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Krishnamoorthy Venkataraman *Editors*

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Why Are Lion-Tailed Macaques Rare?

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Abstract

The intermittent distribution of various animal and plant species in the world, has long been at the core of conservation biology and community ecology. It is therefore vital to know the processes and factors that impact rarities and endemism in the plant and animal world. The mechanism that regulates this rarity and limits a species' distribution and abundance is still not fully understood. We are now beginning to understand that certain plants play an important role during periods of food scarcity. Generally, the plants that sustain animals during periods of food shortage are themselves not abundant (relative to other food trees), and during periods of food abundance, these plants may not be eaten at all. But *Cullenia* and *Ficus* species are the most sought after by the lion-tailed macaques and are important food resources throughout the year. Here we show how these much-favored food trees govern the distribution and very existence of this primate.

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14.1 Introduction

This world is replete with rare and endemic animal and plant species that are patchily distributed. Understanding the processes that cause this rarity has always been a moot point in community ecology and conservation biology (Soulé 1986). While various hypotheses and theories have been put forward to explain this paradigm (Hubbell and Foster 1986; Preston 1962a, b; Rabinowitz et al. 1986), the mechanisms that regulate and limit a species' distribution and abundance are still not fully understood. The "top-down" school holds that predators limit herbivores and thereby prevent them from overexploiting vegetation. "Bottom-up" proponents stress the role of plant chemical defenses in limiting plant depredation by herbivores. Although "top-down" and "bottoms-up" proponents battle on the synecological front (Polis and Strong 1996; Terborgh et al. 2001), ecological and evolutionary forces that govern animals and/or plants are not fully understood. Of particular interest is why certain animals are always rare?

Generally, animals at the top of an ecological pyramid are scarce when compared to the secondary consumers at the bottom of the pyramid. This is true of predators that are at the apex of a food chain because they are controlled by the abundance of their herbivorous prey. Then again smaller species tend to be more abundant than their larger counterparts. Moreover, the distribution and abundance of an animal are dictated by the "quality" of the habitat it occupies. In among these generalizations, if any animal is a large predator, then it is all more rare. Similarly, altitudinal changes could also make an animal uncommon. Equally, folivorous species tend to be more abundant than frugivores and nectarivores. Frugivores generally have large home ranges because of the ephemeral and patchy nature of the availability of the fruits (Fleming 1992). Animals with low reproductive rates and higher inter-birth intervals are also rare. Taking into consideration all these factors, our attention was drawn toward the lion-tailed macaque (*Macaca silenus*).

Although the modern primates and angiosperms appear to have a very tight coevolutionary relationship (Sussman 1991), Howe (1986) opined that it was more of a co-occurrence than otherwise. Angiosperms made their appearance in the early Cretaceous (65 million years ago (MYA)), and the modern rainforests along with modern primates appeared around the same time in mid-Eocene (50 MYA: Sussman 1991). The adaptive radiation and eventual dominance of angiosperms during the Cretaceous opened up a variety of dietary opportunities for the primates (Regal 1977). If present-day primates are any indication, early primates appear to have taken strong advantage of arboreal plant foods since almost all potential food comes from dicotyledonous species using the C_3 carbon pathway and not from the monocotyledonous species (like grass) using the C_4 pathway (Milton 1987).

The genus *Macaca* made its appearance around the mid-Miocene (10 Ma), and the lion-tailed macaque may have evolved around 3 Ma. It is generally considered the ancestor of all extant Asian macaques (Fooden 1975) and hence is the earliest and longest resident in the tropical rainforests of the Western Ghats of southern India.

The lion-tailed macaque is one of the most endangered primates of India. It inhabits the dense tropical rainforests of the Western Ghats between 100 and 1500 m (msl). It is an obligate frugivore and has adapted to a highly arboreal life. Nearly 60% of its diet consists of fruits, and the balance is made up of seeds, flowers, invertebrates, and vertebrates. Females stay with the natal group throughout their lives while males migrate between groups. The home range varies from 1 km² to around 7 km² depending upon the "quality" of the habitat. Lion-tailed macaques live in groups of 8–40 animals, with an average of about 18 animals. Typically, groups have one adult male, one subadult male, five to seven adult females, and the remaining being juveniles and infants. The average adult sex ratio is about five females to one male. Births occur throughout the year with a peak between late November and February (Kumar 1995; Lindburg 1987). Females become primiparous at an average age of 6.6 years, and the inter-birth interval is around 2.5 years, which is considerably higher compared to other macaques. The mean mortality rate irrespective of age/sex classes is around 0.045 per year, which is considerably lower than other macaques. The low population growth of these macaques is due to a delayed primiparity and very low birth rates, but it is compensated by its relatively high survival rate (Kumar 1995). Hence the lion-tailed macaques have always been rare when compared to the other primates of India. Recent population surveys suggest that there are about 4000 individuals in the wild. Here we show how the distribution and existence of a rare and endemic primate, the lion-tailed macaque, are governed by the abundant and much favored food tree, *Cullenia exarillata*, and trees of the genus *Ficus*. The lion-tailed macaque is endemic to the Western Ghats of southern India, whereas the tree, *Cullenia*, is present in the Western Ghats (Kadambi 1954) and Sri Lanka.

14.2   Methods

We surveyed the vegetation of the lion-tailed macaque habitats in the rainforests of the Western Ghats, during 1999–2000 with particular reference to *Cullenia* and *Ficus*. The floristic composition was studied using 48 belt transects by dividing their habitat into two regions based on the vegetation patterns. The area of each belt transect was 0.25 ha (250 × 50 m), and the distance between the first and the 48th belt transect was around 720 km. The lion-tailed macaque habitat was split into two regions and the Palakkad Gap, at around 11° N (Fig. 14.1). The number of individuals and basal areas of each woody plant species were calculated – representing different altitudinal and latitudinal gradients. The woody plant species are represented by trees (≥30 cm gbh) and lianas (≥10 cm gbh). The altitudinal range was between 100 and 1500 m, and the latitudinal range was between 8°3′ and 14°17′ N. The *Ficus* densities were calculated using the software Distance 3.5 (Thomas et al. 1998).
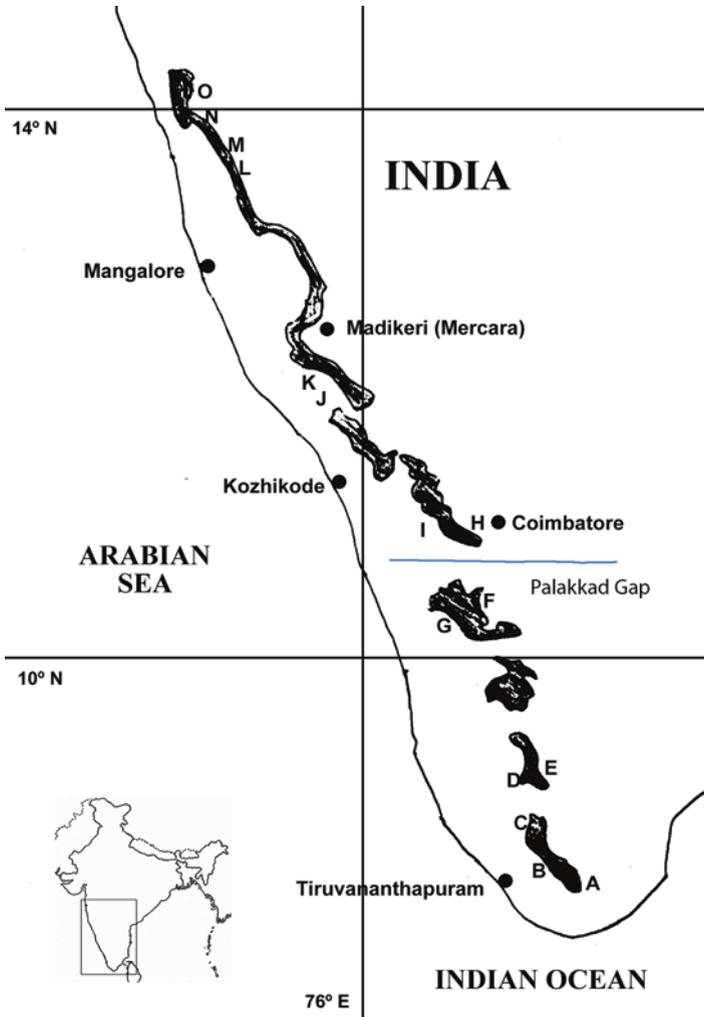
Fig. 14.1 The distributional range of the lion-tailed macaques and the location of the study areas

14.3   Results and Discussion

We sampled 391 woody plant species consisting of 341 trees and 50 lianas (hereinafter referred to as "sampled species") in the lion-tailed macaque habitats, of which 114 woody plant species were lion-tailed macaque food species consisting of 10 lianas and 104 trees (hereinafter referred to as "food species"). This formed 29.16% of the known food trees and lianas. The 15 most important species that contributed

to a large portion of the lion-tailed macaque's diet are only 11.23% of the total number of individuals of the sampled trees, and their basal area contributed to only 20.11% of the total.

Studies in different parts of the Western Ghats show that a total of 218 plants are used as food resource by the lion-tailed macaques from 61 plant families (Krishnamani and Kumar 2000). For the lion-tailed macaque, leaves constitute less than 1% of its diet, and nearly 60% of its food items are fruits. The number of individuals in the sampled species and food species did not vary among zones, and there was no north-south gradation (one-way ANOVA: $F = 0.854, 1.179$, df = 3, $P > 0.0$), whereas the basal areas of the sampled species showed variation among zones, and the basal areas were higher in the sampled species ($F = 6.92$, df = 3, $P < 0.01$), but the basal areas of the food species showed none ($F = 2.484$, df = 3, $P > 0.05$). The number of individuals of all the species of the sampled species decreased with altitude ($r = -0.371$, $n = 48$, $P < 0.01$), and it increased with latitude ($r = 0.317$, $n = 48$, $P < 0.05$), both being weakly significant. But the number of individuals of food species did not show any altitudinal or latitudinal pattern ($r = 0.099, 0.124$, $n = 48$, $P > 0.05$), whereas the basal areas of the sampled species and food species showed marked patterns, with both altitude ($r = 0.431, 0.547$, $n = 48$, $P < 0.01$) and latitude ($r = -0.558, -0.301$, $n = 48$, $P < 0.01, <0.05$).

Cullenia is an important food tree of the lion-tailed macaque. It is the predominant tree in the southern region, and its dominance progressively decreases toward the north and is scarcely present in the northern region (Table 14.1). In fact the northern most limit of *Cullenia* is at 11°75′ N (Pascal 1988; Pascal et al. 1982), and the northern limit of the lion-tailed macaque habitat is at 14°5′ N. Despite this tree's rarity and/or absence in the northern region, the lion-tailed macaques are present there. The lion-tailed macaques feed on *Cullenia* flowers and seeds for most of the year. Flowering in *Cullenia* occurs during periods of fruit scarcity (February–April) and also when most of the other plant species do not flower (Ganesh and Davidar 1997; Green and Minkowski 1977). During this time the lion-tailed macaque feeds heavily on the flowers of *Cullenia*. Although the macaques do depend on nectar, because of its low volume, the fleshy and sweet sepals are readily consumed. The dominance of *Cullenia* results in an overabundance of flowers during this period and is the only species producing such high-quality flowers in the southern region. It is also a remarkably predictable food resource, flowering with the same intensity year after year.

Primates generally give birth when the food resources are abundant (Lindburg 1987), whereas the lion-tailed macaques give birth during December to February, and their favored food trees are not in fruit during February to April. During this time the macaques depend on the flowers of *Cullenia* and the aseasonal and nonsynchronous fruits of *Ficus*. Seasonal reproduction allows animals to be exposed to a varying environment to anticipate and prepare for changes that would adversely affect their fitness. The high survival rates of the neonates in these macaques prove that the macaques may not face problems associated with nonavailability of food resources during the time when they are born. However it is difficult for the lion-tailed macaques to proliferate since the lean season seems to be a bottleneck. The

Table 14.1 The top-ranked food species ($n = 5$–10) contribute to a major portion of a primate's diet. Taxonomy and nomenclature follow Rowe 1996

Primate species	Top-ranked food species (n)	% age of its diet	Source
Blue monkey,	10	69.23	Rudran (1978)
Cercopithecus mitis stuhlmanni	5	34.70	Struhsaker (1978)
Tana river red colobus,	10	>50	Medley (1993)
Procolobus rufomitratus			
(= *Colobus badius rufomitratus*)			
Red colobus,	5	34.3	Struhsaker (1978)
Procolobus badius tephrosceles			
(= *Colobus badius tephrosceles*)			
Black and white colobus,	5	59.8	Struhsaker (1978)
Colobus guereza occidentalis			
Gray-cheeked mangabey,	5	50.9	Struhsaker (1978)
Lophocebus albigena johnstonii			
(= *Cercocebus albigena johnstoni*)			
Red-tailed monkey,	5	36.5	Struhsaker (1978)
Cercopithecus ascanius schmidti			
Bonnet macaque,	5	54.9	Krishnamani (1994)
Macaca radiata			
Barbary macaque,	8	≈65	Ménard and Vallet (1996)
Macaca sylvanus			
Sulawesi crested black macaque,	5	≈50	O'Brien and Kinnaird (1997)
Macaca nigra			

severity of this impediment might vary temporally and spatially depending the "quality" of the habitat. Coping up with this selection pressure may be very crucial to the very survival of these macaques. Considering the fact that these macaques had always been rare (Kumar 1985), we believe these ecological pressures seem to have operated in the same way in the past.

The lion-tailed macaques living in the northern region are at a double disadvantage. The phenological patterns exhibited for the northern region are unimodal, whereas for the southern region, it is bimodal. Hence the availability of fruits in the northern region is limited to a shorter period due to an increased dry period, whereas in the southern region, fruits are available for a considerable longer period. Of the 84 plant species used as food plants, 23 species (27.38%) accounted for a whopping 70.9% (mean for 2 years, SE = 1.7) of the lion-tailed macaque's annual diet (Kumar 1987). Other researchers have also observed the fact that a small percentage of the food species contribute to a major portion of a primate's diet (Table 14.1). This is of paramount importance since only a few food trees sustain the survival of the lion-tailed macaques and the species diversity of the sampled species is lesser in the northern region compared to the south. The sampled species richness for zones 1 and 2 in the northern region was 164 and 183, respectively, and for zones 3 and 4, in the southern region, were 187 and 210, respectively. This means that the southern

Table 14.2 Densities and basal areas of sampled species, food species, *Cullenia*, and *Ficus* spp. in the two regions of the lion-tailed macaque habitats

		Southern region	Northern region	Overall
Sampled area (ha)		6	6	12
Sampled species	Density/ha	430.00	477.17	453.58
	Basal area/ha (m²)	50.59	41.59	45.99
Food species	Density/ha	245.17	255.50	250.33
	Basal area/ha (m²)	33.28	24.99	29.14
Cullenia exarillata	Density/ha	28.00	4.83	16.42
	Basal area/ha (m²)	6.59	0.85	3.72
Ficus spp.	Density/ha	3.01	4.4	3.49
	No. of species	9	9	11

region is more species-rich when compared to the northern region. Also the nonavailability of *Cullenia* in most of the areas in the northern region leaves the macaques with only one choice: *Ficus*. Fortunately, the *Ficus* density in the lion-tailed macaque habitat is higher for areas north of Palakkad Gap compared to the southern region (Table 14.2). The *Ficus* density in the Western Ghats (3.49 trees/ha) is comparable to other areas (Krishnamani and Kumar 2000), whereas the *Ficus* density at the southern extreme of its distribution is very low (1 tree/ha) (Ganesh and Davidar 1997).

Two main attributes determine *Ficus* species as an important food resource for primates during periods of fruit scarcity. Firstly, fruiting patterns of *Ficus* species exhibit spatiotemporal patchiness (Gautier-Hion and Michaloud 1989; Janzen 1979; Milton et al. 1982) ensuring that some individual *Ficus* species are in fruit throughout the year within the same habitat. Secondly, *Ficus* species are usually present at low densities, when compared to other trees in forest ecosystems, and individual trees are usually clumped (Heithaus and Fleming 1978; Gautier-Hion and Michaloud 1989). Owing to these characteristics, it appears that *Ficus* species can be exploited as a major fruit resource only by an animal with a relatively large home range (Borges 1993).

Ficus species form a major portion of lion-tailed macaque's diet. *Ficus* species contain high amounts of amino acids, such as leucine, lysine, valine, and arginine and minerals, such as potassium, calcium, magnesium, sodium, and phosphorous (Wendeln et al. 2000). Although no single species of *Ficus* may be sufficient to sustain frugivores; a mix of *Ficus* species can provide a complete set of nutrients (Wendeln et al. 2000). There are more than 750 species of *Ficus* in this world (Berg 1989), and southern India is the home to 30 *Ficus* species (Sasidharan and Augustine 1999). Of this, 16 species are present within the range of the lion-tailed macaques, and they eat at least 15 species. *Ficus* is a keystone genus that supports a large number of frugivores during periods of fruit scarcity (Terborgh 1986a) since their asynchronous fruiting habit assures that crops will ripen at all times of the year (Milton 1980; Morrison 1978). Some non-*Ficus* fruits also act as keystone resources, although quantitatively they are of minor importance (Terborgh 1986b), but here we

see that a non-*Ficus* species like *Cullenia* seems to be very important for the frugivore community. Usually a species is considered to be a "keystone" when its effect is large compared to its biomass or because of its large density (Jordán et al. 1999). Here *Cullenia* and *Ficus* fit this description. Although carnivorous predators limit the population densities of primary consumers like primates, it is these keystone food resources that regulate the carrying capacity of the frugivorous community during periods of food (fruit) scarcity (Terborgh 1986a). Since plant genera evolve far more slowly than animal genera, "keystone plant species" may act over an evolutionary time as a decisive factor in the evolution of whole faunal assemblages (Terborgh 1986b).

The density of fruit trees, especially some *Ficus* species, regulates the overall density of the orangutans (van Schaik and Djojosudharmo 1992). Sumatran orangutans (*Pongo abelii*) are rare at higher altitudes where *Ficus* densities are also low along with other soft-pulped fruit trees. Similarly, the rarity of a tamarin species (*Saguinus fuscicollis*) has been attributed to two keystone species. The flowers of *Combretum assimile* and *Quararibea cordata* provide them with nectar during periods of food scarcity (Terborgh and Stern 1987).

In the southern region of the Western Ghats, *Ficus* trees are at low densities, and hence *Cullenia* is the major keystone species (Ganesh and Davidar 1997). In the northern region, *Ficus* densities are relatively higher, and hence the lion-tailed macaques do not suffer during periods of fruit scarcity even in the absence of *Cullenia*. Hence the absence of *Cullenia* cannot be a limiting factor for the lion-tailed macaques, in the northern region. The only difference is that the densities of *Cullenia* far outweigh the densities of *Ficus*, but the asynchronous and year-round fruiting pattern of the *Ficus* may compensate for the predictable flowering in *Cullenia*. It is likely that *Ficus* is the keystone species for the lion-tailed macaque in the northern parts and *Cullenia* in the southern parts. The high survival rates of the infant lion-tailed macaques prove that the macaques may not face problems associated with nonavailability of food resources during the time when they are born; however, it is difficult for them to proliferate since the lean season seems to be a bottleneck. Hence, these tree species could well be the limiting factors on which the densities of these macaques depend.

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