



Brief communication

Far from home: The synurbisation of a rainforest-evolved primate, the lion-tailed macaque *Macaca silenus*, and its recent adaptations to anthropogenic habitats in southern India

ASHNI KUMAR DHAWALE^{1,2*,†}  and ANINDYA SINHA^{1,3,4,†}

¹*Animal Behaviour and Cognition Programme, National Institute of Advanced Studies, Bengaluru, India*

²*University of Trans-Disciplinary Health Sciences and Technology, Bengaluru, India*

³*Indian Institute of Science Education and Research, Kolkata, India*

⁴*Centre for Wildlife Studies, Bengaluru, India*

*Corresponding author (Email, ashnidhawale@gmail.com)

†Ashni Kumar Dhawale and Anindya Sinha contributed equally to this work.

MS received 29 January 2022; accepted 24 August 2022

The lion-tailed macaque is an endangered species, endemic to the Western Ghats of southern India. The Anamalai hills harbour 63 groups of the species, several of which occur in rainforest fragments, amidst tea and coffee plantations, on the Valparai plateau. Being highly arboreal, these populations have always been assumed to be largely restricted to their fragmented forest patches and possibly unable to navigate successfully through the surrounding plantation–human habitation matrix. While adult males have occasionally been sighted along roadsides between forest fragments, we now provide evidence for the emigration of an entire troop out of a forest fragment into nearby human settlements, leading to the inclusion of areas completely devoid of natural vegetation into the core home range of the troop. We argue that a combination of hostile inter-troop encounters, a natural urge to expand their range and the discovery of novel and relatively easily accessible food resources may have led to such unusual ranging patterns, accompanied by significant changes in troop behavioural profiles, which we consider as inexorable processes of synurbisation.

Keywords. Anamalai hills; habitat fragmentation; nonhuman primate; provisioning; ranging; synurbisation; urbanisation; Valparai plateau; Western Ghats

1. Introduction

Globally, wild species populations, belonging to various taxa, are increasingly showing a marked tendency to utilise ever-expanding urbanised areas, often in search of novel ecological opportunities (Griffin *et al.* 2017). This process, by which wildlife adapt and continue to exist in now anthropogenically modified, urbanised or semi-urbanised environments, is known as *synurbisation* (Andrzejewski *et al.* 1978; Babińska-Werka *et al.* 1979). From a nonhuman perspective, anthropogenic habitats have been

described as ‘new’, ‘complex’ or ‘strange’, characterised by high degrees of anthropogenic pressures and a host of associated threats to survival (Luniak 2004). Conversely, urban areas also offer novel food resource – human-utilised foods – that are abundantly available, easily accessible and energy rich (Griffin *et al.* 2017), making them attractive habitats for wild species to occupy. Nonhuman populations that colonise anthropogenic habitats show a suite of ecological and behavioural adaptations, including altered behavioural patterns (Altmann and Muruthi 1988; Riley 2007; El Alami *et al.* 2012; Jaman and

Huffman 2013), drastically modified diets (Sinha *et al.* 2005; Baruch-Mordo *et al.* 2014; Yirga *et al.* 2015) or increased mortality due to anthropogenic causes (Beckmann *et al.* 2008), all of which are often consistent across taxa. Here, we draw attention to certain Asian nonhuman primate species, typically of the genus *Macaca* – including the bonnet macaque *Macaca radiata*, rhesus macaque *M. mulatta* and the long-tailed macaque *M. fascicularis* – which have earlier been referred to as the ‘weed macaques’, as they are particularly capable of thriving in anthropogenic habitats. We, however, prefer using the term ‘prolific macaques’ to refer to these species, not only to avoid this somewhat derogatory nomenclature but also to recognise their unique life-history characteristics that set them apart from all the other macaques. Such species are often referred to as *synanthropic*, while those that still remain largely isolated from humans but, more importantly, apparently fail to adapt completely to humans, even when in contact with them, as, for example, the northern pig-tailed macaque *M. leonina* or the stump-tailed macaque *M. arctoides*, are termed *non-synanthropic*. It has become especially crucial to focus, in these times of the Anthropocene, on the behavioural ecology of these latter species, whose capacities to adapt or their recent adaptations to anthropogenic regimes, if any, continue to remain virtually unknown.

The lion-tailed macaque *Macaca silenus*, an endangered species endemic to the rainforests of the Western Ghats of southern India, exists today as 49 subpopulations at only eight key locations, including the Anamalai hills (Molur *et al.* 2003). It has traditionally been observed to be a highly arboreal, primarily frugivorous, habitat-specialist species, completely dependent on the native vegetation of its rainforest landscape and, hence, always considered to be non-synanthropic in its habit.

Since the late 1800s, however, logging of the native vegetation for the expansion of commercially grown tea and coffee plantations, especially on the Valparai plateau in the Anamalai hills, has resulted in extensive forest fragmentation and isolation of lion-tailed macaque troops, which now remain scattered within these remaining rainforest patches (Singh *et al.* 2002; Jegannathan *et al.* 2018). Despite the degraded nature of these last remnant habitats of the macaque, the Anamalai hills, being contiguous with the Parambikulam Tiger Reserve and Neliampathy in the north, and the Chalakudi hills in the south, have been identified as crucial landscape for the conservation of the species (Singh *et al.* 2002).

The Valparai plateau today is a matrix of tea and coffee plantations, interspersed with about 45 rainforest fragments, ranging in size from <10 to >100 ha (Umapathy and Kumar 2000a, b; Mudappa and Shankar Raman 2007). Of these, one particular patch, measuring 92 ha, borders the Valparai town and is surrounded on all other sides by tea plantations – the Puthuthottam forest fragment (figure 1). Generally classified as a small-sized fragment, Puthuthottam has faced perpetual anthropogenic pressures, first being underplanted with coffee and cardamom, which has since been left untended, thus severely affecting the understory, and subjected to largely uncontrolled selective logging, leading to an overall degradation of the habitat (Singh *et al.* 2001). Over the last three decades, a combination of factors, including the continual degradation of habitat and canopy cover, steady growth of the lion-tailed macaque population, expansion of human settlements within the fragment and increased tourism along the Puthuthottam road, has led to the species becoming exposed to human habitations and the resources found within them. This process has, however, been a gradual one, where, as recently as 2015, only certain troops showed a propensity to explore human settlements, while other troops continued to avoid interactions with humans (Dhawale 2016).

While prior to 1991, researchers reported only a single lion-tailed macaque troop in Puthuthottam (Kumar 1987), today the population contains ~190 lion-tailed macaques distributed across five troops (Dhawale, pers. obs.). What is most remarkable is that over the last 5 years, all the troops of the Puthuthottam forest fragment have begun to visit human habitations – either the homes of the plantation labour force within the fragment itself or the neighbouring town of Valparai. These troops have also now developed certain adaptations to these anthropogenic habitats, including a significant reduction of time spent foraging, with a concomitant increase in the time spent resting or the display of altered social dynamics under regimes of perceived competition over human-utilised foods (Dhawale *et al.* 2020). Like many other macaque species (Greenwood 1980), male lion-tailed macaques typically disperse from their natal troops at sexual maturity. This dispersal pattern is thought to reduce inbreeding (Moore 1992), thus playing a crucial role in their long-term survival and reproductive fitness. In fragmented landscapes like the Valparai plateau, however, male migration in lion-tailed macaques appears to be severely impeded (Singh *et al.* 2002), and as a result, males tend to stay back in their natal troops. This, we believe, has led to an unusual multimale,

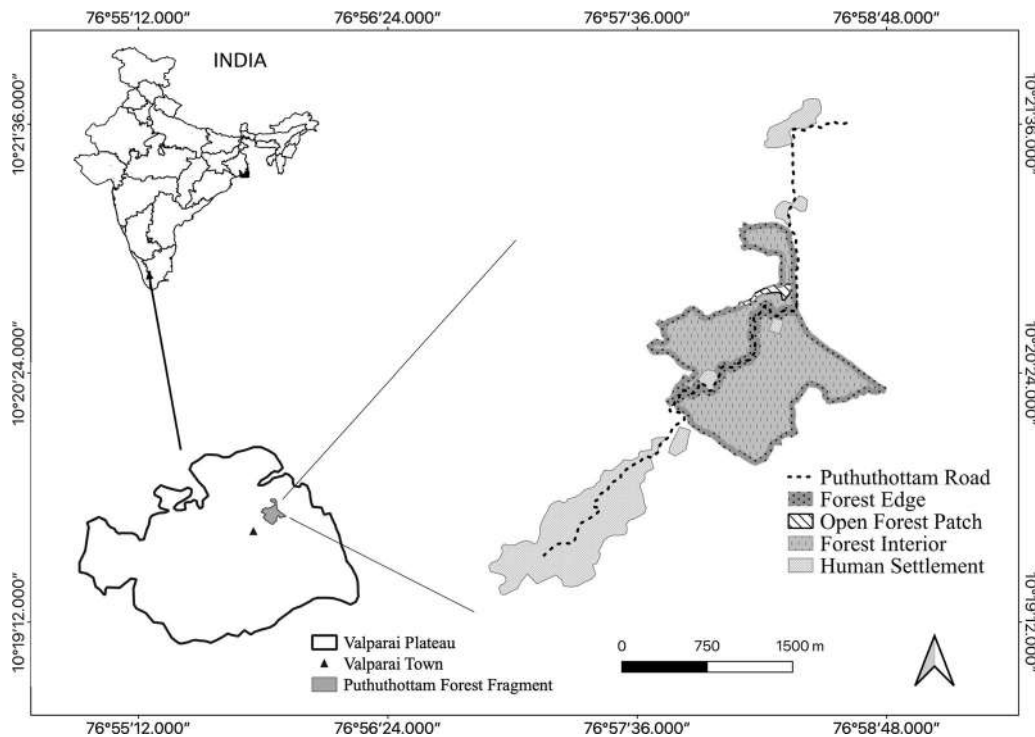


Figure 1. The study area, including the Puthuthottam forest fragment and surrounding human settlements, located on the Valparai plateau in the Anamalai hills, southern India (adapted from Dhawale *et al.* 2020).

multifemale social organisation among the lion-tailed macaque troops of Puthuthottam (Umapathy and Kumar 2000a; Umapathy *et al.* 2011).

In this article, we present the first evidence of an entire lion-tailed macaque troop moving out of the Puthuthottam forest fragment and travelling across a seemingly impermeable matrix of anthropogenic habitats to visit novel human settlements, displaying, in the process, significantly reduced daily movements as well as home-range size, patterns congruent with those observed in other *synurbic* macaque species populations (Aggimarangsee 1992; Hansen *et al.* 2020).

2. Methods

The study troop, henceforth referred to as the RT Troop, consisted of 25 individuals at the time of the study, including 8 adult females, 2 adult males, 1 subadult female, 1 subadult male and 13 juveniles (see Dhawale *et al.* 2020 for a definition of these age classes). The troop left its semi-natural forest fragment for the first time, as confirmed by our earlier field records and on-ground informants, in September 2018, and then once again in November 2018. On

both these occasions, the troop moved 1 km north of the forest fragment towards a dense human settlement, returning to the forest fragment later the same day. We began to systematically track the movements of the RT Troop, using a GPS device to record its location at 15-min intervals from 7:00 to 17:00 h over 15 ± 10 days each month, from January to December 2019. We categorised our movement data into two field seasons, Field Season 1, from January to May 2019, and Field Season 2, from August to December 2019, separated by the monsoon months, when field work could not be conducted, to describe the change in home range of the study troop, as it explored its novel environment. We additionally collected behavioural data *ad libitum* on the troop, as it moved over substrata rather unusual for the species, such as roads, tea bushes and swamps, and as it foraged in the human settlement. A kernel density estimation (KDE; Laver and Kelly 2008) allowed us to determine home range (95% use area) and core use area (50% use area) of the RT Troop over the two field seasons, using an optimal bandwidth selection method to delineate kernels (Fotheringham *et al.* 2000). KDE calculations and visualisation were completed in QGIS (QGIS 2011 version 2.18.3) using the Heatmap plugin.

3. Observations

Field season 1: During the first field season, the RT Troop had a mean daily range of $0.30 \pm \text{SE } 0.04$ km. Initially, the troop would exit the fragment from the northern edge, spending some time at the adjacent Iyerpadi Hospital to forage in its open garbage bins before quickly moving along the edge of the road for 1 km to the Rottikadai human settlement. In this season, the troop would entirely avoid the swamps and tea bushes, walking only on the single road connecting the two settlements, even as traffic continued to ply along the road. The troop would then spend long periods of time, up to 20 days, at the Rottikadai settlement, foraging almost entirely at a large open garbage pit, and occasionally on the few fruiting trees in the settlement, including ones grown in gardens by the local community. In the evenings, it would roost on an *Acacia* stand adjacent to the Rottikadai settlement. The troop returned to the Puthuthottam forest fragment only on three occasions during this entire field season, remaining at its northern edge and returning to the Rottikadai settlement within the same day each time. Our home-range estimate clearly captured this ranging behaviour, with the core use area of 25.6 ha overlapping the Iyerpadi Hospital and Rottikadai settlement, and with the troop's total home range measuring 48.3 ha in this season (figure 2).

Field season 2: During the second field season, the RT Troop had a mean daily range of 0.59 ± 0.09 km. In this season, the troop returned to the Puthuthottam forest fragment more frequently while still spending long periods of time in the Rottikadai settlement, and ultimately visiting a third human settlement, Iyerpadi, 0.5 km north of Rottikadai. During this time, the tea fields adjacent to the Rottikadai and Iyerpadi settlements were pruned, and members of the troop began to move over the stumps to forage for insects. The adult and subadult males would also intently explore the edges of the swamp, presumably to forage. When visiting the Iyerpadi settlement, the troop moved along an overhead cable wire that linked this settlement to Rottikadai, thus avoiding walking through the surrounding scrubland. When in Rottikadai, the troop discovered and began to roost in trees in an unoccupied property within the settlement itself, a practice that continued over the season. Our home-range estimates indicated that while the core use area of the RT Troop was limited to the Rottikadai settlement and measured an area of 22.3 ha, its entire home range extended over an area of 197.43 ha and included parts of the

Puthuthottam forest fragment and the Iyerpadi settlement (figure 2).

4. Discussion

Wild populations are undergoing synurbisation at alarming rates, given the unceasing expansion of human activities across the globe. Human-modified habitats pose a serious threat to the long-term survival of species, especially those that are unable to quickly adapt to the urbanisation of their environments. Lion-tailed macaque populations in isolated forest fragments are known to face human-induced threats, like collision with vehicles and electrocution, and also suffer from biological effects, such as inbreeding depression, presumably due to lack of dispersal between fragments (Ram *et al.* 2015). While it was previously thought that lion-tailed macaque dispersal across the human-modified landscape of Valparai was simply not possible, we present here the first evidence for troop migration of this endangered species, over short distances but across a matrix of human-origin habitats, including tea plantations.

We observed one of the five troops of Puthuthottam, the RT Troop, begin migrating out of the semi-natural forest fragment in September 2018, culminating in a stable shift in its home range from the fragment to a previously unexplored human settlement, almost entirely devoid of natural vegetation, by November 2019. The Rottikadai settlement, situated 1 km north of Puthuthottam and immediately adjacent to an *Acacia* stand, contains densely packed houses, including grocery shops, residential structures, abandoned plots and a large open garbage pit. This troop, which had, till then, predominantly experienced semi-natural forest habitats, initially began to roost in the apparent safety of an *Acacia* stand next to the settlement but, remarkably, shifted its permanent roosting site to the core of this busy settlement within the same year.

The Rottikadai settlement is only one of the seven human settlements in and around Puthuthottam, the others including the town of Valparai and several smaller labour lines in the area. While multiple lion-tailed macaque troops, resident in Puthuthottam, frequently visit the immediately adjacent town of Valparai to primarily forage at its garbage bins, there is no previous record of a troop moving north of the fragment towards Rottikadai. The northern section of the Puthuthottam forest fragment tapers to form a semi-isolated, highly degraded forest patch, bottlenecked by

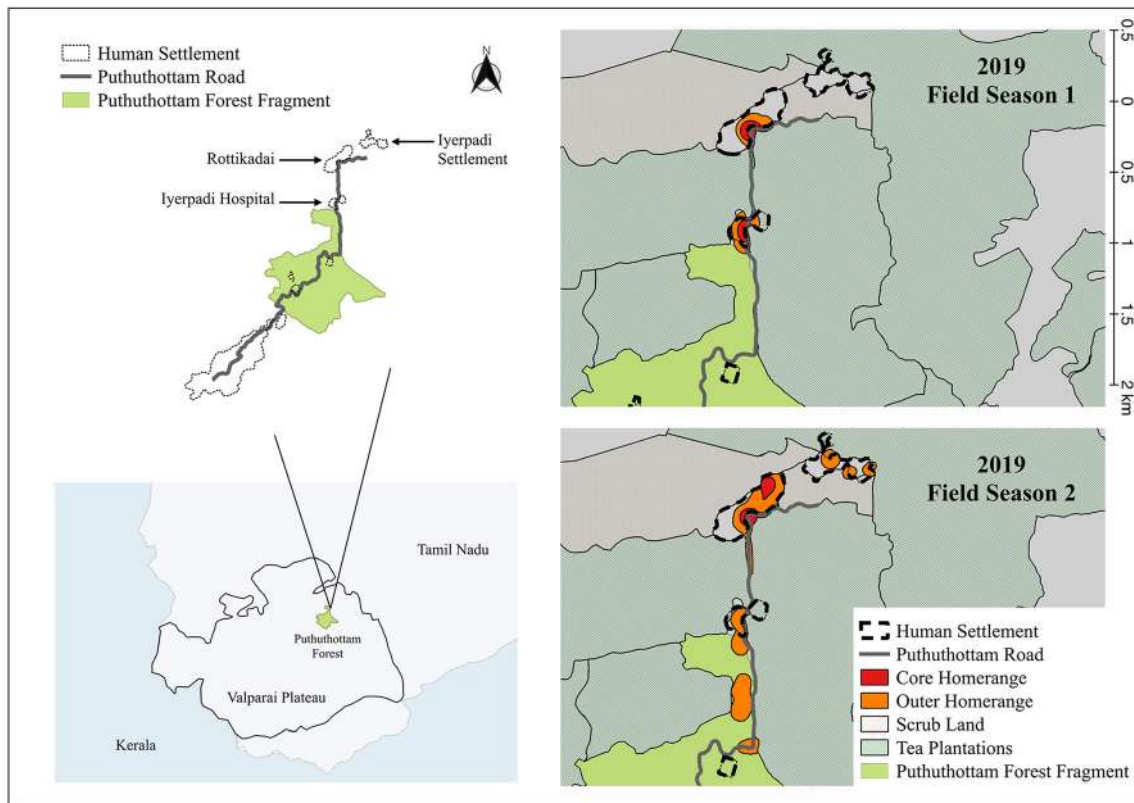


Figure 2. Kernel density estimation of home-range expansion of the RT Troop of lion-tailed macaques over the two field seasons, from January to December 2019.

tea plantations, but this did not appear to deter the exploratory movements of our study troop in any way.

Our previous observations of the lion-tailed macaque troops in Puthuthottam indicated that an inter-troop hierarchy prevails in this population, with the largest, the Big Troop (BT), containing ~90 individuals, being the most dominant and frequently engaging in inter-troop aggression, often chasing away the other troops in their vicinity (Dhawale, pers. obs.). We thus observed heightened vigilance in the male members of smaller troops, in response to the presence of the BT Troop, sometimes leading to pre-emptive troop movements away from the latter, clear evidence of inter-troop scramble competition in the population (van Schaik and van Noordwijk 1988). When we first observed the RT Troop moving north of Puthuthottam, the presence of the BT Troop was also recorded at the northern edge of the fragment. We believe that the initial movement by the RT Troop in the northern direction was possibly a result of avoiding a direct encounter with the BT Troop. Once the smaller RT Troop explored and discovered a set of yet uncontested, new food resources in Rottikadai, it possibly began to revisit the settlement more frequently. We also suggest that the presence of the *Acacia* stand near Rottikadai,

which was initially used as a roosting site, may have allowed the troop to transition between their semi-natural forest habitat and the core of the human settlement. The Iyerpadi settlement, which the troop visited in November 2019, is about 0.5 km from Rottikadai and connected by a narrow mud path. We, therefore, believe that the natural process of home-range expansion from its new urban core home range led to the RT Troop ultimately exploring a second, not too distant, human settlement.

Understanding the patterns of behavioural modifications in wild species in response to rapidly changing anthropogenic habitats is becoming a crucial aspect for the management of wildlife in urban settings (Luniak 2004). We suggest that unimpeded dispersal is crucial for the long-term survival of endangered lion-tailed macaque populations, especially across increasingly fragmented landscapes. While the events that we have presented here pertain to a single macaque troop, we believe that these observations indicate the realisation of the potential ability of lion-tailed macaques to disperse across human-modified habitats, at least over short distances. Whether such migration could also span long distances, essential to maintain a natural inter-population gene flow in the species, awaits long-

term studies in Puthuthottam and the other fragments of the Valparai plateau. It is, nevertheless, critically important to promote native habitat connectivity across the surviving rainforest fragments of the region to ensure the ultimately essential natural dispersal of lion-tailed macaques across this and similarly fragmented landscapes that harbour the last populations of this unique rainforest species.

Acknowledgements

AKD was supported by a fellowship from a research grant (SB/IR/NIAS/2016) awarded to AS by the Science and Engineering Research Board of the Department of Science and Technology, Government of India. We also thank our friends and colleagues at the Nature Conservation Foundation field station in Valparai for logistical and academic support over the years.

References

- Aggimarangsee N 1992 *Survey for semi-tame colonies of macaques in Thailand*. Doctoral Dissertation, Mahidol University, Bangkok, Thailand
- Altmann J and Muruthi PM 1988 Differences in daily life between semiprovisioned and wild-feeding baboons. *Am. J. Primatol.* **15** 213–221
- Andrzejewski R, Babińska-Werka J, Gliwicz J and Goszczyński J 1978 Synurbanization processes in population of *Apodemus agrarius*. I. Characteristics of populations in an urbanization gradient. *Acta Theriol.* **23** 341–358
- Babińska-Werka J, Gliwicz J and Goszczyński J 1979 Synurbanization processes in a population of *Apodemus agrarius*. II. Habitats of the striped field mouse in town. *Acta Theriol.* **24** 405–415
- Baruch-Mordo S, Wilson KR, Lewis DL, *et al.* 2014 Stochasticity in natural forage production affects use of urban areas by black bears: Implications to management of human-bear conflicts. *PLoS One* **9** e85122
- Beckmann JP, Lackey CW and Lackey CW 2008 Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Hum. Wildlife Conflicts* **2** 168–174
- Dhawale AK 2016 *Changing ecologies, shifting behaviours: behavioural responses of lion-tailed macaques *Macaca Silenus* to a matrix of anthropogenic habitats in southern India*. Master's Dissertation, National Centre for Biological Science – Tata Institute of Fundamental Research, Bangalore, India
- Dhawale AK, Kumar MA and Sinha A 2020 Changing ecologies, shifting behaviours: Behavioural responses of a rainforest primate, the lion-tailed macaque *Macaca silenus*, to a matrix of anthropogenic habitats in southern India. *PLoS One* **15** e0238695
- El Alami A, Van Lavieren E, Rachida A and Chait A 2012 Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered Barbary macaque (*Macaca sylvanus*) in the Central High Atlas Mountains. *Morocco. Am. J. Primatol.* **74** 210–216
- Fotheringham AS, Brunson, C and Charlton M 2000 *Quantitative geography: Perspectives on spatial data analysis* 1st edition (London: Sage Publications)
- Greenwood PJ 1980 Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28** 1140–1162
- Griffin AS, Netto K and Peneaux C 2017 Neophilia, innovation and learning in an urbanized world: a critical evaluation of mixed findings. *Curr. Opin. Behav. Sci.* **16** 15–22
- Hansen MF, Ellegaard S, Moeller MM, *et al.* 2020 Comparative home range size and habitat selection in provisioned and non-provisioned long-tailed macaques (*Macaca fascicularis*) in Baluran National Park, East Java. *Indonesia. Contrib. Zool.* **89** 393–411
- Jaman MF and Huffman MA 2013 The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates* **54** 49–59
- Jeganathan P, Mudappa D, Raman TRS and Kumar MA 2018 Understanding perceptions of people towards lion-tailed macaques in a fragmented landscape of the Anamalai Hills, Western Ghats. *India. Primate Conserv.* **32** 205–215
- Kumar A 1987 *The ecology and population dynamics of the lion-tailed macaque (*Macaca silenus*) in South India*. Doctoral Dissertation, Cambridge University, Cambridge, UK
- Laver PN and Kelly MJ 2008 A critical review of home range studies. *J. Wildlife Manage.* **72** 290–298
- Luniak M 2004 Synurbanization: adaptation of animal wildlife to urban development; in *Proceedings of the 4th International Symposium on Urban Wildlife Conservation* (eds) WW Shaw, LK Harris and L VanDruff (Tucson, AZ, USA: School of Natural Resources, College of Agriculture and Life Sciences, University of Arizona) pp 50–55
- Mckinney T 2011 The effects of provisioning and crop-raiding on the diet and foraging activities of human-commensal white-faced capuchins (*Cebus capucinus*). *Am. J. Primatol.* **73** 439–448
- Molur S, Brandon-Jones D, Dittus W, *et al.* 2003 *The status of South Asian primates: Conservation assessment and management plan (CAMP) workshop report*. Coimbatore, India: Zoo Outreach Organisation/CBSG-South Asia
- Moore J 1992 Dispersal, nepotism, and primate social behavior. *Int. J. Primatol.* **13** 361–378

- Mudappa D and Shankar Raman TR 2007 Rainforest restoration and wildlife conservation on private lands in the Western Ghats; in *Making conservation work* (eds) G Shahabuddin and M Rangarajan (Ranikhet, India: Permanent Black) pp 210–240
- QGIS DT 2011 Quantum GIS geographic information system. Open Source Geospatial Foundation Project (github.com/qgis/QGIS)
- Ram MS, Marne M, Gaur A, *et al.* 2015 Pre-historic and recent vicariance events shape genetic structure and diversity in endangered lion-tailed macaque in the Western Ghats: Implications for conservation. *PLoS One* **10** e0142597
- Riley EP 2007 Flexibility in diet and activity patterns of *Macaca tonkeana* in response to anthropogenic habitat alteration. *Int. J. Primatol.* **28** 107–133
- Singh M, Kumara HN and Kumar AM 2001 Behavioural responses of lion-tailed macaques (*Macaca silenus*) to a changing habitat in a tropical rain forest fragment in the Western Ghats. *India. Folia Primatol.* **72** 278–291
- Singh M, Singh M, Kumar MA, *et al.* 2002 Distribution, population structure, and conservation of lion-tailed macaques (*Macaca silenus*) in the Anaimalai Hills, Western Ghats. *India. Am. J. Primatol.* **57** 91–102
- Sinha A, Mukhopadhyay K, Datta-Roy A and Ram S 2005 Ecology proposes, behaviour disposes: Ecological variability in social organization and male behavioural strategies among wild bonnet macaques. *Curr. Sci.* **89** 1166–1179
- Umapathy G, Hussain S and Shivaji S 2011 Impact of habitat fragmentation on the demography of lion-tailed macaque (*Macaca silenus*) populations in the rainforests of the Anamalai Hills, Western Ghats. *India. Int. J. Primatol.* **32** 889–900
- Umapathy G and Kumar A 2000a The demography of the lion-tailed macaque (*Macaca silenus*) in rain forest fragments in the Anamalai Hills, South India. *Primates* **41** 119–126
- Umapathy G and Kumar A 2000b The occurrence of arboreal mammals in the rain forest fragments in the Anamalai Hills, South India. *Biol. Conserv.* **92** 311–319
- Yirga G, Leirs H, De Iongh HH, *et al.* 2015 Spotted hyena (*Crocuta crocuta*) concentrate around urban waste dumps across Tigray, northern Ethiopia. *Wildlife Res.* **42** 563–569

Corresponding editor: UMA RAMAKRISHNAN