

Differences Between Vervets (*Cercopithecus aethiops*) and Patas Monkeys (*Erythrocebus patas*) in Agonistic Interactions Between Adult Females

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*We examined agonistic interactions between adult females in wild, unprovisioned patas monkeys (*Erythrocebus patas*) and vervets (*Cercopithecus aethiops*). The dominance hierarchy of patas is far less clear than that of vervets. Patas had fewer interactions per dyad, fewer dyads with interactions, and a high percentage (18%) of reversals in which lower-ranking females won in agonistic interactions with higher-ranking females. Although the rank ordering of the kinds of interactions patas and vervets displayed is similar, with avoidance being the most frequently observed agonistic response to approaches by other females, patas were chased and supplanted more often than vervets were. The resources over which females were supplanted also differ between species. Supplants over food comprise smaller proportion of total supplants patas than for vervets. Patas appear to feed on less usurpable foods than vervets. We conclude that (1) *Erythrocebus* and *Cercopithecus* spp., except *C. aethiops*, should not be categorized with other *Cercopithecinae*, and *C. aethiops* should not be categorized with other *Cercopithecus* spp. and *Erythrocebus*, in discussions and analyses of relationships between females within groups and (2) ecological conditions, i.e., usurpability of foods, can override phylogenetic history as the selective pressure determining the nature of female competitive relationships within groups.*

KEY WORDS: dominance; food resources; rank inheritance; usurpability.

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INTRODUCTION

Competitive relationships between females are of central importance in understanding variation in female reproductive success because females that compete most effectively against other females to gain access to limiting resources are likely to achieve greater reproductive success than females that are less effective competitors (Silk, 1993; Pusey *et al.*, 1997). An expression of relative competitive ability in group-living animals is the dominance hierarchy, in which higher-ranking individuals have preferential access to resources over lower-ranking individual (Pusey and Packer, 1997).

The norm for Old World female primates is to live with other females in social groups (Wrangham, 1987). In many group-living species, females form dominance hierarchies within their groups that are linear, in which female A has priority of access to resources over all other females, female B has priority of access to resources over all females except for female A, and female C has priority of access to resources over all females except for females A and B. In stable dominance hierarchies, relative rankings are consistent over time. Reversals, in which a lower-ranking female sometimes wins in agonistic interactions with a higher-ranking female, are rare in stable, linear dominance hierarchies. Stable, linear dominance hierarchies are typical of some savannah baboons [*Papio cynocephalus* (Hausfater, 1975; Hausfater *et al.*, 1982; Samuels *et al.*, 1987), *P. anubis* (Barton and Whiten, 1993)], macaques [*Macaca mulatta* (Missakian, 1972), *M. sylvanus* (Deag, 1977), *M. radiata* (Silk *et al.*, 1981), *M. fuscata* (Chapais, 1988a)], and vervets [*Cercopithecus aethiops* (Seyfarth, 1980; Whitten, 1983; this study)]. In these species, reversals against the hierarchy are rare even when maturing females enter the dominance hierarchy (Missakian, 1972; Hausfater *et al.*, 1982). Maturing females typically assume ranks near or directly below that of their mothers (Missakian, 1972; Hausfater *et al.*, 1982; Horrocks and Hunte, 1983; Samuels *et al.*, 1987). Inheritance of rank and stability of dominance relationships are achieved both by maternal support of daughters and by nonkin alliances against lower-ranking individuals (Hausfater, 1982; Silk, 1987; Walters and Seyfarth, 1987; Chapais, 1988a, b; Chapais *et al.*, 1991; Pereira, 1992).

This pattern of stable, linear, matrilineally determined dominance hierarchies is not typical of all Old World primates (Isbell, 1991; Silk, 1993; Strier, 1994). In gorillas (*Gorilla gorilla*), for example, agonistic interactions are infrequent and dominance hierarchies are weak at best (Harcourt, 1979; Harcourt and Stewart, 1987; Watts, 1985, 1994). Inheritance of maternal rank does not occur partly because female gorillas typically leave their mothers and transfer between groups (Harcourt, 1978). In some colobine species, females also regularly, or at least occasionally, transfer out of their natal groups

[red colobus, *Colobus badius* (Struhsaker, 1975; Marsh, 1979); capped langurs, *Presbytis pileata* (Stanford, 1991); Thomas's langurs, *Presbytis thomasi* (Sterck, 1997; reviews in Moore, 1984, and Isbell and Van Vuren, 1996)]. The fact that dominance hierarchies among females in most colobines are either undetectable (Struhsaker and Leland, 1987; Newton and Dunbar, 1994) or are unstable over time [e.g., Hanuman langurs, *Presbytis entellus* (Hrdy and Hrdy, 1976; Borries *et al.*, 1991)] may suggest a causal link between female residency in natal groups and stable, matrilineally based dominance hierarchies (Silk, 1993). However, although female residency in natal groups may be necessary for the formation of stable, linear, matrilineally inherited dominance hierarchies, it does not appear to be sufficient in all cases. In Hanuman langurs, dominance hierarchies are unstable over time, rank is not inherited, and maturing females rise in rank above older adult females including their mothers, despite the fact that females typically remain in their natal groups (Hrdy and Hrdy, 1977; Borries *et al.*, 1991; Borries, 1993).

These differences in dominance relationships among female Old World primates have been hypothesized ultimately to reflect differences in food quality or distribution (Wrangham, 1980; van Schaik, 1989; Isbell, 1991). When foods are usurpable, higher-ranking individuals can take them away from lower-ranking individuals either directly or indirectly (by supplanting), and dominance hierarchies are clearly identifiable by human observers. Usurpability has been suggested to be a function of food distribution (Whitten, 1983; Harcourt, 1987; Boccia *et al.*, 1988; Barton and Whiten, 1993), but more specifically, it is likely an interactive function of abundance and food-site depletion time (FSDT) (Shopland, 1987; Janson, 1990; Isbell *et al.*, 1998). Baboons, macaques, and vervets typically feed on seeds, fruits, gums, or corms, or other foods that can have long depletion times (Altmann and Altmann, 1970; Post *et al.*, 1980; Wrangham and Waterman, 1981; Barton and Whiten, 1993), whereas some colobines, some guenons, patas monkeys (*Erythrocebus patas*), and gorillas typically feed on leaves or arthropods or other foods that are either ubiquitous (and thus not worth usurping) or quickly ingested (and thus difficult to usurp) (Struhsaker, 1975; Isbell, 1983, 1998; Watts, 1985; Stanford, 1991; Oates, 1994).

If usurpability of foods is ultimately responsible for differences in female dominance relationships, then the patterning of dominance relationships should be effectively independent of phylogeny (except that closely related species often have broadly similar diets) and more dependent on ecology. This can be examined in closely related species that eat foods differing in usurpability.

Patas monkeys and vervets are excellent subjects for such a comparison. They are closely related (Disotell, 1996), and both live in cohesive groups with stable female residency, i.e., females remain in their natal

groups throughout their lives. They are also sympatric in parts of their biogeographical ranges. Although both species feed extensively on gums (patas, 14–37%; vervets, 39–57%), patas also feed more extensively than vervets on arthropods and other small food items (~40%; vervets, ~6%), whereas vervets feed more extensively on plant reproductive parts (flowers, seeds, and fruit) and other food items that are depleted more slowly at feeding sites (~17%; patas, ~8%) (Isbell, 1998; Isbell *et al.*, 1998). These differences suggest that the foods of patas and vervets differ in their usurpability.

Although patterns of dominance relationships are well-known for vervets, disagreement exists about patterns of dominance relationships in patas monkeys. Patas groups have been described both as having stable, linear dominance hierarchies (Kaplan and Zucker, 1980; Jacobus and Loy, 1981; Loy and Harnois, 1988; Nakagawa, 1992; Goldman and Loy, 1997) and as having only poorly defined dominance hierarchies at best (Rowell and Olson, 1983; Cords, 1987; Walters and Seyfarth, 1987). Before our study no data on dominance had been presented from free-ranging, unprovisioned patas monkeys, however, and the possibility exists that the dominance hierarchies observed in provisioned patas monkeys are a direct result of artificially high concentrations of food that increase the ability of individuals to usurp foods beyond that normally experienced by unprovisioned animals.

Here we examine dyadic agonistic interactions between adult females in patas monkeys and vervets to describe the pattern of dominance relationships in free-ranging, unprovisioned female patas relative to vervets and to determine whether dominance relationships in these two species are consistent with the hypothesis that variation in usurpability of foods can explain differences in female dominance relationships within groups of primates.

STUDY SITE AND METHODS

The study was conducted as part of a long-term, ongoing comparative study of patas monkeys and vervets at Segera Ranch on the Laikipia Plateau of north-central Kenya (36°50'E, 0°15'N). Segera is a cattle ranch and conservation area that operates with a nearly complete complement of native animals; at least 17 species of ungulates and 5 species of large carnivores inhabit the area. Researchers, water troughs, fences, cattle, and cattle herders are the only anthropogenic intrusions into the lives of the monkeys; the latter two factors have been present for several centuries. Rainfall is variable, but averages 700 mm per year, with September and

January–February typically being the drier months (Isbell, 1998; Isbell *et al.*, 1998).

From June 1993 to April 1997 we observed two groups of vervets and one group of patas monkeys. The smaller group of vervets had only 2 adult females and is not included in analyses below. The large group of vervets varied from 26 to 30 individuals and included 6–9 adult females. The patas group varied from 28 to 50 monkeys and included 10–15 adult females. All individuals were habituated to the presence of observers, and all vervets and adult patas were individually recognizable by observers via tail kinks, differences in pelage, coloration of ischial callosities, nipple coloration, and other natural characteristics as markers. Adult female status in vervets is operationally defined by larger body size and the presence of elongated nipples, which indicated reproduction before the study. Adult female status in patas is operationally defined by larger body size, pelage of a darker red-orange than that of smaller individuals, a nose covered completely by white fur (in East African patas, individuals have more extensively white noses as they mature), and the presence of elongated nipples.

We did not know exact dates of birth for the one female vervet or the five female patas that became adult during the study. We based our classification of maturational stage for the female vervet on experience with vervets of known ages elsewhere (Isbell *et al.*, 1991), body size, the absence of elongated nipples, and a generally younger appearance (i.e., healthy pelage, no scars, robust body). She was estimated to be a subadult (3 years old) when she was first recognized individually. We estimated maturational stages for the five female patas by the presence of incompletely white pelage on the nose, light orange pelage darkening over time to reddish-orange on the torso, the absence of elongated nipples, and smaller body size. There was no female in the patas group with reddish-orange pelage and completely white nose but without elongated nipples, indicating that all the adult females had reproduced at least once before or during the study and were accounted for. The five female patas that matured during the study were first recognized as individuals either during pregnancy or upon reproducing. All females included in the dominance hierarchies are limited to subadults just before transition to adult status and adults.

Seven observers collected data on agonistic interactions via identical data sheets and operational definitions. Whenever agonistic interactions were observed, the observers recorded the date, group, identities of the actor and recipient, and the recipient's response to the actor's approach. Approaches could range in intensity from walking to running but were limited to approaches to ≤ 2 m of the recipient. The recipient's response to the approach was recorded as leaving, avoiding, being supplanted, or being chased. Leaving is moving casually away to a distance of at least two meters.

Because leaving does not necessarily indicate submission by the recipient (but see Seyfarth, 1976, for baboons), we omit it from our analyses. Avoiding is cringing, flinching, cowering, or abruptly moving away from the approacher but to a distance ≤ 2 m. The recipient was supplanted when the approacher replaced her in its exact spot. We also recorded the resource that was given up during the supplant. Chases were obvious, with the approacher running at or toward the recipient, which responded by running away. Supplants and chases precluded continued use of a given resource by the recipient, whereas avoids did not, and so are considered functionally higher in intensity than avoids.

Observers differed consistently in the rates at which they recorded aggressive interactions, i.e., observers who recorded interactions frequently for patas also recorded interactions frequently for vervets; and vice versa. They also differed in the kinds of dominance interactions they recorded ($\chi^2 = 39.84$, $df = 6$, $P < 0.001$). Analyses of rates and kinds of interactions are therefore limited to the observer, Pruettz, who recorded the highest rates of interactions and recorded interactions between adult females whether or not their identities could be determined. We used data from all observers to construct dominance matrices. Dominance hierarchies using all data were constructed to minimize the number of reversals, i.e., interactions below the diagonal. We also constructed dominance matrices over subsets of time—each 15 months or longer—for patas to examine the mobility of females over time. Construction of these dominance hierarchies is based on minimizing (1) the number of reversals, (2) the distance of reversals from the diagonal, and (3) in the case of the second and third periods of time, changes against the previous period's hierarchy.

RESULTS

Over the 46-month period, we observed in vervets 127 aggressive interactions in 26 of 36 (72%) possible dyads (Fig. 1A). No reversal occurred in nearly 4 years, even as a maturing female (MOO) entered the adult hierarchy. Using a test based on the number of circular triads (Appleby, 1983), we found the dominance hierarchy to be significantly linear [$d = 6.25$, $P < 0.001$; Table I of Appleby (1983)]. Although alternative tests may be somewhat more conservative, they would not change our conclusion of linearity (de Vries, 1995). Moreover, the index of linearity is high ($K = 0.79$; 0 = no linearity and 1 = complete linearity). The index of linearity is < 1 because there is a lack of information for some dyads. The long-term (3.8-year) temporal stability and linearity of the dominance hierarchy in

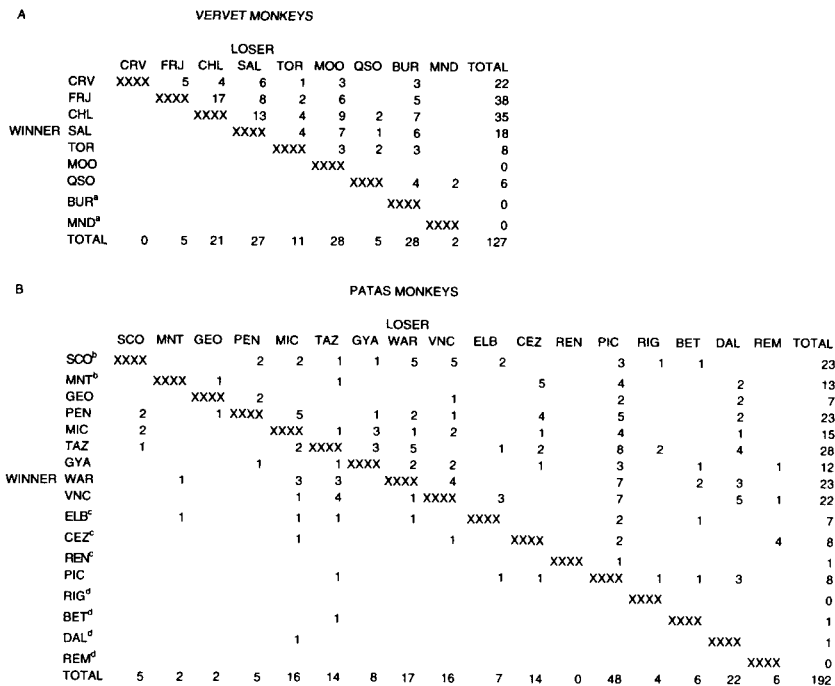


Fig. 1. Dominance matrices of female vervets (A) and patas monkeys (B) constructed from supplants, chases, and approach-avoidance interactions to minimize reversals (records below the diagonal). The dominance hierarchy of patas monkeys is less confidently determined than the dominance hierarchy of vervets because patas had more reversals, fewer dyads with interactions, and fewer interactions per dyad. The females sharing a superscript could be interchanged without affecting the number of reversals; note that there are 2 such vervets but 9 such patas.

Table I. Differences Between Patas Monkeys and Vervets in Types of Agonistic Interactions Displayed by Adult Females Toward Other Adult Females^a

	Patas monkeys		Vervets	
	%	n	%	n
Approach-avoid	47	(92)	70	(63)
Chase	13	(25)	8	(7)
Supplant	40	(77)	22	(20)
Total	100	(194)	100	(90)

^a $\chi^2 = 12.64, P < 0.01, df = 2.$

this group of vervets agree with and extend the findings for vervets elsewhere (Seyfarth, 1980; Cheney *et al.*, 1981; Whitten, 1983).

Over the same 46-month period, we observed in patas 192 aggressive interactions in which both interactants were identified in 69 of 118 (58%) possible dyads; not all dyads were possible because some females died before others matured (Fig. 1B). Although we constructed a dominance matrix, the dominance hierarchy not significantly linear ($d = 160.2$, $\chi^2 = 30.4$, $df = 24$, $P = 0.17$). The degree of linearity is also much less than that of vervets ($K = 0.21$). Reversals accounted for 18% (34/192) of the agonistic interactions. Eleven of 17 females sometimes lost to lower-ranking females.

Dominance hierarchies constructed for patas over three subsets of time revealed shifts in the relative positions of some females (as measured by the percentage of females outranked) and continued high frequencies of reversals (Fig. 2). In the first 15 months of the study, reversals accounted for 6% (3/52) of all agonistic interactions. In the second 15 months, reversals increased to 14% (13/91 interactions). During the second period, two females (SCO and MIC) rose higher than others in the hierarchy, with SCO moving from outranking 61% to outranking 92% of the females and MIC from 23 to 69%. One female (WAR) fell considerably farther in rank than others, from outranking 100% of the females initially to 77% by the end of the second period. In the last period, reversals accounted for 10% (5/49) of all agonistic interactions. Compared to the immediately preceding 15 months, relative ranks changed again for some females, with two females rising in rank (ELB and GYA) and two females falling (WAR and MIC). Compared to the first 15 months of the study, four females rose in rank (SCO, GYA, VNC, and MIC), increasing their average percentage of females outranked from 46 to 71%. The highest-ranking female in the first 15 months (WAR) fell in rank to become midranking by the end of the third period. The mean percentage of reversals for the three time periods is lower than the overall percentage because more reversals could be eliminated by changing the positions of females over different periods.

Over the entire duration of the study, two females (SCO and TAZ) accounted for almost half (16/34) of all reversals (Fig. 1B). They were the only younger, primiparous females during the first period of the study. During the first 15 months, SCO and TAZ initiated only 10% (5/52) of the agonistic interactions ($\chi^2 = 0.91$, $df = 1$, $P > 0.30$; expected values based on percentage representation among the females). As the study progressed, however, they initiated increasingly more agonistic interactions with other females [second period, 23% (21/91), $\chi^2 = 5.74$, $df = 1$, $P < 0.02$; third period, 51% (25/49), $\chi^2 = 60.6$, $df = 1$, $P < 0.001$], indicating that they challenged others increasingly over time as they entered into adult relationships (Rowell and Olson, 1983). This was not contradicted by the

		LOSER													TOTAL	
		WAR	MNT	GEO	PEN	TAZ	SCO	GYA	VNC	CEZ	REN	MIC	PIC	DAL	REM	TOTAL
A	WAR	XXXX	1						1							5
	MNT		XXXX	1		1				1			2	1		6
	GEO			XXXX	2				1				2	2		7
	PEN				XXXX	1		1	1	4		1	2	2		12
	TAZ					XXXX	1		1	1		1	1		4	
	SCO						XXXX		1						1	
	GYA							XXXX	2						1	5
	WINNER VNC						1		XXXX				2		1	3
	CEZ									XXXX			1		4	5
	REN										XXXX		1			1
	MIC											XXXX		1		1
	PIC												XXXX	1		1
	DAL													XXXX		1
	REM														XXXX	0
	TOTAL		0	1	2	2	3	2	0	6	6	0	2	13	9	6

		MNT	SCO	PEN	WAR	MIC	VNC	TAZ	GYA	ELB	CEZ	REN	PIC	DAL	REM	TOTAL
B	MNT	XXXX									4		2	1		7
	SCO		XXXX	1	1	2	1	1	1				1			8
	PEN			XXXX	2	4		1					2			9
	WAR				XXXX	1	3	1					6	1		12
	MIC			1		XXXX	2	1	3		1		3	1		13
	VNC						XXXX	3		1			4	5		14
	TAZ				1	1		XXXX	3	1	1		3	3		13
	WINNER GYA			1	1				XXXX		1		1			5
	ELB		1							XXXX			2			3
	CEZ					1	1				XXXX		1			3
	REN											XXXX				0
	PIC									1	1		XXXX	2		4
	DAL													XXXX		0
	REM														XXXX	0
	TOTAL		1	1	2	6	10	7	7	8	3	8	0	0	13	0

		MNT	SCO	PEN	GYA	VNC	ELB	TAZ	WAR	MIC	CEZ	REN	PIC	RIG	BET	DAL	TOTAL
C	MNT	XXXX															0
	SCO		XXXX	1		3	2		4				2	1	1		14
	PEN			XXXX									1				2
	GYA				XXXX				1						1		2
	VNC					XXXX	2	1	1				2				5
	ELB						XXXX	1	1	1					1		4
	TAZ							XXXX	4	1			4	2			11
	WINNER WAR								XXXX	2			1	2			6
	MIC			1						XXXX							1
	CEZ										XXXX						0
	REN											XXXX					0
	FC								1				XXXX	1	1		3
	RIG													XXXX			0
	BET								1						XXXX		1
	DAL															XXXX	0
TOTAL		0	2	1	0	3	4	4	11	4	0	0	0	6	4	0	49

Fig. 2. Dominance matrices of female patas monkeys over 3 successive periods of time. A is based on data collected from June 1993 to August 1994; B from September 1994 to November 1995; and C from December 1995 to April 1997. Reversals accounted for 6, 14, and 10%, respectively, of all agonistic interactions and several females changed ranks through time. All matrices were constructed to minimize reversals, distance of reversals away from the diagonal, and, for the second and, third matrices, changes from the previous hierarchy.

behavior of three other younger adult females, one of which (ELB) matured during the second period, and two others (RIG and BET) during the third period. Excluding the two youngest females that became adult in the last period of the study (because of the patterns shown by SCO and

TAZ that maturing females do not initially demonstrate increased agonism), younger adult females initiated significantly more interactions with others than expected based on their percentage representation among the females ($\chi^2 = 20.9$, $df = 1$, $P < 0.001$). Nonetheless, challenges by younger adult females cannot explain all the ambiguity in dominance relationships. Excluding all interactions involving the 5 younger adult females, over the entire study reversals still accounted for 10% (12/114) of all agonistic interactions.

The high frequency of reversals, the increasingly frequent initiation of agonistic interactions by younger adult females as they became older, and the mobility of females over time within the hierarchy suggest that dominance ranks of female patas are not acquired through maternal inheritance as is the case in vervets, baboons, and macaques. We did not know maternal relationships of adults in either species.

Pruetz observed that, including interactions with unidentified females, patas monkeys had 194 agonistic interactions over 546 hr at a rate of 0.36/hr, and vervets had 90 aggressive interactions over 620 hr at a rate of 0.14/hr. The higher rate of interaction among patas monkeys is most likely because there were more females in the patas group than in the vervet group. Patas actually had fewer recorded interactions per dyad (1.9; $n = 101$ possible dyads during JDP's observation tenure) than vervets (2.5; $n = 36$ possible dyads) and a lower rate of interactions per dyad (0.31/dyad \times 100 hr) than vervets (0.44/dyad \times 100 hr).

Although the rank ordering of the kinds of interactions is similar between species, patas and vervets differ the extent to which they displayed different kinds of agonistic interactions ($\chi^2 = 12.6$, $df = 2$, $P < 0.01$) (Table I). Patas avoided approachers about one-third less often than vervets did but were supplanted twice as often as vervets were. The greater percentage of higher-intensity agonistic interactions in patas, as measured by the extent of displacement from either locations or resources, may be associated with an absence of clear behaviors indicating submission (Rowell and Olson, 1983; Loy *et al.*, 1993), which may be important in minimizing escalated aggression in other species (de Waal, 1989).

Patas monkeys and vervets also differed in the resources over which they were supplanted ($\chi^2 = 12.0$, $df = 5$, $P < 0.05$) (Fig. 3). Female patas sometimes supplanted each other over water and proximity to adult males and adult females; female vervets exhibited no supplantation over these resources. Female patas supplanted each other over grooming three times more often than female vervets did. Supplants over these resources do not differ significantly between species (χ^2 tests; all P 's > 0.10). In contrast, vervets supplanted each other over food proportionately more often than female patas did ($\chi^2 = 9.47$, $df = 1$, $P < 0.010$) (Fig. 3).

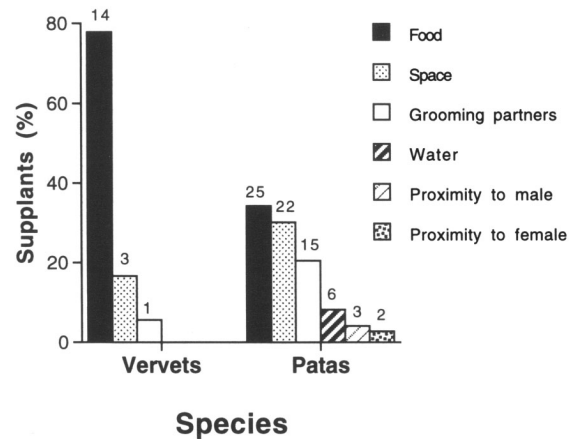


Fig. 3. Differences between vervets and patas monkeys in the resources over which adult females were supplanted. Overall $\chi^2 = 12.0$, $P < 0.05$, $df = 5$. Among individual resources, vervets and patas differed significantly only in the frequency of supplants over food ($\chi^2 = 9.47$, $P < 0.01$). Sample sizes are listed above the bars. Excluded are supplants over unidentified resources (vervets; $n = 2$; patas; $n = 4$).

DISCUSSION

Disparity in the Dominance Hierarchies of Provisioned and Unprovisioned Patas Monkeys

Provisioned patas groups, both free-ranging and captive, are reported to have stable, linear dominance hierarchies among females (Kaplan and Zucker, 1980; Jacobus and Loy, 1981; Loy and Harnois, 1988; Nakagawa, 1992; Goldman and Loy, 1997; but see Rowell and Olson, 1983). In contrast, we found that the dominance hierarchy among unprovisioned female patas is not linear, with a high number of reversals. A possible explanation for these contrasting results is that the time frame of our study included a relatively short period of instability in a group with an otherwise stable dominance hierarchy (Samuels *et al.*, 1987). When the study was separated for analysis into three shorter periods, however, each included a higher percentage of reversals than has been observed in vervets, macaques, baboons, or provisioned patas.

A more likely explanation for the difference between our results and those from captive or wild, provisioned patas is that there is a difference in the usurpability of the foods of unprovisioned and provisioned patas.

The foods of provisioned patas occur at high concentrations over limited areas. Under such conditions, the frequency of agonistic interactions is expected to increase as items become more usurpable (Rowell, 1967; Southwick, 1967; Gartlan, 1968; Boccia *et al.*, 1988; Brennan and Anderson, 1988). In Kaplan and Zucker's (1980) study of provisioned patas, the majority of agonistic interactions (60%) occurred at food hoppers. In Goldman and Loy's (1997) study of provisioned patas, the detectability of dominance hierarchies was likely enhanced by conducting observations around feeding time. Indeed, provisioning has been deliberately applied as a tool to determine relative dominance ranks quickly in wild patas (Nakagawa, 1992). Contrarily, unprovisioned patas eat small, widely distributed foods such as arthropods and small globules of gum on small trees (Isbell, 1998; Isbell *et al.*, 1998). The foods of unprovisioned patas are undoubtedly less usurpable than those of provisioned patas, and they do not encourage contests. They are also apparently less usurpable than the foods of vervets. Isbell *et al.* (1998) showed that patas spend significantly less time feeding at individual food sites and eat smaller foods (determined by greater difficulty in identifying the foods of patas). Shorter handling times and smaller food sizes are likely to decrease usurpability because they decrease the food-site depletion time (FSDT).

Hill and Okayasu (1996) suggested that provisioning can have a measurable influence on dominance relationships in macaques. They point out that the principle of younger sister ascendancy does not exist in all macaque populations but is apparently seen only in ones that are provisioned. By increasing the frequency or intensity of agonism and therefore the risk of injury to younger females, provisioning may facilitate stronger maternal support of youngest offspring than is necessary in nonprovisioned macaques.

The finding here that nonprovisioned patas have more ambiguous dominance relationships and a less linear dominance hierarchy than nonprovisioned vervets suggests that some of these differences are based on environmental (food) differences. Nonetheless, provisioned patas do not become identical to nonprovisioned vervets, baboons, and macaques, for which dominance is still a central theme in the organization of their social behavior (Silk, 1987). Provisioned patas do not have obvious signals of submission (Rowell and Olson, 1983; Loy *et al.*, 1993), which indicate species with unambiguous dominance relationships and a formal dominance structure (de Waal, 1989), and many studies of provisioned patas question the importance of dominance in organizing social behavior within their groups (Kaplan and Zucker, 1980; Loy and Harnois, 1988; Loy *et al.*, 1993; Goldman and Loy, 1997). Moreover, although kinship appears to be important in social relationships of provisioned patas (Loy and Harnois, 1988; Gold-

man and Loy 1997), the high frequency at which daughters develop ambiguous dominance relations with their mothers (70%) or rise above their mothers in the hierarchy (30%) (Goldman and Loy, 1997) argues for a less codified kin structure than that which occurs in nonprovisioned vervets, baboons, and macaques. These differences between provisioned patas and nonprovisioned vervets, baboons, and macaques suggest that patas have been subjected to different selection pressures than vervets, baboons, and macaques.

Phylogenetic Patterns

Patas monkeys are perhaps more closely related to vervet monkeys than they are to other guenons (Disotell, 1996), and yet dominance relationships between females within groups of these species are quite different. These differences parallel other behavioral differences between members of the tribe Cercopithecini (excluding vervets) and members of the tribe Papionini (Kaplan 1987; Rowell, 1988). Despite their inclusion in the Cercopithecini, vervets are more closely aligned in their dominance relationships with the Papionini (including baboons and macaques). Baboons, macaques, and vervets have stable, linear dominance hierarchies, with reversal rates typically <2% and rarely as high as 4% (Missakian, 1972; Hausfater, 1975; Cheney *et al.*, 1981; Seyfarth, 1980; Silk *et al.*, 1981; Hausfater *et al.*, 1982; Smuts, 1985; Barton and Whiten, 1993; Ron *et al.*, 1996).

Blue monkeys (*Cercopithecus mitis*), a species of the Cercopithecini, appear to be similar to patas in the ambiguity of their dominance relations. The dominance hierarchy in one group of blue monkeys is not statistically significantly linear ($d = 134.75$, $\chi^2 = 27.18$, $df = 23.3$, $P > 0.20$) and the index of linearity is low ($K = 19.8$) (our analysis of data from Rowell *et al.*, 1991). Reversals in blue monkeys also account for a relatively high proportion of interactions (15%) (Rowell *et al.*, 1991). More recent analyses from this group confirmed the lack of a linear dominance hierarchy within most years but showed significant linearity when data over multiple years were combined (Cords, 1998). Maternal relationships within groups have not been determined for unprovisioned blue monkeys or patas monkeys but the relatively high percentage of reversals in both species suggests little, if any, maternal or nonkin support for females and therefore, little rank inheritance in either species. No detailed data are available for other unprovisioned guenons but it appears that these conditions may be typical of most guenons (see Rowell, 1988).

Excluding vervets, guenons appear to be more similar to many colobines than to other cercopithecines in the nature of female relationships

within groups. Like most guenons, many colobines have unstable or undiscernible dominance hierarchies (Newton and Dunbar, 1994). Interactions between female colobines are infrequent, reversal rates are high, though apparently not as high as in guenons, and rank is not inherited despite stable female residency in some species and the consequent opportunity for maternal support (Borries *et al.*, 1991; Borries, 1993).

In summary, four patterns suggest that the expression of female relationships within groups of Old World primates is a labile characteristic, largely but not entirely responsive to the qualities of foods and not particularly constrained by phylogenetic history: (1) the divergence of patas and vervets in female dominance relationships, (2) the divergence of guenons and other cercopithecines in female dominance relationships, (3) the similarity between guenons and many of the less closely related colobines in female dominance relationships, and (4) the ability of patas to form stable, linear dominance hierarchies when their foods are manipulated.

Similar patterns of divergent female relationships within groups in closely related pairs of species can be found in ring-tailed lemurs (*Lemur catta*) and brown lemurs (*Eulemur fulvus*), and in western black-and-white colobus (*Colobus polykomos*) and guerezas (*C. guereza*). Ring-tailed lemurs and western black-and-white colobus have detectable female dominance hierarchies whereas brown lemurs and guerezas have no discernible female dominance hierarchy (Oates, 1977a; Sussman, 1975; Dasilva, 1989, cited by Newton and Dunbar, 1994; Pereira and Kappeler, 1997). Ring-tailed lemurs and western black-and-white colobus feed extensively on fruits or seeds (Sussman, 1977; Oates, 1994), much of which may be usurpable because they have long food-site depletion times (FSDT). In contrast, brown lemurs and guerezas feed extensively on leaves (Sussman, 1975; Oates, 1977b), much of which may not be usurpable because they either are ubiquitous or have short FSDT. Phylogenetic history may be associated with the nature of female dominance relationships only to the extent that closely related species are more likely than distantly related species to eat foods that are similar in usurpability by virtue of species similarities in, for example, digestive morphology or dietary requirements: phylogenetic niche conservatism (Harvey and Pagel, 1991; Westoby *et al.*, 1995).

In conclusion, many of the differences among Old World primates in female relationships within groups may be ascribed ultimately to differences in food abundance and usurpability. The stability of the dominance hierarchy appears to be to a large extent dependent on maternal support and nonkin alliances. Whether maternal support and nonkin alliances occur are likely to depend on the effectiveness of such support in gaining access to resources. Support from mothers and other allies may be effective only

when foods are limited in abundance and usurpable. Such complex social relationships and the complex social signals that help maintain them might evolve in any primate species in which females living together face persistent conditions of usurpable foods that can limit reproductive success.

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