



OVERVIEW

Responses of animals to habitat alteration: an overview focussing on primates

Christoph Schwitzer^{1,*}, Livvy Glatt¹, K. Anne-Isola Nekaris², Jörg U. Ganzhorn³

¹Bristol Conservation and Science Foundation, c/o Bristol Zoo Gardens, Clifton, Bristol BS8 3HA, UK

²Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford Brookes University, Oxford OX3 0BP, UK

³Department of Animal Ecology and Conservation, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

ABSTRACT: Original habitat of animal species is being destroyed at an accelerating rate. This is usually associated with an alteration of the remaining habitat, which becomes degraded and/or fragmented. In many regions, forests are cleared to make way for plantations or other agricultural use, and animal species are forced to coexist with humans. In some countries, forests are in the process of being restored for wildlife. As even long-established and well-protected areas typically comprise mosaics of habitats with different degrees of degradation, the future conservation of many species will depend on the capacity of such altered habitats to support their populations. During the last 15 yr, more and more studies have addressed the way that different species respond to the human-induced change of their habitats. These responses are varied, and range from population decline to adaptation and development of new behavioural strategies. Whereas some species rely heavily on intact primary forests, others can adapt to secondary forests and forest-agriculture mosaics. Habitat change has been shown to affect many aspects of the ecology and behaviour of animals. Changes in dietary composition and diversity, population density, group size and adult sex ratio in groups are some examples. This Theme Section of *Endangered Species Research* collates a number of case studies on how animals, and particularly primates, respond to the alteration of their habitat.

KEY WORDS: Habitat alteration · Degradation · Fragmentation · Agricultural use · Restoration · Primates

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INTRODUCTION

Natural habitat for animal and plant species is being destroyed at a high rate. MacKinnon & MacKinnon (1986, 1991) stated that by 1986 there had been a loss of 65% of wildlife habitat in Africa south of the Sahara, with more than 50% of habitat lost in 33 out of 42 countries and more than 70% loss in just 20 of those. Sussman et al. (1996) estimated that the rate of deforestation of Madagascar's eastern rainforests between 1950 and 1985 was 111 000 ha yr⁻¹ and that, if habitat destruction continued at the same rate, only forests on the steepest slopes would survive the next 35 yr. The current rate of forest loss in Madagascar is roughly 150 000 ha yr⁻¹, which means that if this rate continues, all of the is-

land's primary vegetation will have disappeared by 2067 (Moat & Smith 2007). In parts of the neotropics (Peres et al. 2010) and Asia (Sodhi et al. 2010) the situation is similar. MacKinnon & MacKinnon (1991) assessed that 31 to 96% of the original habitat of 42 primate species in the Indomalayan realm had been lost by the early 1990s. Habitat loss is usually associated with an alteration of the remaining habitat, which becomes degraded (e.g. through selective logging, disturbance of sapling growth by cattle, wild and feral pigs, goats etc.) and/or fragmented. Animals left residing in degraded forests or forest fragments may face reduced food resources and loss of sleeping or hiding places, and in some cases pressure from invasive species. Populations may also be more vulnerable in the event of

*Email: cschwitzer@bcsf.org.uk

natural disasters such as hurricanes, and changes in habitat brought about by global climate change, such as seasonal droughts (Malhi et al. 2008). Habitat degradation can mean easier access for predators and, hence, increased predation pressure (Wilcove 1985, Wilcove et al. 1986, Andr n & Angelstam 1988, Estrada & Coates-Estrada 1996, Irwin et al. 2009 but see Onderdonk & Chapman 2000). Better visibility and accessibility resulting from logging and fragmentation has been discussed as one reason for increases in some raptor populations (Karpanty 2003, Colquhoun 2006). In forests exposed to human activity, hunters can be an additional and novel predation threat for many animal species.

When forested areas become fragmented, the enduring fragments do not remain structurally intact. The edges of forest which border human-altered habitats undergo changes as a result of penetrating biotic and abiotic conditions, known as edge effects, which are a dominant driver of forest dynamics (Ries et al. 2004, Lehman et al. 2006a,b). Edge effects change the dynamics of forest fragments, affecting forest microclimate, tree mortality, and the fauna residing there (Laurance et al. 2011).

Habitat alteration can have very different effects, even on closely related animal populations. A recent review of responses of species to anthropogenic disturbance in Madagascar by Irwin et al. (2010) concluded that: (1) responses were generally negative, but remained poorly known, (2) the importance of different proximate factors varied between taxonomic groups, (3) responses within taxonomic groups differed between ecoregions, (4) phylogenetic relatedness or ecological similarity did not reliably infer similarity in responses, and (5) anthropogenic disturbance usually led to a reduction in species diversity, especially of native and/or endemic species.

FORESTS DEGRADED BY HUMAN ACTIVITIES

Irwin et al. (2010) summarised the responses of Malagasy lemurs to habitat alteration. Whereas at the community level some species might have benefitted from increased resource abundance after intermediate disturbance, higher disturbance led to the decline and eventual disappearance of all species through food shortage and/or hunting (Ganzhorn et al. 1997). Species varied in their responses and showed higher, lower, or equal densities in disturbed relative to moderately disturbed forest (Petter et al. 1977, Lehman et al. 2006a,b, Lehman 2007)

Irwin (2006, 2008a,b) found that diademed sifaka *Propithecus diadema* in disturbed fragments had lower mass, smaller home ranges, consumed less canopy tree fruit and more mistletoe, and showed reduced scent

marking, aggression and play behaviour than in undisturbed forest. In a study by Arrigo-Nelson (2006) in selectively logged rainforest, Milne-Edwards' sifaka *P. edwardsi* exhibited reduced fruit consumption, reduced mass and less social interaction. Whereas *P. edwardsi* had reduced mass in disturbed fragments, *Eulemur* spp. had similar mass but increased home ranges (Dehgan 2003, Schwitzer et al. 2007a, Irwin et al. 2010). Grey bamboo lemurs *Hapalemur griseus* in selectively logged rainforest or forest remnants in agricultural landscapes showed dietary differences and smaller ranges, but no sign of reduced health (Grassi 2001, Martinez 2008). Of the few lemur species studied, relatively folivorous species (*H. griseus*) were generally less susceptible than more frugivorous species (*Propithecus* spp., *Eulemur* spp., *Varecia* spp.). This was consistent with data showing that frugivores were more easily extirpated (Irwin & Raharison 2009). It has been suggested that there is great variation in the responses of bamboo lemurs to degraded habitat; for example, the golden bamboo lemur *H. aureus* is absent from fragments, whereas the greater bamboo lemur *Prolemur simus* survives for decades (Wright et al. 2008).

Notwithstanding hunting, most studies suggest that food resources are the primary driver of lemur density (Balko & Underwood 2005) and behavioural changes (Irwin 2007). Other factors, such as higher parasite loads in degraded habitats (Raharivololona et al. 2007, Wright et al. 2009, Schwitzer et al. 2010, this Theme Section) are less well-studied but are potentially important in Madagascar (Irwin et al. 2010).

In peninsular Malaysia and Sabah, Johns (1992) found long-term responses of primate communities to logging events to be depressed breeding rates and a drop in abundance (6 and 12 yr after the logging event, respectively). Populations of Sumatran (*Pongo abelii*) and Bornean orang-utans (*P. pygmaeus*) showed temporary declines in sites that had experienced reduced-impact logging (Morrogh-Bernard et al. 2003, Knop et al. 2004, Johnson et al. 2005, Marshall et al. 2006). However, these populations seem to have the potential to rebound if there is sufficient fruit available (Knop et al. 2004) and sustainable logging practices are strictly adhered to (Ancorenaz et al. 2005). Johns (1986), who studied a community of 5 diurnal and 1 nocturnal primate species in Sungai Tekam, West Malaysia, did not observe a reduction in viability in any of the populations in older logged forest, and numbers of infants, which were initially reduced following logging events, 'rapidly returned to normal' during his observations. He suggested that primates at Sungai Tekam were able to persist in logged forest due to a high degree of ecological and behavioural flexibility, especially in lar gibbons *Hylobates lar* and Sumatran surili *Presbytis melalophos*.

FORESTS DEGRADED BY EXTREME WEATHER EVENTS AND CLIMATE CHANGE

Human activities within and around forests are not the only sources of habitat degradation. Natural disasters affect not only human populations but also animal and plant communities. Hurricanes are a particularly destructive example of natural habitat alteration, resulting in abrupt changes to ecosystem processes, vegetative structure and animal populations (Pavelka et al. 2003). An opportunistic study carried out by Pavelka et al. (2003) after a hurricane event in southern Belize in 2001 found that the resident population of black howler monkeys *Alouatta pigra* suffered a population decline of 42% following an almost complete loss of forest canopy habitat, and that those left suffered social disorganisation characterised by higher numbers of solitary and transient individuals and smaller and more highly fragmentary social groups than before the hurricane. For many wildlife populations, the low levels of food availability following a hurricane pose a high risk of mortality (Johns & Skorupa 1987). As a species with a rather generalised frugifolivorous diet (Silver et al. 1998), the black howler monkeys were able to adjust to changes in food availability and after 12 wk of social disorganisation the stability of larger groups increased; however, home ranges were still not stable at 35 wk after the hurricane (Pavelka et al. 2003).

Black-and-white ruffed lemurs *Varecia variegata* at Manombo, eastern Madagascar (Ratsimbazafy 2002, Ratsimbazafy et al. 2002), altered their behaviour after a cyclone destroyed >50% of their preferred fruit trees. The animals fed more on shrubs and invasive plants, reduced travel, increased resting, lost body mass and halted reproduction for 4 yr (J. Ratsimbazafy unpubl., cited in Irwin et al. 2010).

Berenstain (1986) gave an account of a group of long-tailed macaques *Macaca fascicularis* in the Bornean rainforest adapting to habitat damage following severe drought and fire by altering their diet to less preferred items such as insects and charred and desiccated fruits, increasing their home range and adopting more terrestrial travel.

Whereas the effects on primate populations of localised natural disasters such as hurricanes and droughts are relatively easy to observe, as they occur over days and years, global climate change, which can be expected to have dramatic implications for the distribution of vegetational zones (Dunbar 1998), and so primate ecology, is difficult to study. This is due to the relatively long time frames associated with increases in global temperatures, as well as the detailed information necessary on population characteristics of the species concerned, their rates of survival and fecundity

and their variability (Dunham et al. 2008). Due to these constraints, only species that have been subject to long-term studies over years with suitably varying temperatures may provide appropriate case studies for evaluating the effects of global climate cycles on population dynamics (Dunham et al. 2008). The latter authors used population modelling to predict the effects of climate change on lemur populations, using data from 2 long-term studies of Milne Edward's sifakas *Propithecus edwardsi*, which together covered 8 El Niño years. In Madagascar and southern Africa, El Niño southern oscillation (ENSO) events have been documented to cause drought and vegetational changes which may negatively affect wildlife (Gould et al. 1999, Dunham et al. 2008). The model predicted that changes in ENSO frequencies and intensities resulting from climate change could lead to reduced *P. edwardsi* fecundity. Studies of sifaka species found that low body weights of adults were associated with prolonged drought seasons, which may cause reduced birth rates, as in other primates (King et al. 2005, Dunham et al. 2008).

Wiederholt & Post (2010) modelled the influence of ENSO and climatic conditions on the abundance of 4 genera of large-bodied, neotropical ateline primates: woolly monkey *Lagothrix lagotricha*, Colombian red howler monkey *Alouatta seniculus*, muriqui *Brachyteles arachnoides* and Geoffroy's spider monkey *Ateles geoffroyi* and their resource levels. Analyses indicated a strong effect of climatic variability and El Niño events on primate resources, and an immediate or lagged effect of resource availability on primate populations. The greatest population declines following El Niño events were for those species with a higher degree of frugivory, i.e. muriquis, woolly and spider monkeys (Wiederholt & Post 2010).

FRAGMENTED FORESTS

Forest fragmentation is one of the main threats to the conservation of species worldwide and can affect species richness and distribution, predator-prey interactions and habitat suitability (Tabarelli & Gascon 2005, Boyle 2008a), along with seed dispersal, which may result in a positive-feedback loop, changing plant populations and communities (Chapman & Onderdonk 1998). Boyle (2008a,b) evaluated the large-scale effects of Amazon forest fragmentation on a community of 6 primate species at the Biological Dynamics of Forest Fragments Project study site, 80 km north of Manaus, Brazil. The species studied were red howler monkey *Alouatta seniculus*, black spider monkey *Ateles paniscus*, brown capuchin *Cebus apella*, northern bearded saki *Chiropotes satanas chiropotes*, golden-

faced sakis *Pithecia chrysocephala* (L. K. Marsh pers. comm.) and red-handed tamarin *Saguinus midas*. Several forest characteristics predicted primate species richness, including fragment size, proportion of secondary growth in the human-altered matrix connecting the fragments, and distance to closest forest patch. Primates with large home range sizes and large proportions of fruit in their diet are thought to be the most vulnerable to negative effects of forest fragmentation (Johns & Skorupa 1987). Correspondingly, the species with the smallest home range size and the highest degree of folivory in Boyle's (2008a,b) study, the red howler monkey, was present in all fragments regardless of size and had the largest distribution and persistence throughout the fragments of all 6 studied species. The ability of howler monkeys to adapt to habitat alteration and to live in patches where other neotropical primate species cannot persist is relatively well documented (e.g. Lovejoy et al. 1986, Schwarzkopf & Rylands 1989, Silver et al. 1998, Bicca-Marques 2003, Garber et al. 2006, Van Belle & Estrada 2006, Pozo-Montuy & Serio-Silva 2007, Arroyo-Rodriguez & Dias 2010). Howlers can increase the proportion of leaves in their diet when fruit is in short supply and can also improve foraging efficiency in several ways, i.e. by group fission, adjustment of activity patterns to minimise energy expenditure, reducing travel time or resting for longer periods and decreasing foraging time (Asensio et al. 2007, Pozo-Montuy & Serio-Silva 2007). However, in their review of howler monkey responses to habitat fragmentation and disturbance, Arroyo-Rodriguez & Dias (2010) cited evidence indicating that habitat loss negatively affected the distribution and abundance of howlers in fragmented habitats.

Bearded sakis *Chiropotes* spp. are seed predators with typically large home ranges and large social groups. Boyle et al. (2009) and Boyle & Smith (2010) compared the social groupings, foraging behaviour and diet as well as spatial habitat use of northern bearded sakis *C. satanas chiropotes* between fragmented and continuous forest at the same study site as Boyle's 2008 study (see previous paragraph). In fragmented forest, bearded sakis did not utilise the entire fragment, avoiding certain areas of forest. When compared with those living in continuous forest, fragment-dwelling individuals also occupied smaller home ranges, lived in smaller groups, travelled shorter daily distances and used circular and repetitive routes. There was little overlap in the diet of *C. satanas chiropotes* living in forest fragments versus continuous forest, even when the same fruiting trees were present in both habitats.

Different studies on responses of Malagasy lemurs to forest fragmentation yielded similar results as for the above-mentioned neotropical primates. Deterministic

species extirpations (causing 'nested' distributions) in forest fragments were reported in several studies (Ganzhorn et al. 2003). At Tsinjoarivo in eastern-central Madagascar (Irwin & Raharison 2009), species loss increased with decreasing fragment size (which correlated with disturbance). Larger-bodied and more frugivorous species were more susceptible to extirpation from fragments. In the humid forest of south-eastern Madagascar (Dehgan 2003), forest fragments had lower species richness, with fragment size not predicting richness. Lemur species showing 'behavioural plasticity' were more resilient than those that did not. In Sahamalaza, north-western Madagascar, blue-eyed black lemurs *Eulemur flavifrons* were found in higher densities, had lower parasite loads, smaller home ranges and lower nocturnal activity levels in primary as compared to secondary forest fragments, suggesting low suitability of isolated secondary forest fragments for the long-term survival of the species (Schwitzer et al. 2007a,b, 2010). According to Ganzhorn et al. (2000), populations of ~40 adult individuals can persist in isolated fragments for 20 to 40 yr. Populations of this size require between 20 and 800 ha of suitable forest; fragments of ~1000 ha are needed to maintain all species.

FOREST EDGES

Forest fragmentation increases the ratio of forest edge to forest interior. After an area of forest is cleared, the new forest edge allows sunlight and wind to penetrate into the remaining fragment, resulting in microclimate changes that affect forest structure, leaf fall, turnover in the plant community, seedling recruitment patterns and the distribution of animals within the fragment (Gascon et al. 2000). Forest areas close to edges are vulnerable to higher levels of desiccation as well as tree mortality, and old growth, such as large tree species associated with climax communities are replaced by pioneer species (Gascon et al. 2000, Malhi et al. 2008). Lehman et al. (2006a) studied the biotic edge effects that influenced the distribution and density of several lemur species in Madagascar, where, in 2000, over 45% of forest consisted of patches of <500 km², and more than 80% of forest area was less than 1 km from an edge (Harper et al. 2007, Irwin et al. 2010). Lehman et al.'s (2006a) study site was the Vohibola III Classified Forest in south-eastern Madagascar, where both the density and size of lemur food trees decreased near forest edges. Compared with fruit, a relatively high availability of leaves and insect prey was found at forest edges. In a study by Quéméré et al. (2010), golden-crowned sifakas *Propithecus tattersalli* in the Daraina region of northern Madagascar were found to have neutral responses to edge effects, possi-

bly due to their flexible feeding behaviour, but it was noted that the study took place in the dry season when the species seemed to be less dependent on fruit.

NON-NATURAL HABITATS

In Madagascar, anthropogenic habitat is unsuitable for most lemur species, although tree plantations can provide buffer zones around forests that can sometimes benefit smaller lemur species such as *Microcebus* and *Mirza* through seasonal food provision (Ganzhorn 1987, Ganzhorn et al. 1999, Irwin et al. 2010). The grey mouse lemur *Microcebus murinus* may exist in pure garden environments, such as in Fort Dauphin (Irwin et al. 2010), but does not maintain populations in secondary habitats, even if linked to primary forests (Ganzhorn & Schmid 1998). Only aye-aye *Daubentonia madagascariensis* and black lemur *Eulemur macaco* seem able to survive in anthropogenic landscapes for extended periods (Colquhoun 1993, Sterling 2003, Simmen et al. 2007). Similarly, Fitzherbert et al. (2008, cited in Sodhi et al. 2010) reported that species richness of bats and primates in rubber and oil palm plantations in Malaysia and Indonesia was relatively lower than in primary forests.

FOCUS OF THE THEME SECTION

Thus, in general, primates do less well in disturbed, degraded and fragmented habitats than in primary forest habitats. However, unlike the situation with bees (Williams et al. 2010), it has not been possible so far to identify specific life history traits of primates and environmental conditions that would permit us to predict the response of any given species to different forms of habitat change (Cowlshaw & Dunbar 2000, Marsh 2003). Being able to predict population changes in relation to habitat characteristics is not only relevant in view of ongoing habitat degradation, but is equally important for efforts of habitat restoration. In view of these deficits, we compiled a number of reports on responses of animals to habitat alteration at the 22nd Congress of the International Primatological Society held in Edinburgh, Scotland, in 2008. The contributions provide an array of important case studies and illustrate new methods and issues that have only recently emerged but will become more important in the near future. Urbanisation is such an emerging field that will warrant further study. Moore et al. (2010, this Theme Section) describe the interactions of the highly endangered purple-faced langurs in an urban setting. In principle, the animals seem to adapt well to the urban situation, but the ultimate survival of this species

will depend on the tolerance of humans, and represents a challenge for urban planning. These types of human–non-human primate interactions will become more and more important in urban as well as in agricultural settings.

Strum (2005) and Donati et al. (2007) tackle the problem from a different angle, describing how, in many instances, populations can only survive if moved to areas that are better protected, restored or designed to serve multiple purposes, including provision of an economic livelihood for the human population. Along the same lines, Shedden-González & Rodríguez-Luna (2010, this Theme Section) discuss how howler monkeys dealt with a new environment to which they have been translocated. The new site represented a fragment that combined economic palm cultivation in a matrix of natural forest. The animals adapted well. Although howler monkeys seem to be among the most flexible monkey species, this example is encouraging in that it combines conservation with economic benefits for the local people.

Link et al. (2010, this Theme Section) report increased densities of brown spider and red howler monkeys in recently fragmented forest remnants in Colombia, while white-fronted capuchin densities varied unpredictably. They relate this to the inability of spider and howler monkeys to move out of the forest and cross non-forested matrix. Thus, the remaining individuals seem to be compressed in fragments until populations adapt to the new environmental capacity. Their study illustrates that time scales and generation times are important factors to be considered in fragmentation studies.

This leads to the important question of data quality. It is difficult to provide reliable estimates of primate densities, and estimates can vary considerably depending on the methods applied (Whitesides et al. 1988). This makes conservation planning difficult, particularly in the case of elusive species or difficult habitats. Guillera-Aroita et al. (2010, this Theme Section) use the bamboo lemurs in a marsh of central Madagascar as a model to introduce more sophisticated models to arrive at more robust density estimates of elusive species.

Schwitzer et al. (2010) demonstrate that the prevalence of intestinal and ectoparasites of blue-eyed black lemurs was higher in secondary than in primary forests. Parasite prevalence was high in general. This could be due to the high degree of habitat degradation of the area. Their study is complemented by the study of Raharivololona & Ganzhorn (2010, this Theme Section), who illustrate seasonal variation in the incidence of gut parasite excretion in mouse lemurs, thus illustrating the need for repeated sampling of known individuals.

Studies on climate change responses of white-sided dolphins by Salvadeo et al. (2010, this Theme Section), recruitment patterns in Scottish freshwater pearl mussels (Hastie et al. 2010, this Theme Section) and altered predator–prey relationships between coyotes and desert turtles in areas where predators are subsidised (Esque et al. 2010, this Theme Section) complement this special issue of *Endangered Species Research*.

These studies certainly did not solve the problem that we are still unable to produce general models on primate reactions to habitat changes. However, they have added new aspects to the complex picture of primate population responses that might advance the field towards a more cohesive understanding of the survival of primates in altered habitats.

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