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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 and 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 overrepresented 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 provisioned items, and as differences in activity, ranging, grouping patterns, and

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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 (cf. 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 that is equivalent to human-dominated or human-impacted habitats, among similar terms (see McKinney 2015 for a 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 (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 that 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 review 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™ 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 7, 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 the 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: 1) 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 (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; 2) behavioral responses of primates to novel aspects of, or risks associated with, anthropogenic habitats; 3) direct interactions between primates and humans (including tourists, local people, and researchers) in anthropogenic habitats; 4) human perceptions of, attitudes toward, or

beliefs about, primates; and 5) 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), or articles focused 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 returned mostly 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 behavior, 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 by others (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 grow: The first 7 years of the 2010s (until December 2016) account for 57% of publications in our dataset (Fig. 1).

Which Primates and Where?

Most publications in our dataset concerned primates in mainland Africa (40%) and Asia (39%) (Fig. 2); 16% concerned Neotropical primates, whereas 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

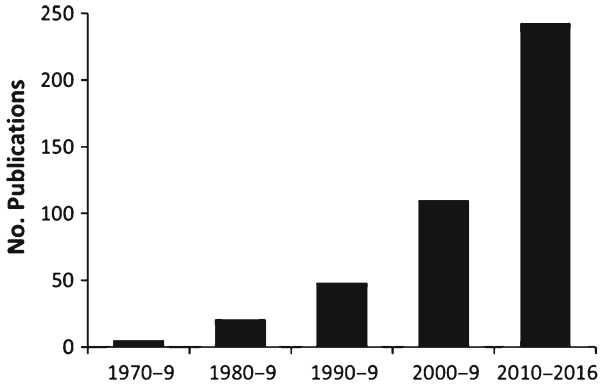

Fig. 1 The number of publications about primates in anthropogenic habitats published in each decade since the 1970s from a Web of Science™ literature search (1970 to December 7, 2016; $N = 427$).

(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 subjects of the most publications.

The most common anthropogenic habitat in which primates interface with humans could 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 habitats including 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 SI–SIII). 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

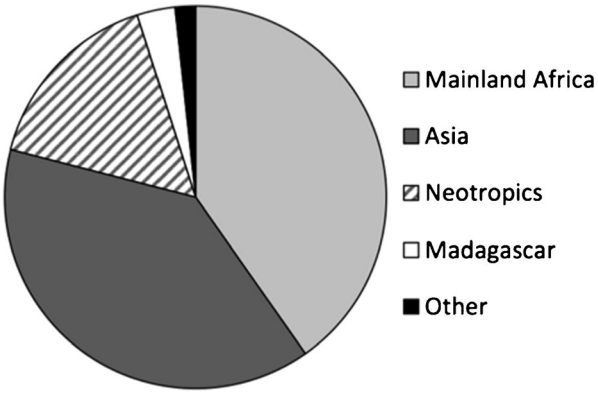

Fig. 2 Pie chart showing the distribution of publications about primates in anthropogenic habitats according to geographical region, from a Web of Science™ literature search covering the period 1970 to December 7, 2016 ($N = 405$ publications specific to a particular geographic region). "Other" comprises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

species accounted for half (51%) of the records for individual species ($N = 415$) (Fig. 3a; see ESM Table SI for a complete list).

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

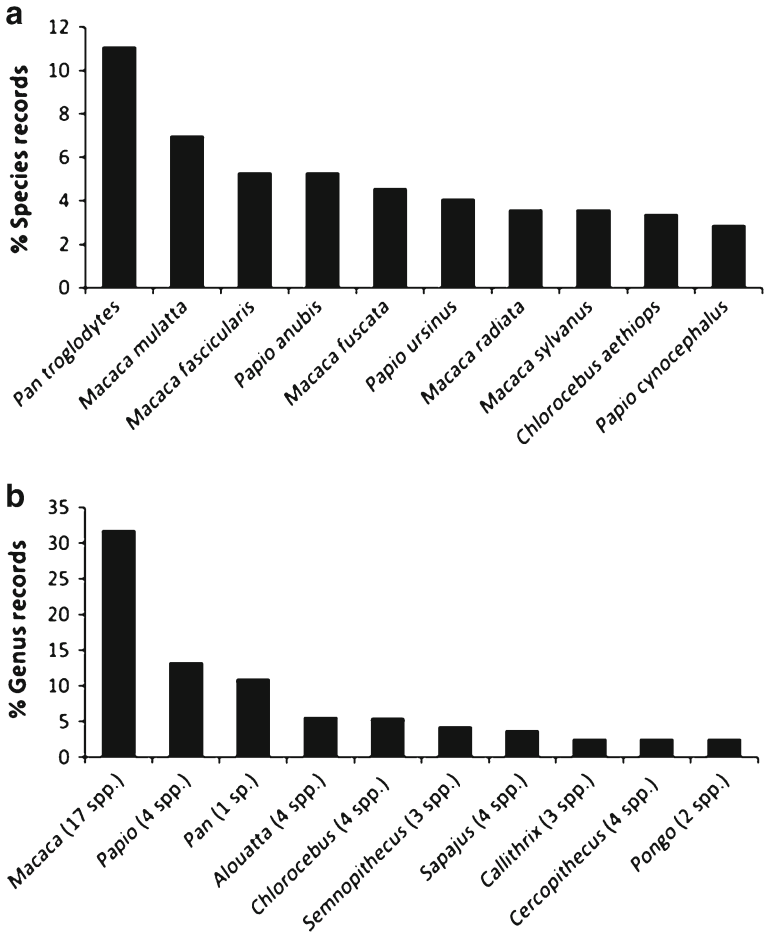

Fig. 3 The 10 primate species and genera most commonly featured in publications about primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December 7, 2016). We recorded up to two focal species and genera per publication. Bars show the percentage of the total number of 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 parentheses below the bars in **(b)**.

species. By comparison, some other species that exploit anthropogenic environments were the focus of relatively few studies in our dataset, for example, members of *Cercopithecus* and *Sapajus*, and *Erythrocebus patas*.

Three genera (*Macaca*, *Papio*, and *Pan*) accounted for more than half of the records for individual genera ($N = 420$; ESM Table SII). *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. (howlers) and *Chlorocebus* spp. (including grivet and vervet monkeys) also featured relatively often in the dataset.

Most publications (63%) in the dataset concerned the Cercopithecidae (ESM Table SIII). However, the distribution of research across primate families has changed over time (Fig. 4). The proportion of studies focused on the Cercopithecidae decreased after the 1990s while those focused 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.

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 SI).

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 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

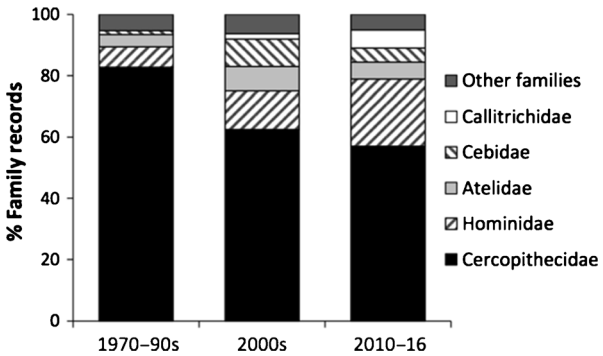

Fig. 4 The distribution of research focused on individual families of primates in three time periods, from a Web of Science™ literature search about primates in anthropogenic habitats (1970 to December 7, 2016). We recorded up to two focal families per publication. We calculated percentages from the number of records per family out of the total number of "family records" in each period: 1970–1990s ($N = 75$ family records), 2000s ($N = 112$), and 2010–2016 ($N = 237$). "Other families" are the combined records for Aotidae, Daubentoniidae, Hylobatidae, Indriidae, Lemuridae, Lorisidae, and Tarsiidae, each of which was the focus of one to nine publications in the dataset only (see ESM Table SIII).

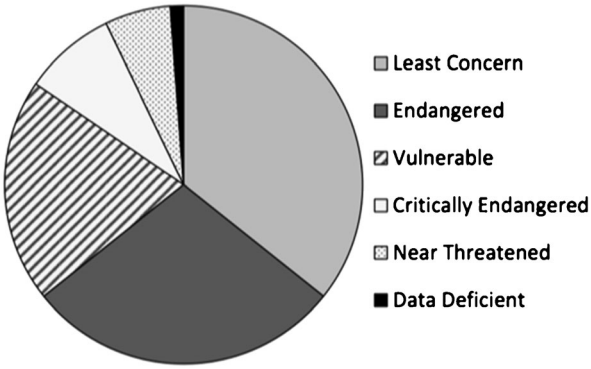

Fig. 5 Pie chart showing the conservation status of 84 species of focal primate in publications about primates in anthropogenic habitats, from a Web of Science™ literature search (1970 to December 7, 2016). IUCN Red List Categories follow Estrada *et al.* (2017).

religious sites. In rare instances baboons and chimpanzees also ate domestic animals, while capuchins were observed consuming a chicken carcass (Cunha *et al.* 2006).

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) and *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).

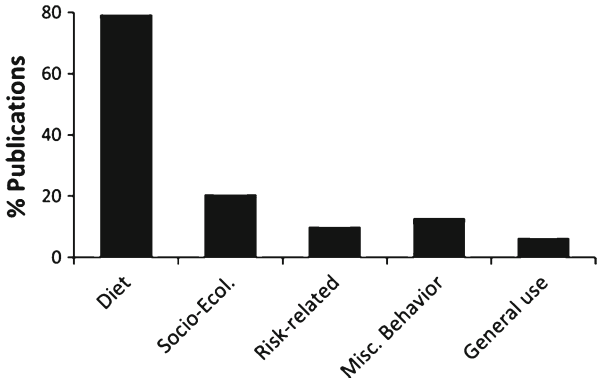

Fig. 6 The % of publications reporting behavioral adjustments of primates living in anthropogenic habitats from a Web of Science™ literature search (1970 to December 7, 2016; $N = 427$). We categorized behaviors as dietary, socioecological, risk-related, miscellaneous, and general use of the habitat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

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 toward 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" (*Pan troglodytes*: Hockings *et al.* 2007). Increased intragroup aggression or harassment of human visitors for food was common in provisioned primates, e.g., *Macaca sylvanus* (El Alami *et al.* 2012) and *Macaca thibetana* (Zhao and Deng 1992). A further 6% of publications described general use of anthropogenic habitats by primates, for example, long-term persistence in exotic plantations or agroforestry landscapes, e.g., *Alouatta pigra* (Zárate *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 (or wildlife including 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 toward, perceptions of, or beliefs about, primates. Of these, 10% were published in the 1970–1990s, 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 biodiversity conservation (Bennett *et al.* 2017). For example, ethnoprimatology uses interdisciplinary methods and perspectives to understand the social and ecological interconnectedness of humans and other primates (Fuentes 2012; Fuentes and Hockings 2010). Although relatively few publications in our dataset explicitly adopted an ethnoprimatological approach ($N = 17$; 4%), only one was published before 2010 (Riley 2007).

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 centered 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,

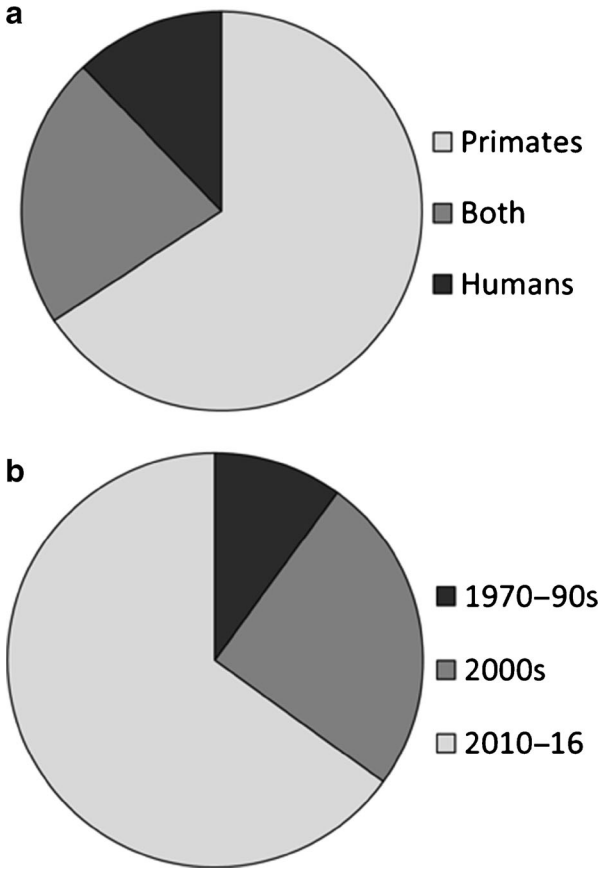

Fig. 7 Pie charts showing **(a)** the proportion of publications about primates in anthropogenic habitats that focused primarily on primates, humans, or both, from a Web of Science™ literature search (1970 to December 7, 2016; $N = 427$); **(b)** the proportion of publications that included an assessment of human attitudes toward, perceptions of, or beliefs about, primates ($N = 88$) that were published in each of three time periods: 1970–1990s, 2000s, and 2010–2016.

including observations of farmers chasing or throwing objects to deter primates, e.g., *Papio anubis* (Warren *et al.* 2011).

Thirty-three percent 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 emphasized 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 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 SI). 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 (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. Although 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 focused on this great ape.

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.* (2017) explore seed dispersal in a novel anthropogenic context, by studying patterns of dispersal of a cultivated crop (cacao, *Theobroma cacao*) by western chimpanzees (*P. t. verus*). Nowak *et al.* (2017) 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 (2017) compared camera trap footage of crop foraging by moor macaques (*Macaca maura*) with farmer perceptions of macaque behavior on farms gleaned from semistructured interviews. Spagnoletti *et al.* (2017) 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 (2017) examined crop foraging and its potential economic costs

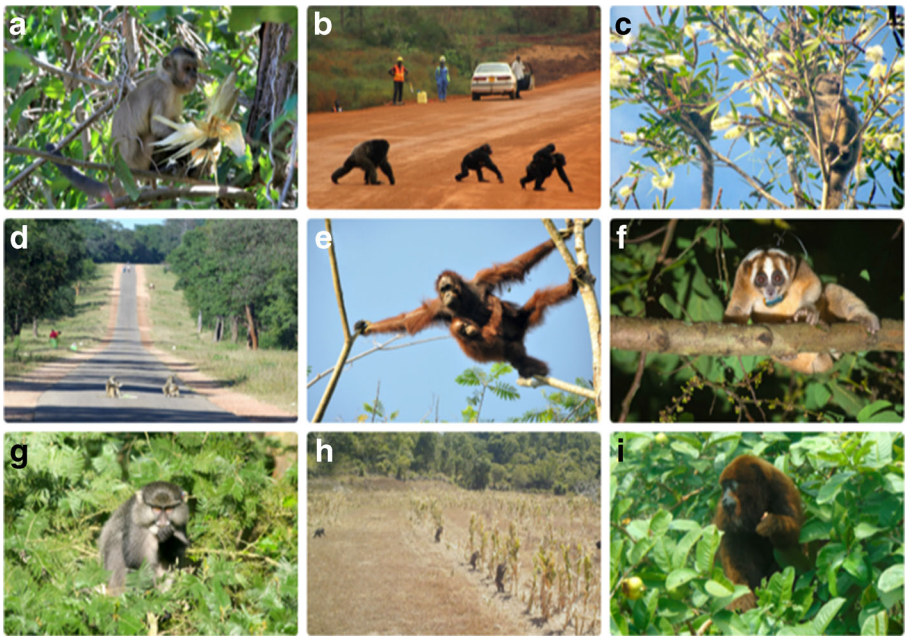

Fig. 8 Primate species in anthropogenic habitats included in this Special Issue. **a** Adult male bearded capuchin monkey (*Sapajus libidinosus*) feeding on maize, *Zea mays* (photo by N. Spagnoletti). **b** Eastern chimpanzees (*Pan troglodytes schweinfurthii*) crossing a newly widened road at Bulindi, 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).

by brown howlers (*Alouatta guariba clamitans*), combined with interviews to understand landowners' perceptions of this issue. Despite significant crop losses to primates, farmers in these latter two studies did not perceive 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 that 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 *Pan troglodytes 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 traveling. McCarthy *et al.* (2017) 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.* (2017) 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 behavior, 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 crop feeding by primates. Finally, Setchell *et al.* (2017) 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 such as 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.* (2017), 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 sociopolitical environment in which they conduct their research. Human–primate interactions rarely stand alone 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 twenty-first century and beyond.

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