

1 **THE IMPLICATIONS OF PRIMATE BEHAVIORAL FLEXIBILITY FOR SUSTAINABLE**
2 **HUMAN–PRIMATE COEXISTENCE IN ANTHROPOGENIC HABITATS**

3

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24 **ABSTRACT**

25 People are an inescapable aspect of most environments inhabited by nonhuman primates today.
26 Consequently, interest has grown in how primates adjust their behavior to live in anthropogenic
27 habitats. However, our understanding of primate behavioral flexibility and the degree to which it will
28 enable primates to survive alongside people in the long-term remains limited. This Special Issue
29 brings together a collection of papers that extend our knowledge of this subject. In this introduction,
30 we first review the literature to identify past and present trends in research, then introduce the
31 contributions to this Special Issue. Our literature review confirms that publications on primate
32 behavior in anthropogenic habitats, including interactions with people, increased markedly since the
33 2000s. Publications concern a diversity of primates but include only 17% of currently recognized
34 species, with certain primates over-represented in studies (e.g., chimpanzees and macaques).
35 Primates exhibit behavioral flexibility in anthropogenic habitats in various ways, most commonly
36 documented as dietary adjustments (i.e., incorporation of human foods including agricultural crops
37 and other exotic plants, and provisioned items) and differences in activity, ranging, grouping
38 patterns, and social organization, associated with changing anthropogenic factors. Publications are
39 more likely to include information on negative rather than positive or neutral interactions between
40 humans and primates. The contributions to this Special Issue include both empirical research and
41 reviews that examine various aspects of the human–primate interface. Collectively, they show that
42 primate behavior in shared landscapes does not always conflict with human interests, and
43 demonstrate the value of examining behavior from a cost–benefit perspective without making prior
44 assumptions concerning the nature of interactions. Careful interdisciplinary research has the
45 potential to greatly improve our understanding of the complexities of human–primate interactions,
46 and is crucial for identifying appropriate mechanisms to enable sustainable human–primate
47 coexistence in the 21st Century and beyond.

48

49 **Keywords:** Anthropocene, behavioral adaptability, behavioral plasticity, ethnoprimateology, human-
50 dominated landscapes, human–wildlife interactions

51 **INTRODUCTION**

52 Flexible behavior – sometimes referred to as ‘adaptability’ or ‘plasticity’, although these terms are
53 not strictly synonyms (Strier 2017) – evolves in response to heterogeneous environments (Jones
54 2005). An animal’s ability to adjust its behavior under changing conditions can determine its survival
55 in a fast-changing world dominated by humans (Wong and Candolin 2015). Until quite recently, how
56 nonhuman primates (hereafter referred to as ‘primates’) respond behaviorally to human-induced
57 environmental changes and increased contact with people was not a primary focus of research (but
58 see Horrocks and Hunte 1986; Kavanagh 1980; Maples et al. 1976 for early examples of such work).
59 However, rapid human population growth and associated land-use changes such as agriculture and
60 urbanization are transforming primate habitats (Estrada et al. 2012; McKinney 2015). Consequently,
61 much field primatology today is conducted in ‘anthropogenic habitats’, a broad term which is
62 equivalent to ‘human-dominated’ or ‘human-impacted’ habitats, among similar terms (see McKinney
63 2015 for detailed analysis of anthropogenic influences on primate habitats). With the acceptance
64 that modified environments offer habitat for many primates, theoretical and applied interest in how
65 primates behave in anthropogenic habitats has increased (Hockings et al. 2015; Humle and Hill 2016;
66 Nowak and Lee 2013; Strier 2017).

67 Consistent with the wider literature on human–wildlife interactions (Angelici 2016; Seoraj-
68 Pillai and Pillay 2017; Woodroffe et al. 2005), research on primates in anthropogenic habitats has
69 tended to concentrate on negative aspects of human–primate interactions, such as primates
70 ‘raiding’ agricultural crops and other ‘conflicts’ that challenge the sustainability of primate
71 coexistence with people (Hill 2005). This reminds us that not all behavioral adjustments to
72 anthropogenic habitats are beneficial (see Sih et al. 2011; Tuomainen and Candolin 2011; Wong and
73 Candolin 2015), with some behaviors compromising the survival of primate populations, for example
74 by inciting persecution by people. Understanding primates’ behavioral flexibility in response to
75 human influence on their habitat, and how local people perceive and respond to changing primate

76 behavior, can inform conservation management to aid the long-term survival of primates in a fast-
77 changing world (Hockings et al. 2015; Nowak and Lee 2013).

78 To explore these issues in more depth, we organized a Symposium entitled “Behavioral
79 flexibility by primates in anthropogenic habitats” at the VIth European Federation for Primatology
80 Congress held in Rome in August 2015, inviting presentations from researchers studying human–
81 primate interactions. In response to the interest shown during the symposium, Joanna M. Setchell,
82 Editor-in-Chief of the *International Journal of Primatology*, invited us to guest edit a Special Issue on
83 this topic. This Special Issue presents papers which illustrate different and novel ways that primates
84 exhibit behavioral flexibility in response to human-induced habitat changes, and how this affects the
85 long-term sustainability of their interactions with humans. We refer to these themes more generally
86 in this introduction as “primates in anthropogenic habitats”. To provide context to the contributions,
87 we first reviewed the literature to identify past and present trends in research focus in primates in
88 anthropogenic habitats. We discuss which primates are most studied and where, what kinds of
89 behavioral adjustments are reported, and the nature of interactions reported between primates and
90 people, with representative examples from the literature search. Next, we introduce the
91 contributions to this Special Issue. We conclude with reflections on the current state of research in
92 this evolving field, and suggest future lines of inquiry for its development.

93

94 **RESEARCH TRENDS**

95 We searched the literature for publications reporting primate behavior in anthropogenic habitats
96 using the Web of ScienceTM database. We searched using ‘All Databases’, which included the Web of
97 Science core collection, MEDLINE, and BIOSIS and SciELO citation indexes, covering articles published
98 from 1970 to December 7th 2016. We searched for full-length research articles, short
99 communications, commentaries and reviews, but excluded studies published as abstracts only. We
100 used the key words ‘primate’, ‘monkey’, ‘ape’ and ‘lemur’ in all searches, as well as common names
101 (e.g., macaque, baboon, capuchin, chimpanzee) in some searches. We combined key words with

102 relevant search terms, repeating searches using alternative or synonymous terms. Search terms that
103 returned greatest numbers of relevant articles were human–wildlife conflict, human–wildlife
104 interactions, crops, crop raiding, agriculture, plantation, anthropogenic, human-dominated, tourism,
105 provisioning, and urban.

106 Our criterion for inclusion was that articles include information on any of the following: (i)
107 primate behaviors that may be regarded as adjustments to, or consequences of, living in
108 anthropogenic habitats, and thus broadly indicative of flexibility in such environments. While
109 behavioral ‘adjustments’ included reports of differences between primates in anthropogenic
110 habitats compared to those in less human-impacted ones, we refer to these behavioral differences
111 as ‘adjustments’ for consistency with the wider literature (e.g., Sol et al. 2013; Wong and Candolin
112 2015). Reported adjustments include behaviors associated with diet (i.e., feeding on exotic items),
113 activity, ranging, social organization and reproduction; (ii) behavioral responses of primates to novel
114 aspects of, or risks associated with, anthropogenic habitats; (iii) direct interactions between
115 primates and humans in anthropogenic habitats (tourists, local people or researchers); (iv) human
116 perceptions of, attitudes towards, or beliefs about, primates; and (v) the conservation implications
117 or likely sustainability of these interactions.

118 We did not consider publications reporting only general effects of human disturbance such
119 as forest fragmentation, logging, and hunting on primate occurrence, densities, distribution or
120 ecology (including influences on primates’ natural diet, for example in forest fragments), or articles
121 focussed solely on the ecological characteristics of human-modified habitats used by primates.
122 Likewise, we excluded publications about primate health, population genetics or physiology, unless
123 these also included relevant information on behavior. We limited searches to studies of wild or free
124 ranging primates, excluding (ex-)captive or pet primates, but note that some ‘wild’ or free ranging
125 populations included in our review – especially those at tourism or religious sites – are managed by
126 humans to considerable extents (e.g., through food provisioning or population control).

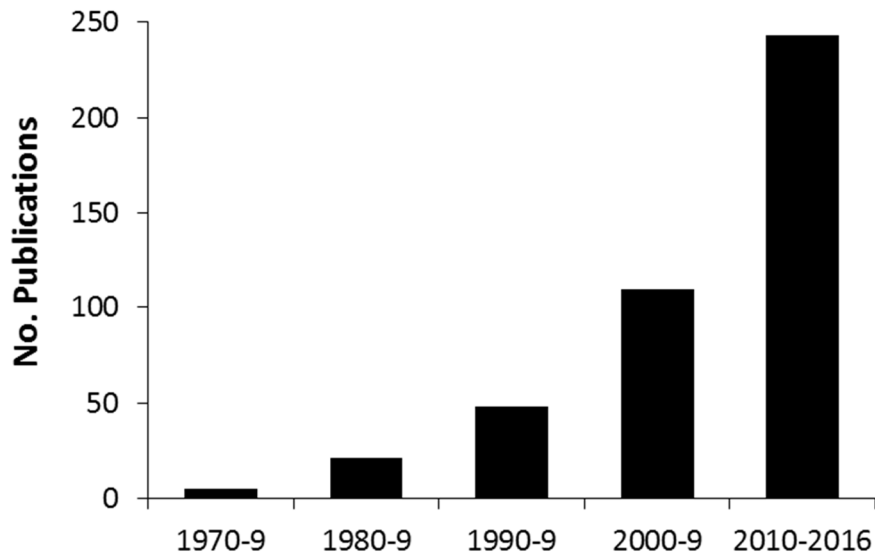
127 Our searches returned 517 publications that potentially met our criteria. After examining
128 each abstract, in most cases we consulted the full article to confirm the publication's relevance or to
129 establish additional details about the study. The final dataset comprised 427 publications.

130 Our review is not intended to be exhaustive. Contributions to edited volumes were not well-
131 represented in our searches, which mostly returned journal articles. Additional relevant studies can
132 be found in Fa and Southwick (1988), Fuentes and Wolfe (2002), Gumert et al. (2011), Paterson and
133 Wallis (2005), Radhakrishna et al. (2013) and Waller (2016), and in journals and newsletters
134 published by the IUCN/SSC Primate Specialist Group, which are not indexed by Web of Science.
135 Nevertheless, Web of Science has a wide coverage of science journals including all major animal
136 behaviour, ecology and conservation periodicals (including the 'big four' primatology journals,
137 *American Journal of Primatology*, *Folia Primatologica*, *International Journal of Primatology*, and
138 *Primates*). Thus, we are confident that results of our literature search are representative of the field.

139

140 ***Growth in research***

141 As noted elsewhere (Humble and Hill 2016), publications concerning primates in anthropogenic
142 habitats have increased since the earliest reports from the 1970s (Fig. 1). Studies were relatively few
143 until the 1990s when research interest began to increase, particularly in primates' use of agricultural
144 crops (usually termed 'crop raiding'), and following the publication of several influential studies
145 (Altmann and Muruthi 1988; Hill 1997; Naughton-Treves et al. 1998; Siex and Struhsaker 1999;
146 Strum 1994). By the 2000s, primate behavior in anthropogenic environments was an established
147 topic of research (26% of publications in our dataset were published in this decade), and research
148 interest continues to rise: the first seven years of the 2010s (until December 2016) account for 57%
149 of publications in our dataset (Fig. 1).



150

151 **Fig. 1.** The number of publications about primates in anthropogenic habitats published in each
 152 decade since the 1970s from a Web of Science™ literature search (1970 to December 7th 2016; N =
 153 427).

154

155 ***Which primates and where?***

156 Most publications in our dataset concerned primates in mainland Africa (40%) and Asia (39%) (Fig.
 157 2); 16% concerned Neotropical primates while only 3% concerned Madagascan primates.

158 Historically-introduced populations of *Macaca mulatta* in the United States and *M. sylvanus* in

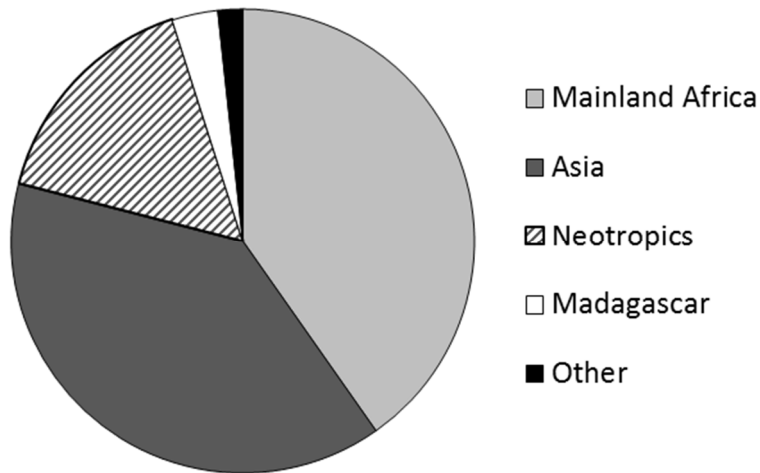
159 Europe accounted for one and seven publications, respectively. Forty-eight countries were

160 represented, including 44 of the 90 where primates occur naturally (Estrada et al. 2017), as well as

161 four countries where primates were introduced historically. India (12%), Uganda (11%), Indonesia

162 (11%), Brazil (9%), South Africa (5%), Japan (5%) and Kenya (5%) were the subject of the most

163 publications.



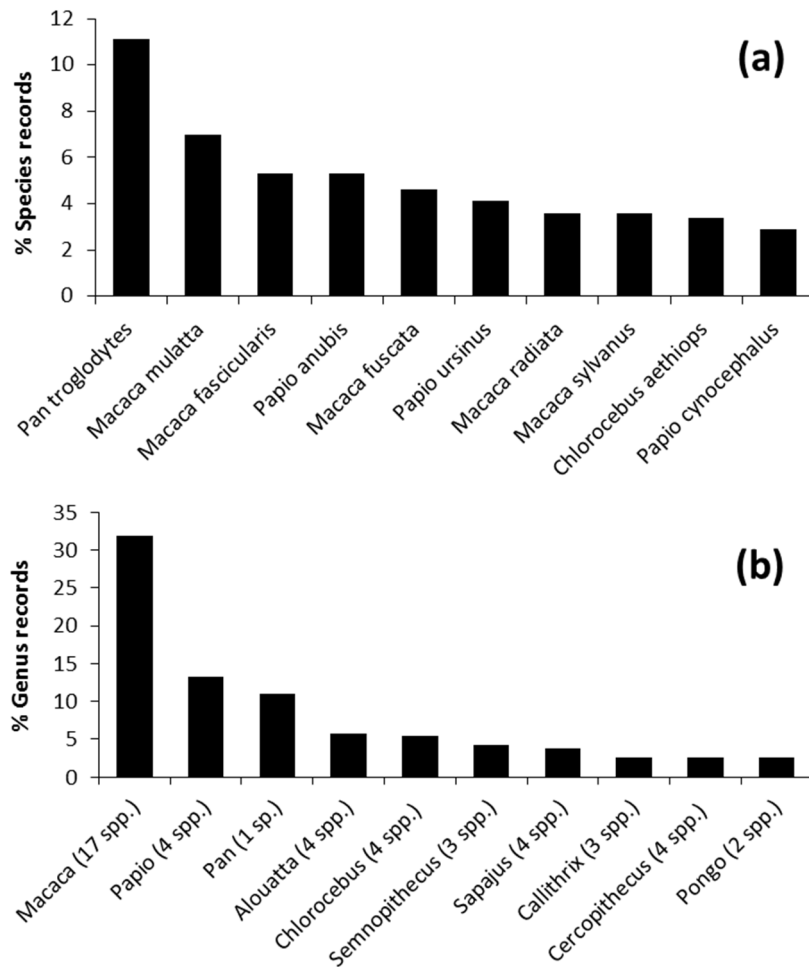
164

165 **Fig. 2.** Pie chart showing the distribution of publications about primates in anthropogenic habitats
 166 according to geographical region, from a Web of Science™ literature search covering the period
 167 1970 to December 7th 2016 (N = 405 publications specific to a particular geographic region). ‘Other’
 168 comprises publications on historically-introduced primates in Europe and the United States.
 169

170 The most common anthropogenic habitat in which primates interface with humans can be
 171 broadly categorized as ‘rural agricultural’ (50% of publications). These were typically mosaic
 172 landscapes with areas of ‘natural’ vegetation such as forest fragments bordered by or intermixed
 173 with household farms and villages, or where protected areas border agricultural land. In 14% of
 174 publications, primates were studied in large commercial timber or agricultural plantations. Twenty
 175 percent of publications concerned primates at sites visited by tourists or religious devotees, while
 176 15% of publications described primate behavior in urban settings such as towns and cities. These
 177 habitat categories were not mutually-exclusive; for example, primate tourism sites were often in
 178 urban locales.

179 We recorded the focal primate species, genera and families in publications (see Electronic
 180 Supplementary Material [ESM] Tables S1–S3). The dataset included 84 species in 32 genera from 12
 181 families, corresponding to 17% of 504 species, 41% of 79 genera, and 75% of 16 families recognized
 182 in Estrada et al. (2017). Ten primate species accounted for half (51%) of the records for individual
 183 species (N = 415) (Fig. 3a; see ESM Table S1 for a complete list).

184



185

186 **Fig. 3.** The 10 primate species and genera most commonly featured in publications about primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December 7th 2016). We
 187 recorded up to two focal species and genera per publication. Bars show the percentage of the total
 188 number of records for (a) individual species (N = 415 ‘species records’) and (b) individual genera (N =
 189 420 ‘genus records’). The number of focal species in each genus in the dataset is shown in
 190 parenthesis below the bars in (b).
 191

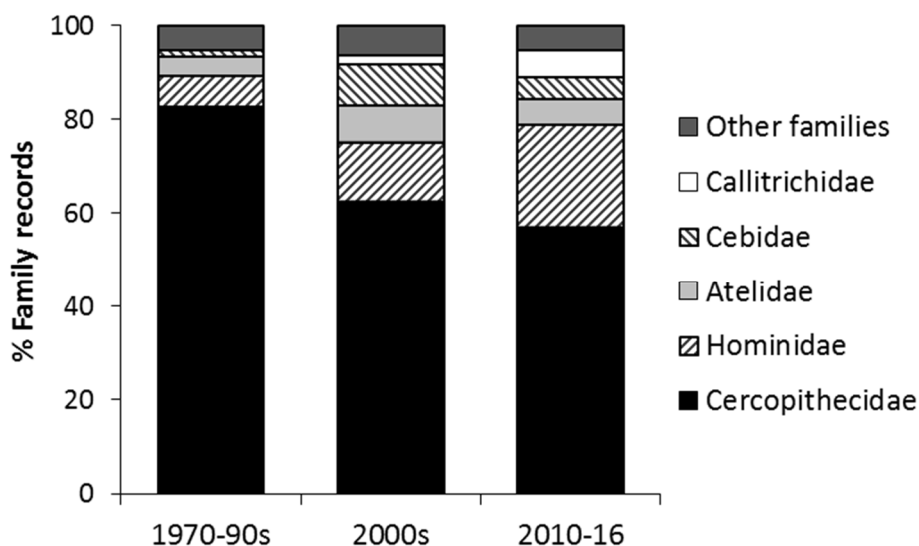
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193 One species of great ape (*Pan troglodytes*) featured in the greatest number of publications
 194 (11% of species records; Fig. 3a). Other focal species common in the dataset include those well-
 195 known for inhabiting human-dominated habitats: five macaque species (*Macaca* spp.), three baboon
 196 species (*Papio* spp.) and grivet monkeys (*Chlorocebus aethiops*). The prevalence of chimpanzee
 197 studies does not imply that this species is especially numerous or prospers in modified habitats in
 198 association with people – unlike some macaques, for example (Richard et al. 1989). Rather, it mostly
 199 reflects recent interest in this species’ responses to anthropogenic habitat modifications (e.g.,
 200 Hockings and McLennan 2012; Krief et al. 2014; McLennan and Hockings 2014). Other primate

201 genera that have been well-studied in anthropogenic habitats are more speciose than chimpanzees
 202 (especially *Macaca*), with research effort spread over several species. By comparison, other genera
 203 that exploit anthropogenic environments were the focus of relatively few studies in our dataset, for
 204 example *Cercopithecus*, *Sapajus*, and *Erythrocebus*.

205 Three genera (*Macaca*, *Papio* and *Pan*) accounted for over half of the records for individual
 206 genera (N = 420; ESM Table S2). *Macaca* alone accounted for one third, and included 17 focal
 207 species (Fig. 3b). Four species of *Papio* accounted for 13% of genus records. *Alouatta* spp. (howler
 208 monkeys) and *Chlorocebus* spp. (including grivet and vervet monkeys) also featured relatively often
 209 in the database.

210 Most publications (63%) in the dataset concerned the Cercopithecidae (ESM Table S3).
 211 However, the distribution of research across primate families has changed over time (Fig. 4). The
 212 proportion of studies focussed on the Cercopithecidae decreased after the 1990s while those
 213 focussed on the Hominidae increased, particularly since 2010. The proportion of studies of
 214 Neotropical primates (Atelidae, Callitrichidae and Cebidae) also increased after the 1990s. Only 5%
 215 of publications in the dataset concerned other primate families.



216

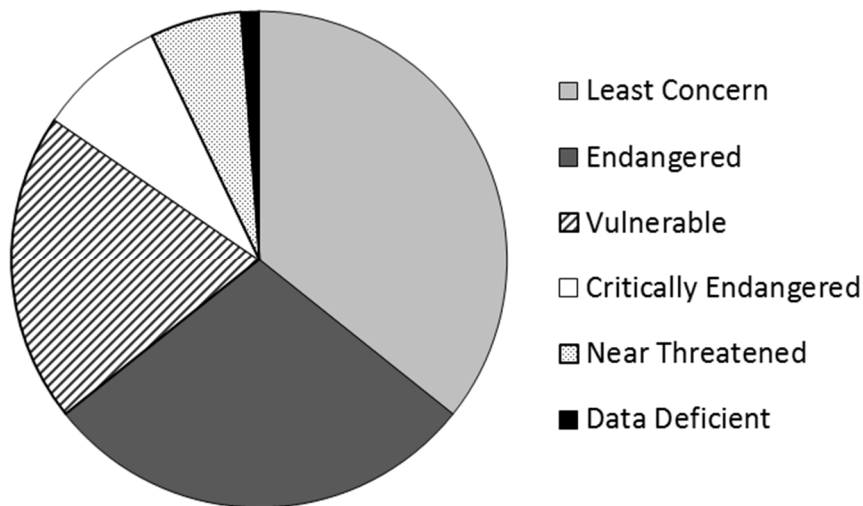
217 **Fig. 4.** The distribution of research focussed on individual families of primate in three time periods,
 218 from a Web of Science™ literature search (1970 to December 7th 2016). We recorded up to two focal
 219 families per publication. We calculated percentages from the number of records per family out of
 220 the total number of ‘family records’ in each period: 1970–90s (N = 75 family records), 2000s (N =

221 112) and 2010–16 (N = 237). ‘Other families’ are the combined records for Aotidae, Daubentoniidae,
222 Hylobatidae, Indriidae, Lemuridae, Lorisidae and Tarsiidae, each of which was the focus of 1–9
223 publications only (see ESM Table S3).

224

225 Of the 84 species in the dataset, 36% are currently classified as Least Concern (Fig. 5,
226 following IUCN Red List Categories reported in Estrada et al. 2017). Fifty-seven percent of species are
227 currently in the IUCN Red List ‘Threatened’ categories: 20% are Vulnerable, 29% are Endangered,
228 and 8% are Critically Endangered (Fig. 5) (ESM Table S1).

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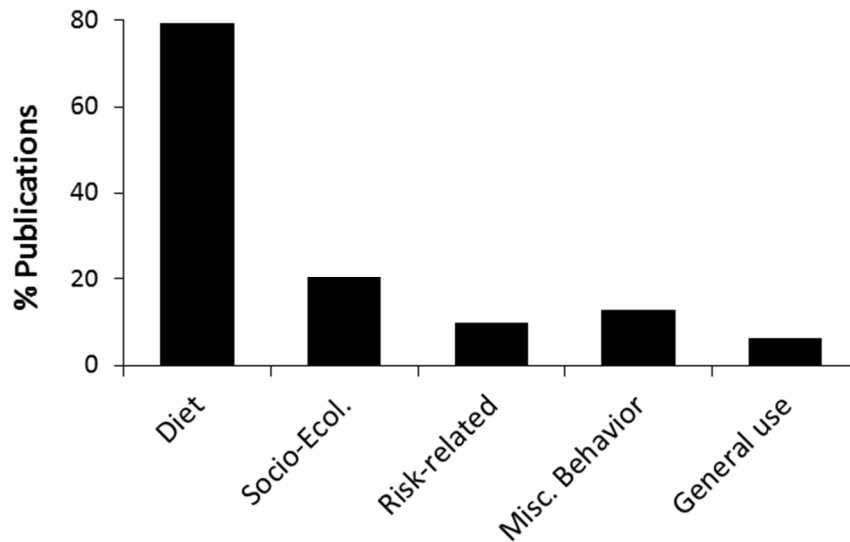
231 **Fig. 5.** Pie chart showing the conservation status of 84 species of focal primate in publications about
232 primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December
233 7th 2016). IUCN Red List Categories follow Estrada et al. (2017).

234

235 ***Behavioral adjustments***

236 We classified behavioral adjustments by primates living in anthropogenic habitats as ‘dietary’,
237 ‘socioecological’, ‘risk-related response’, ‘miscellaneous’ (for novel or rare behaviors) and ‘general
238 use’ (for publications reporting primates’ active use of anthropogenic environments but without
239 specifying a particular behavioral adjustment). The most commonly reported behavioral adjustment
240 exhibited by primates in anthropogenic habitats was dietary (Fig. 6): primates in anthropogenic
241 habitats were widely reported to feed on exotic plants including agricultural crops and plantation

242 trees among other introduced species, as well as garbage and provisioned items; 19% of these
243 publications concerned wild and free-ranging primates at tourist or religious sites. In rare instances
244 baboons and chimpanzees also consumed domestic animals, while capuchins were observed
245 consuming a chicken carcass (Cunha et al. 2006).



246

247 **Fig. 6.** The % of publications reporting behavioral adjustments in primates living in anthropogenic
248 habitats from a Web of Science™ literature search (1970 to December 7th 2016; N = 427). We
249 categorized behaviors as dietary, socioecological, risk-related, miscellaneous, and 'general use'
250 of the habitat (see text for details). Some studies reported behaviors in more than one category.
251

252 Socioecological adjustments – described in 21% of publications – included changes in
253 activity, ranging and habitat use, grouping and social organization, and reproduction. For example,
254 primates that regularly eat energy-rich agricultural crops or garbage often, but not always, travel
255 and forage less, have smaller ranges, and spend more time resting and socializing (e.g., *Chlorocebus*
256 *pygerythrus*, Saj et al. 1999). Crop foraging primates may exhibit flexible grouping patterns with
257 certain age-sex classes (often adult males) most likely to participate in risky forays into agricultural
258 fields (e.g., *Cercopithecus ascanius*, Baranga et al. 2012; *Pan troglodytes*, Hockings et al. 2012).
259 Habitat use, including sleeping site locations, may facilitate primates' access to human foods (e.g.,
260 *Macaca fascicularis*; Brotcorne et al. 2014) but can also reflect avoidance of areas of busy human
261 activity (e.g., *Hylobates moloch*, Reisland and Lambert 2016). In some publications, frequent

262 consumption of human foods is linked to shorter interbirth intervals, earlier reproductive onset and
263 reduced infant mortality (e.g., *Papio anubis*; Higham et al. 2009; Strum 2010).

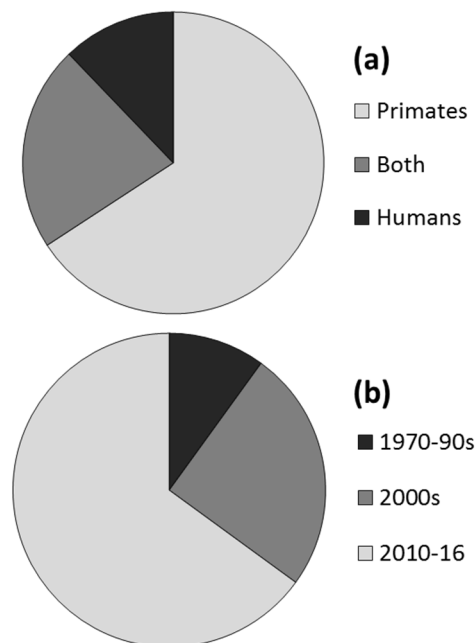
264 Ten percent of publications report specific behavioral responses of primates to novel risks in
265 anthropogenic habitats, such as roads, domestic dogs and cats, and humans. Behaviors described
266 include cryptic behavior to avoid detection (e.g., *Chlorocebus tantalus*, Kavanagh 1980), vigilance
267 (e.g., *Papio cynocephalus*; Maples et al. 1976), group cohesion and protective behavior towards
268 vulnerable group members (e.g., *Pan troglodytes*; Cibot et al. 2015; Hockings et al. 2012), choice of
269 sleeping sites to minimize predation by domestic animals (e.g., *Callithrix penicillata*, Duarte and
270 Young 2011), and aggression directed at humans and dogs (e.g., *Pan troglodytes*: McLennan and Hill
271 2010). Counter-aggression in response to threats from humans was reported at some tourist sites
272 (e.g., *Macaca mulatta*, Beisner et al. 2015).

273 Miscellaneous behavioral adjustments (13% publications) included use of exotic trees for
274 sleeping (e.g., *Pongo pygmaeus*, Ancrenaz et al. 2015), use of artificial structures such as roofs and
275 fences for travelling or resting (e.g., *Semnopithecus vetulus*; Moore et al. 2010), use of human water
276 sources for drinking (*Erythrocebus patas*, de Jong et al. 2008), and use of high-valued agricultural
277 fruits as potential 'commodities' (e.g., *Pan troglodytes*, Hockings et al. 2007). Increased intragroup
278 aggression or harassment of human visitors for food were common in provisioned primates (e.g.,
279 *Macaca sylvanus*, El Alami et al. 2012; *Macaca thibetana*, Zhao and Deng 1992). A further 6% of
280 publications describe 'general use' of anthropogenic habitats by primates, for example, long-term
281 persistence in exotic plantations or agroforestry landscapes (e.g., *Alouatta pigra*, Zarate et al. 2014).
282 Nineteen percent of publications identified the behavioral or ecological flexibility (or 'adaptability')
283 of focal primates as a likely factor contributing to their persistence in anthropogenic habitats (e.g.,
284 *Sapajus xanthosternos*, Canale et al. 2013).

285

286 ***People and primates***

287 Most publications in our dataset (66%) were studies of primates and included only incidental or
 288 brief, anecdotal information about humans. However, humans were the primary focus in 12% of
 289 publications, while 22% were studies of both people and primates (Fig. 7a). Overall, 21% of
 290 publications included some assessment of human attitudes towards, perceptions of, or beliefs
 291 about, primates. Of these, 10% were published in the 1970–90s, 25% were published in the 2000s,
 292 and 65% were published during 2010–2016 (Fig. 7b). This substantial growth in primate research
 293 concerned with people reflects increasing forays by primatologists into the realm of social science,
 294 and mirrors a general shift across the biological sciences in recognition of the need to engage with
 295 human dimensions of wildlife and biodiversity conservation (e.g., Bennett et al. 2017). For example,
 296 ethnoprimatology uses interdisciplinary methods and perspectives to understand the social and
 297 ecological ‘interconnectedness’ of humans and other primates (e.g., Fuentes 2012; Fuentes and
 298 Hockings 2010). While relatively few publications in our dataset explicitly adopted an
 299 ethnoprimatological approach (N = 17; 4%), only one of these was published before 2010 (Riley
 300 2007).



301

302 **Fig. 7.** Pie charts showing (a) the proportion of publications about primates in anthropogenic
 303 habitats that focussed primarily on primates, humans, or both, from a Web of Science™ literature
 304 search (1970 to December 7th 2016; N = 427); (b) the proportion of the total number of publications

305 that included an assessment of human attitudes towards, perceptions of, or beliefs about, primates
306 (N = 88) that were published in each of three time periods: 1970–90s, 2000s, and 2010–16.
307

308 Direct behavioral interactions between people and primates were reported in 23% of publications,
309 many concerning interactions that can be regarded as ‘negative’. Descriptions of interactions
310 occurred disproportionately in studies of provisioned primates or primates in urban settings (56% of
311 publications reporting direct interactions), and centred mostly on the acquisition of human food by
312 primates (e.g., *Chlorocebus aethiops*, Brennan et al. 1985). Reported interactions in agricultural
313 settings revolved mostly around protection of crops, including observations of farmers chasing or
314 throwing objects to deter primates (e.g., *Papio anubis*, Warren et al. 2011).

315 33% of publications in our dataset overtly emphasized ‘negative’ or competitive aspects of
316 people–primate interactions, through use of terms such as ‘conflict’, ‘killing’, ‘pest’ and ‘damage’.
317 Conversely, only 7% explicitly emphasised ‘positive’, ‘peaceful’ or neutral interactions (e.g., *Callithrix*
318 *penicillata*, Leite et al. 2011); these were reported mostly in the context of human cultural attitudes
319 that serve to protect or promote tolerance of coexisting primates, and hence allow for more
320 sustainable interactions (e.g., *Macaca tonkeana* and *M. ochreata*: Riley and Priston 2010). Most such
321 publications discussed both positive and negative aspects of coexistence, with local people
322 expressing tolerance of primates in addition to concerns over crop losses or aggression from
323 primates (e.g., *Pan troglodytes*: McLennan and Hill 2012).

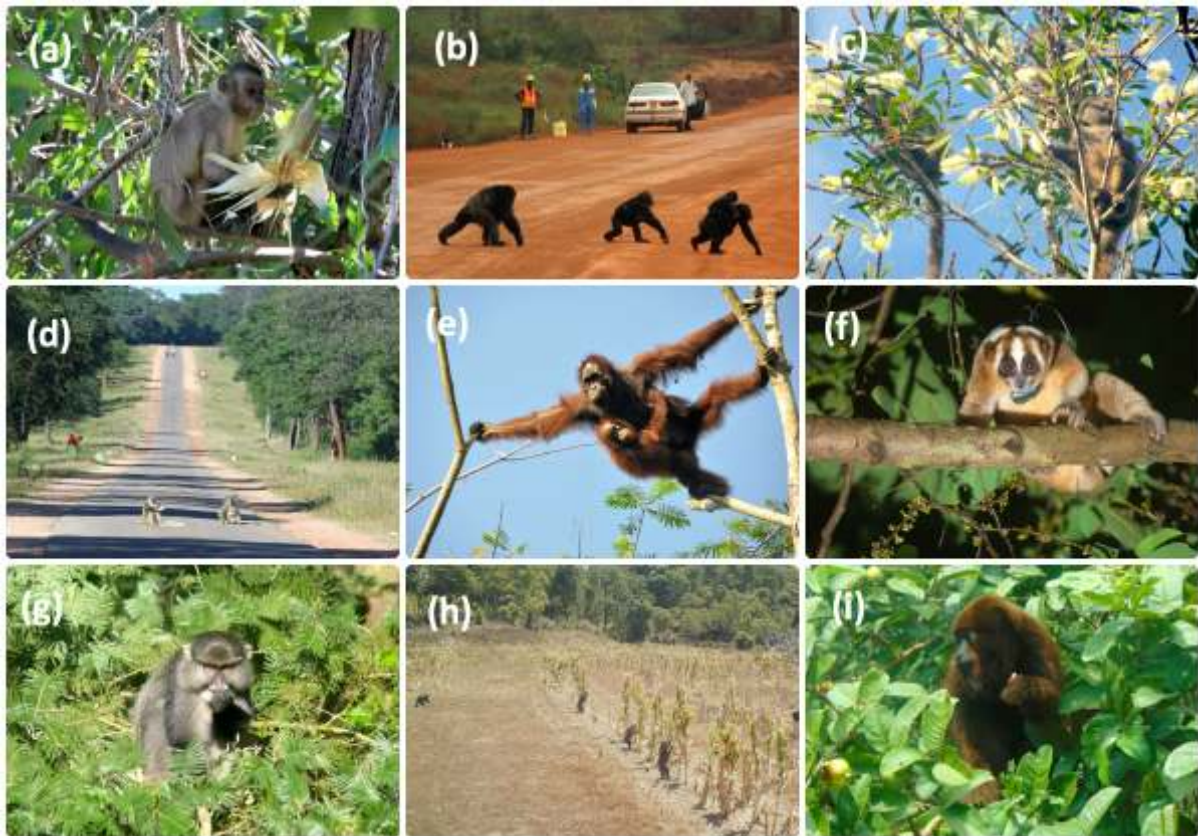
324 In summary, our review confirms that primate behavior and interactions with people in
325 anthropogenic habitats are major topics of inquiry in primatology today. Most species that were
326 prominent in publications are classified as ‘Least Concern’ in the IUCN Red List, although
327 chimpanzees are an exception (ESM Table S1). Least-concern primates are often generalists that can
328 fare well in landscapes dominated by human activities (e.g., some macaques and baboons).
329 Examples of flexible behavior concerned a diversity of primates, however, including highly
330 threatened and so-called ‘specialist’ species (see Nowak and Lee 2013). Nevertheless, the majority of
331 primate species were not represented in any publications in our dataset (e.g., members of the

332 Cheirogaleidae, Galagidae, Lepilemuridae and Pitheciidae), which may be because they are less likely
333 to occur in human-modified environments – perhaps owing to a lack of flexibility – or are
334 understudied generally, or both. Evident from our review is the predominant focus on ‘negative’
335 (i.e., conflict) compared to ‘positive’ (coexistence) aspects of people–primate interactions. While
336 studies often provided recommendations to reduce conflict, few included an in-depth exploration of
337 mechanisms that could enable sustainable human–primate coexistence in the long-term.

338

339 **CONTRIBUTIONS TO THIS SPECIAL ISSUE**

340 For this Special Issue we invited contributions from researchers working in all main geographic
341 regions where primates occur naturally – mainland Africa, Asia, the Neotropics and Madagascar.
342 Research articles concern a variety of primates (Fig. 8), with additional species covered in two review
343 articles. Three focal primates (*Cercopithecus albogularis*, *Eulemur collaris*, and *Macaca maura*) were
344 not represented by any publications in our literature review, thus contributions provide new
345 information about the behavior of these species in human-modified environments. The current
346 strong research interest in chimpanzees, evident from our review, is reflected in four contributions
347 focussed on this great ape.



348

349 **Fig. 8.** Primate species in anthropogenic habitats included in this Special Issue. (a) Adult male
 350 bearded capuchin monkey (*Sapajus libidinosus*) feeding on maize, *Zea mays* (photo by N.
 351 Spagnoletti); (b) Eastern chimpanzees (*Pan troglodytes schweinfurthii*) crossing a newly widened
 352 road at Bulindi, Uganda (photo by J. Rohen); (c) Southern bamboo lemurs (*Hapalemur meridionalis*)
 353 foraging on flowers of exotic *Melaleuca quinquenervia* in the Mandena littoral forest, southeast
 354 Madagascar (photo by T. M. Eppley); (d) Chacma baboons (*Papio ursinus*) eating maize on the road
 355 after foraging in crop fields (photo T. Gaillard); (e) Mother and infant Bornean orangutan (*Pongo*
 356 *pygmaeus morio*) moving arboreally in a plantation of *Paraserianthes falcataria* in East Kalimantan
 357 (photo by Y. Rayadin); (f) Javan slow loris (*Nycticebus javanicus*) using a cultivated avocado plant
 358 (photo by A. Walmsley); (g) Juvenile samango monkey (*Cercopithecus albogularis labiatus*) eating
 359 exotic black wattle seeds (photo by K. Wimberger); (h) Camera trap photograph (captured by a
 360 Bushnell 8 MP remote sensor camera) showing moor macaques (*Macaca maura*) foraging on maize
 361 (photo by A. Zak and E. Riley); (i) Adult female brown howler (*Alouatta guariba clamitans*) eating
 362 guava, *Psidium guajava*, in an orchard in Itapuã settlement, southern Brazil (photo by J. P. Back).

363

364 As our literature review revealed, feeding on exotic plants is a primary behavioral
 365 adjustment of primates in modified habitats, and many contributions to this Special Issue concern
 366 aspects of this dietary adjustment. McLennan and Ganzhorn (2017) evaluate the common
 367 assumption that crops offer high nutritional returns compared to wild forage for primates by

368 comparing the chemical content of wild and cultivated foods in the diet of eastern chimpanzees (*Pan*
369 *troglodytes schweinfurthii*). Wimberger et al. (2017) examine the role of exotic plants in the feeding
370 ecology of samango monkeys (*Cercopithecus albogularis labiatus*) in a matrix of residential gardens
371 and native forest. Hockings et al. (2016) explore seed dispersal in an anthropogenic context, by
372 studying patterns of dispersal of a cultivated crop (cacao, *Theobroma cacao*) by western
373 chimpanzees (*P. t. verus*). Nowak et al. (2016) take an experimental approach to examine risk-
374 sensitive foraging in samango monkeys (*C. a. labiatus*) in a habitat matrix of indigenous forest and
375 residential gardens, where food acquisition was most risky. Schweitzer et al. (2017) examine
376 individual participation, decision-making, and collective movements by chacma baboons (*Papio*
377 *ursinus*) when foraging on crops along the periphery of a National Park.

378 Three research articles use multidisciplinary methods to study human–primate interactions.
379 Zak and Riley (2016) compared camera trap footage of crop foraging by moor macaques (*Macaca*
380 *maura*) with farmer perceptions of macaque behavior on farms gleaned from semi-structured
381 interviews. Spagnoletti et al. (2016) combined interviews with local people with observations of crop
382 foraging in bearded capuchins (*Sapajus libidinosus*) and other vertebrates using experimental plots
383 established with the participation of local farmers. Chaves and Bicca-Marques (2016) examined crop
384 foraging and its potential economic costs by brown howlers (*Alouatta guariba clamitans*), combined
385 with interviews to understand landowners' perceptions of the issue. Despite significant crop losses
386 to primates, farmers in these latter two studies did not perceive these crop losses as problematic.
387 These examples remind us that the extent of primate crop damage does not necessarily equate to
388 the resulting level of 'conflict' (Hockings 2016), and that human perceptions of primates which
389 influence tolerance of them vary in time and space (Hill and Webber 2010).

390 Several contributions consider how primates adjust their behavior to landscape
391 characteristics in anthropogenic habitats. Bryson Morrison et al. (2017) examined the activity
392 budgets of *P. t. verus* in a mosaic habitat to examine the influence that 'risky' parts of their home
393 range – cultivated fields, roads and paths – have on their foraging behavior. Nekaris et al. (2017)

394 studied the behavior of Javan slow lorises (*Nycticebus javanicus*) in response to the introduction of a
395 cash crop, chayote, finding that the bamboo frames used to support chayote provided lorises with a
396 novel substrate network for foraging and travelling. McCarthy et al. (2016) adopt a landscape-level
397 approach to reveal how *P. t. schweinfurthii* respond to anthropogenic land-use changes through
398 their use of cultivated and exotic tree plantation species for nesting. Eppley et al. (2016) assessed
399 the ecological flexibility of two lemurids (*Eulemur collaris* and *Hapalemur meridionalis*) in a degraded
400 habitat by comparing their use of exotic and pioneer plants. Spehar and Rayadin (2017) conducted
401 camera trapping and nest surveys to examine habitat use by Bornean orangutans (*Pongo pygmaeus*
402 *morio*) in a plantation forestry landscape.

403 Hill (2017) reviews current knowledge about primate crop foraging behaviour, and highlights
404 key areas for future research to promote human–primate coexistence in shared landscapes.
405 Additionally, she outlines current debates over terms such as ‘human–wildlife conflict’ and ‘crop-
406 raiding’, arguing that these obscure the complex nature of human–primate interactions, and can
407 exacerbate associated problems. In recognition of these debates, contributors to this issue
408 endeavored to use neutral terminology when discussing primate crop feeding. Finally, Setchell et al.
409 (2016) present three case studies that demonstrate how careful integration of biological and
410 ethnographic methods and perspectives can greatly improve our understanding of the complexities
411 of human–primate interactions, and thus are crucial for addressing conservation challenges
412 effectively.

413 Collectively, these articles illustrate recent advances in the field, including new insights on
414 prominent themes in the literature (e.g., primate crop feeding) as well as traditional themes in
415 behavioral ecology (e.g., seed dispersal, nutritional ecology, collective movements and risk
416 perception), and an emphasis on interdisciplinary methods and perspectives to study people–
417 primate interactions (e.g., camera traps combined with farmer interviews, and ethnoprimateology
418 approaches).

419

420 **WAYS FORWARD**

421 Primates have slow life histories and some human-induced changes likely occur too quickly for
422 genetic adaptations to accrue. Given severe threats to the survival of primates globally (Estrada et al.
423 2017), it is critical to understand how different species respond to anthropogenic change, and the
424 extent to which behavioral flexibility will help them survive in the face of ongoing changes. A goal of
425 this Special Issue is to stimulate increased interest and new ideas on this topic.

426 As our review indicates, we still know little about how most primates respond behaviorally
427 to humans and their activities, underscoring the need for research on additional, understudied
428 species. Few primate field sites are wholly unaffected by human influence, providing researchers
429 with opportunities to incorporate anthropogenic variables into studies of primate behavior
430 (Hockings et al. 2015). A lack of flexible responses should be reported along with evidence of
431 flexibility. Greater examination of the adaptive value of behavioral changes is needed: do these
432 adjustments help primates succeed in human-impacted environments or do they incite persecution
433 from humans, potentially leading to extirpation of primate populations? To this end, long-term
434 studies and comparisons among populations exposed to different forms and degrees of
435 anthropogenic influence are invaluable.

436 We cannot hope to conserve primates without considering the wider political,
437 socioeconomic, ecological, and cultural conditions under which coexistence with humans is possible,
438 or not. Thus, we must be interested in people too. As emphasized by Setchell et al. (2016), this
439 requires that primate researchers become “skilled at bridging disciplinary boundaries”. Care must be
440 taken, however, when researching potentially controversial topics such as ‘conflicts’ involving
441 humans and primates to avoid misrepresenting or exacerbating problems (Hill 2015; Redpath et al.
442 2013). Anthropological investigations should be undertaken by researchers trained in the social
443 sciences and with experience of the local socio-political environment in which they conduct their
444 research. Human–primate interactions rarely stand alone and are usually associated with broader
445 conservation issues. Thus, we should strive for a more holistic approach to primate conservation.

446 This requires a shift from a predominant focus on constraints to coexistence to careful
447 interdisciplinary research to identify appropriate mechanisms that will enable sustainable human–
448 primate coexistence in the 21st Century and beyond.

449

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458

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Electronic Supplementary Material

The Implications of Primate Behavioral Flexibility for Sustainable Human–Primate Coexistence in Anthropogenic Habitats

Matthew R. McLennan · Noemi Spagnoletti · Kimberley J. Hockings

Table SI Focal primate species featured in publications about primates in anthropogenic habitats, from a Web of Science™ literature search covering the period 1970 to December 7, 2016 ($N = 427$). Species are listed alphabetically and in descending order of frequency in the dataset (number of publications).

Primate species ^a	Common name	IUCN Red List category ^b	No. of Publications	% Species records ^c
<i>Pan troglodytes</i>	Chimpanzee	EN	46	11.1
<i>Macaca mulatta</i>	Rhesus macaque	LC	29	7.0
<i>Macaca fascicularis</i>	Long-tailed macaque	LC	22	5.3
<i>Papio anubis</i>	Olive baboon	LC	22	5.3
<i>Macaca fuscata</i>	Japanese macaque	LC	19	4.6
<i>Papio ursinus</i>	Chacma baboon	LC	17	4.1
<i>Macaca radiata</i>	Bonnet macaque	LC	15	3.6
<i>Macaca sylvanus</i>	Barbary macaque	EN	15	3.6
<i>Chlorocebus aethiops</i>	Grivet monkey	LC	14	3.4
<i>Papio cynocephalus</i>	Yellow baboon	LC	12	2.9
<i>Macaca thibetana</i>	Tibetan macaque	NT	9	2.2
<i>Semnopithecus vetulus</i>	Purple-faced langur	EN	9	2.2
<i>Alouatta pigra</i>	Central American black howler	EN	8	1.9
<i>Semnopithecus entellus</i>	Bengal sacred langur	LC	8	1.9
<i>Callithrix penicillata</i>	Black-tufted-ear marmoset	LC	7	1.7
<i>Macaca tonkeana</i>	Tonkean macaque	VU	7	1.7
<i>Pongo pygmaeus</i>	Bornean orangutan	EN	7	1.7
<i>Alouatta palliata</i>	Mantled howler	LC	6	1.4
<i>Chlorocebus pygerythrus</i>	Vervet monkey	LC	6	1.4
<i>Lemur catta</i>	Ring-tailed lemur	EN	6	1.4
<i>Sapajus nigrinus</i>	Black-horned capuchin	NT	6	1.4
<i>Alouatta guariba</i>	Brown howler	LC	5	1.2
<i>Cercopithecus mitis</i>	Blue monkey	LC	5	1.2
<i>Leontopithecus chrysomelas</i>	Golden-headed lion tamarin	EN	5	1.2
<i>Macaca ochreata</i>	Booted macaque	VU	5	1.2
<i>Ptilocolobus kirkii</i>	Zanzibar red colobus	EN	4	1.0
<i>Pongo abelii</i>	Sumatran orangutan	CR	4	1.0
<i>Sapajus apella</i>	Guianan brown capuchin	LC	4	1.0
<i>Sapajus libidinosus</i>	Bearded capuchin	LC	4	1.0
<i>Trachypithecus geei</i>	Golden langur	EN	4	1.0

<i>Alouatta caraya</i>	Paraguayan howler	LC	3	0.7
<i>Callithrix kuhlii</i>	Wied's black-tufted-ear marmoset	NT	3	0.7
<i>Cebus capucinus</i>	Colombian white-faced capuchin	LC	3	0.7
<i>Cercopithecus sclateri</i>	Sclater's monkey	VU	3	0.7
<i>Colobus guereza</i>	Guereza	LC	3	0.7
<i>Erythrocebus patas</i>	Patas monkey	LC	3	0.7
<i>Gorilla gorilla</i>	Western gorilla	CR	3	0.7
<i>Macaca leonina</i>	Northern pig-tailed macaque	VU	3	0.7
<i>Macaca sinica</i>	Toque macaque	EN	3	0.7
<i>Tarsius dentatus</i>	Dian's tarsier	VU	3	0.7
<i>Theropithecus gelada</i>	Gelada	LC	3	0.7
<i>Cercopithecus ascanius</i>	Red-tailed monkey	LC	2	0.5
<i>Chlorocebus tantalus</i>	Tantalus monkey	LC	2	0.5
<i>Macaca assamensis</i>	Assamese macaque	NT	2	0.5
<i>Macaca munzala</i>	Arunachal macaque	EN	2	0.5
<i>Macaca nemestrina</i>	Southern pig-tailed macaque	VU	2	0.5
<i>Macaca nigra</i>	Crested macaque	CR	2	0.5
<i>Nycticebus javanicus</i>	Javan slow loris	CR	2	0.5
<i>Papio hamadryas</i>	Hamadryas baboon	LC	2	0.5
<i>Saguinus leucopus</i>	White-footed tamarin	EN	2	0.5
<i>Aotus lemurinus</i>	Lemurine night monkey	VU	1	0.2
<i>Callithrix jacchus</i>	Common marmoset	LC	1	0.2
<i>Cebus imitator</i>	Panamanian white-faced capuchin	LC	1	0.2
<i>Cercocebus agilis</i>	Agile mangabey	LC	1	0.2
<i>Cercocebus galeritus</i>	Tana River mangabey	EN	1	0.2
<i>Cercopithecus campbelli</i>	Campbell's monkey	LC	1	0.2
<i>Chlorocebus djamdjamentis</i>	Bale monkey	VU	1	0.2
<i>Colobus angolensis</i>	Angolan colobus	LC	1	0.2
<i>Colobus vellerosus</i>	White-thighed colobus	VU	1	0.2
<i>Daubentonia madagascariensis</i>	Aye-aye	EN	1	0.2
<i>Eulemur macaco</i>	Black lemur	VU	1	0.2
<i>Gorilla beringei</i>	Eastern gorilla	EN	1	0.2
<i>Haplemur meridionalis</i>	Southern bamboo lemur	VU	1	0.2
<i>Hoolock leuconedys</i>	Eastern hoolock gibbon	VU	1	0.2
<i>Hylobates lar</i>	Lar gibbon	EN	1	0.2
<i>Hylobates moloch</i>	Moloch gibbon	EN	1	0.2
<i>Macaca cyclops</i>	Taiwanese macaque	LC	1	0.2
<i>Macaca siberu</i>	Siberut macaque	VU	1	0.2
<i>Macaca silenus</i>	Lion-tailed macaque	EN	1	0.2
<i>Nycticebus bengalensis</i>	Bengal slow loris	VU	1	0.2
<i>Ptilocolobus badius</i>	Upper Guinea red colobus	EN	1	0.2
<i>Ptilocolobus pennantii</i>	Pennant's red colobus	EN	1	0.2
<i>Presbytis comata</i>	Javan langur	EN	1	0.2
<i>Presbytis femoralis</i>	Banded langur	NT	1	0.2
<i>Presbytis hosei</i>	Hose's langur	DD	1	0.2
<i>Presbytis siberu</i>	Siberut langur	EN	1	0.2
<i>Propithecus tattersalli</i>	Tattersall's sifaka	CR	1	0.2
<i>Propithecus verreauxi</i>	Verreaux's sifaka	EN	1	0.2
<i>Rungwecebus kipunji</i>	Kipunji	CR	1	0.2
<i>Saguinus bicolor</i>	Pied tamarin	EN	1	0.2
<i>Sapajus xanthosternos</i>	Yellow-breasted capuchin	CR	1	0.2
<i>Semnopithecus johnii</i>	Nilgiri langur	VU	1	0.2
<i>Tarsius tarsier</i>	Selayar tarsier	VU	1	0.2
<i>Trachypithecus auratus</i>	East Javan langur	VU	1	0.2

699 ^aFor each publication, we recorded up to two focal primate species. Primate taxonomy follows the most recent
700 taxonomic compilation of Estrada *et al.* (2017). The diversity of species in our dataset ($N = 84$ species) may be
701 slightly underestimated because not all publications identified primates to species level and we did not compile
702 species information for 44 publications (of the 427 in the dataset) that concerned >2 species.

703
704 ^bIUCN Red List categories follow Estrada *et al.* (2017). LC = Least Concern; NT = Near Threatened; DD =
705 Data Deficient; VU = Vulnerable; EN = Endangered; CR = Critically Endangered. The seven CR species in the
706 dataset were crested macaque, Javan slow loris, Kipunji (highland mangabey), Sumatran mangabey, Tattersall's
707 sifaka, western gorilla, and yellow-breasted capuchin.

708
709 ^c% Species records refers to the % representation of each species of the total number of publication records for
710 individual species ($N = 415$).

711

712 **Table SII** Primate genera (and number of focal species within each genus) featured in publications
 713 about primates in anthropogenic habitats, from a Web of Science™ literature search covering the
 714 period 1970 to December 7, 2016 ($N = 427$). Genera are listed alphabetically and in descending order
 715 of frequency in the dataset (number of publications).

Primate genus (no. of species) ^a	No. of publications	% Genus records ^b
<i>Macaca</i> (17)	134	31.9
<i>Papio</i> (4)	56	13.3
<i>Pan</i> (1)	46	11.0
<i>Alouatta</i> (4)	24	5.7
<i>Chlorocebus</i> (4)	23	5.5
<i>Semnopithecus</i> (3)	18	4.3
<i>Sapajus</i> (4)	16	3.8
<i>Callithrix</i> (3)	11	2.6
<i>Cercopithecus</i> (4)	11	2.6
<i>Pongo</i> (2)	11	2.6
<i>Lemur</i> (1)	6	1.4
<i>Ptilocolobus</i> (3)	6	1.4
<i>Cebus</i> (2)	5	1.2
<i>Colobus</i> (3)	5	1.2
<i>Leontopithecus</i> (1)	5	1.2
<i>Presbytis</i> (4)	5	1.2
<i>Trachypithecus</i> (2)	5	1.2
<i>Gorilla</i> (2)	4	1.0
<i>Tarsius</i> (2)	4	1.0
<i>Erythrocebus</i> (1)	3	0.7
<i>Nycticebus</i> (2)	3	0.7
<i>Saguinus</i> (2)	3	0.7
<i>Theropithecus</i> (1)	3	0.7
<i>Cercocebus</i> (2)	2	0.5
<i>Eulemur</i> (1)	2	0.5
<i>Hylobates</i> (2)	2	0.5
<i>Propithecus</i> (2)	2	0.5
<i>Aotus</i> (1)	1	0.2
<i>Daubentonia</i> (1)	1	0.2
<i>Hapalemur</i> (1)	1	0.2
<i>Hoolock</i> (1)	1	0.2
<i>Rungwecebus</i> (1)	1	0.2

716 ^aFor each publication, we recorded up to two focal primate genera (we did not compile this information for 36
 717 publications that concerned more than two genera). Primate taxonomy follows Estrada *et al.* (2017).
 718

719 ^b% Genus records refers to the % representation of each genus of the total number of publication records for
 720 individual genus in the dataset ($N = 420$); a single record was made for publications concerned with plural
 721 species of a genus.
 722

723 **Table SIII** Primate families featured in publications about primates in anthropogenic habitats, from a
 724 Web of Science™ literature search covering the period 1970 to December 7, 2016 ($N = 427$). Families
 725 are listed in descending order of frequency in the dataset (number of publications).

Primate family ^a	No. of publications	% Family records ^b
Cercopithecidae	267	63.0
Hominidae	71	16.7
Atelidae	25	5.9
Cebidae	22	5.2
Callitrichidae	16	3.8
Lemuridae	9	2.1
Tarsiidae	4	0.9
Hylobatidae	3	0.7
Lorisidae	3	0.7
Indriidae	2	0.5
Aotidae	1	0.2
Daubentoniidae	1	0.2

726 ^aFor each publication, we recorded up to two focal families (we did not compile this information for 20
 727 publications concerning more than two primate families).

728
 729 ^b% Family records refers to the % representation of each family of the total number of publication records for
 730 individual families in the dataset ($N = 424$); a single record was made for publications concerned with plural
 731 taxa within a family.

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 734 **Reference**

735 Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., *et al.* (2017). Impending
 736 extinction crisis of the world's primates: Why primates matter. *Science Advances*, 3, e1600946.

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