

1 Ranging patterns of the rainforest-adapted lion-tailed macaque *Macaca silenus* in a human-
2 dominated landscape in the Anamalai hills of the Western Ghats, India

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25 Running title: *Ranging patterns of rainforest primate in a human-dominated landscape*

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35 **Abstract**

36 The ranging patterns of five lion-tailed macaque *Macaca silenus* troops, forming the
37 Puthuthottam sub-population, were studied over a three year period to determine
38 road/habitation visitation rate, home ranges and habitat preference. Each troop visited the road
39 or human habitation at varying rates, with the largest troop visiting most frequently. Home
40 ranges sizes were observed to be highly reduced when compared to wild populations, and also
41 greatly varied across troops, with relatively low overlap given the macaque density in the
42 available area. All five macaque troops showed a preference for human-modified habitats such
43 as roads and human settlements where anthropogenic food was easily available. Our study
44 shows an increasing dependence amongst members of the Puthuthottam troops on
45 anthropogenic foods, which has led to many threats faced by individuals including fatal
46 collisions with vehicular traffic and electrocutions.

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55 Introduction

56 Animal movements in a landscape are largely determined by the availability and distribution
57 of food, predation risk, intra- and inter- species competition, reproductive investments and
58 behavioural adaptations (Clutton-Brock, 1975; Pontzer & Kamilar, 2009; South, 1999; Wiens
59 et al., 1993), all of which are heavily influenced by human disturbance. Globally, natural
60 habitats are being razed for agricultural purposes, having already resulted in the loss of up to
61 50% of forest land (Defries et al., 2004). The resultant fragmentation of natural habitats into
62 isolated patches is known to drastically affect the spatial movement of animals, often restricting
63 them to certain areas beyond which the habitat becomes impermeable (Andren, 1994; Bladon
64 et al., 2002; Mborá et al., 2009). Patch resource quality and heterogeneity directly influences
65 animal home range (Levins, 1968; Rolstad, 1999), which is typically defined as the total area
66 used by an individual or group (Jay, 1965). Additionally, fragmentation indirectly shapes
67 ranging behaviour through the introduction of unnatural features into the landscape, such as
68 linear intrusions and barriers (Jakes et al., 2018). Ranging behaviour, thus, becomes a useful
69 tool to capture the interactions of animals with their changing environment, especially insofar
70 as human activity is concerned.

71 Humans developmental activities directly and indirectly impact the ranging behaviour of
72 animals. For example, the construction in windfarms in Scotland caused resident Golden eagles
73 *Aquila crysaetos* to change their ranging in order to avoid the manmade structures (Walker et
74 al., 2005). The red fox *Vulpes vulpes* selectively used human-dominated areas in Central Italy,
75 based on the tolerance exhibited by people towards them (Lucherini et al., 1995). Another
76 species from Central Italy, the Least weasel *Mustela nivalis* showed a strong preference for
77 remnant natural habitats, such as hedges, in a predominantly agricultural landscape (Magrini
78 et al., 2009). A species of stone curlew *Burhinus oedicnemus* in southern England preferentially
79 chose breeding grounds that were greater than three kilometres from a major road (R. E. Green
80 et al., 2000). Home range expansion was observed to be multi-fold in some populations of
81 South Andean deer *Hippocamelus bisulcus* in response to hunting and other such human
82 disturbances in Chilean Patagonia (Gill et al., 2008). Closer to home, in the Western Ghats of
83 India, movement patterns of many large mammals including the Asian elephant *Elephas*
84 *maximus*, spotted deer *Axis axis* and tiger *Panthera tigris* are radically affected by linear
85 intrusions such as pipelines, railway tracks, electric wires and fences (Menon et al., 2013;
86 Nayak et al., 2020).

87 Of the many mammals impacted by human activity, primates perhaps have the longest history
88 of interactions with humans and human habitations. For example, the Bonnet macaque *Macaca*
89 *radiata*, endemic to peninsular India, has featured in literature from 2000 years ago, being
90 described as a regular fixture in the town's commons (see Sinha, 2001 for source). With a
91 population of 2 billion people in primate range countries, as of 2005 (Estrada et al., 2012), it is
92 hardly surprising that primates across the world are increasingly encountering humans and their
93 infrastructure. In fact, many species the world over, are able to persist in agroecosystems, or
94 habitats dominated by crops but having some remnant natural vegetation (Estrada et al., 2006,
95 2012). These trends, however, are usually observed in primate species that show a high
96 propensity for adapting to human-dominated landscapes, such as habitat generalists or species
97 that are non-reliant on dense canopy for movement. Even those that find their way through a
98 human-modified habitat matrix, and are able to exploit new food sources or find shelter
99 (Adhikari et al., 2018; Estrada et al., 2012; Ganguly & Chauhan, 2018; Nijman, 2021), face
100 numerous caveats including intra-species and human-primate conflict (Defries et al., 2004;
101 Jaman & Huffman, 2013; Radhakrishna & Sinha, 2011; Ram et al., 2003; Riley, 2007; Sinha
102 et al., 2005; Tracie, 2011; Warren et al., 2011), fatal encounters with vehicles , increased
103 parasite load (Hussain et al., 2013; Mborera et al., 2009) and hunting pressures (Gill et al., 2008;
104 Richard-Hansen, 2000).

105 These caveats are especially pronounced in those primate species that display a further
106 specialisation in their ecology or behaviour. For example, the highly arboreal proboscis
107 monkey *Nasalis larvatus* completely avoided clear-felled habitats surrounding human
108 habitation (Salter et al., 1985) and abandoned roosting sites along riversides where tourism-
109 associated infrastructure was established (Marsh & Chapman, 2013). The Yunnan snub-nosed
110 monkey, inhabiting the highest elevation of any non-human primate species, displayed greatly
111 varied daily movements in response to severe human disturbance, which were further
112 exacerbated by the seasonality of natural food resources (Li et al., 2020). The habitat-specialist
113 diademed sifaka *Propithecus diadema* showed a drastically reduced home range size and daily
114 path length in fragmented habitats (Irwin, 2008). A similar trend was observed in frugivorous
115 primates, such as the moustached guenon *Cercopithecus cephus* and hoolock gibbon *Hylobates*
116 *hoolock* and *Hylobates agilis* (Yanuar & Chivers, 2010), wherein home range size in
117 fragmented habitats is drastically reduced. This pattern could perhaps be explained by the
118 surrounding human-dominated matrix creating a “hard edge”, restricting the species entirely

119 within the fragment, as is the case with the highland mangabey *Rungwecebus kipunji* in
120 Tanzania (Bracebridge et al., 2013). It is also noteworthy that folivorous species that have
121 inherently small home ranges tend to fare better in fragmented habitats, as they are able to
122 maximise resources within restricted areas (Yanuar & Chivers, 2010).

123 The lion-tailed macaque *Macaca silenus*, while belonging to the highly adaptable genus of
124 macaques, has been categorised as an arboreal, primarily frugivorous, habitat-specialist
125 species, dependent on the wet evergreen native vegetation type (Kumar, 2013). This is a species
126 endemic to the Western Ghats, existing today in 49 subpopulations, in only eight key locations,
127 including the Anamalai Hills (Kumara & Singh, 2003; Kurup & Kumar, 1993; Molur et al.,
128 2003). Since the late 1800s, logging of the native vegetation for the expansion of commercially
129 grown tea and coffee plantations on the Valparai plateau in the Anamalai hills has resulted in
130 forest fragmentation and the isolation of lion-tailed macaque troops now scattered within these
131 remaining pockets of rainforest (Jeganathan et al., 2018; Singh et al., 2002). Despite the
132 degraded nature of these remaining habitats, the Anamalai hills, being contiguous with
133 Parambikulam Tiger Reserve and Neliampathy in the North, and the Chalakudi hills in the
134 south, has been identified as a crucial landscape for the conservation of the lion-tailed macaque
135 (Singh et al., 2002).

136 The Valparai plateau is a matrix of tea and coffee plantations interspersed with 45 rainforest
137 fragments ranging in size from <10ha to >100ha (Mudappa & Shankar Raman, 2007;
138 Umopathy & Kumar, 2000). In the surrounding shola forest of Varagaliyar, lion-tailed macaque
139 groups are reported to maintain a home range of 131ha, while covering 10.75ha and moving
140 between 0.75km to 2.5km on a daily basis (Kurup & Kumar, 1993). In contrast, this study
141 focuses on one of the larger forest fragments in the Valparai plateau, measuring 92ha. The
142 Puthuthottam forest fragment, neighbouring the town of Valparai, and surrounded on all other
143 sides by tea-plantations, contains ~190 lion-tailed macaque individuals divided into five troops.
144 All of the five troops present in the Puthuthottam forest fragment visit human habitations, either
145 labour lines within the fragment or the neighbouring town of Valparai (Dhawale Pers. Obs.).

146 Troops in this population already exhibit adaptations to these anthropogenic habitats,
147 significantly reducing time spent foraging while increasing time spent resting, and display
148 altered social dynamics under regimes of potentially perceived competition in the presence of

149 human-use foods (Dhawale et al., 2020). Like many other macaque species (Greenwood,
150 1980), male lion-tailed macaques typically disperse from the natal troop at sexual maturity.
151 This dispersal pattern is thought to reduce inbreeding in species (Moore, 1992), thus playing a
152 crucial role in their long-term survival. In fragmented landscapes like the Valparai plateau,
153 however, male migration in lion-tailed macaques is severely impeded (Singh et al., 2002). As
154 a result, males tend to stay back in the natal troops, which has led to an unusual multimale/
155 multifemale social organisation in the troops present in Puthuthottam (Dhawale, pers. obs.).
156 Given these relatively recent shifts in the species' ecology and behaviour in this particular
157 population, we sought to examine the ranging behaviour, and habitat use and preference of the
158 five Puthuthottam troops, as they traversed over a human-dominated habitat matrix.

159 **Objective and Questions**

160 Examining movement, habitat use and competition across the multiple lion-tailed macaque
161 troops residing in Puthuthottam forest fragment through ranging behaviour.

- 162 1) How does the home range differ between troops and across field seasons?
163
- 164 2) How much overlap is observed across troop core- and outer- home ranges?
165
- 166 3) What is the degree of movement for each troop per day over the study period?
167
- 168 4) What pattern of habitat use is observed by the Puthuthottam population over the study
169 period?
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171

172 **Methods**

173 **Field Methods**

174 GPS locations were taken at the centre of two pre-determined marker adult females of the troop
175 at 15 min intervals during the simultaneous and systematic following of all troops present in
176 the Puthuthottam forest fragment, as they ranged over both natural and anthropogenic habitats.

177 Data was collected for 8 ± 1 months (over 14 ± 1.7 days/ month) for each season (September to
178 May), on each of the five troops present in Puthuthottam from 2018 to 2021. A total of ~5000
179 location data points were collected with 250 ± 100 data points per month.

180 *Habitation Visitation Rate*

181 The Puthuthottam highway and human settlements were monitored continuously for 12 months
182 between October 2018-October 2019, with a GPS location recorded at every encounter with
183 any troop present in Puthuthottam. If the troop continued to remain by the human habitation,
184 the GPS record was repeated at 15 min intervals. These locations were later mapped to describe
185 the patterns of road visitation by the lion-tailed macaques in the Puthuthottam population.

186 *Home range estimation, overlap and habitat use*

187 GPS locations over the field seasons and total study period were mapped using GIS software
188 to calculate distances travelled, directions of movement and rates of ranging across and outside
189 the study area for each troop. Such an analysis is essential to map the new-found home range
190 of these macaque troops, particularly in so far as they overlap with human habitations, orchards
191 and roads, potential areas for escalated human-primate conflict.

192 **Analysis**

193

194 *Habitation Visitation Rate*

195

196 A habitation visitation rate was calculated as the proportion of days over the monitoring period
197 during which lion-tailed macaques were encountered near roads or human settlements (adapted
198 from Singh 2001).

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201 *Home range estimation and overlap:*

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203 A kernel density estimation (Laver & Kelly, 2008) allowed us to determine outer home range
204 (95% use area) and core use area (50% use area), using an optimal bandwidth selection method
205 to delineate kernels from Fotheringham et al., 2000. KDE calculations and visualisation were
206 completed in QGIS (QGis, 2011 version 2.18.3) using the Heatmap plugin. Additionally we

207 visually present overlap of home range across all troops in Puthuthottam to describe prevailing
208 inter-troop competition.

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211 *Degree of movement:*

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213 Daily paths were calculated for each troop over each field season in QGIS (QGis, 2011 version
214 2.18.3) and their lengths presented as average per troop per field season.

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217 *Habitat Use and Preference:*

218 To describe habitat use and preference, troop locations were sampled such that a single unique
219 location was considered per day over the entire study period, and compared to a randomly
220 generated set of points of comparable sample size using a non-parametric test (Wilcoxon Test)
221 in R, revised version 3.2.4. The random points were weighted as density dependent, based on
222 the available area of any given habitat type using QGIS (QGis, 2011 version 2.18.3).
223 Additionally, the study area was rasterized such that each raster pixel (50mx50m) contained a
224 corresponding 'Habitat Type' value and the frequency of each habitat type (available area) was
225 compared to the sampled troop locations to provide a visual comparison of availability versus
226 use.

227 All graphs were created in R, revised version 3.2.4. The habitat types considered are as follows:

228 *Forest Edge:* A 50-m-wide belt around the edge of the Puthuthottam forest fragment,
229 containing native and non-native tree species and bordered on one side by a national highway.
230 We chose to demarcate the boundary at 50m from the edge as we observed that the troop spread
231 at any given time was $\leq 50\text{m}$. This habitat contained Natural food sources, and occasionally
232 Human-use foods, either dropped along the roadside or in the form of handouts provided by
233 tourists.

234 *Forest Interior:* An area of forest contained by the Forest Edge, described above, consisting of
235 native and non-native tree species, all of which constituted Natural food sources.

236 *Open Forest Patch*: A relatively open space, largely without canopy cover, present within the
237 Puthuthottam forest and recently planted with coffee saplings. It included only Natural food
238 sources.

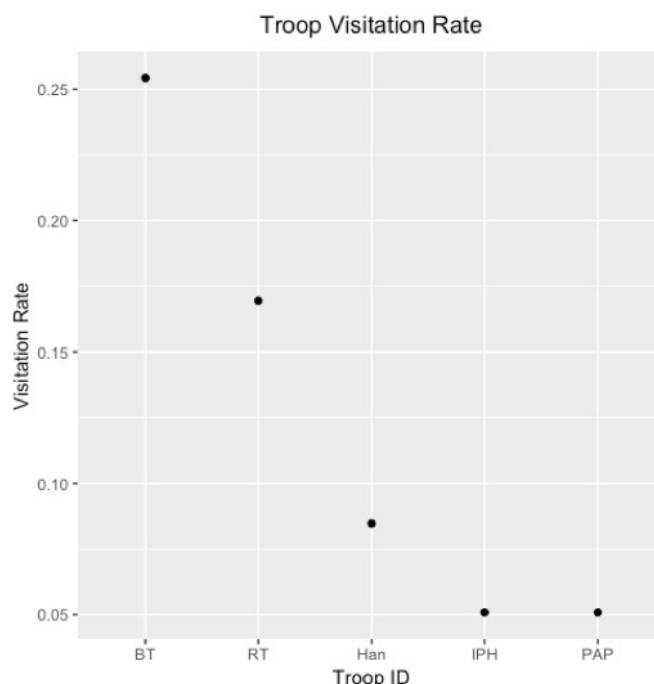
239 *Human Settlement*: Six separate human habitations were present within and surrounding the
240 Puthuthottam forest fragment, including two high-density towns, three labour lines housing
241 plantation workers, and a hospital building. These areas were considered as Human Settlement
242 habitat type which was characterised by the presence of both Natural and Human-origin food
243 resources.

244 *Puthuthottam Road*: The section of the Puthuthottam Highway beginning from the Human
245 Settlements to the north of the forest fragment and ending at the southern end of the forest
246 fragment.

247 **Results**

248 **Habitation Visitation Rate**

249 Each of the five troops visited habitation at varied rates (Figure 1), with the BT troop and RT
250 troop visiting habitation most frequently. The overall habitation visitation rate was calculated
251 to be 0.57 times a day.

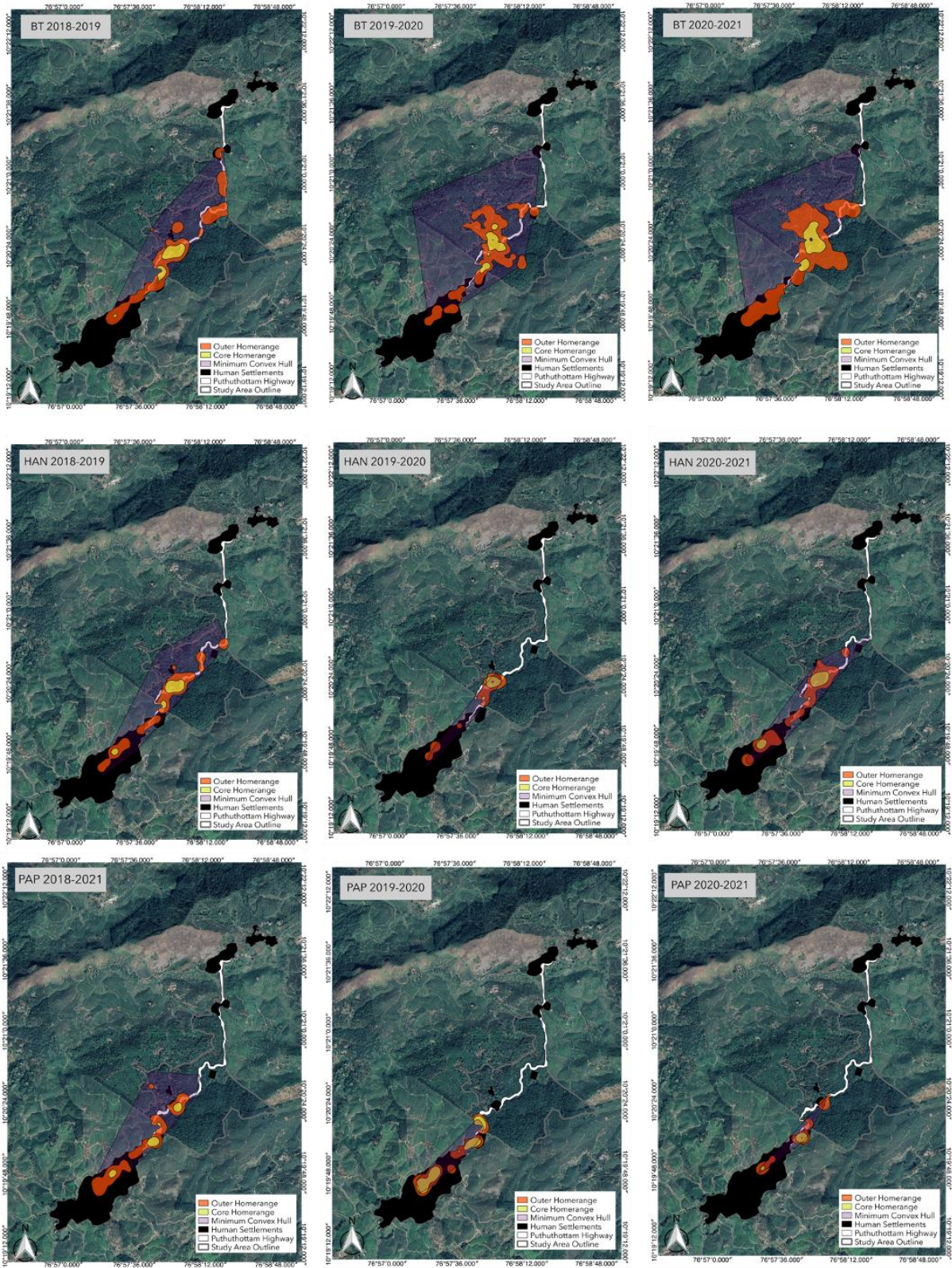


252 **Fig 1.** Habitat visitation rate of the five Puthuthottam troops during October 2018-October 2019

253

254 **Outer- and core- home range**

255 Figure 2 depicts the home ranges for each field season (Sept 2018-May 2019; Aug 2019-Apr
256 2020; Oct 2020-Mar 2021) of all troops present in Puthuthottam. Three of the troops were
257 present for only a few of the field seasons due to fission-fusion and reforming of certain troops.
258 Home ranges varied both across field seasons and troops. The home range of the biggest troop,
259 BT, seemed to expand over the three field seasons while the RT home range seemed to become
260 concentrated in certain areas. NTT, a troop which formed when two smaller troops joined
261 together, seemed to show the most varied home range over field seasons. Figure 3 depicts the
262 overall home range of each troop measured over the entire study period. Three of the troops,
263 namely BT, PAP and HAN ranged primarily over the southern part of the forest fragment,
264 while the other two troops, NTT and RT, were mostly observed in the northern part of the
265 fragment. Table 1 contains the overall home range sizes of each troop. The largest troop, BT,
266 also had the largest home range, however, the smallest troop, HAN, did not have the smallest
267 home range. Figure 4 shows the correlation between total home range area and total troop size.
268 There is a slight correlation between home range and troop size (Spearman rank correlation,
269 $R= 0.6$, $p=0.35$), and home range and number of adult males per troop (data not shown),
270 however, these were not statistically significant.



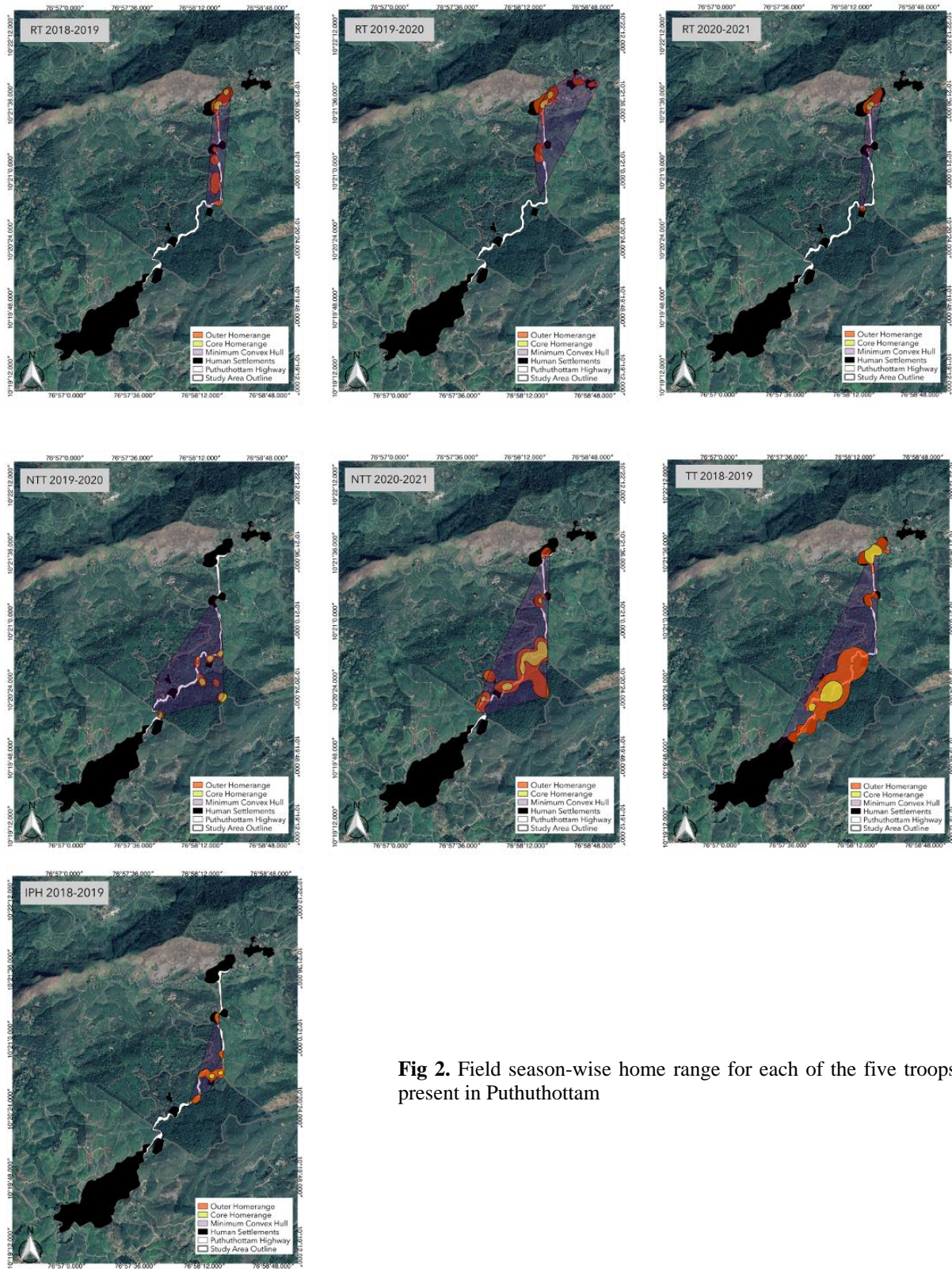


Fig 2. Field season-wise home range for each of the five troops present in Puthuthottam

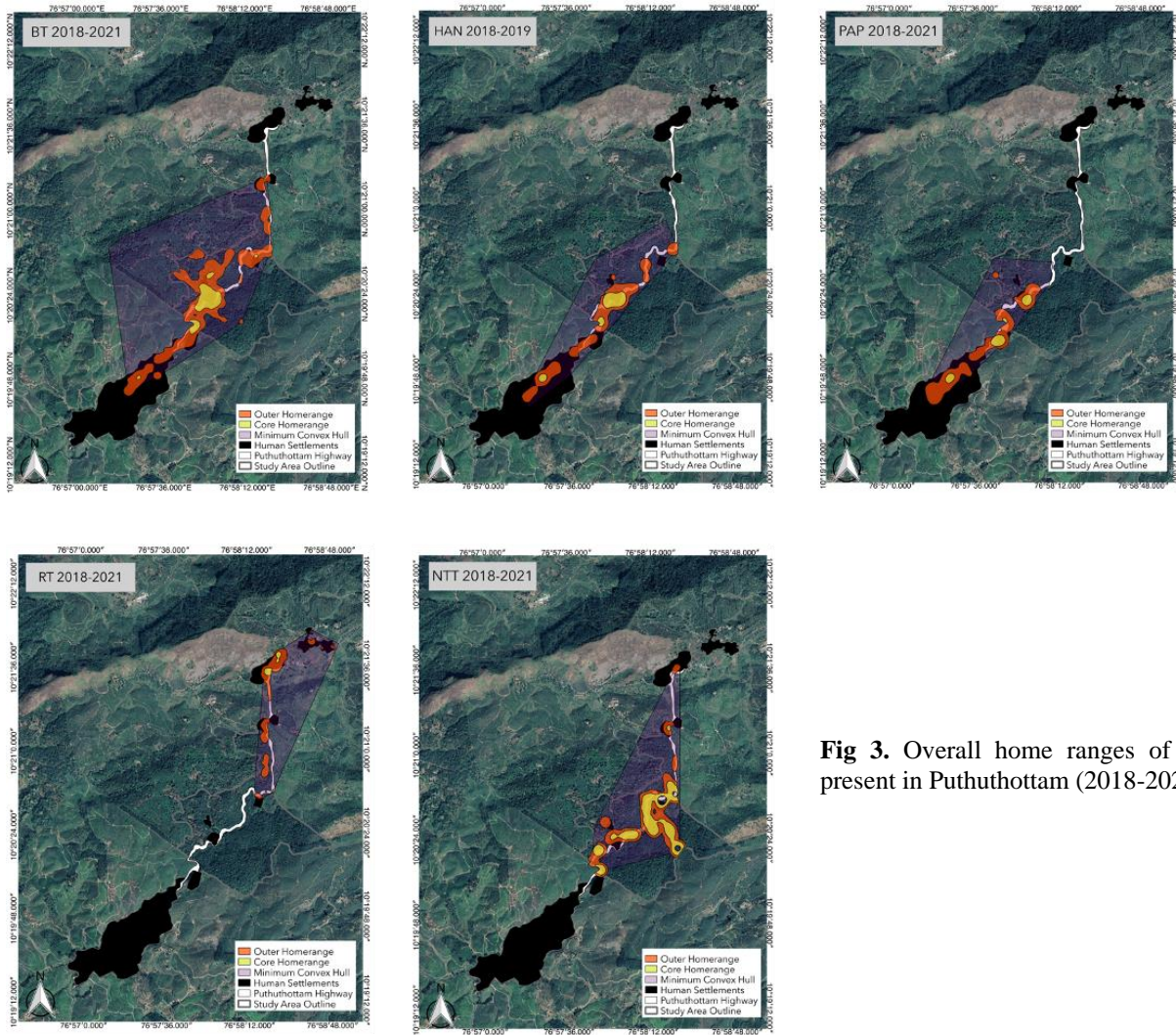


Fig 3. Overall home ranges of all troops present in Puthuthottam (2018-2021)

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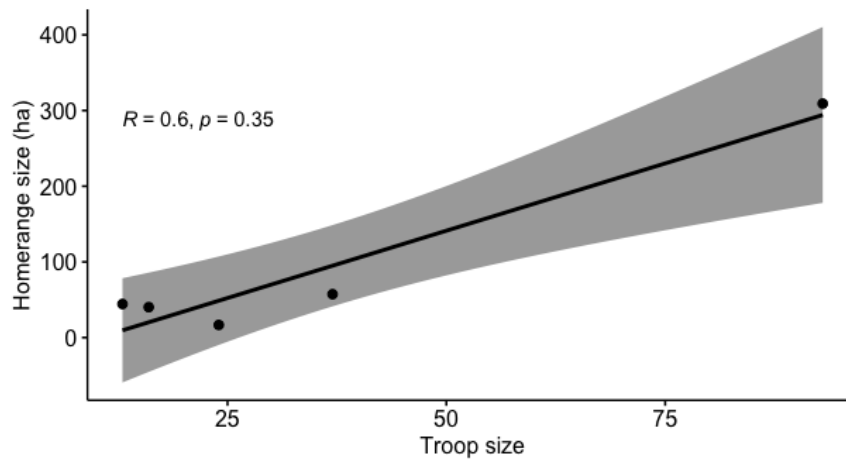
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Table 1. Overall home range sizes (ha) of all troops in Puthuthottam 2018-2021

TROOP NAME	OUTER-HOME RANGE	CORE-HOME RANGE	TOTAL
BT	297.9	11.2	309.1
HAN	37.2	7.1	44.3
PAP	34.9	5.3	40.2
RT	15.1	1.6	16.7
NTT	52.06	5.22	57.28
IPH	8.6	1.1	9.7
TT	80.8	17.2	98

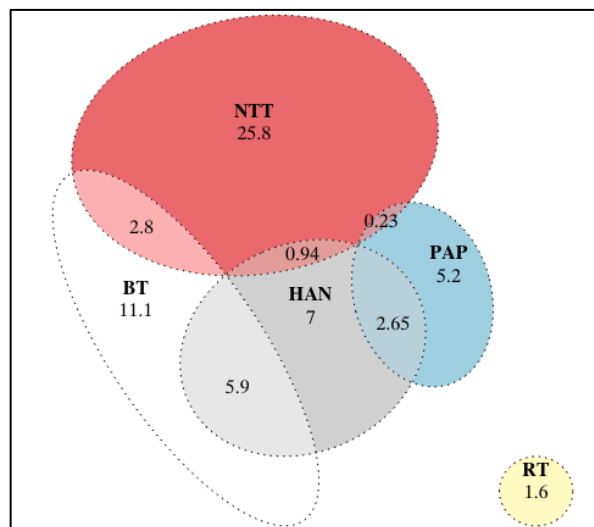
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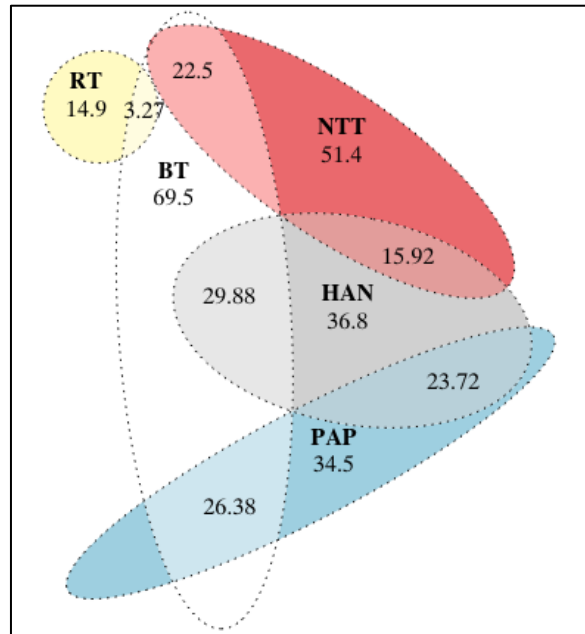
277 **Fig 4.** Correlation between total home range area and total troop size for all troops in Puthuthottam

278 Home range Overlap

279 The outer- and core- home ranges of most troops overlapped to a certain degree. There was
280 relatively less overlap between troop core-home ranges than the outer home range. Figures 4
281 and 5 depict the pairwise overlap of core- and outer- home ranges respectively. Three troops,
282 which were primarily observed in the southern part of the forest fragment, showed the most
283 home range overlap while the two troops near the northern half did not show much overlap.



284 **Fig 5.** Pairwise overlap of core-home ranges across all troops present in Puthuthottam. Numbers indicate area in
285 hectares



286 **Fig 6.** Pairwise overlap of outer-home ranges across all troops present in Puthuthottam. Numbers indicate area
 287 in hectares

288 **Degree of Movement**

289 Over the study period, troops moved an average of 393.3 – 722.3m per daily field session
 290 (Table 2). The two troops that joined to form a single troop, NTT, during the first field season
 291 moved the most on average per day, however, the largest troop recorded the maximum daily
 292 path length at 3.8 km on a single day. Overall, daily path length was not significantly correlated
 293 with troop size ($R=0.57$, $p=0.2$).

294 **Table 2.** Observed degree of movement (m) per day for each troop in Puthuthottam 2018-2021

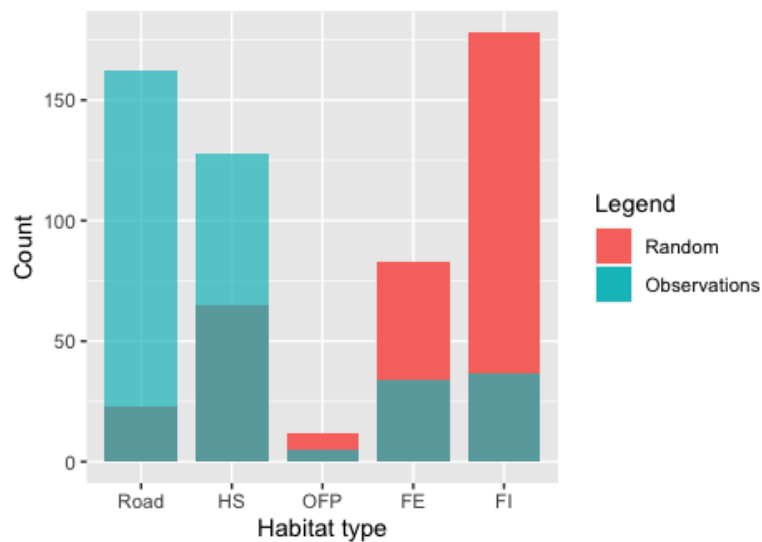
TROOP ID	AVERAGE OBSERVED MOVEMENT/ DAY (M)	RANGE OF MOVEMENT/ DAY (M)
BT	650.5	26.5 - 3774.7
HAN	585.3	8.6 - 2467.2
PAP	393.3	6.3 - 1256.4
RT	468.4	4.7 - 2962.9
NTT	722.3	65.1 - 2397.4
IPH	285.3	50.6 - 546
TT	721.93	64 - 2565

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297 **Habitat Preference**

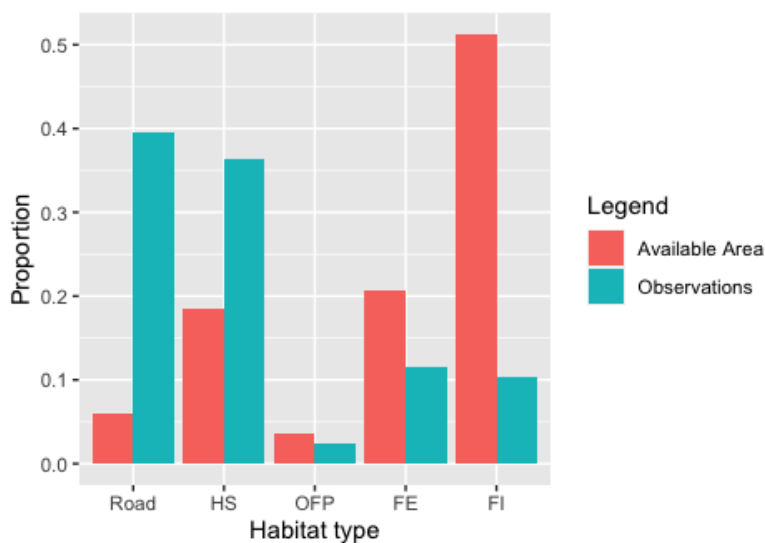
298 A non-parametric Wilcoxon test revealed a significant difference between density-dependent
299 randomly generated points and observed macaque locations ($W=24312$; $p < 0.0001$; Figure 7).
300 The macaques also used human-dominated habitats such as the road and human settlements
301 disproportionately more than the area available in these habitat types (Figure 8).

302



303 **Fig 7.** Randomly generated locations versus observed lion-tailed macaque locations across each habitat type.
304 HS= Human Settlement; OFP= Open Forest Patch; FE= Forest Edge; FI= Forest Interior

305



306 **Fig 8.** Available area in each habitat type versus observed lion-tailed macaque locations. HS= Human
307 Settlement; OFP= Open Forest Patch; FE= Forest Edge; FI= Forest Interior

308

309 **Discussion**

310 Each of the five Puthuthottam troops visited human habitation at varying rates, with the largest
311 troop, BT, visiting most frequently, followed by RT, the newly formed troop in the population.
312 The HAN troop, which split from the BT troop most recently in 2017 also visited human
313 habitations relatively frequently. Interestingly, the two smaller troops, IPH and PAP, which
314 infrequently visited human settlements or the road, both contained a single adult male up until
315 2016, after which an additional male joined each troop. Both troops were observed to increase
316 habitation visitation after this time, with IPH mainly frequenting the Iyerpadi Garden Hospital
317 and some stretches of road towards the north of the fragment, and PAP moving along the edges
318 of the Valparai town towards the south. The rate at which Puthuthottam monkeys visited houses
319 and buildings was calculated at 0.43/day in 2001 (Singh et al., 2001) while this study indicates
320 an increased habitation visitation rate of 0.57/day. Additionally, our measurement, which
321 required continuous monitoring of the road and settlements, was carried out for a year between
322 2018-2019; based on our further observations of troops, these rates were noted to increase in
323 the following years between 2019-2021.

324 All of the five Puthuthottam troops incorporated, into their core- or outer- home range, one or
325 more of the six human settlements situated within and bordering the Puthuthottam forest
326 fragment, listed from North to South as follows: Rottikadai, Iyerpadi Garden Hospital, 10-
327 Acre, Puthuthottam lines, PAP colony and the Valparai town. Energy-rich human-use foods
328 were, naturally, accessible at each of these settlements, however, Rottikadai, Puthuthottam
329 lines and the Valparai town contained large areas where garbage was openly disposed and were
330 presumably the most contested sources for this precious food type. While Rottikadai is a
331 kilometre to the North of the fragment and requires traversing a dangerous highway, tea fields
332 and swamps, the Puthuthottam lines and Valparai are located to the South of the fragment,
333 where we see a corresponding concentration of troop activity. Of the five troops, home ranges
334 of three were located entirely in the southern half of fragment, and the remaining two troops
335 maintained home ranges towards the northern half of the fragment.

336 Across taxa, home range size is largely determined by diet, body size and corresponding energy
337 requirements (Harestad & Bunnell, 1979; McNab, 1963). Within primate species as well, home
338 range size is dependent on body size and diet, with folivorous and terrestrial species

339 maintaining smaller home ranges than frugivorous and arboreal species (Milton & May, 1976).
340 Additionally, group-size plays an important role in determining home ranges, most primates
341 being group-living, with larger groups maintaining larger home ranges, to fulfil the metabolic
342 requirements of all troop members (Clutton-Brock & Harvey, 1977). The lion-tailed macaque,
343 an arboreal and primarily frugivorous species, has been reported to maintain a home range size
344 ranging between 1.25km (Kumar, 1987) to 5km (Green & Minkowski, 1977) in the wild. In
345 selectively logged forests of Sirsi-Honnava, the reported home range for lion-tailed macaque
346 groups is a maximum of 3km, with an average daily path length of 500-1500m (Santhosh et
347 al., 2015). The unique habitat composition of the Puthuthottam forest fragment, however,
348 creates a hard boundary beyond which troops are unable to move, due to the presence of
349 impermeable tea plantations and swamps; with the exception of the largest BT troop, which
350 contains c. 96 individuals, the Puthuthottam troops all showed drastically reduced home range
351 sizes ranging between 9.7ha to 98ha. Further, the total home range size did not vary
352 significantly across the five troops, although BT, the largest troop, did maintain the largest
353 home range. Consequently, the daily path length were also observed to be reduced, ranging
354 between 285-722m/day, and were also comparable across troops. The ability for this population
355 to sustain small home ranges, despite requiring much larger areas, is explained by the presence
356 of easily available human-use foods, which allow individuals to acquire greater energy per unit
357 food (Altmann & Muruthi, 1988), thus, resulting in a patterns of altered ranging behaviour also
358 observed in many provisioned species (e.g. Berman et al., 2007; Sengupta et al., 2015; Sinha
359 & Mukhopadhyay, 2013).

360 Since the Puthuthottam forest fragment restricts macaque movement beyond certain edges,
361 inter-troop encounters are inevitable. In primates, inter-troop encounters are observed to
362 typically be agonistic in nature (Dorothy L Cheney, 1987) as they increase inter-group feeding
363 competition and, thus, directly influence movements of troops (e.g. Spironello, 2001). In this
364 connection, variations in troop size are thought to be of benefit in defending territories, both in
365 terms of food resource and mates (Wrangham, 1980), a theory which supports our observations
366 of a prevailing inter-troop dominance hierarchy in the Puthuthottam population, wherein the
367 smaller troops tend to avoid encounters with the largest BT troop. A similar trend was also
368 observed in Amboseli, where a large troop of vervet monkeys expanded their range over those
369 of smaller troops, restricting them to certain areas (Cheney & Seyfarth, 1987). Previously, the
370 rate of encounters between troops in Puthuthottam has been reported at 0.1/hour, however, this

371 measure has perhaps increased with the increased troop numbers. We, thus, expected this
372 highly competitive environment to have led to scramble competition across the troops in the
373 Puthuthottam, as is often seen with competing primate troops (Isbell, 1991), and evidence from
374 the present study seems to indicate this is indeed the case. Of the three troops that had relatively
375 larger overlaps in home range in the southern part of the study site, two were the smallest troops
376 comprising of 14-16 individuals, allowing them to roam over the same areas without
377 encountering the largest BT troop often. The two northern troops were also able to avoid
378 frequent encounters, especially after one troop migrated entirely out of the forest fragment into
379 neighbouring human settlements, and was able to maintain a core-home range that did not
380 overlap with any other troop.

381 Finally, while it was evident that human settlements were incorporated in the home ranges of
382 each of the Puthuthottam troops, it was equally important to determine the extent to which
383 these habitat types were being used. Other primate species that have been provisioned often
384 preferentially seek out these resources, thus, gravitating towards human settlements (e.g. Sinha
385 & Mukhopadhyay, 2013). This preference can be an indicator of the degree to which a species
386 is dependent on human-use foods, and its vulnerability to the suite of threats that accompany
387 provisioning. The Puthuthottam troops showed an unfortunate, albeit expected, pattern wherein
388 human-dominated habitats where human-use foods were easily available, such as the
389 Puthuthottam Road and Human Settlement, were used disproportionately more than the
390 available forest habitats, despite these being larger in area. Nevertheless, all troops did use the
391 Forest Interior and Open Forest Patch habitats where they maintained roosting sites throughout
392 the study period. A pertinent point to be made is that despite the troops relying on resources
393 available in human-dominated habitats, the species is still highly dependent on the remaining
394 natural vegetation, without which the population's survival would be questionable.

395 Dependence on human-use foods has led to many threats faced by individuals of the
396 Puthuthottam population, some of which are fatal. Singh et al., 2001 reported Puthuthottam
397 troops crossing the main road at 0.7/day, and once again the current measure is perhaps much
398 higher. During the three year study period, five deaths were recorded due to collisions with
399 vehicles on the Puthuthottam Road. Other linear intrusions, such as electric lines passing
400 through the fragment and human settlements, caused two deaths and two minor electrocutions
401 in the population. We also observed numerous injuries to the hands and legs of macaques, most

402 likely from manipulating man-made structures in order to access human-use foods, such as
403 garbage dumpsters, windows and roof tiles. Most importantly, the frequent visits to human
404 settlements has led to a precipitous human-macaque conflict situation, especially in the two
405 settlements, Rottikadai and Puthuthottam lines, where home-raiding occurs most often. A
406 strong presence by the local forest department has averted hunting or retaliatory poisoning
407 cases, however, local community members have continued to build pressure, calling for the
408 capture and translocation of macaques. Historically, such measures have not been successful,
409 leading to the shifting of a problem to a new location, rather than a solution. Furthermore, in
410 all likelihood, macaques from Puthuthottam could culturally transmit home-raiding tendencies
411 and the affinity for human-use foods to neighbouring populations, thus, drastically aggravating
412 the situation. So far, the Puthuthottam population has managed to survive and grow
413 exponentially with the added help of this new food resource, however, our data (see Chapter
414 2) shows a gradual steadying of the population as resources become increasingly limited. These
415 natural underlying processes would perhaps exert the desired control on the population far
416 better than those offered by further human intervention.

417 **References**

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