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Socioecology, Predation, and Cognition in a Community of West African Monkeys

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The Ivory Coast's Taï Forest is home to a diverse primate fauna, including eight monkey species that interact daily with the environment, each other, and a web of predators. These interactions have led to an array of adaptations, some of which conform to theoretical expectations, and others are at odds with current behavioral ecology models. In this paper, we draw on fifteen years of observations to examine two central issues. First, how do broad trends in diet and resource distribution influence group size and levels of sociality? Second, what mechanisms are used to counter pressures exerted by the predator community? The general picture that emerges is that while the pressure exerted by predators at Taï has led to a host of behavioral and cognitive adaptations, it is food preferences and foraging habits, not predation pressure, that are the main determinants, not only of group size, but also its direct consequences - mating systems and sociality levels.

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The Taï cercopithecids are descendents of migrants from central Africa that became isolated in the Upper Guinea Forest.[1–4] In terms of total biomass, these monkeys are evolutionarily successful mammals. Their community composition mirrors the pattern of primate faunas in other African forests.[5] Of the four guenon species present, one, *Cercopithecus nictitans stampflii*, is found at low densities only in the park's northern latitudes (Fig. 1a). The three remaining guenon species are much more abundant and found throughout the forest. The most conspicuous of these is the Diana monkey, *Cercopithecus diana*, a brightly colored, loud, active primate that moves quickly and easily throughout all forest layers (Fig. 1b). Campbell's monkey, *Cercopithecus campbelli* (Fig. 1c), and the lesser spot-nosed monkey, *C. petaurista* (Fig. 1d), are more subdued in virtually all aspects of their behavior and appearance, and have adopted more cryptic lifestyles. The fourth cercopithecine is the sooty mangabey, *Cercocebus atys* (Fig. 1e). This papionin is the largest and only terrestrial monkey at Taï, making its living on foods gleaned from the forest floor.[6,7]

Taï is one of the few forests where three colobine species live sympatrically. The dominant species is the Western red colobus, *Procolobus badius* (Fig. 1f). In areas where human poaching has not altered the forest's natural balance, red colobus are the most abundant monkeys, comprising the largest percentage of primate biomass. Taï red colobus live in large, loud groups that spend most of their time in the main canopy. The Western black-and-white or King colobus, *Colobus polykomos,* (Fig. 1g), lives in smaller, quieter groups. Black-and-white colobus use all forest levels, particularly the emergent layer, for morning sunning; the understory, is often used for foraging on liana leaves. The third colobine, the olive colobus *Procolobus verus* (Fig. 1h), is a peculiar monkey that has fascinated researchers since the pioneering studies of Booth.[8–11] Olive colobus are not only the smallest colobines, but the only anthropoids known to carry dependent young in their mouths. These elusive primates are the most active leapers at Taï. They spend most of their time in the understory, where they frequent vine tangles and other areas of dense vegetation. Table 1 summarizes some of the key species characteristics.

SOCIOECOLOGY

A central model of primate behavioral ecology is that resource distribution and defensibility limits group size, influences dispersal tendencies, and determines levels of sociality within and between sexes.[19–23] When food is distributed in patches that exceed the feeding requirements of a single group, groups will be large. Also, competition between females will be low both within and between groups. Under these conditions, females develop little interest in each other and complex social behavior is less likely to evolve. If access to food is linked to high travel costs, groups will be smaller and females will benefit from each other's support, both to defend resources against other group members and against neighboring groups. Consequently, complex social skills are likely to emerge and be selected for. The dietary diversity and array of social systems at Taï provides an excellent opportunity to test this general model.

The four Taï guenons rely to varying extents on fruits that typically are available in isolated patches and that require significant travel between food trees (Table 1).[24–28] Fleshy fruits preferred by guenons are high quality and of limited availability, not abundant enough to support large aggregations of individuals. Consequently, these fruits are worth defending. All guenon groups are relatively small; they consist of related females and a single adult male. The spatio-temporal availability of food limits viable group size to approximately 20 individuals. Intergroup competition is high. Episodes of resource scarcity are common and, during these times, guenons employ various fallback foods (for example, invertebrates) and become highly intolerant of competitors.[29]

Although the guenons' patchy and contestable diets should, in theory, promote high degrees of sociality, guenons are not known for complex social behavior; their levels of intragroup social interactions are considerably lower than those of other frugivorous cercopithecids such as macaques and baboons.[17] They exhibit little evidence of sophisticated behaviors such as intragroup coalition formation or tactical deception.[30] One explanation is that the behavioral cues used by forest guenons are so subtle that humans find it difficult to discern them. Indeed, recent studies

Figure 1. a: Stampflii's putty-nosed guenon, *Cercopithecus nictitans stampflii.* b: The Diana monkey, *Cercopithecus diana diana.* c: Campbell's monkey, *Cercopithecus campbelli.* d: The lesser spot-nosed monkey, *Cercopithecus petaurista.* e: The sooty mangabey, *Cercocebus atys.* f: The Western red colobus, *Procolobus badius badius.* g: The Western black-and-white or King colobus, *Colobus polykomos.* h: The olive colobus monkey, *Procolobus verus.*

TABLE 1. Comparative Ecology of Taï Primates

	Procolobus badius	***Colobus polykomos***	***Procolobus verus***	***Cercocebus atys***	***Cercopithecus diana***	***Cercopithecus campbelli***	***Cercopithecus petaurista***	***Cercopithecus nictitans stampflii***
Morphology								
♂/♀ Weight	8.3/8.2	9.9/8.3	4.7/4.4	11.0/6.2	5.2/3.9	4.5/2.7	4.4/2.9	6.7/4.2
Dimorphism	Small	Medium	Small	Large	Large	Large	Large	Large
IMI	90.5	81.6	80.1	84	80.8	84.6	80	82
Habitat Use & Activity Pattern								
Stratum Preference	High	High-low	Low	Ground	High	Low	Low	High
Home range	0.58	0.78	0.56	5	0.59	0.6	0.69	0.93
Population density	123.8	17.3	17.3	11.9	48.2	24.4	29.3	2.1
Cryptic ?	No	Yes	Yes	Yes	No	Yes	Yes	Yes
Resting %	29.9	33.9	35	18.5	8.8	20.2	32.5	?
Sociality								
IBI	2.4	1.7	1.6	2.5	1.6	1.6	1.9	2.0
♀ swelling	Yes	Yes	Yes	Yes	No	No	No	No
Testes	Large	Small	Large	Large	Small	Small	Small	Small
Group size	52.9 (32-73)	15.4 (11-19)	6.7 (4-12)	69.7 (45-96)	20.2 (11-29)	10.8 (7-14)	17.5 (11-24)	10.5 (7-14)
Philopatry	♂	♂&♀	0	♀	♀	♀	♀	♀
Mating	Multi ♂	Single ♂ (Multi ♂)	Single ♂/ Multi ♂	Multi ♂	Single ♂	Single ♂	Single ♂	Single ♂
Feeding								
Fruits	28.8	48	9	68.4	70.9	46.3	33.7	58.9
Leaves	50	48	91	2.4	1.6	8.4	39.7	4.2
Invertebrates	–	–	–	26.4	26.5	33.1	12.3	31.3
Flowers	19.5	3	–	1.3	0.4	1	6.2	2.5
Fungi	–	–	–	0.9	0.2	1.6	1.1	1.3
Other	2.1	1	–	0.6	0.5	9.3	6.4	1.8

Body weight: adult body weight in kg;[12] IMI: intermembral index;[14] IMI for *C. nictitans stampflii* is for *C. nictitans;*[15] Home range: annual home range size (km^2);[14,16,17] Pop. density: estimated individuals/km;[2–13] Resting: estimated annual percent of activity budget;[14] IBI: average interbirth interval in years;[13] Group size: estimated average number of individuals per group; observed range in parentheses;[13] Feeding: estimated annual percentage of food items.[18]

on captive Campbell's monkeys have revealed surprisingly sophisticated social behavior among female guenons, suggesting that we may be missing many of the less overt, but no less important, social interactions.[31,32]

Coalitionary behavior at Taï emerges primarily during intergroup interactions when females regularly fight with those in neighboring groups over access to food trees.[17,33] These interactions can be extreme: Adult females have been observed to kill those of neighboring groups.[34] Thus, while rates of intragroup interactions appear to be low, guenon females will coordinate their activities, and with deadly force, when their resource base is threatened. In contrast, adult males in all four guenon species show little interest in social interactions, almost never grooming and rarely attacking other group members.[17] This tendency is particularly marked in Diana monkeys. As Buzzard notes, Diana monkey males are far less integrated into their groups than are the males of other Taï guenon species, rarely participating in intergroup encounters.[17] Diana monkeys are the most frugivorous of the Taï guenons. Also, their groups are larger than those of both the lesser spot-nosed monkey and Campbell's monkey. Diana monkeys consistently dominate the other guenon species, particularly Campbell's monkeys, with which dietary overlap is greatest.[26]

Although sooty mangabeys are also highly frugivorous, these papionins feed on hard, bitter fruits acquired from the forest floor. Intra-group feeding competition is comparatively low.[35–44] Resource contestability is not as great a constraint on group size, so that mangabey groups, sometimes numbering over 100 individuals, are the largest of any Taï primate (Table 1). During periods of extreme resource scarcity, mangabey groups often divide into subgroups. Foraging and traveling on the ground is energetically more efficient than is arboreal locomotion, allowing sooty mangabeys to cover larger home ranges and gain access to a greater number of food trees at comparatively low costs. However, terrestrial foraging and locomotion is associated with high predation risk. Indeed, sooty mangabeys at Taï suffer particularly high predation rates.[13,45–49] The large size of sooty mangabey groups at Taï can be viewed as a response to two associated factors: less contestable resources and the potential dangers associated with acquiring those resources from the ground.

While moderate feeding competition appears to limit the need to develop complex social behavior, sooty mangabeys are, nevertheless, highly social primates. Males and females form well-differentiated relationships with preferred partners and support each other during conflicts.[41] Individuals form stable dominance hierarchies and well-differentiated relationships with preferred partners. These relationships follow patterns resembling those observed in other matrilineal primate species.[38,39] Access to food and to preferred feeding sites is rank-related and high-ranking members tend to be surrounded by multiple group members near the group's center. High-ranking males are preferred by females. If high-ranking females benefit by having access to priority feeding sites, and if these sites afford better predator protection, then social strategies that lead to ascendency in social status should result in increased reproductive success.[41] Studies designed to test the associations between rank, feeding priority, and reproductive success are currently underway at Taï.

The three colobines species have strongly contrasting diets and show great variation in their social systems.[50] Taï red colobus rely on foods that are abundant and readily accessible. Because food patches are close together, red colobus travel costs are low. The socio-ecological model predicts that red colobus groups will be large and that affiliative relationships among females will be weak. The model is strongly supported by data from Taï; red colobus groups often number close to one hundred individuals and affiliative behavior among females is uncommon. Due to the abundance of their food supply, females have little need to defend food and red colobus are one of the few cercopithecids in which male philopatry is the general rule. Females groom males more often than they groom other females; coalitionary behavior between females is rare. At Taï, females have never been observed participating in intergroup encounters. The territories of neighboring groups do not strongly overlap and territory defense is solely a male activity. Males regularly engage in agonistic interactions during which they form coalitions with each other. Male-male embracing and grooming is common. Males also cooperate with each other in predator defense, particularly against crowned eagles.

The foods preferred by black-and-white colobus are more widely distributed, unpredictable, and contestable. Groups of this species are more territorial; intergroup encounters are comparatively frequent and aggressive episodes between groups usually involve both males and females.[51] Consistent with socio-ecological theory, groups of *Colobus polykomos* are small and comprised of related females that aggressively defend patchy resources that include highly prized seeds. Despite a strong reliance on seeds from fruit, intragroup aggression between females is rare. Indeed, females groom each other more than they groom males. Korstjens[50] attributes the reduced aggression to the long processing times required by the most contestable food items, the seeds of *Pentaclethera macrophylla*. Monkeys routinely take fifteen minutes or more to remove the flat, poker-chip-sized seeds from their woody husks. Because the seeds are small, they cannot be shared, which reduces the potential for conflicts and keeps groups small. Contestability between groups is a different matter, with female black-and-white colobus frequently attacking those in other groups. Thus, while black-and-white colobus females do not cooperate to defend food within groups, they readily cooperate to defend food against outsiders. Additional features supporting the notion that this species is adapted to living in small groups are that males have relatively small testes and females display no obvious signs of estrus (Table 1). Sexual dimorphism in body size is the greatest among all Taï colobines, suggesting that males have been selected to compete with each other to monopolize a group of females.

Olive colobus have diets consisting largely of young leaves. We would expect small groups to form around such ephemeral and patchy resources and, indeed, olive colobus groups are the smallest of any Taï cercopithecid (Table 1). Such modest group sizes with single males make sense in terms of resource distribution. However, olive colobus display several features indicative of large multi-male groups.[51] Body size dimorphism is small, yet males have large testes and females develop impressive sexual swellings to advertise their estrous. Individuals from all age-sex classes disperse and neither sex can be considered philopatric.[52,53] Females show hardly any affiliative interactions with each other, while males are not only tolerant of each other, even in mating contexts, but are known to form alliances.[53]

One explanation for this unusual pattern of dispersal and group formation is that olive colobus do, in fact, form multi-male groups, but that individuals in these groups are distributed across groups of another species.[52] At all sites where olive colobus are sympatric with *Cercopithecus diana*, Diana monkey groups typically have one or more olive colobus males and several adult females attached to them.[54] These bi-specific associations are a behavioral strategy in which olive colobus co-mingle with Diana monkeys for predator protection.[55] Associations between the two species range from short admixtures during the olive colobus estrus period to those lasting several years or more.[16,52] Even as adults, both male and female olive colobus move between Diana monkey groups, where migrating members have a high chance of meeting members of the opposite sex.[52,53] Bi-male groups are common and the dispersal of females across several Diana monkey groups may make it impossible for a single male to monopolize multiple females. In groups containing more than one adult male, males are known to cooperate during intergroup encounters; pairs of males will jointly threaten and chase individuals in neighboring groups during aggressive episodes. There is no evidence that olive colobus seek Diana monkeys for foraging benefits. Olive colobus social units are formed around Diana monkeys and in this scenario the limiting resource is not food, but the protection afforded by another species.

Our observations suggest that the quality and distribution of a species' diet, as well as its general anti-predator strategy, have a significant impact on the maximum group size that can be realized. High degrees of frugivory limit group size in most Taï primates, while low-quality foods, including the hard, bitter fruits preferred by mangabeys, tend to favor larger groups. Olive colobus monkeys are an interesting exception because, although this species shows all the hallmarks of a large multi-male multi-female social system, individuals aggregate in very small and unstable groups, almost always in close proximity to a Diana monkey group. Complex social behavior is more commonly seen in large group species, regardless of species-specific diet differences, but the two sexes are often affected in different ways. Predation pressure is equally high for all Taï primates, but fails to explain species differences in group size.

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PREDATION

Adaptations to Predation

Chimpanzees, crowned eagles (*Stephanoaetus coronatus*), leopards and, more recently, human poachers form a complex predator fauna at Taï. Long-term observations and natural experiments involving the manipulation of predator effects have revealed several mechanisms that monkey species use to counter predation. These data can be compared with known predation rates in direct assessment of the effectiveness of several common anti-predation adaptations.

Group size

A central tenet of animal behavior is that gregariousness evolved wholly or in part as a response to predation pressure.[56] Group living offers a variety of advantages. If monkeys can increase their safety by living with others, predation should favor the evolution of large groups. The most obvious benefit of increased group size is numerical: Individual risk of death by a predator declines as groups become larger, a principle known as the dilution effect. All Taï cercopithecids live in groups; the only solitary individuals normally observed are young adults transferring from their natal groups. (The major exception to this pattern is the olive colobus monkey. Individuals of all age/sex classes have been observed migrating.) Species group sizes vary considerably (Table 1), but our data indicate that individuals in large groups are not better protected than those in small groups. Predation by crowned eagles does decline with increasing group size, but this is true only for arboreal species. Sooty mangabeys have the largest groups of all the Taï cercopithecids, but are killed by crowned eagles at rates significantly higher than their densities predict.[45,46] Similarly, the percentage of the red colobus population captured by chimpanzees (3.2%) is significantly higher than that of black-and-white colobus (1.4%), despite the much larger groups in the former.[50] The pattern is similar for leopard predation: Species living in larger groups are at much higher risk than those living in smaller groups.[13] For leopards, different prey species may even be in competition with each other to avoid preference formation,[47] with species living in smaller groups appearing to be at an advantage.

Janson[57,58] explored this paradox by employing the concept of "intrinsic predation risk," which considers predator densities, attack rates of individual predators, attack success, and individual prey vulnerability. Using life-history data, his model predicts that because of the significant size disparity between most predators (large) and their prey (smaller), intrinsic predation rates should not decrease significantly with body size. Janson[57] reasoned, "If predation risk does not decline while longevity increases with increasing body mass, then larger species will pay the cost of high predation rates over more years than will smaller species, and thus will gain a greater fitness benefit by reducing predation rates to low values. This trend should favor increased sociality in larger species even if intrinsic predation risk declines slightly with body mass" (p. 131). The size disparity between some predators, such as chimpanzees and leopards, and their monkey prey is considerable, which is consistent with the model's assumptions. When body sizes of crowned eagles and their preferred primate prey are considered, the scenario becomes more complex.

Body size

Body size (Box 1) is frequently cited as a direct adaptation to predation, based on the notion that larger individuals are at less risk than smaller ones.[59–61] Although this may be true for a broad range of animals, the hypothesis is difficult to defend with the Taï monkeys since chimpanzees, leopards, and crowned eagles prey on monkeys of all sizes, including full-grown adult males.[45] Moreover, two of the three main monkey predators, leopards and chimpanzees, appear to prefer the larger monkey species.

Taï leopards are known to favor large prey and are particularly successful at killing red and black-and-white colobus monkeys (Fig. 2a).[13,47] Chimpanzees preferentially hunt red and black-and-white colobus but are rarely successful at capturing the smaller, more agile guenons (Fig. 2b).[62–64] Crowned eagles routinely capture all monkey species, and while there is a negative relationship between the number of arboreal monkeys killed by eagles and body size, the relationship dissolves when terrestrial mangabeys are included in the analysis (Fig 2c).[65,66] Monkey-eating eagles at Taï specifically target mangabeys, the largest monkey in the forest, most likely due to their substrate preference.[45,46] The conclusion from these data is that the major monkey predators produce a selection pressure that favors small rather than large body size. Large body size, when considered alone, is not an effective deterrent to predation at Taï.

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Crypsis and responses to predators

Many primates make consistent efforts to remain inconspicuous.[57] Crypsis can be an effective strategy if behaviors that reduce the likelihood of detection do not compromise feeding and reproduction. One of the simplest measures of a species' reliance on crypsis is how easily unhabituated groups can be located. Olive colobus lead extremely cryptic lives and unhabituated individuals are difficult to find. Diana monkeys and red colobus, on the other hand, are easily detected by the commotion of their daily routines. Both species produce frequent, highly audible calls, move noisily through the main canopy, and make little attempt to remain hidden. The black-and-white colobus and other guenon species are intermediate in their general crypsis. Groups of these species can usually be located only after the adult male in a group produces loud calls. Mangabeys are also relatively cryptic, particularly given their large group size and substrate preference.

Morphological and behavioral crypsis is correlated with habitat preference among the Taï cercopithecids. The loudest, most conspicuous, brightly colored monkeys, red colobus and Diana monkeys, are typically found in the highest portions of the canopy, while monkeys preferring lower forest levels have adaptations that draw less attention to themselves. Species frequenting the understory, among them olive colobus, Campbell's monkey, and lesser spot-nosed monkeys, are not brightly adorned, produce fewer and softer vocalizations, and engage in more stealthy locomotion. Adaptations that increase a monkey's ability to avoid being detected may, of course, be dictated by other fitness components, such as foraging behavior, or may also reflect the proximity of perceived dangers. If the latter is true, then the more subdued markings and behavior of olive colobus, Campbell's monkey, and the lesser spot-nosed monkey might indicate that the low forest levels they frequent most often pose greater predator risks than does the high

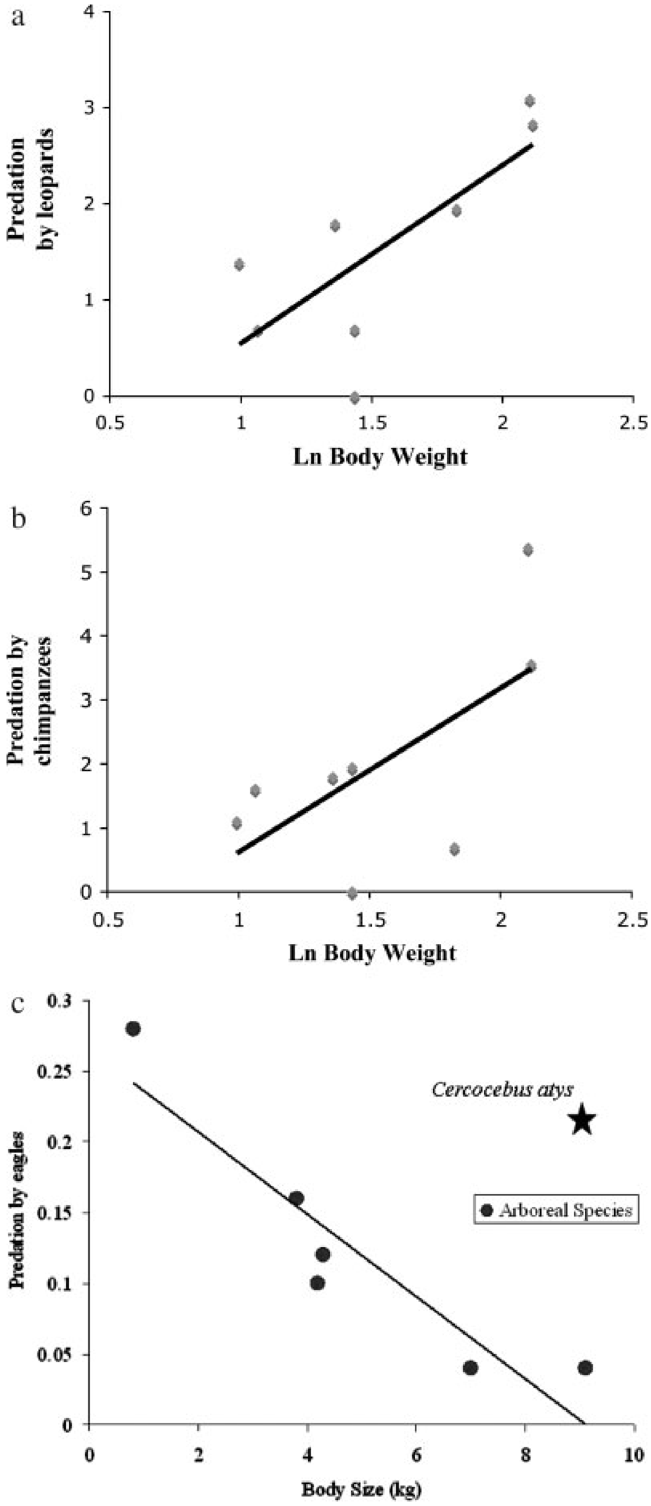

Figure 2. a: Relationship between leopard predation and body size of Taï monkeys.[13] b: Relationship between chimpanzee predation and body size of Taï monkeys.[61] c: Relationship between eagle predation and body size of Taï monkeys.[45,63]

canopy.[59,60] Testing this hypothesis requires comparing the frequencies of attacks on primates at different forest levels.

Despite their varied reliance on crypsis, monkeys of all species, once they have detected a predator, respond to its presence in generally uniform ways. These responses are determined by the hunting strategies of the three main monkey predators, each of which is likely to have exerted different selection pressures. The presence of chimpanzees elicits cryptic behavior in all monkey species; after a brief alarm call is sounded, groups of all species become silent. This common strategy has most likely evolved because chimpanzees hunt by locating monkeys through auditory cues and will continue pursuing even after being detected. Sustained alarms by monkeys would serve only as locational beacons.

Leopards, in contrast, are ambush hunters; they hide in thick vegetation to stalk and attack monkeys foraging in the low canopy or on the ground. Because of this, leopards rely strongly on surprise. Monkeys detecting leopards tend to produce sustained alarm calls, most likely as a means of signaling the leopard that it has been discovered. During encounters with leopards, monkeys routinely descend to low forest levels and direct alarm calls at the threat. Radio-tracking data have shown that this strategy is highly effective, with forest leopards usually leaving an area after receiving monkey alarm calls.[13,47]

Crowned eagles also depend on surprise, sitting motionless in apparent attempts to ambush unsuspecting monkey groups. All monkey species typically respond to crowned eagles with sustained alarm calls, while adult males of several species are known to attack these raptors. Adult male black-and-white colobus will not hesitate to charge directly at crowned eagles while emitting their roaring calls, suggesting that these calls function not only as signals to deter the predator, but also to warn group members about the nature of the danger. These observations indicate that, regardless of the usual crypsis of each monkey species, once a predator has been detected tendencies to remain cryptic or advertise perception are consistent across species and are a function of the hunting idiosyncrasies of the three individual predators.

Polyspecific associations

Mixed-species associations are a behavioral maneuver that provides safety-in-number benefits, including heightened vigilance, early warning, and dilution. There is considerable evidence that the high frequencies of polyspecific associations at Taï are not caused by attraction to common dietary resources or the result of chance encounters, but are, rather, a direct adaptation to predator pressure.[24,25,67–69] If predation favors the formation of mixed species groups, then differences in association rates should vary with predation pressure. Two examples provide strong support for this notion.

Red colobus monkeys are the preferred monkey prey of Taï chimpanzees. Experimental evidence has shown that of all the arboreal cercopithecids, Diana monkeys are the best at detecting predators, including chimpanzees, approaching from the ground.[70] During the season when chimpanzees hunt monkeys, associations between red colobus and Diana monkeys reach their highest levels. During the season when chimpanzee communities are dispersed and opportunities for males to form cooperative hunting parties are reduced, association rates between Diana monkeys and red colobus are lowest. The tendency for red colobus to seek the protection of Diana monkeys during chimpanzee hunts has been experimentally manipulated using playbacks of chimpanzee vocalizations. During the nonhunting season, when red colobus and Diana monkey groups are not mixed, chimpanzee playbacks immediately cause red colobus to seek the proximity of nearby Diana groups. If the two species are already associated, red colobus maintain the association for significantly longer than they would have if chimpanzee vocalizations had never been produced. These associations have nothing to do with diet, but rather are a function of the Diana monkeys' ability to serve as early warning mechanisms.[71]

Mixed-species associations are known to occur even between species with similar diets and habitat use patterns. As noted, Stampflii's putty-nosed monkeys occur only in northern portions of Taï National Park and at very low densities, most likely because they have lost their natural habitat in the forest-savannah transition zone. The disjunct distribution of putty-nosed monkeys across West Africa has been explained as a function of competitive exclusion by Diana monkeys.[72–75] Also, observations at Taï confirm that the two guenons occupy virtually identical niches and have strongly overlapping home ranges.[29,76] Despite their ecological similarity, the two species can still form near-permanent mixed-species associations. Diana monkeys do become intolerant of putty-nosed monkeys during periods of low fruit availability, yet agonistic encounters are relatively rare.[29] There is good evidence that Diana monkeys accept the presence of competing putty-nosed monkeys because they provide anti-predation benefits. Putty-nosed monkeys are one of the few Taï primates that will aggressively attack crowned eagles. We have witnessed simultaneous attacks on eagles by the males of mixed groups of putty-nosed and Diana monkeys. In addition, playback experiments demonstrate that putty-nosed monkeys produce eagle alarm calls that Diana monkeys recognize and respond to.[29] In this case, Diana monkeys absorb the cost of feeding competition from putty-nosed monkeys because of the anti-predation benefits afforded by the latter.

None of the Taï primates has evolved specialized morphological anti-defense weapons. Also, monkeys probably do not have access to as many safe microhabitats as do some other animals. We contend that the primary way in which Taï monkeys deal with predation is by means of their cognitive skills.

COGNITION

Compared to most other animals, primates are unusual in the high amount of energy they devote to their brains.[77] What are the advantages of having a large and metabolically expensive brain? One popular idea is the social-intelligence hypothesis, which states that "the higher intellectual faculties of primates have evolved as an adaptation to the complexities of social living."[78] Higher intellectual facilities allow an individual to navigate its social world effectively by better recognizing others' social relations and predicting their behavior. In Taï, where socially complex problems regularly emerge when monkeys interact with other species, we suspect that predation is a major driving force behind much of their behavioral complexity.[79] None of the Taï primates has evolved specialized morphological anti-defense weapons. Also, monkeys probably do not have access to as many safe microhabitats as do some other animals. We contend that the primary way in which Taï monkeys deal with predation is by means of their cognitive skills. For example, diurnal primates cannot hide in a burrow to avoid an approaching predator, but must continuously monitor the threat's location and behavior while simultaneously adjusting their own behavior. Among the Taï monkeys, as in many organisms, there is good evidence of a sophisticated understanding of a predators' hunting behavior, as well as the relationship between each predator and its different prey species. The following examples illustrate these points.

As noted, red colobus monkeys are heavily preyed on by chimpanzees.[80,81] Taï chimpanzees search for red colobus groups by auditory cues. Once a group is located, hunting parties approach silently and ascend trees in hopes of isolating individual prey. Upon hearing chimpanzees at a distance, red colobus monkeys usually move silently through the canopy in the opposite direction. However, if Diana monkeys are nearby, red colobus move toward the Diana monkeys even if it means moving in the direction of the approaching chimpanzees, probably because Diana monkeys are excellent sentinels that produce brief but recognizable alarm calls if they visually spot a chimpanzee. Alert monkeys, including those of a different species, make hunting more difficult. The presence of Diana monkeys seems to deter chimpanzees from hunting.[68]

Diana monkeys are able to assess the chances of an impending attack by attending to the chimpanzees' vocal behavior. The Diana monkeys' main response to chimpanzees is to become cryptic. This behavior is usually followed by one adult female giving several conspicuous alarm calls, behavior that can be experimentally elicited by playing back typical vocalizations of chimpanzees, such as pant hoots or social screams.[82,83] Chimpanzee screams are a highly variable class of vocalizations containing information about the external situation to which a caller is responding. For example, individuals engaged in agonistic interactions produce screams that are acoustically different depending on whether they act as aggressors or victims.[84] Chimpanzees also produce screams in alarm situations, particularly when encountering a leopard. A playback experiment has shown that Diana monkeys discriminate between chimpanzees' agonistic and alarm screams, although the two signals are acoustically very similar. Moreover, Diana monkey groups having home ranges in the core area of the resident chimpanzee community were better at discriminating screams than were Diana monkey groups living at the periphery.[85,86] The only way to learn how to discriminate between the two chimpanzee scream types is by directly observing an interaction between a leopard and chimpanzees, and this is likely to happen more frequently in the chimpanzees' core area.

A third study reinforces the notion that awareness of another species' predator detecting capabilities can be used to expand one's habitat use. Taï red colobus prefer the main canopy, foraging only occasionally in the shrub and ground layers. Sooty mangabeys obtain most of their food from the ground. Their home ranges overlap those of several groups of other species, including red colobus. Because of the disparity in home range size, red colobus groups do not encounter sooty mangabeys on a regular basis. However, when the foraging routes of mangabeys bring them into polyspecific association, red colobus respond by dramatically altering their habitat use, descending to low understory levels and the ground. We strongly suspect the reaction of red colobus is due to their knowledge of the leopard-detecting abilities of mangabeys.[87] During experimental trials, sooty mangabeys consistently responded to an approaching leopard threat not only by producing alarm calls before any other monkey species noticed the threat, but also doing so from much greater distances. Sustained activities at low forest levels by red colobus are rarely, if ever, observed when mangabeys are absent, suggesting that red colobus recognize the early warning capabilities of mangabeys and take advantage of mangabey sentinel abilities by using an otherwise dangerous area of the forest when mangabeys are in the vicinity.

DISCUSSION

Taï monkeys live in a variety of social organizations, ranging from small family groups (olive colobus) to polygynous one-male groups (all four guenons, black-and-white colobus monkeys), to large multi-male, multi-female groups (red colobus, sooty mangabeys). Predation rates alone, as distinguished from predation risk,[58] cannot explain these differences in social organization. Strong reliance on fruit leads to high intragroup contest competition, which limits the maximum number of females per group. We observe this pattern in the four guenon species and the black-and-white colobus monkeys, all of which have large proportions of fruit in their diet and typically live in polygynous groups with ten or fewer females that are hostile to their neighbors.

Sooty mangabeys also consume much fruit, but have specialized on low-quality items collected from the forest floor, which are difficult to process and usually are not consumed by other primates. Their terrestrial locomotion is energetically efficient, but also dangerous. Sooty mangabeys can cover large distances but suffer substantially from predation by eagles and leopards. Low feeding competition, large home ranges, and high predation pressure induce females to live in large groups, leading to the large multi-male, multi-female groups observed in this species. At present, we are unable to determine whether feeding ecology or predation pressure was the primary selective force favoring larger groups in sooty mangabeys. Olive colobus live in the smallest groups, but because they often associate with Diana monkeys, groups are forced to split into small and relatively unstable subgroups. Red colobus monkeys appear to be the least constrained by these factors, and the species is regularly found in large groups consisting of more than fifty individuals.

A species' mating system, dispersal pattern, and general social behavior follows more or less directly from female group size. If female group size increases beyond ten or so individuals, single males will find it increasingly difficult to monopolize them and protect their offspring from infanticidal intruders. In polygynous species, adult males are generally intolerant toward adult same-sex group member, and will eventually expel their adolescent male offspring, as do the guenons and black-and-white colobus monkeys. Consequently, female philopatry and male dispersion is the rule in most primates; female dispersion is the exception. If access to food is competitive, individuals will be forced to interact with each other and social skills will evolve, allowing individuals to form differentiated relationships. In large multi-male groups, males will compete over access to estrous females, which will favor the evolution of social skills in

BOX 1: Diet, Body Size, and Positional Behavior

Figure B1. The association between diet and locomotion is weak among the Taï cercopithecids and most other primate groups.[93]

A central goal of primatology is to establish predictive associations between variables in extant taxa in order to make more accurate interpretations of fossil behavior. No variable is more important in this regard than body size, so it is worthwhile to examine the extent that species differences in body size co-vary with characteristics of diet, foraging behavior, and habitat use.

Despite pronounced dietary differences among the Taï monkeys (Table 1), there are no simple associations between major food categories and body size among the Taï cercopithecids. Moreover, the colobine = folivore/cercopithecine = frugivore dichotomy is not only over simplistic, but obscures important interspecific variation and is, in many instances, completely inaccurate.[89] The most frugivorous monkeys, Diana monkeys and sooty mangabeys, eat similar quantities of fruit, but mangabeys weigh more than twice as much as Diana monkeys do. The body weight of the most folivorous monkey, the olive colobus, falls within the range of the Taï guenons, each of which is characterized by a unique dietary profile. Insects make up one-third of the diet of Campbell's monkeys, while the same-sized lesser spot-nosed monkey eats 8% fewer leaves than does the much larger black-and-white colobus. The fact that the diminutive olive colobus eats more than twice the amount of leaves as do the larger colobines is further proof that folivory need not increase with body size, a point highlighted by others.[90,91] The guiding principle is that potential diet quality, independent of food category, should decline as body size increases. The young leaves preferred by olive colobus may in fact be of higher quality than many foods, including some fruits, preferred by other sympatric cercopithecids. In addition, the lack of a strong association between body size and diet in the Taï monkeys is likely due to the flexibility of cercopithecids' diets, a point that has been well established elsewhere. For example, long-term data from Uganda's Kibale Forest demonstrate that dietary variation within species routinely exceeds that between species.[89,92,93]

Given the poor correlation between diet and body size, it is not surprising that relationships between diet and locomotor behavior in the Taï cercopithecids are also weak (Fig. B1). Differences in locomotor tendencies are well established (Table 1), but overall locomotor profiles do not co-vary consistently with dominant elements of diet, nor is diet an accurate predictor of any single behavior such as leaping.[14,94–96] What becomes apparent is that there are

Figure B2. The association between diet and posture is stronger. Elevated rates of sitting in black-and-white colobus are a product of a folivorous diet and reliance on highly prized fruits that requires long processing times. Accessing the seeds of a single *Pentaclethera macrophylla* fruit, seen suspended, routinely requires 15 minutes or more.

multiple locomotor avenues for monkeys with similar diets to meet their nutritional needs. At the same time, species with similar locomotor behaviors often have strongly contrasting diets. These conclusions are consistent with broader surveys that have found few correlates between feeding and locomotion.[97] Within this array of taxa, locomotion has less to do with foraging than with long-distance travel between sites and anti-predator adaptations that include cryptic, stealthy movement.

Studies of posture provide more promising links between diet, foraging behavior, and positional behavior.[96,98] High frequencies of sitting are associated with both folivorous and frugivorous diets when the latter includes fruits requiring long handling times. The three colobine species are the most folivorous monkeys and have the highest sitting frequencies. Black-and-white colobus also rely to a great extent on *Pentaclethera macrophylla* seeds.[99–103] These seeds are housed in large woody pods that require extended processing times and are accompanied by long bouts of sitting (Fig. B2). The frequent sitting postures that characterize black-and-white colobus are therefore as much a function of highly prized and labor intensive fruits as they are related to folivory.[101–104] Most other arboreal monkeys with large frugivorous components sit less and have positional repertoires that include elevated frequencies of standing and other “upright” postures. Such positions facilitate rapid, efficient movement to the next feeding source. Taken together, postural tendencies have less to do with body weight than with the spatial distribution, processing requirements, and competition accompanying different food types.

males. When weak female-female relations due to low feeding competition are combined with strong male-male relations due to mating competition, they determine whether female dispersal and male philopatry will emerge in a species, as observed most clearly in red and olive colobus monkeys.

All three colobine species have been observed in multi-male groups, but the trait is habitual only among red colobus. The most likely explanation is that all three species are derived from a multi-male ancestral species, but that under current conditions this mating system is viable only for red colobus. Long-term observations support this hypothesis. Female dispersal has been observed in all colobine species; it is a regular occurrence in both red and olive colobus and is occasionally seen in black-and-white colobus.[16] As predicted, female relationships are relatively weak among all three colobines species and female-female interactions are rare.[16] In contrast, and consistent with their dispersal patterns, males in both olive and red colobus groups regularly interact with each other.

By monopolizing access to relatively high-quality nutrition, monkeys are able to afford large brains, allowing them to develop complex behavioral strategies in response to important environmental problems. Among the Taï monkeys, many social problems center on understanding relations between other species and predicting their behavior. Such cognitive challenges are particularly important in the context of predation. Predation is an extremely important and domineering daily factor in the lives of the Taï monkeys. Long-term data indicate that those monkey species with the highest predation risk form the largest groups, as theory predicts.[13,57,58] Predation has led to a host of adaptations, including sophisticated warning and vigilance behavior, suggesting that the evolutionary effects of predation on these monkeys have been especially significant at the cognitive level. Taï monkeys differ in how much emphasis they put on cryptic behavior, which is strongly associated with their ecological niche. Foraging in the high forest canopy is associated with conspicuous morphology and behavior, while foraging in dense lower portions of the canopy is associated with adaptations that favor crypsis.

In sum, long-term studies at Taï by many researchers have yielded results that are consistent with theoretical expectations, as well as others that are at odds with prevailing models. For example, multiple data sets support the hypothesis that philopatry is a byproduct of strongly developed social relations with other group members of the same sex. Frequent social interactions favor the evolution of social intelligence. However, whether adolescent males or females leave their natal group depends on the development of social networks that are determined by dietary considerations. At Taï, large-bodied monkeys and individuals found in the largest groups experience the greatest predation risk; our data indicate that individuals in these classes are targeted more often by several primate predators. Predation pressure has been critical in the development of behavior flexibility, as well as a host of underlying cognitive skills across the Taï cercopithecids. Additional long-term data on sociality, responses to resource fluctuations, and predation rates, combined with experimental manipulations of predation effects, should provide further insight into how the behavior of forest-dwelling monkeys is shaped by a complex of evolutionary forces.

Our research to date on the relationship between resource distribution and competitive regimes across the seven Taï cercopithecids has been guided by several influential models directly linking sociality and ecology. Although these constructs have been valuable templates for testing hypotheses, variations on the model need not be viewed as “exceptional”; they also should not serve as an impetus to adjust models so they better accommodate the data. Perhaps a more honest approach is to acknowledge that a single socioecological model cannot accommodate the diversity of relationships within the Order, a point recently made in this journal.[88]

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