks, whereas a group of 20–30 grayfoot-like animals at WP 85 included several with lighter cheeks and ventral hair, suggesting kinda admixture (Fig. 4). One, at least, had a distinct ''mohawk'' crest. All 35 Grayfoot Zone specimens typed for mitochondria carried grayfoot haplotypes, but 5/15 male specimens had a kinda Y-haplotype. Nine of the males typed for both genetic variables had concordant genotypes (both Y-chromosome and

TABLE II. Mitochondrial and Y-Haplotype Combinations in Male Specimens Where Both Could be Typed

Transition zone				Kinda zone				Grayfoot zone			
WP	Specimen ♯	Y-microsat.	Mt/Y	WP	Specimen ♯	Y-microsat.	Mt/Y	WP	Specimen ♯	Y-microsat.	Mt/Y
88	BZ107043	296	K/K	26	BZ104060	300	K/K	74	BZ107006	285	*G/K*
88	BZ107050		*G/K*	26	BZ104061	296	K/K	74	BZ107009	285	*G/K*
88	BZ107048	285	*G/K*	26	BZ104062	292	K/K	74	BZ102066	272	G/G
88	BZ107046	292	*G/K*	30	BZ104064	288	K/K	74	BZ107010	220/252	G/G
88	BZ107045	292	*G/K*	63	BZ102084	292	K/K	76	BZ107011	281	G/G
88	BZ107041	281	*G/K*	105	BZ107126	292	K/K	76	BZ107019	262	G/G
88	BZ107049	265	G/G	105	BZ107121	289	K/K	78	BZ107026	274	G/G
88	BZ107042	274	G/G	105	BZ107127	285	*G/K*	82	BZ107031		*G/K*
89	BZ107057	296/292	*G/K*	108	BZ107135	302/299	K/K	82	BZ107033	292	*G/K*
89	BZ107056	300	*G/K*	108	BZ107139	300	K/K	82	BZ107032	281	G/G
89	BZ107055	238	G/G	108	BZ107145	300	K/K	82	BZ107034	274	G/G
98	BZ107106	303	K/K	108	BZ107141	292	K/K	125	BZ108005	296	*G/K*
98	BZ107103		K/K	108	BZ107144	292	K/K	125	BZ108002	272	G/G
98	BZ107097	303	K/K	108	BZ107133	281	K/K	"Lake ITT"	BZ102072	280	G/G
98	BZ107096		K/K	108	BZ107137	281	K/K				
129	BZ108011	300	*G/K*	108	BZ107140	281	K/K				
129	BZ108009	294	*G/K*	108	BZ107142	281	K/K				
				110	BZ107147	289	K/K				
				113	BZ102079	292	K/K				
				113	BZ107152	289	K/K				
				116	BZ107167	292	K/K				
				116	BZ107164	285	K/K				
				116	BZ107165	285	K/K				
				132	BZ108014	288	K/K				

"Lake ITT": a locality close to Lake Itezhi-Tezhi, precise coordinates not available. Individuals with discordant mitochondrial and Y-haplotype are emphasized.

Fig. 3. Typical grayfoot baboons at WP 82.

Fig. 4. Subadult hybrid male with light cheeks and kinda-like coloration, WP 85.

mitochondrial haplotypes grayfoot), but five were discordant, combining a grayfoot mitochondrial haplotype with a kinda Y-chromosome. Remarkably, two of these apparently Y-mitochondrial discordant specimens were collected at Choma (WP 74), far to the south of the present or historically recorded range of Kinda baboons or phenotypically recognizable hybrids.

Between these two regions (in the "Transition Zone"), we observed several groups in which a majority of animals were of mixed appearance. The most northerly of these was a group of 20–30 observed at WP 129, close to the western shore of the artificial Lake Itezhi-Tezhi. In phenotype, members of this group appeared large and generally grayfoot-like, but some individuals had kinda-like crown hair and tail carriage. Their mitochondria

Fig. 5. Kinda-like hybrids at WP 98. Front: adult male; rear: juvenile.

Fig. 6. Adult male hybrid, WP 89. General kinda coloration, but large with long face and white muzzle patches.

Fig. 7. Adult female grayfoot-like hybrids, WP 89.

were all grayfoot, but both male samples tested contained kinda Y-chromosomes. At WP 98, on the banks of the Musa River, a seasonal right bank tributary of the Kafue that now runs into Lake Itezhi-Tezhi, we observed a troop of approximately 30 animals. Most had pelage features close to kindas (overall yellowish coloration, light ''spectacles,'' light cheeks, and ventral hair) but showed some signs of admixture (Fig. 5). Adults appeared larger and stockier in build than typical kindas. Some animals were distinctly chacma-like in coloration, with dark ventral hair, and some had chacma-like tail length and carriage, and white muzzle patches. At least one adult male had a visibly asymmetrical muzzle, but it was impossible to judge whether this was congenital [Ackermann et al., 2006] or the result of trauma. All 12 fecal samples from WP 98 carried kinda mitochondria and all 3 male specimens tested carried a kinda Y-chromosome. At WP 130, 8 km north of the Musa River, three animals of kinda phenotype were observed, but no fecal specimen was collected.

At several Transition Zone locations immediately south of Lake Itezhi-Tezhi, we encountered groups of baboons that included many individuals of mixed phenotype. Most were predominantly grayfoot-like in size and proportions, but many of these had some features of kinda baboons, especially in pelage color (Figs. 6 and 7). Two such groups were observed at neighboring WPs 88 and 89, respectively. Each numbered 40–50 animals. Seventeen of the 18

fecal samples typed from these two groups carried the grayfoot mitochondrial haplotype, the other was kinda. Of the 13 Y-chromosomes typed from these two groups, 10 were kinda.

At WP 97, 3 km south of the National Park Headquarters at Ngoma, we observed a group of about 40 animals from about 300 m away. At that distance, all appeared to be predominantly grayfoot-like, but nine of ten samples typed carried kinda mitochondria. The most physically diverse group, also consisting of about 40 animals, was observed and photographed at close range of about 5 km further south (WP 92/93) (Figs. 8 and 9). Here, animals ranged in appearance from near-typical grayfooted chacmas to individuals that had kinda coloration and linear build, but were larger than typical kindas. We observed several infants with typical, blackish pelage, and at least one with kinda-like white fur. Of the fecal samples from this group, four yielded kinda and seven grayfoot mitochondria, but no Y-chromosomes could be typed.

Overall, 15 male-derived specimens, 5 of them from the Grayfoot Zone, 9 from the Transition Zone, and 1 from the edge of the Kinda Zone, exhibited

Fig. 8. Two adult male hybrids at WP 92. Foreground: smaller, shorter-faced, more kinda-like in coloration; behind: more grayfoot-like; left background: hybrid juveniles or females with robust build but kinda-like ''mohawks.''

Fig. 9. Hybrids, WP 92. Left: grayfoot-like adult male; right: female with white infant.

Y-mitochondrial discordance, i.e. grayfoot mitochondria combined with a kinda Y-chromosome. Of these, 13 were typed for the Y-microsatellite. Of the ten different kinda-associated Y-haplotypes seen in the Kafue, six were represented among the discordant males (Table II).

Overall, kinda Y-chromosomes were significantly more common than kinda mitochondria, both in the phenotypically intermediate group at WP 88/89 ($P = 0.0008$, Fisher's exact test) and in the chacma groups to the south ($P = 0.0006$, Fisher's exact test). Moreover, all 15 male samples with Y-mtDNA discordance combined a kinda Y-chromosome with a grayfoot mitochondrial haplotype, and therefore were either the product of a male kinda × female grayfoot mating or had such a mating in their paternal lineage. The 13 discordant males typed for the Y-linked microsatellite showed six different microsatellite alleles. The more common alleles

occurred in multiple social groups, and in two groups the Y-chromosomes of discordant males were polymorphic for the microsatellite allele (Table II).

DISCUSSION

Ansell [1960, 1978] suggested that the two species might coexist without interbreeding in a zone extending approximately between 15.25 and 15.80 S. He reported grayfoot chacmas as far north as Lubalunsuki Hill and Ithumba. Neither of these places could be relocated exactly in our surveys, but as reported in Ansell [1978] they must be situated close to our WP 110 where we observed kindas. Ansell also reported that the range of kindas (called ''yellow baboons'' in his account) covered the northern part of the Kafue National Park, and might extend as far south as the Musa River, thus overlapping with the grayfoot range in a band of about 75 km wide. In general, we found the ranges of the two taxa to be remarkably similar to his account [Ansell, 1960, 1978]. We observed only kindas north of latitude 15.50 S, and found almost all animals to the south of Ngoma to be grayfoot in appearance. Moreover, our observation of phenotypically grayfoot-like baboons at WP 129 and kindas to their south, at WP 130, suggests that separate groups of the two species might still coexist in this area. Unfortunately, a stretch of about 55 km along the right bank of the Kafue and the western shore of Lake Itezhi-Tezhi between WP 129 and WP 110, encompassing much of the putative overlap zone, was inaccessible at the time of our surveys.

Unlike Ansell, however, we also found several groups in the zone of contact and overlap that showed strong phenotypic evidence of extensive interspecific introgression, an inference supported by genetic evidence unavailable to earlier investigators. The baboons observed and sampled at the Musa River (WP 98) in 2007, though close to the kinda phenotype, showed phenotypic signs of admixture. The mixed heritage of the groups around Ngoma was even more phenotypically obvious, suggesting substantial contributions from both parental species, and successful back- and interhybrid crossing. Some animals with phenotypes suggesting kinda admixture could be seen in grayfoot Zone groups as far as WP 81, about 35 km south of Ngoma.

In the half-century since Ansell [1960, 1978] recorded the distribution of baboons in this area, changes have occurred in the central part of the Kafue National Park and its surroundings. The area most affected is around the site of the Itezhi-Tezhi gorge (approximately 15.7S, 25.9E), where the Kafue River makes a right-angled eastwards turn from its middle course and enters its swampy lower reaches. The construction of the Itezhi-Tezhi dam at this site in 1974–1977 formed an extensive reservoir (Lake Itezhi-Tezhi), and most of the region bordering the

National Park to the east, immediately north of the dam and town of Itezhi-Tezhi, is urban or farmed. The environmental changes raise the question of human influence on the formation of hybrid baboon groups. In particular, it has been informally suggested to us that the Itezhi-Tezhi dam has promoted hybridization by creating a corridor between populations of the two species previously isolated by the river. This is unlikely, however, because, as documented by Ansell [1960, 1978] and by museum specimens, both species were already present on the right (western or southern) bank of the river where hybrids have now been found, long before the dam was constructed. It is likely that the treeless, swampy grasslands of the Kafue Flats have always prevented baboon dispersal across much of the *lower* course of the Kafue River, which runs approximately west to east [Ansell, 1960, 1978]. There is, however, no indication that the *middle* course of the Kafue (running north-south, approximately 14.6 S–25.9 S), which is flanked on both sides by hilly woodland inhabited by baboons, has ever formed a barrier or boundary between the species. Construction of the Itezhi-Tezhi dam at the junction of the middle and lower segments of the Kafue River's course would not have altered this situation.

Similarly, although we found the most obviously mixed and hybridized groups within a few tens of kilometers of the National Park Headquarters at Ngoma, there is no evidence that human activities in this area have influenced baboon biology in ways likely to promote introgression. The settlement includes a few houses and other facilities, but no cultivation, and wild animals are not harassed. The habitat of the hybrid groups is no more disturbed than other parts of the National Park. In particular, there are no indications that human influence has disproportionately affected one of the baboon species, a situation known to promote interspecific hybridization in cercopithecine monkeys [Bernstein, 1966; Detwiler et al., 2005].

The genetic evidence (summarized in Figs. 10 and 11) is still quantitatively inadequate for a full analysis of the relationship between grayfoot and kinda populations in the Kafue basin, but some provisional conclusions can be drawn. Most obviously, the genetics strongly support the inference from phenotypes that kindas and grayfoots are not reproductively isolated. Groups in the center of the transition zone that include a great variety of intermediate phenotypes also have both mitochondrial and Y-chromosome contributions from both parental species. Of the three known female specimens from WP 92, one had kinda mitochondria and two had grayfoot. Because females, unlike males, can probably be assumed to have been born in the group, these observations confirm the participation of females as well as males of both species in the ancestry of the hybrid groups. Mixed-taxon troops might have been initially formed by the amalgamation of whole groups [Beyene Gebru, 1998] or by intertroop migration of subgroups that included both males and females. Very rarely female chacmas in some populations have been seen to migrate between
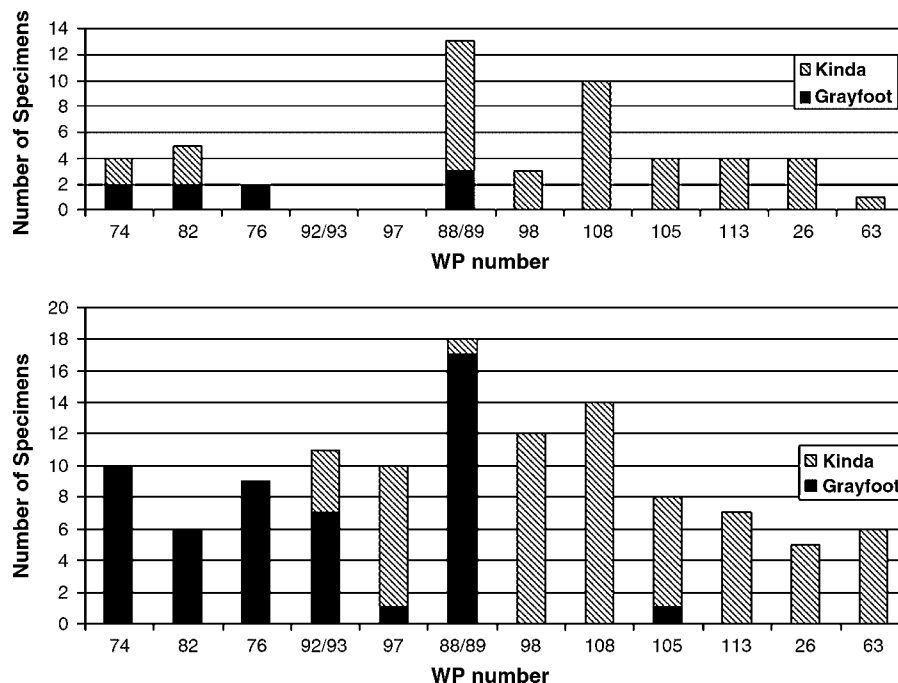

Fig. 10. Frequencies of taxon-specific types at Waypoints with >4 mitochondrial determinations. Above: Y-chromosome types; below: mitochondrial haplotypes.
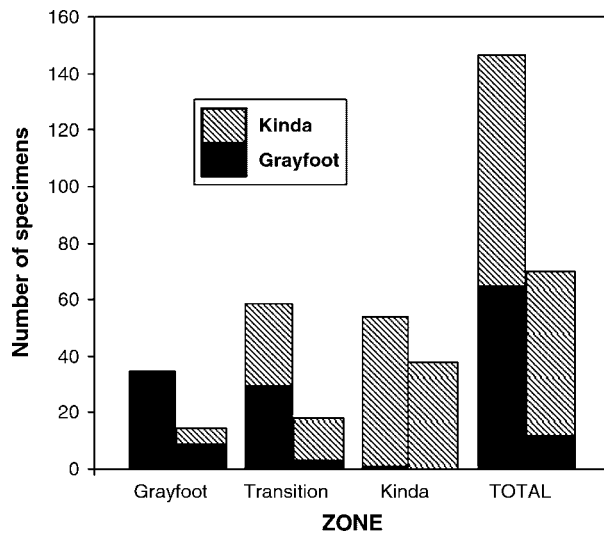
Fig. 11. Frequencies of taxon-specific types in three zones across the intertaxon boundary. Left column in each zone: mitochondrial haplotypes; right column: Y-chromosome types.

groups with the putative father of their dependent infants [Henzi et al., 2000], but whether female kindas ever migrate in this way is unknown. On a broader scale, kindas show patterns of genetic structuring in maternal, paternal, and biparentally inherited genes, strongly indicative of female philopatry and male dispersal [Burrell, 2009].

The occurrence of males with discordance between mtDNA and Y-haplotype supports the inference from phenotypic variation that, though they probably originated as mixed-taxon associations, these groups now include many animals with dual-taxon ancestry. Clearly, contemporary populations of kinda and grayfoot baboons in the Kafue basin do not comprise the reproductively incompatible end-forms of a ring species [Mayr, 1942].

A second less strongly supported inference from the genetic evidence is that the hybrid zone has moved northwards over time. On the grayfoot side of the hybrid zone, there is a low but widespread incidence of phenotypic hybrids and kinda Y-chromosomes, but on the kinda side of the zone extensive genetic sampling and observation of phenotypes failed to find a corresponding extended tail of grayfoot genes. This pattern may prove to be less pronounced when the west side of the river between WP 98 and WP 110 is investigated more fully. Present evidence, however, suggests an asymmetry in the transhybrid zone gene clines. Though not definitive, such a pattern is generally interpreted as a footprint of the hybrid zone's movement in the past [Barton & Hewitt, 1985; Buggs, 2007]—in this case, moving northwards as grayfoot populations expanded, displacing kindas, and hybridizing with them. This interpretation must remain hypothetical until tested against the transzone distribution of variation at other autosomal loci, as well as the

structure of variation within the grayfoot and kinda populations.

A third, unexpected, inference is suggested by the fact that kinda Y-chromosomes significantly outnumber kinda mitochondria in the hybrid zone, and were carried by all males with Y-mitochondrial discordance. It appears from this observation that the kinda contribution to hybridization came predominantly from males. Moreover, the diversity of Y-linked microsatellite alleles carried by the discordant animals suggests that multiple cross-matings occurred. Even if each of the six Y-haplotypes seen in discordant males represented only one event of primary hybridization, it is statistically significant that none of the discordances involved the reciprocal cross, between male chacmas and female kindas ($\chi^2 = 6$, $P = 0.014$). On the not unlikely assumption that all the observed cases of discordance resulted from independent hybridization events, this represents a very significant departure from the 50% frequency predicted from the null hypothesis of equal success for either type of cross-mating ($\chi^2 = 15$; $P = 0.0001$, two-tailed).

The distribution of genetic variation in *Papio* baboon populations includes many cases in which phenotypic, mitochondrial, and Y-chromosome variation are not concordant [Burrell, 2009; Burrell et al., 2010; Keller et al., 2010; Zinner et al., 2009]. As in other organisms, where males are the dispersing sex, most of these cases can be attributed to a history of strongly unidirectional male introgression or "swamping" (also known as "mitochondrial capture" or "transpatric migration") that changes a population's nuclear genome (and hence its phenotype), but leaves the native mitochondrial gene pool intact [Good et al., 2008; Roca et al., 2004; Rohwer et al., 2001; Verkaar et al., 2004]. In *Papio*, many populations exhibit mitochondrial–phenotypic discordance [Burrell, 2009; Keller et al., 2010; Zinner et al., 2009] and, as predicted in a scenario of swamping by male dispersal, the distribution of Y-haplotypes in these cases coincides with phenotype [Burrell et al., 2010]. For instance, the TSPY haplotype carried by grayfoot chacmas is identical to those of other chacma baboons [Burrell et al., 2010], even though all grayfoots carry mitochondrial haplotypes that are descended from haplotypes, evidently "captured" by nuclear swamping, from an ancestral population of yellow baboons [Burrell, 2009; Keller et al., 2010], and are quite distinct from those of chacmas further south.

Among groups sampled in the contemporary Kafue hybrid zone, the group at WP 97 (although it was not observed at close range and its Y-chromosomes could not be typed) apparently shows the combination of grayfoot-like phenotype and (mostly) kinda mitochondria that is the expected outcome of nuclear swamping. In the Kafue hybrid zone as a whole, however, it is the Y-chromosome that is

discordant, with kinda Y-chromosomes occurring frequently in groups that are phenotypically and mitochondrially grayfoot, as well as in hybrid groups with mostly grayfoot mitochondria. Such Y-chromosome–phenotype discordance is much rarer than mitochondrial–phenotype discordance in species where females are philopatric and males disperse. It is predicted, however, in a situation where one species owing to ecological advantage is expanding at the expense of its neighbor, but males of the invaded species are advantaged in one-on-one mating competition. For example, discordance between phenotype and Y-chromosome haplotype in a population of long-tailed macaques (*M. fascicularis*) has been attributed to larger, more aggressive male rhesus monkeys (*M. mulatta*) from a neighboring population, transmitting their Y-chromosomes into the *M. fascicularis* population without modifying the recipient group's phenotype or mitochondrial gene pool [Tosi et al., 2003a].

Though unusual in showing Y-phenotype discordance, the macaque case conforms to the usual pattern in hybridizing vertebrates, in that the "father species" is the larger sized of the parental taxa [Wirtz, 1999]. Kinda × chacma mating involves a much greater size discrepancy than in the macaques and, remarkably, in the baboons it is the *smaller* species that is disproportionately contributing Y-chromosomes to the hybrid zone. A male kinda in a mixed-taxon group would have to compete for mates with male chacmas approximately twice his body weight, which aggressively defend access to estrous females they are consorting. Most exceptions to "Wirtz's Rule," in which males of the smaller and apparently weaker species are disproportionately successful, occur in the context of "sneaky" matings [Redenbach & Taylor, 2003; Wirtz, 1999]. We hypothesize that male kindas may occasionally be able to capitalize upon their small size and immature appearance to sneak matings with female chacmas.

With a body mass of about 16 kg, a full-grown male kinda is the size of a male chacma that has reached about 50–55% of its adult body mass. It has the short face correlated with small size [Leigh, 2006] and the linear build and high-pitched voice characteristic of subadulthood in larger baboons [Ey et al., 2007; Fischer et al., 2002]. Subadults with these characteristics normally pose little reproductive threat to adult male baboons. Among Ethiopian Anubis baboons [Phillips-Conroy & Jolly, 2004], for example, a male of 50–55% mean adult body mass is typically entering the second half of its 6th year. Its serum testosterone level is still in the juvenile range and testicular volume, although it increases markedly during this interval, is less than 40% of the adult mean. Permanent canine teeth are in the early stages of emergence [Phillips-Conroy & Jolly, 1988]. Robusticity (measured as cube root of body mass/summed limb lengths) reaches its lowest level during this interval

(Awash National Park Baboon Project, unpublished). Among East African yellow baboons, developmental milestones appear to be comparable. Six males of 50–55% adult body mass from Mikumi National Park, Tanzania, had testes less than 30% of adult volume [J. Rogers and J. Phillips-Conroy, unpublished]. At Amboseli, male yellow baboons undergo rapid testicular enlargement in the middle of their 6th year. In this subadult phase, they may be fertile but they rarely mate with estrous females, and their reproductive success is very low [Alberts & Altmann, 1995; Alberts et al., 2006; Altmann et al., 1981].

Thus, an adult male kinda would present the gestalt of a young subadult to both male and female chacmas. If the chacmas respond in kind, females will not consider the kinda male in the calculus of paternity confusion [Moscovice et al., 2010; Palombit, 2009] and, more significantly, male chacmas may not perceive him as a serious rival in the context of mating. A comparable situation has been observed in captive hamadryas baboons, where fully adult males seem not to prevent reproductively active, juvenile or younger subadult males from copulating with estrous females [Zinner et al., 2006]. An additional factor in the Kafue case may be the male kinda's propensity to actively initiate and maintain an extended grooming bout with a female, even when she is not estrous [Phillips-Conroy et al., 2009; Weyher, 2010]. Among chacmas, as in most baboons, grooming is mainly a female activity and the male kinda's behavior has no parallel in male chacmas of any age [Wittig et al., 2008]. In the absence of direct observation, we can only speculate about the response it might elicit from chacmas. It seems likely that it would be pleasant for the female groomee [Wittig et al., 2008] and at the same time might appear "feminine" (and therefore nonthreatening) to a male chacma. As a result, male kindas may be able to approach a consorting pair closely enough to permit occasional furtive copulations, perhaps when the consorting male's attention is distracted by a conspecific rival. Cross-species mating could also result if male kindas mate with and sometimes fertilize young, nulliparous female chacmas, whose first few estrous cycles usually do not attract the interest of full adult males of their own species [Beehner, personal communication].

The apparent rarity of the reciprocal (male chacma × female kinda) cross might be similarly explained. "Wirtz's Rule" [Wirtz, 1999] assumes that males of the two species are equally motivated to compete over fertile females of the smaller species, but in fact female kindas may be relatively unattractive to full-grown male chacmas, because they appear to be immature. Body mass of an adult female kinda (mean~10 kg) is about 2/3 that of a full grown female chacma's [Barrett & Henzi, 1997; Delson et al., 2000; Dunbar, 1990]. Two-thirds grown female baboons are typically either prepubescent or are in their first year

of cycling. Cross-sectional data from Awash National Park suggest that female anubis attain 2/3 of adult body weight about 4 years of age and begin cycling soon after, but rarely become recognizably pregnant before attaining 80% of mean adult body mass in their 6th year [Phillips-Conroy & Jolly, 2004; Jolly & Phillips-Conroy, unpublished]. More precise longitudinal data from Amboseli show median age at menarche in yellow baboons to be 4.5 years, with median first conception at about 5.3 years [Alberts & Altmann, 1995]. Thus, a male chacma judging an adult female kinda by chacma size standards would see her either as prepubertal or, if visibly estrous, as an adolescent in the ~10 month interval in which cycling occurs without conception. Among chacmas, as in other baboons [Anderson, 1986], high-ranking males show little interest in such young females and generally ignore their sexual solicitations [J. Beehner, personal communication]. If this speculative interpretation proves to be correct, the apparently juvenile-to-subadult appearance of kindas has a double effect, both allowing cross-breeding by male kindas in mixed troops and also inhibiting the reciprocal cross. Another possibility is that the dearth of offspring resulting from grayfoot × kinda mating is explained by a genetic incompatibility between the chacma-Y and the kinda autosomal genotype, a situation with no known parallel in the genus *Papio*. A more likely alternative, not incompatible with prezygotic selection mediated by behavior, is obstetrically driven, postzygotic selection. It is conceivable that the size discrepancy between the taxa makes it difficult or even impossible for a female kinda to successfully carry and deliver the large fetus sired by a grayfoot male.

Whether by pre- or postzygotic selection, the effect of the size difference between the taxa would be to bias the direction of *initial* hybridization in favor of male kindas. It is important to note, however, that this effect would not necessarily impede the movement of the hybrid zone toward the kinda side. Such movement could be driven by simple population pressure from the grayfoot side. Alternatively (or in addition), it could occur by selection in favor of grayfoot-like phenotypic characters (especially, perhaps, larger body size) in kinda populations that received grayfoot genes via immigrant male hybrids. If the latter (as our results suggest) were almost always carriers of kinda Y-chromosomes, there would be no impact upon the Y-gene pool of the recipient kinda population. (The immigrants' grayfoot-derived mitochondria, of course, would not be propagated.) The result would be a population that carried only kinda mitochondria and Y-chromosomes, but was phenotypically somewhat "grayfootized." Our findings from WP 98 (K/K males in a kinda-like hybrid group) and WP 105 (one G/K male specimen from a kinda group) are compatible with this speculation.

Much more genetic and phenotypic information and systematic observations of behavior in unmixed, mixed, and hybridized troops in the Kafue are needed to test this hypothetical scenario of interbreeding. Also, yet to be investigated are the dynamics of interaction among grayfoot, kinda, and larger yellow baboons in and around the lower Luangwa Valley where a three-taxon hybrid zone has been found [Bergey et al., 2009; Burrell, 2009; Jolly & Phillips-Conroy, 2007]. Here, too, there is the potential for interactions to be influenced by taxon-specific behavioral and size-related differences. Finally, we note that the external appearance of some Kafue hybrids is very similar to that of "large" or "typical" yellow baboons (*Papio cynocephalus cynocephalus*) of Malawi, northern Mozambique, and eastern Tanzania. This observation suggests the intriguing hypothesis that, requiring genetic testing, the latter taxon itself had an ancient hybrid origin.

ACKNOWLEDGMENTS

REFERENCES

Ackermann R, Rogers J, Cheverud J. 2006. Identifying the morphological signatures of hybridization in primate and human evolution. Journal of Human Evolution 51:632–645.

Alberts SC, Altmann J. 1995. Preparation and activation: determinants of age at reproductive maturity in male baboons. Behavioral Ecology and Sociobiology 36:397–406.

Alberts SC, Altmann J. 2001. Immigration and hybridization patterns of yellow and anubis baboons in and around Amboseli, Kenya. American Journal of Primatology 53: 139–154.

Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. Animal Behaviour 72:1177–1196.

Altmann J, Altmann S, Hausfater G. 1981. Physical maturation and age estimates of yellow baboons, *Papio cynocephalus*, in Amboseli National Park, Kenya. American Journal of Primatology 1:389–399.

Anderson C. 1986. Female age: male preference and reproductive success in primates. International Journal of Primatology 7:305–326.

Ansell WFH. 1960. Mammals of Northern Rhodesia. Lusaka, Northern Rhodesia: The Government Printer. 24p.

Ansell W. 1978. The mammals of Zambia. Chilanga, Zambia: The National Parks and Wildlife Service. 243p.

Barrett L, Henzi SP. 1997. An inter-population comparison of body weight in chacma baboons. South African Journal of Science 93:436–438.

Barton NH, Hewitt NH. 1985. Analysis of hybrid zones. Annual Review of Ecological Systems 16:113–148.

Bergey CM, Jolly CJ, Phillips-Conroy JE, Barrell A, Disotell TR. 2009. Mitochondrial population structure of a baboon contact zone. American Journal of Physical Anthropology 138:89.

Bernstein I. 1966. Naturally occurring primate hybrid. Science 154:1559–1560.

Beyene Gebru S. 1998. The role of female mating behavior in hybridization between anubis and hamadryas baboons in Awash, Ethiopia. Dissertation Abstractions International 59:1648.

Buggs R. 2007. Empirical study of hybrid zone movement. Heredity 99:301–312.

Burrell A. 2009. Phylogenetics and population genetics of Central African baboons [PhD]. New York: New York University. 323p.

Burrell AS, Jolly CJ, Tosi AJ, Disotell TR. 2009. Genetic data suggest the kipunji mangabey (Rungwecebus kipunji) is hybrid in origin. American Journal of Physical Anthropology 138:99.

Burrell AS, Jolly CJ, Phillips-Conroy JE, Disotell TR. 2010. Conflicting mitochondrial and Y-chromosomal phylogenies indicate complex evolutionary history of Papio baboons. American Journal of Physical Anthropology 74.

Delson E, Terranova CJ, Jungers WL, Sargis EJ, Jablonski NG, Dechow PC. 2000. Body mass in Cercopithecidae (Primates, Mammalia): estimation and scaling in extinct and extant taxa. Anthropological Papers of the American Museum of Natural History 83:1–159.

Detwiler KM, Burrell AS, Jolly CJ. 2005. Conservation implications of hybridization in African cercopithecine monkeys. International Journal of Primatology 26:661–684.

Di Fiore A. 2005. A rapid genetic method for sex assignment in non-human primates. Conservation Genetics 6:1053–1058.

Dunbar RIM. 1990. Environmental determinants of intraspecific variation in body weight in baboons. Journal of Zoology, London 220:157–169.

Erler A, Stoneking M, Kayser M. 2004. Development of Y-chromosomal microsatellite markers for nonhuman primates. Molecular Ecology 13:2921–2930.

Ey E, Hammerschmidt K, Seyfarth RM, Fischer J. 2007. Age- and sex-related variations in clear calls of Papio ursinus. Intenational Journal of Primatology 28:947–960.

Fischer J, Hammerschmidt K, Cheney DL, Seyfarth RM. 2002. Acoustic features of male baboon loud calls: influences of context, age, and individuality. Journal of the Acoustical Society of North America 111:1465–1474.

Frost SR, Marcus LF, Bookstein FL, Reddy DP, Delson E. 2003. Cranial allometry, phylogeography, and systematics of large-bodied papionins (Primates: Cercopithecinae) inferred from geometric morphometric analysis of landmark data. Anatomical Record 275A:1048–1072.

Good J, Hird S, Reid N, Demboski J, Steppan S, Martin-Nims T, Sullivan J. 2008. Ancient hybridization and mitochondrial capture between two species of chipmunks. Molecular Ecology 17:1313–1327.

Groves CP. 2001. Primate taxonomy. Washington, DC: Smithsonian Institution Press. 350p.

Grubb P. 1999. Evolutionary processes implicit in distribution patterns of modern African mammals. African biogeography, climate change and human evolution. New York: Oxford University Press. p 150–164.

Hapke A, Zinner D, Zischler H. 2001. Mitochondrial DNA variation in Eritrean hamadryas baboons (Papio hamadryas hamadryas): life history influences population genetic structure. Behavioral Ecological Sociobiology 50:483–492.

Harrison R. 1990. Hybrid zones: windows on evolutionary process. In: Futuyuma D, Antonovics J, editors. Oxford surveys in evolutionary biology. Oxford: Oxford University Press. p 69–128.

Henzi SP, Barrett L, Weingrill A, Dixon P, Hill RA. 2000. Ruths amid the alien corn: males and the translocation of female Chacma baboons. South African Journal of Science 96:61–62.

Jolly CJ. 1993. Species, subspecies, and baboon systematics. Species, species concepts, and primate evolution. New York: Plenum Press. p 67–107.

Jolly CJ. 2001. A proper study for mankind: analogies from the Papionin monkeys and their implications for human evolution. Yearbook of Physical Anthropology 44:177–204.

Jolly CJ, Phillips-Conroy JE. 2007. Ecology, history and society as determinants of hybrid zone structure in baboons. American Journal of Physical Anthropology 138.

Keller C, Roos C, Groeneveld L, Fischer J, Zinner D. 2010. Introgressive hybridization in southern African baboons shapes patterns of mtDNA variation. American Journal of Physical Anthropology 142:125–136.

Kingdon J. 1997. The Kingdon guide to African mammals. London: Academic Press.

Leigh SR. 2006. Cranial ontogeny of Papio baboons (Papio hamadryas). American Journal of Physical Anthropology 130:71–84.

Mayr E. 1942. Systematics and the origin of species. New York: Columbia University Press.

Moscovice L, Di Fiore A, Crockford C, Kitchen D, Wittig R, Seyfarth R, Cheney D. 2010. Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. Animal Behaviour 79:1007–1015.

Nagel U. 1973. A comparison of Anubis baboons, Hamadryas baboons and their hybrids at a species border in Ethiopia. Folia Primatologica 19:104–165.

Palombit R. 2009. ''Friendship'' with males: a female counter-strategy to infanticide in chacma baboons of the Okavango Delta. Sexual coercion in primates and humans: an evolutionary perspective on male aggression against females. Cambridge, MA: Harvard University Press. p 377–409.

Phillips-Conroy JE, Jolly CJ. 1986. Changes in the structure of the baboon hybrid zone in the Awash National Park, Ethiopia. American Journal of Physical Anthropology 71:337–350.

Phillips-Conroy JE, Jolly CJ. 1988. Dental eruption schedules of wild and captive baboons. American Journal of Primatology 15:17–29.

Phillips-Conroy JE, Jolly CJ. 2004. Male dispersal and philopatry in the Awash baboon hybrid zone. Primate Report 68:27–52.

Phillips-Conroy JE, Jolly CJ, Weyher AH. 2009. Observations of ''kinda'' baboons (Papio cynocephalus kindae) in Zambia: adult males as the active partner in male-female grooming dyads. American Journal of Primatology 71:65.

Redenbach Z, Taylor E. 2003. Evidence for bimodal hybrid zones between two species of char (Pisces: Salvelinus) in northwestern North America. Journal of Evolutionary Biology 16:1135–1148.

Roca A, Georgiadis N, O'Brien S. 2004. Cytonuclear genomic dissociation in African elephant species. Nature Genetics 37:96–100.

Rohwer S, Bermingham E, Wood C. 2001. Plumage and mitochondrial DNA haplotype variation across a moving hybrid zone. Evolution 55:405–422.

Ronquist F, Huelsenbeck J. 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

Samuels A, Altmann J. 1986. Immigration of a Papio anubis male into a group of Papio cynocephalus baboons and evidence for an anubis-cynocephalus hybrid zone in Amboseli, Kenya. International Journal of Primatology 7: 131–138.

Tosi AJ, Morales JC, Melnick DJ. 2003a. Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. Evolution 57:1419–1435.

Tosi AJ, Disotell TR, Morales JC, Melnick DJ. 2003b. Cercopithecine Y-chromosome data provide a test of competing morphological evolutionary hypotheses. Molecular Phylogenetics and Evolution 27:510–521.

Tung J, Charpentier M, Garfield D, Altmann J, Alberts S. 2008. Genetic evidence reveals temporal change in hybridization patterns in a wild baboon population. Molecular Ecology 17:1998–2011.

Verkaar ELC, Nijman IJ, Beeke M, Hanekamp E, JA L. 2004. Maternal and paternal lineages in cross-breeding bovine species. Has Wisent a hybrid origin? Molecular Biology and Evolution 21:1165–1170.

Weyher A. 2010. Behavior observations of kinda baboons (*Papio cynocephalus kindae*) in Zambia. American Journal of Physical Anthropology 50:241–242.

Wirtz P. 1999. Mother species-father species: unidirectional hybridization in animals with female choice. Animal Behaviour 58:1–12.

Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. 2008. Focused grooming networks and stress alleviation in wild female baboons. Hormones and Behavior 54:170–177.

Zinner D, Krebs E, Schrod A, Kaumanns W. 2006. Early sexual maturity in male hamadryas baboons (*Papio hamadryas hamadryas*) and its reproductive implications. American Journal of Physical Anthropology 129:584–590.

Zinner D, Groeneveld LF, Keller C, Roos C. 2009. Mitochondrial phylogeography of baboons (*Papio* spp.)—indication for introgressive hybridization? BMC Evolutionary Biology 9:83.