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

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ABSTRACT

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

Keywords: Anthropocene, behavioral adaptability, behavioral plasticity, ethnoprimatology, human-dominated landscapes, human–wildlife interactions

INTRODUCTION

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

Consistent with the wider literature on human–wildlife interactions (Angelici 2016; Seoraj-Pillai and Pillay 2017; Woodroffe et al. 2005), research on primates in anthropogenic habitats has tended to concentrate on negative aspects of human–primate interactions, such as primates 'raiding' agricultural crops and other 'conflicts' that challenge the sustainability of primate coexistence with people (Hill 2005). This reminds us that not all behavioral adjustments to anthropogenic habitats are beneficial (see Sih et al. 2011; Tuomainen and Candolin 2011; Wong and Candolin 2015), with some behaviors compromising the survival of primate populations, for example by inciting persecution by people. Understanding primates' behavioral flexibility in response to human influence on their habitat, and how local people perceive and respond to changing primate behavior, can inform conservation management to aid the long-term survival of primates in a fast-changing world (Hockings et al. 2015; Nowak and Lee 2013).

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

RESEARCH TRENDS

We searched the literature for publications reporting primate behavior in anthropogenic habitats using the Web of Science^{TM} database. We searched using 'All Databases', which included the Web of Science core collection, MEDLINE, and BIOSIS and SciELO citation indexes, covering articles published from 1970 to December 7th 2016. We searched for full-length research articles, short communications, commentaries and reviews, but excluded studies published as abstracts only. We used the key words 'primate', 'monkey', 'ape' and 'lemur' in all searches, as well as common names (e.g., macaque, baboon, capuchin, chimpanzee) in some searches. We combined key words with relevant search terms, repeating searches using alternative or synonymous terms. Search terms that returned greatest numbers of relevant articles were human–wildlife conflict, human–wildlife interactions, crops, crop raiding, agriculture, plantation, anthropogenic, human-dominated, tourism, provisioning, and urban.

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

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

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

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

Growth in research

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

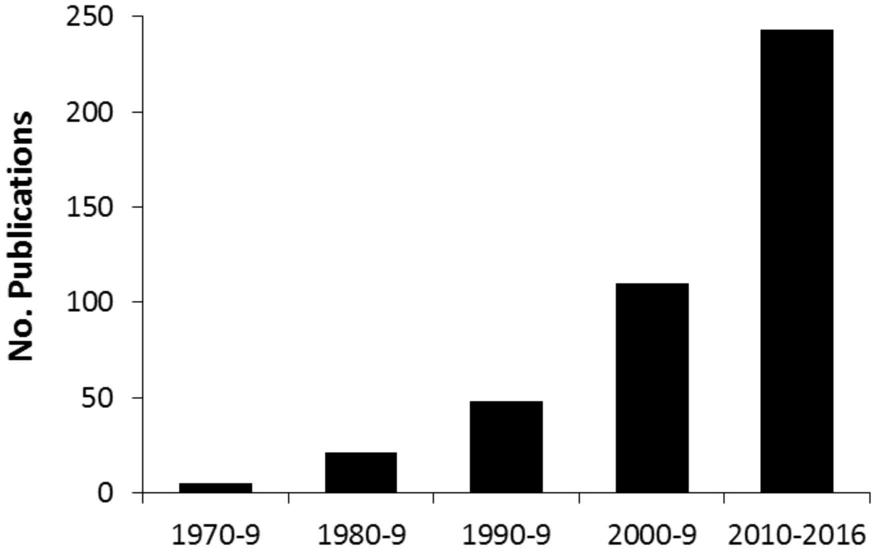

Fig. 1. The number of publications about primates in anthropogenic habitats published in each decade since the 1970s from a Web of Science™ literature search (1970 to December 7th 2016; N = 427).

Which primates and where?

Most publications in our dataset concerned primates in mainland Africa (40%) and Asia (39%) (Fig. 2); 16% concerned Neotropical primates while only 3% concerned Madagascan primates. Historically-introduced populations of *Macaca mulatta* in the United States and *M. sylvanus* in Europe accounted for one and seven publications, respectively. Forty-eight countries were represented, including 44 of the 90 where primates occur naturally (Estrada et al. 2017), as well as four countries where primates were introduced historically. India (12%), Uganda (11%), Indonesia (11%), Brazil (9%), South Africa (5%), Japan (5%) and Kenya (5%) were the subject of the most publications.

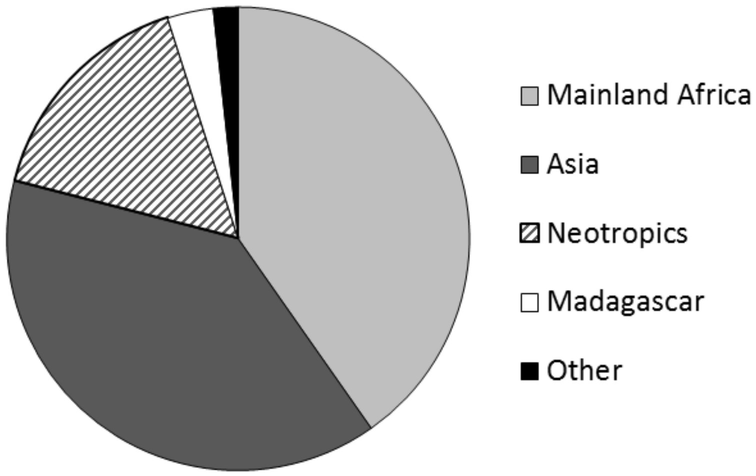

Fig. 2. Pie chart showing the distribution of publications about primates in anthropogenic habitats according to geographical region, from a Web of Science^{TM} literature search covering the period 1970 to December 7th 2016 (N = 405 publications specific to a particular geographic region). 'Other' comprises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

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

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

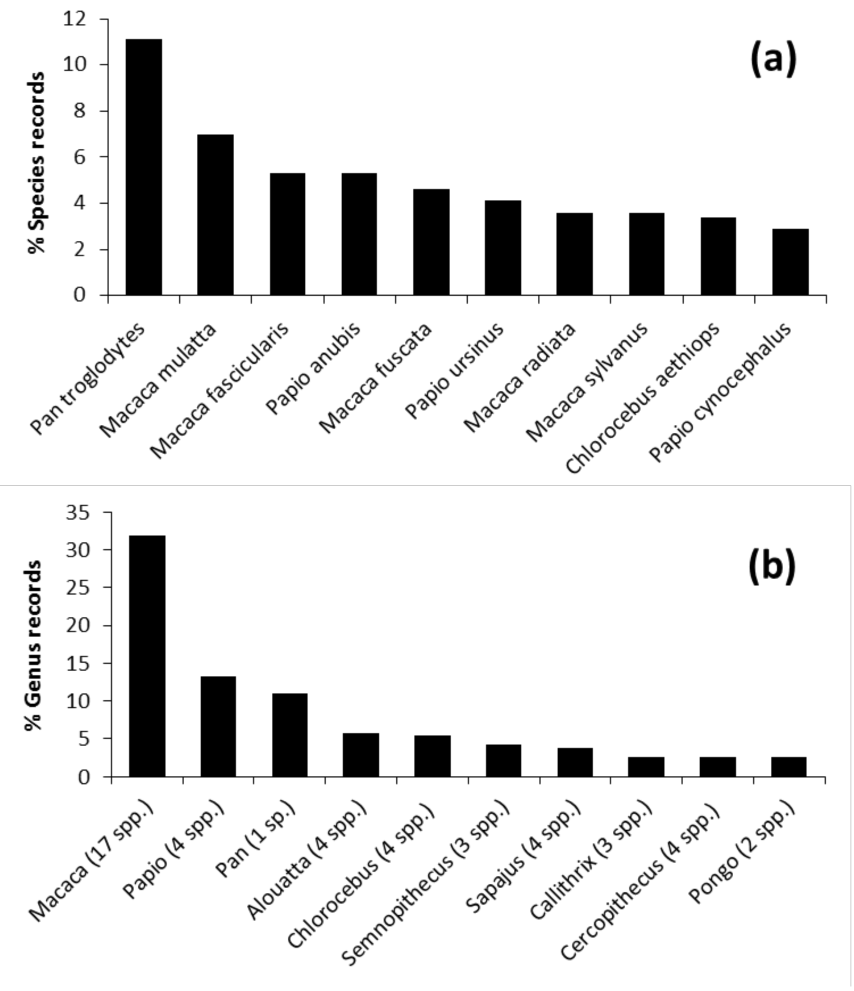

Fig. 3. The 10 primate species and genera most commonly featured in publications about primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December 7th 2016). We recorded up to two focal species and genera per publication. Bars show the percentage of the total number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

One species of great ape (*Pan troglodytes*) featured in the greatest number of publications (11% of species records; Fig. 3a). Other focal species common in the dataset include those well-known for inhabiting human-dominated habitats: five macaque species (*Macaca* spp.), three baboon species (*Papio* spp.) and grivet monkeys (*Chlorocebus aethiops*). The prevalence of chimpanzee studies does not imply that this species is especially numerous or prospers in modified habitats in association with people – unlike some macaques, for example (Richard et al. 1989). Rather, it mostly reflects recent interest in this species' responses to anthropogenic habitat modifications (e.g., Hockings and McLennan 2012; Krief et al. 2014; McLennan and Hockings 2014). Other primate genera that have been well-studied in anthropogenic habitats are more speciose than chimpanzees (especially *Macaca*), with research effort spread over several species. By comparison, other genera that exploit anthropogenic environments were the focus of relatively few studies in our dataset, for example *Cercopithecus*, *Sapajus*, and *Erythrocebus*.

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

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

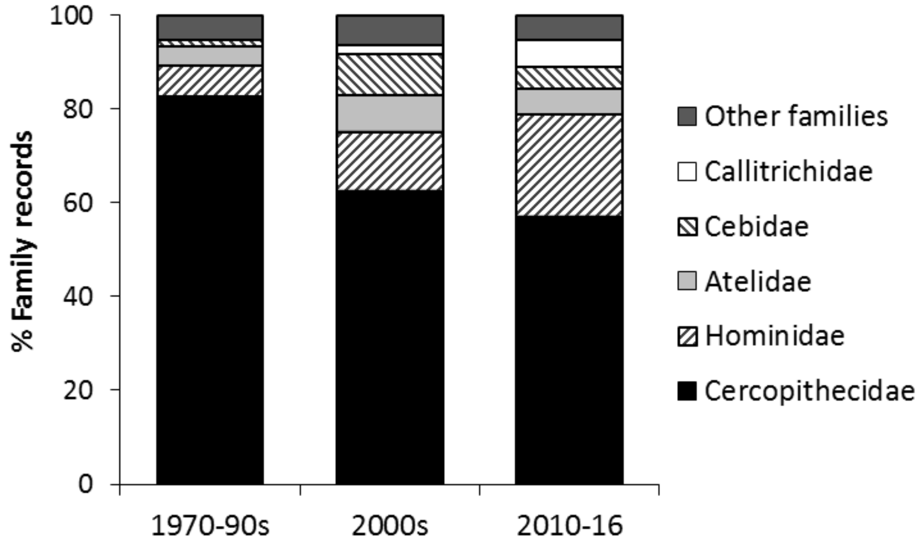

Fig. 4. The distribution of research focussed on individual families of primate in three time periods, from a Web of Science™ literature search (1970 to December 7th 2016). We recorded up to two focal families per publication. We calculated percentages from the number of records per family out of the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

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

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

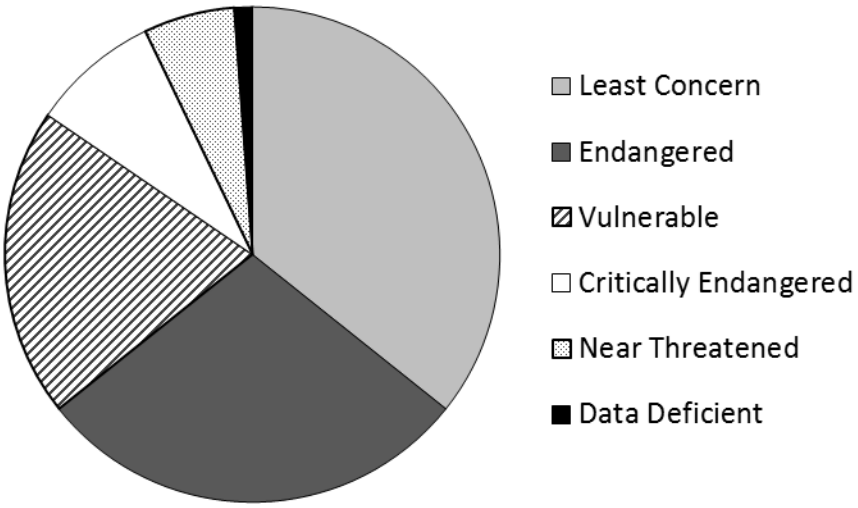

Fig. 5. Pie chart showing the conservation status of 84 species of focal primate in publications about primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December 7th 2016). IUCN Red List Categories follow Estrada et al. (2017).

Behavioral adjustments

We classified behavioral adjustments by primates living in anthropogenic habitats as 'dietary', 'socioecological', 'risk-related response', 'miscellaneous' (for novel or rare behaviors) and 'general use' (for publications reporting primates' active use of anthropogenic environments but without specifying a particular behavioral adjustment). The most commonly reported behavioral adjustment exhibited by primates in anthropogenic habitats was dietary (Fig. 6): primates in anthropogenic habitats were widely reported to feed on exotic plants including agricultural crops and plantation trees among other introduced species, as well as garbage and provisioned items; 19% of these publications concerned wild and free-ranging primates at tourist or religious sites. In rare instances baboons and chimpanzees also consumed domestic animals, while capuchins were observed consuming a chicken carcass (Cunha et al. 2006).

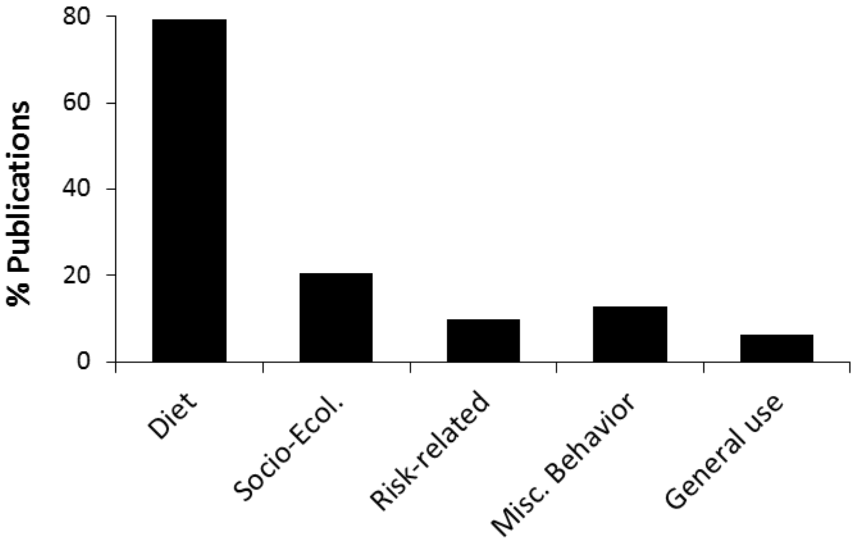

Fig. 6. The % of publications reporting behavioral adjustments in primates living in anthropogenic habitats from a Web of Science™ literature search (1970 to December 7th 2016; N = 427). We categorized behaviors as dietary, socioecological, risk-related, miscellaneous, and 'general use' of the habitat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

Socioecological adjustments – described in 21% of publications – included changes in activity, ranging and habitat use, grouping and social organization, and reproduction. For example, primates that regularly eat energy-rich agricultural crops or garbage often, but not always, travel and forage less, have smaller ranges, and spend more time resting and socializing (e.g., *Chlorocebus pygerythrus*, Saj et al. 1999). Crop foraging primates may exhibit flexible grouping patterns with certain age-sex classes (often adult males) most likely to participate in risky forays into agricultural fields (e.g., *Cercopithecus ascanius*, Baranga et al. 2012; *Pan troglodytes*, Hockings et al. 2012). Habitat use, including sleeping site locations, may facilitate primates' access to human foods (e.g., *Macaca fascicularis*; Brotcorne et al. 2014) but can also reflect avoidance of areas of busy human activity (e.g., *Hylobates moloch*, Reisland and Lambert 2016). In some publications, frequent consumption of human foods is linked to shorter interbirth intervals, earlier reproductive onset and reduced infant mortality (e.g., *Papio anubis*; Higham et al. 2009; Strum 2010).

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

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

People and primates

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

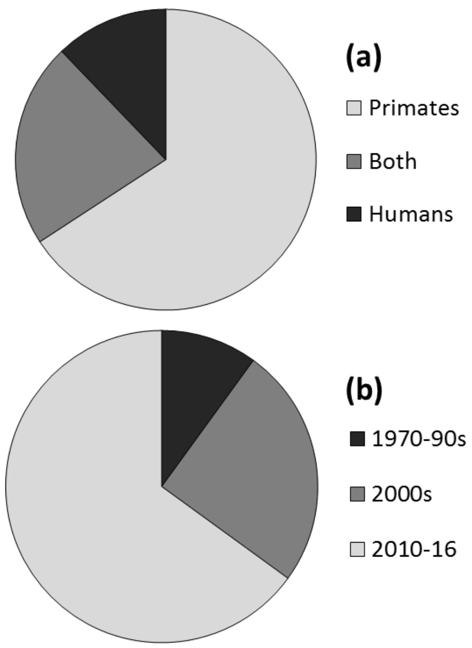

Fig. 7. Pie charts showing (a) the proportion of publications about primates in anthropogenic habitats that focussed primarily on primates, humans, or both, from a Web of Science™ literature search (1970 to December 7th 2016; N = 427); (b) the proportion of the total number of publications

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

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

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

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

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

CONTRIBUTIONS TO THIS SPECIAL ISSUE

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

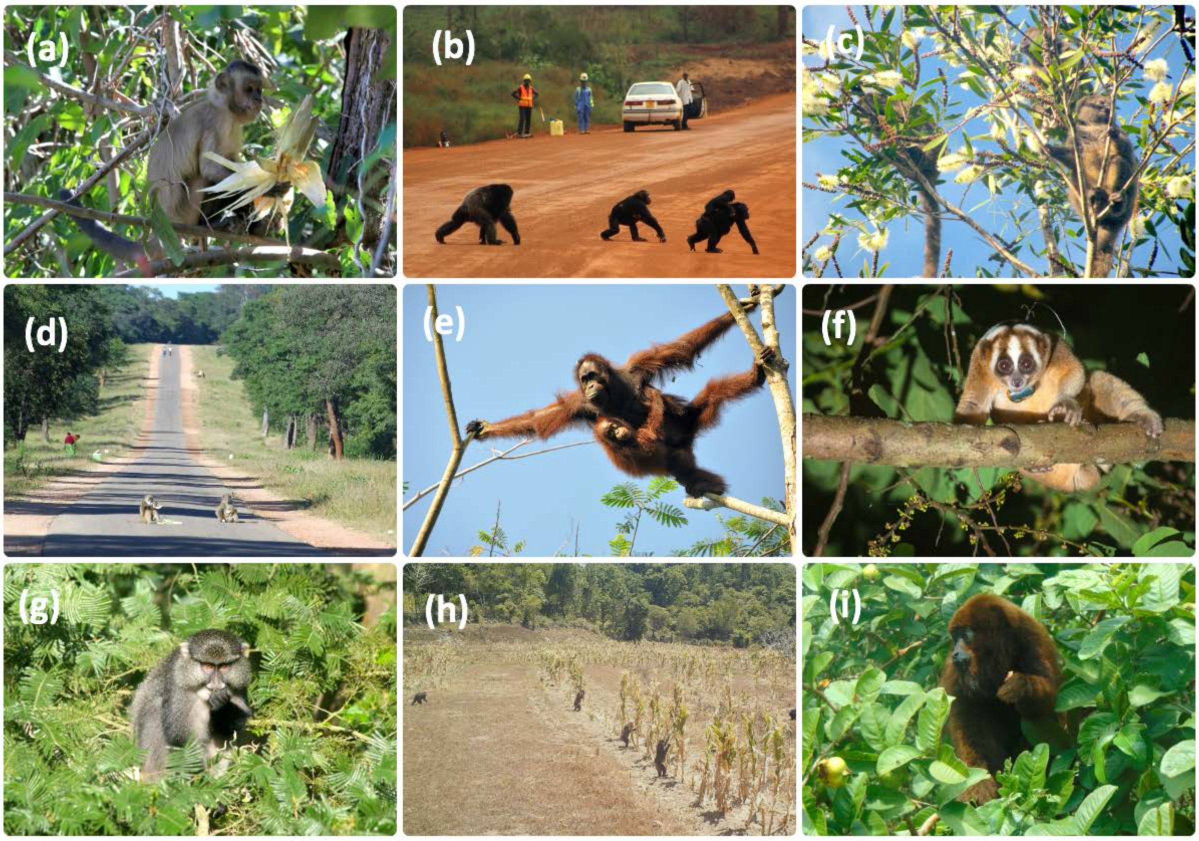

Fig. 8. Primate species in anthropogenic habitats included in this Special Issue. (a) Adult male bearded capuchin monkey (*Sapajus libidinosus*) feeding on maize, *Zea mays* (photo by N. Spagnoletti); (b) Eastern chimpanzees (*Pan troglodytes schweinfurthii*) crossing a newly widened road at Bulindi,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

As our literature review revealed, feeding on exotic plants is a primary behavioral adjustment of primates in modified habitats, and many contributions to this Special Issue concern aspects of this dietary adjustment. McLennan and Ganzhorn (2017) evaluate the common assumption that crops offer high nutritional returns compared to wild forage for primates by comparing the chemical content of wild and cultivated foods in the diet of eastern chimpanzees (*Pan troglodytes schweinfurthii*). Wimberger et al. (2017) examine the role of exotic plants in the feeding ecology of samango monkeys (*Cercopithecus albogularis labiatus*) in a matrix of residential gardens and native forest. Hockings et al. (2016) explore seed dispersal in an anthropogenic context, by studying patterns of dispersal of a cultivated crop (cacao, *Theobroma cacao*) by western chimpanzees (*P. t. verus*). Nowak et al. (2016) take an experimental approach to examine risk-sensitive foraging in samango monkeys (*C. a. labiatus*) in a habitat matrix of indigenous forest and residential gardens, where food acquisition was most risky. Schweitzer et al. (2017) examine individual participation, decision-making, and collective movements by chacma baboons (*Papio ursinus*) when foraging on crops along the periphery of a National Park.

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

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

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

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

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

WAYS FORWARD

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

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

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

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

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Electronic Supplementary Material

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

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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]
Pan troglodytes	Chimpanzee	EN	46	11.1
Macaca mulatta	Rhesus macaque	LC	29	7.0
Macaca fascicularis	Long-tailed macaque	LC	22	5.3
Papio anubis	Olive baboon	LC	22	5.3
Macaca fuscata	Japanese macaque	LC	19	4.6
Papio ursinus	Chacma baboon	LC	17	4.1
Macaca radiata	Bonnet macaque	LC	15	3.6
Macaca sylvanus	Barbary macaque	EN	15	3.6
Chlorocebus aethiops	Grivet monkey	LC	14	3.4
Papio cynocephalus	Yellow baboon	LC	12	2.9
Macaca thibetana	Tibetan macaque	NT	9	2.2
Semnopithecus vetulus	Purple-faced langur	EN	9	2.2
Alouatta pigra	Central American black howler	EN	8	1.9
Semnopithecus entellus	Bengal sacred langur	LC	8	1.9
Callithrix penicillata	Black-tufted-ear marmoset	LC	7	1.7
Macaca tonkeana	Tonkean macaque	VU	7	1.7
Pongo pygmaeus	Bornean orangutan	EN	7	1.7
Alouatta palliata	Mantled howler	LC	6	1.4
Chlorocebus pygerythrus	Vervet monkey	LC	6	1.4
Lemur catta	Ring-tailed lemur	EN	6	1.4
Sapajus nigritus	Black-horned capuchin	NT	6	1.4
Alouatta guariba	Brown howler	LC	5	1.2
Cercopithecus mitis	Blue monkey	LC	5	1.2
Leontopithecus chrysomelas	Golden-headed lion tamarin	EN	5	1.2
Macaca ochreata	Booted macaque	VU	5	1.2
Piliocolobus kirkii	Zanzibar red colobus	EN	4	1.0
Pongo abelii	Sumatran orangutan	CR	4	1.0
Sapajus apella	Guianan brown capuchin	LC	4	1.0
Sapajus libidinosus	Bearded capuchin	LC	4	1.0
Trachypithecus geei	Golden langur	EN	4	1.0
Alouatta caraya	Paraguayan howler	LC	3	0.7
Callithrix kuhlii	Wied's black-tufted-ear marmoset	NT	3	0.7
Cebus capucinus	Colombian white-faced capuchin	LC	3	0.7
Cercopithecus sclateri	Sclater's monkey	VU	3	0.7
Colobus guereza	Guereza	LC	3	0.7
Erythrocebus patas	Patas monkey	LC	3	0.7
Gorilla gorilla	Western gorilla	CR	3	0.7
Macaca leonina	Northern pig-tailed macaque	VU	3	0.7
Macaca sinica	Toque macaque	EN	3	0.7
Tarsius dentatus	Dian's tarsier	VU	3	0.7
Theropithecus gelada	Gelada	LC	3	0.7
Cercopithecus ascanius	Red-tailed monkey	LC	2	0.5
Chlorocebus tantalus	Tantalus monkey	LC	2	0.5
Macaca assamensis	Assamese macaque	NT	2	0.5
Macaca munzala	Arunachal macaque	EN	2	0.5
Macaca nemestrina	Southern pig-tailed macaque	VU	2	0.5
Macaca nigra	Crested macaque	CR	2	0.5
Nycticebus javanicus	Javan slow loris	CR	2	0.5
Papio hamadryas	Hamadryas baboon	LC	2	0.5
Saguinus leucopus	White-footed tamarin	EN	2	0.5
Aotus lemurinus	Lemurine night monkey	VU	1	0.2
Callithrix jacchus	Common marmoset	LC	1	0.2

Cebus imitator	Panamanian white-faced capuchin	LC	1	0.2
Cercocebus agilis	Agile mangabey	LC	1	0.2
Cercocebus galeritus	Tana River mangabey	EN	1	0.2
Cercopithecus campbelli	Campbell's monkey	LC	1	0.2
Chlorocebus djamdjamensis	Bale monkey	VU	1	0.2
Colobus angolensis	Angolan colobus	LC	1	0.2
Colobus vellerosus	White-thighed colobus	VU	1	0.2
Daubentonia madagascariensis	Aye-aye	EN	1	0.2
Eulemur macaco	Black lemur	VU	1	0.2
Gorilla beringei	Eastern gorilla	EN	1	0.2
Hapalemur meridionalis	Southern bamboo lemur	VU	1	0.2
Hoolock leuconedys	Eastern hoolock gibbon	VU	1	0.2
Hylobates lar	Lar gibbon	EN	1	0.2
Hylobates moloch	Moloch gibbon	EN	1	0.2
Macaca cyclopis	Taiwanese macaque	LC	1	0.2
Macaca siberu	Siberut macaque	VU	1	0.2
Macaca silenus	Lion-tailed macaque	EN	1	0.2
Nycticebus bengalensis	Bengal slow loris	VU	1	0.2
Piliocolobus badius	Upper Guinea red colobus	EN	1	0.2
Piliocolobus pennantii	Pennant's red colobus	EN	1	0.2
Presbytis comata	Javan langur	EN	1	0.2
Presbytis femoralis	Banded langur	NT	1	0.2
Presbytis hosei	Hose's langur	DD	1	0.2
Presbytis siberu	Siberut langur	EN	1	0.2
Propithecus tattersalli	Tattersall's sifaka	CR	1	0.2
Propithecus verreauxi	Verreaux's sifaka	EN	1	0.2
Rungwecebus kipunji	Kipunji	CR	1	0.2
Saguinus bicolor	Pied tamarin	EN	1	0.2
Sapajus xanthosternos	Yellow-breasted capuchin	CR	1	0.2
Semnopithecus johnii	Nilgiri langur	VU	1	0.2
Tarsius tarsier	Selayar tarsier	VU	1	0.2
Trachypithecus auratus	East Javan langur	VU	1	0.2

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

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

[c]% Species records refers to the % representation of each species of the total number of publication records for individual species (*N* = 415).

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

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

[a]For each publication, we recorded up to two focal primate genera (we did not compile this information for 36 publications that concerned more than two genera). Primate taxonomy follows Estrada *et al*. (2017).

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

Table SIII Primate families featured in publications about primates in anthropogenic habitats, from a Web of Science[TM] literature search covering the period 1970 to December 7, 2016 (N = 427). Families 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

[a]For each publication, we recorded up to two focal families (we did not compile this information for 20 publications concerning more than two primate families).

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

Reference

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