What matters most in fragmented habitats?

A comparison between resilient and non-resilient primates.

by

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S2871912

16th December 2015

Behavioural & Physiological Ecology and Genomics Research in Ecology & Evolution in Nature

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ABSTRACT

Habitat fragmentation is a leading threat to primate conservation. Agriculture and urbanisation can split continuous forest habitat into smaller patches within a matrix. The ability of a species to persist in a habitat patch depends on the size of the patch, how isolated it is and the configuration of the matrix. This essay compares and contrasts threats and adaptations presented by a resilient and non-resilient species in regards to habitat fragmentation. Howler monkeys can persist in areas where other primates cannot (e.g. *Ateles*) by finding alternate food sources in the patch, surrounding patches or matrix and dispersing through highly modified matrixes. Apes have life history traits that naturally make them more susceptible to lower survival in fragmented areas such as a low fecundity, long generation time, large body size, large home ranges and high frugivory. However, adaptations prove to be similar to those of howler monkeys; apes too have been shown to find alternate food sources, often through crop raiding and increasing their terrestrial movement to disperse or cross matrixes. Nevertheless, the hunting threat is much higher in apes than howler monkeys and is further exacerbated by an increase of edge areas and access for hunters. Hunting threats have a high impact resulting in high mortality despite their adaptations. Furthermore, the presence of humans is the main and often only predicator for ape occupancy in a patch. A lack of studies quantitatively analysing habitat fragmentation in apes is shown, especially when compared with howler monkey studies. This means that the threat from anthropogenic hunting could be masking other factors that are equally important. A shift in studies needs to occur in apes in order to be able to properly assess which threats are most important as to better direct conservation efforts.

Table of Contents

What is habitat fragmentation? 4
Figure 1, landscape scale study 4
Figure 2, different types of habitat fragmentation 6
Threats and adaptations to reduced food availability **7**
Prediction of occupancy table 8
Threats and adaptations to reduced ability to disperse **9**
Primate/human conflict **11**
Conclusion **12**
Reference list **13**

WHAT IS HABITAT FRAGMENTATION?

Habitat fragmentation is the splitting up of habitat such as continuous forest into smaller patches and is one of the leading causes in the loss of biodiversity (Franklin *et al.* 2002, Fischer & Lindermayer 2007). Although natural fragmentation can occur where rivers or fires split up areas of habitat, anthropogenic activity is currently a more pressing threat, causing a rapid decrease in forested habitats worldwide (Cowlishaw & Dunbar 2000, Ewers & Didham 2006). In anthropogenic fragmentation, there is normally a decrease of current habitat (habitat loss) and an increase in new, normally unsuitable, habitat called the matrix such as farmland, pastures, monoculture, roads and so on (Fischer & Lindermayer 2007). Increased agriculture and urbanisation, including legal and illegal logging and forest clearing creates detrimental and, perhaps, irreversible damage to ecosystems (Pardini *et al.* 2010, Barr *et al.* 2014). This makes forest dwelling species particularly vulnerable to habitat fragmentation as when their forest canopy habitat decreases, they are forced to find alternative habitats.

Habitat fragmentation can split up habitats in different ways, affecting the total habitat and edge area as well as the connectivity/isolation of patches. As a habitat patch decreases in size, the edge area: volume ratio increases. The edge of habitat patches are affected by the characteristic of the matrix and are a less suitable habitat compared to the inner area, an effect called 'The Edge Effect' (Sauders *et al.* 1991). Thus, the fragmented landscape can take many forms including but not limited to those shown in Figure 1. The increased edge in more fragmented areas or less compound patches reduces the amount of high quality habitat area. However the chance for an individual to find a patch increases in less compound shapes which could increase connectivity.

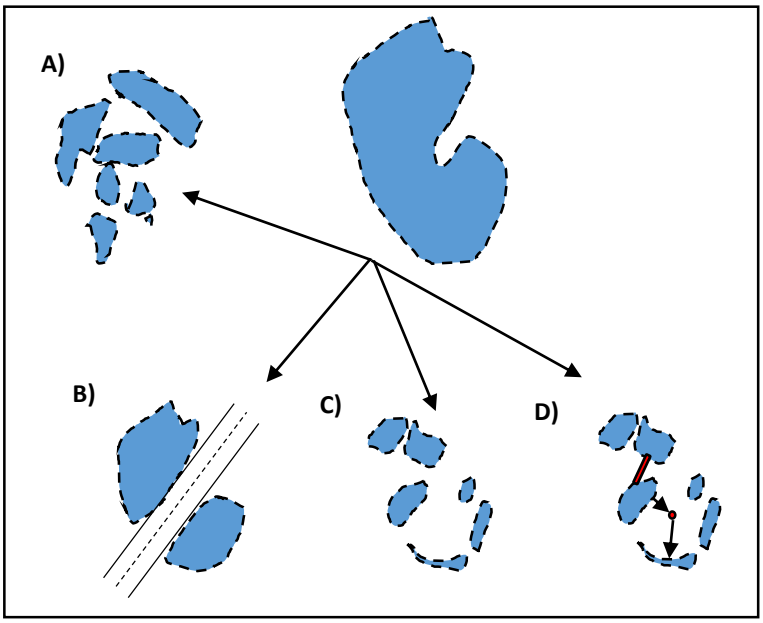

Figure 1, 3 different variations (not all) of habitat fragmentation. A) pure habitat fragmentation increased patches and edge, no decrease in habitat area B) single division (increased patches, increased edge and low decrease in habitat) e.g. by construction of a road C) increased patches, large decrease in area and increased edge D) as C but with inclusion of habitat corridor and stepping stone

The configuration of the matrix should be measured when assessing habitat fragmentation. For example, factors such as number of patches, distance between patches, amount of edge and quality of the matrix should be considered. Connectivity between patches and within the larger landscape can be reduced dependent on the matrix and the species ability to cross it (Benchimol & Peres 2013). Roads, monocultures and urban environments increase the risk for species that could be hunted by natural predators, humans or hit by cars. Increased isolation in habitat patches can reduce dispersal, meaning that individuals are forced to stay in their patch, which can reduce the amount of resources available to them. Furthermore, dispersal from ones natal group at sexual maturity is important in many species to maintain social cohesion and genetic diversity (Clutton-Brock & Lukas 2012). Habitat corridors or stepping stones can provide either a continuous patch of habitat in which to travel down or an in-between patch of habitat, reducing the distance required to travel across matrix in one go (Fig 1, D). Both of which have been shown to greatly increase dispersal in animals (Donald & Evans 2006, Saura *et al.* 2014).

Primates are mostly forest dwelling creatures and rely on continuous forest canopy to survive (Mittermeier 1988), which makes them particularly vulnerable to habitat fragmentation. They are a popular study subject and many species have shown adaptive plasticity to habitat fragmentation (Marsh 2003, Marsh & Chapman 2013). Primates make an interesting study subject as they are spread throughout the world and some species have proven to be particularly resilient to disturbance (e.g. Howler monkeys, *Allouatta sp.*), and some are especially impacted by the effects of habitat fragmentation (e.g. the Great Apes, *Pan sp. Pongo sp. & Gorilla sp.*).

Howler monkeys are one of the most studied primate species in regards to habitat fragmentation. This is most likely the result of a bias of habitat fragmentation studies that occur in South America (Harcourt & Doherty 2005) and the higher occupancy rates of Howler monkeys in patches, meaning they are easier to find and observe than other species e.g. *Ateles sp.* (Estrada & Coates-Estrada 1996). Furthermore, Howler monkeys have a loud dawn chorus meaning that they are easier to locate (e.g. Cristóbal-Azkarate *et al.* 2005). The Great apes are also popular study subjects and their recent dramatic population decline has been well publicised, however are an elusive group and can be difficult study subjects to find and observe.

Apes are naturally more vulnerable to habitat fragmentation due to high degree of frugivory (in *Pan sp*. & *Pongo sp*.), low fecundity, large body and home range sizes and slow life histories. Apes first give birth late in life and have long inter-birth intervals (Gorillas: 6-8 years, 4 years (Czekala & Sicotte 2000), Orangutans: 14-15 year, 8 years (van Noordwijk & van Schaik 2005), Chimpanzee: 13 years, 5-6 years (Nishida *et al.* 2003)) respectively. This means that it is harder for genetic adaptation to occur as generation length is long and even low mortality has a higher impact. Furthermore, home range sizes are vast and often over 1000ha, therefore functional habitat patches are required to be large and intact (Herbinger *et al.* 2001, Singleton & van Schaik 2001, Bermejo 2004). The combination of these aspects has resulted in all the Great apes currently being assessed as either Endangered or Critically Endangered according to the IUCN Red List (IUCN, 2008). In particular, the Sumatran

orangutan, *Pongo abelii* has a conservative population estimate of 6000 (Meijaard *et al.* 2012) and the cross-river gorilla, *Gorilla gorilla diehli*, which is the subject of many fragmentation studies, has a population size of just 300 (Bergl *et al.* 2008).

Contrastingly, howler monkeys are smaller bodied with earlier first reproduction (3 – 4 years) and shorter inter-birth intervals (6-12 months) (Garber & Kowalewski 2011, Van-Belle & Bicca-marques 2015). They can also have very small home range sizes from just 1ha in *A. pigra* (Marsh and Loiselle 2003) to 79 ha in *A. seniculus* (Stevenson *et al.* 2002). Due to high persistence in areas, most are considered least concern. However, two out of eleven species are currently classed as endangered because of heavily fragmented areas and high human densities in their range (IUCN, 2008).

Howler monkeys only occur in central and south America while the Great apes are found in central and western Africa (*Pan sp*. & *Gorilla sp*.) as well as Indonesia (*Pongo sp.).* Despite this, they all experience heavily modified habitats that are fragmented as a result of increased agriculture and urbanisation (Achard *et al.* 2002). Comparisons between two groups of animals and their reactions to habitat fragmentation is rarely done, and in this case, the comparison could result in pinpointing the most important factors that affect these groups in fragmented areas.

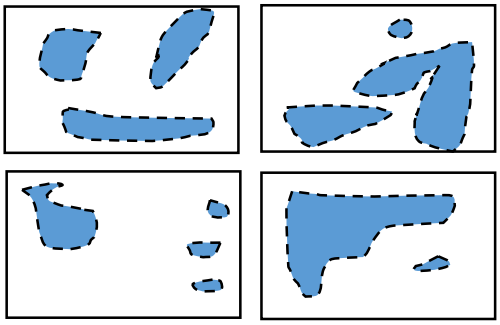

Figure 2, boxes represent 4 different fragmented landscapes made up of habitat patches. In a landscape study the sample size would be n=4.

Adapted from Fahrig, 2003

Habitat fragmentation is extensively studied. However, the recent spike in popularity regarding this term has led to many studies using inconsistent terminology (Fahrig 2003). Arroyo-Rodríguez *et al.* (2013) conducted a study and found that 25% of 100 papers on habitat fragmentation in primates did not compare multiple landscapes resulting in data that only considers local dynamics rather than the larger scale. Habitat fragmentation occurs at a patch scale however it is a landscape process and should be treated as such (Figure 2). This means that it is difficult to extract reliable predictions based on single landscape scale study as the distinct history it has can influence the effect on species living there. Furthermore, it is important to quantitatively analyse how anthropomorphic and ecological factors affect species. One way to do this and ensure that comparisons can be made between species is finding predictors of occupancy or absence in patches. This essay uses this data as well as descriptive studies to compare and contrast the impact of different habitat fragmentation factors on Apes and Howler monkeys in attempt to discover which

are key. This should enable better directed conservation efforts towards areas that are causing most impact which is particularly important to stabilise declining Ape populations and also maintain Howler monkey populations.

THREATS AND ADAPTATIONS TO REDUCED FOOD AVAILABILITY

Howler monkeys are able to live in highly fragmented areas, which is considered to be linked to their highly adaptable diet (Arroyo-Rodriguez & Dias 2009). They are a frugivorous-folivorous species (Silver *et al.* 1998) and are therefore are able to fulfil their nutritional and energetic needs even in small patches by a range of behavioural adaptations. However, Howler monkeys are still more likely to be found in patches that are larger, which could be linked to higher amount of food in that patch (Table 1). However, if individuals can harness food from the matrix, edge areas or other patches, as well as exploring other available foods in the current patch then small patches are able to withstand larger population numbers (Cristobal-Azkarate & Arroyo-Rodriguez 2007).

Landscape supplementation is the process of using more than one patch to fulfil dietary requirements (Dunning *et al.* 1992, Asensio et al 2009, Arroyo-Rodriguiz & Mandujano 2009) and is known to occur in both Howler monkeys and Apes. Howler monkeys are able to cross hostile matrixes despite being arboreal (Pozo-Montuy *et al.* 2011), therefore they can harness food sources from other patches which could be the reason they are able to survive in particularly small areas (3-5ha) (Zunino *et al.* 2007, Asensio *et al.* 2009, Mandujano *et al.* 2006). The edge area is lacking in tall trees meaning there in an increase in light which affects the growth of different plants causing the edge areas to have a different species configuration to the core patch. This could be advantageous for Howler monkeys as references 3 and 4 (Table 1) show a correlation between an increase in floristic composition variety and Howler monkey occupancy. However, positive associations between edge area and occupancy are lacking despite this group previously reported being found in the edge area (Lenz *et al.* 2014). Additionally, correlations between increased edge and absence in a patch have been found (reference 1, Table 1) suggesting edge effects are too strong in patches for positive associations to occur.

Chimpanzees can also use more than 1 patch to supplement their diet as seen in Kibale, Uganda (Onderdonk & Chapman 2000). This is most likely a result of their natural terrestrial movement making it easier to move in the matrix and their fission-fusion social structure meaning they split up into smaller, fluid sub-groups which reduces competition (Symington 1990). Howler monkeys can also switch from multi-male multi-female groups to a fission-fusion foraging structure to reduce competition and energy expenditure if needed (Asensio *et al.* 2007). Orangutans are slow moving, large bodied and arboreal meaning there is high risk for them to cross an open matrix (Ancrenaz *et al.* 2014). This reduces their ability for landscape supplementation, however Orangutans have been known to raid crops is they are less than 50m from the forest (Ancrenaz *et al.* 2015). Crop raiding is much more prevalent in Apes than Howler monkeys due to a bias in arboreal movement and a restriction to the higher canopy in American primates (McKinney 2010). Chimpanzees manage to maintain a highly frugivorous diet, despite seasonal lows in fruit by regularly crop raiding nearby

Table 1, summary of factors that best predict occupancy of a species in a patch in a fragmented landscape. Studies that used multiple landscapes (landscape scale) are highlighted in bold. + occupancy increases with increase in factor, 0 no correlation found, - occupancy decreases with increase in the factor. A dashed line separated the howler monkey and ape studies.

			Occupancy predictors							Study design and scale		
Species	Ref	Site	Patch size	Patch Shape/edge density	Isolation of patch	Nearest human settlement/hunting pressure	Diversity of food species	Age of forest	Inclusion of matrix and habitat configuration	Number of patches	Comparison with continuous forest?	Size of area (ha) (L = landscape area P = patch size(s))
APA	**1**	**LT**	**+**	-	-	-			✓	**208**	**X**	**L: 3 x 500**
												P: 4.7 – 15.2
APA	**2**	**CG**	**0**		**0**			**+**	✓	**6**	**X**	**L: 10,800 12,200 & 500**
												P: 7-9,571
APA	3	LT	+		0	0	+		✓	55	X	L: 7500
												P: 5.63-38.57 (mean)
APA	4	LT	+		-		+		✓	126	X	L: 624,000
												P: 2 – 1000
AG	5	BdR	0		0				✓*	63	X	P: 0.5-992
APA	6	CP	+		-				✓	119	X	L: 12500
												P: 2.9 (4.4) (median ±IQ)
AC	7	LT	+						X	24	X	L: 4800
												P: 9.24 (SD = 7.62)
API	8	CM							X	44	✓	L: 261000
												P: 1-86
APA	9	LT	+				0			21		P:1.3-700
APA	10	LT	+		-		+		✓	92	✓	L: 4960
												P: 20 (mean)
PT	11	GF					0		X	1	X	L: 900
PT	12	GB	+	+	+			+	✓	N/A	X	L: 2,723,000
PT	13	NLC				-	0		X	N/A	X	L: 27,970,000
PP	**14**	**DMC**		**-**		**-**			✓	**N/A**	**X**	**L: 563,330,000**
PA	15	BT		-		+			X	N/A	X	L: 1093000
PPY	16	SB						+	X	19	X	L: 3,366,000
GGD	17	NCB				-	0		X	N/A	X	L: 1000000
GGD	18	NCB				-	-		X	N/A	X	L: 560000
GGD	19	KGS				-			✓	N/A	X	L: 19400

APA = *A. palliate, AC = A. caraya, API = A pigra, AG = A. guariba PT = Pan troglodytes, PP = Pan paniscus, PA = Pongo abeilii, PPY = Pongo pygmaeus, GGD = Gorilla gorilla diehli*

LT = Los Tuxtlas, CG= Area de Conservaci ´on Guanacaste, Costa Rica, BdR = Barra do Ribeiro, Brazil, CP = Corrientes Province, Argentina, CM = Chiapas, Mexico, GF = Gishwati Forest Reserve, GB = SW Gunnea Bussai, SB = Sabah, Borneo, NCB = Nigeria – Cameroon border region, NLC = Ndoki-Likouala, Congo, DMC = Democratic republic of Congo, BT = Batang Toru, KGS = Kagwene Gorilla Sanctuary

References 1 = Arroyo-Rodriguis *et al.* 2008, 2 = DeGama-Blanchet & Fedigan 2006 3 = Cristóbal-Azkarate *et al.* 2005, 4 = Estrade & Coates-Estrada 1996, 5 = Silva & Bicca marques 2013, 6 = Anzures-Dadda & Manson 2007, 7 = Zunino *et al.* 2007, 8 = Estrada *et al.* 2002, 9 = Cristóbal-Azkarate & Arroyo-Rodriguez 2007, 10 = Mandujano *et al.* 2006, 11= Chancellor *et al.* 2012, 12 = Torres *et al.* 2010, 13 = Stokes *et al.* 2010, 14 = Hickey *et al.* 2013, 15 = Wich *et al.* 2011, 16 = Gregory *et al.* , 17 = Imong *et al.* 2013, 18 = Sawyer & Brashares 2013, 19 = De Vere *et al.* 2011

*only included inter-patch distance

plantations (Bessa *et al.* 2015, Hockings *et al.* 2009). For this reason, the edge area of patches has been shown to be important for chimpanzees (ref 12 table 1) as this area is where they exit in order to access the plantations. However, the increase of edge area also increases access for hunters. Moreover, crop raiding increases the probability of primate-human interaction which often results in Apes being met with persecution and endangerment (Hockings & Hulme 2009). This also might be the reason why Chimpanzees have begun crop raiding at night, even when it is not a full moon and therefore visibility is low, increasing the risk (Krief *et al.* 2014).

Howler monkeys have been shown to adapt their diet depending on the environment they are inhabiting. Cristobal-Azkarate & Arroyo-Rodriguez (2007) showed that in Los Tuxtlas, Mexico, Howler monkeys consumed more non-tree growth forms and reduced their fruit intake when the population was high and have been known to shift their ecological niche to herbs, grasses or bird eggs (Asensio *et al.* 2007, Bicca-marques *et al.* 2009). Nevertheless, this shift can cause a problem as, Howler monkeys are important species in regards to seed dispersal and this reduction in frugivory could cause a positive feedback loop where food availability continues to decrease (Arroyo-Rodríguez *et al.* 2015).

Apes, in particular Chimpanzees and Orangutans, have advanced cognitive foraging techniques that are learnt and taught in local populations through social transmission which can then spread with dispersing individuals. Some strategies are too advanced to be continually learned independently. Therefore, they face the unique threat that some foods or foraging techniques will become inaccessible if local populations face extinction and cannot pass on these techniques (van Schaik 2002).

Both Apes and Howler monkeys have behavioural adaptations to cope with the decrease or shift in food availability that occurs with habitat fragmentation. However, the Apes restriction to their respective diets have meant that they are not able to harness all the areas that howler monkeys can. Furthermore, Apes have large body sizes that require larger energy consumption which means that, even with food supplementation, the food availability may not be high enough.

ADAPTATIONS TO REDUCED ABILITY TO DISPERSE

In primates it is common that one or both species will disperse to another group or area at sexual maturity (Clutton-Brock & Lukas 2012). This increases the reproductive success for the migrating individual and genetic variation for the population it migrates to (Pope 2000). In fragmented areas, patches can be increasingly isolated, therefore preventing landscape supplementation and could lead to inbreeding, which in turn causes a decline of genetic variation within populations (Oklander *et al.* 2010).

Dispersal between patches depends on the ability of an individual to cross the matrix (Clobert *et al.* 2004). Arboreal animals such as Howler monkeys or Orangutans have added difficulty as in order to cross a non-forested matrix, they must move terrestrially. Nevertheless, terrestrial movement in the matrix has been observed in both animals (Mandujano *et al.* 2004, Zunino *et al.* 2007, Pozo-Montuy *et al.* 2011, Ancrenaz *et al.* 2014).

Despite this, some studies have still shown that isolation of patches is a key predictor in the occupancy of Howler monkeys in a patch (Table 1). Studies that show no relationship between occupancy and isolation either contain patches of above 1000ha (references 2 and 5, (reference 5, Table 1) or isolation measurements were not really possible due to 50% of the patches being less than 100m apart (reference 3, Table 1). Therefore is it likely that these studies do not reflect the relationship between isolation and presence in a patch.

In contrast, the impact of isolation does not yet seem to have been quantitatively measured in Apes. However, studies have reported excessive males and reduced dispersal in Orangutan natal groups in fragmented areas of Borneo (Marshall *et al.* 2009, Meijaard *et al.* 2012). Furthermore, a Chimpanzee population in Guinea has become so isolated that despite the species ability for long migration and terrestrial movement, females are no longer dispersing (Sugiyama 1999). This has resulted in a change from a male-bonded group to a bisexually bonded group and decreased genetic flow (Sugiyama 1988, Morin *et al.* 1993). Despite no recent investigations into this shift at this area, similar patterns have been shown in Cote d'Ivoire (Lehmann & Boesch 2005) showing the effect habitat fragmentation can have on social structure.

Reduced gene flow has also been reported in Howler monkeys and other Apes. Howler monkey populations that currently seem stable have been shown to have reduced genetic variation which could have implications for future generations (Oklander *et al.* 2007). For example, there have been disease outbreaks in past populations that resulted in local extinctions due to high population density and reduced genetic variation (Bicca-Marques 2009; Bicca-Marques and Freitas 2010, Freitas and Bicca-Marques 2011). Apes too have been shown to have a recent decrease in genetic variation (Goossens *et al.* 2006) which is more present in fragmented than continuous areas (Bradley *et al.*, 2004, 2005; Bergl *et al.* 2008). However, in contrast, direct causes from climatic changes and habitat loss and fragmentation will likely cause extinctions in many ape populations before genetic causes take place.

Stepping stones or habitat corridors can be implemented in order to increase connectivity between patches. These can increase the viability of a population (Estrada *et al.* 2006), although become much less effective in homogenous landscapes such as monocultures (Mandujano *et al.* 2004). Studies that do not include the matrix configuration, as is the case with many studies in Table 1, can miss small patches of habitat that might increase connectively and find unrealistic correlations based on false data. Many models have predicted the future success of increasing connectivity. For example, the chance for extinction of a population went from 35% to 1% when connectivity was increased for Howler monkeys in Los Tuxtlas, Mexico (Mandujano *et al.* 2006). In orangutans, a reduction in population decline was also predicted if corridors were placed linking patches to long term habitat (Gregory *et al.* 2014). Many studies therefore predict corridor success and encourage linking patches which although seems logical, there is very little empirical evidence detailing its success in these species.

HUMAN/PRIMATE CONFLICT

In less economically developed countries, hunting of primates is common, especially large bodied species as they are a great source of protein (Estrada 2013). However, small bodied primates or infants are often sold to the pet trade (Duarte-Quiroga & Estrada 2003, Nijman 2009). When a continuous landscape is fragmented, it increases the access to habitats where primates reside. For the Great apes in particular, the increase of logging in their respective geographical areas has brought with it access to previously inaccessible areas and an increase of transport and guns (Robinson *et al.* 1999).

The threat of hunting or distance to the nearest human settlement is a much stronger predictor of occupancy in patches for Apes than for Howler monkeys (Table 1). This pattern was found in all Ape species and sometimes linked with edge density that allows greater access for hunters. One study (reference 15, Table 1) found a positive correlation between occupancy of patch and distance to human settlements however, this is likely a result of hunters moving to areas with high Orangutan density and not a true occupancy predictor.

Apes have found some behavioural mechanisms to counteract habitat loss and fragmentation, however, their long generation times and low fecundity means that they are vulnerable to even low hunting pressure (Kormos *et al.* 2003; Rizkalla *et al.* 2007). It was found that for Orangutans, that it was possible for them to survive in low level logged forests, however this became untrue when in near proximity to hunting villages (Marshall *et al.* 2006). It has been suggested through population variance analysis that if this level of hunting is continued, then Orangutan extinction is imminent (Marshall *et al.* 2009). Furthermore, in the border region of Nigeria and Cameroon it has been shown that the fragmentation of the Cross River Gorilla has occurred as a result of human population increase and the threat from hunting and human activities opposed to ecological factors such as food availability or patch size (Imong *et al.* 2014). This is also shown as predictor variables in Table 1 (reference 17).

Howler monkeys also experience low level hunting pressure and are reasonably common in the pet trade (Peres 1997, Duarte-Quiroga & Estrada 2003). However, this low level sustenance hunting does not impact this species as much due to a much shorter generation times, high fecundity and longer inter-birth intervals. Nevertheless, Peres (1997) showed a marked decrease in overall population in hunting areas, however this did not affect likelihood to occupy a patch.

Apes too are commonly captured as pets, although this only occurs with infants or young juveniles, often many adult individuals are killed as they try and protect their young (Rijksen 2001, Tutin & Vedder 2001, Meijaard & Wich 2007, Lopresti-Goodman *et al.* 2012). Furthermore, gorillas in Virunga National Reserve are so extensively hunted; they are now continuously guarded by field staff to prevent poaching and hunting (Robbins *et al.* 2011).

Decreased occupancy in patches close to human settlements is possibly due to local extinctions resulting from hunters or behavioural adaptations where individuals relocate to less dangerous areas. However, either way is resulting in decreased populations as hunters

flock to areas where the apes are found. In stark contrast to Howler monkeys, there are few studies in Apes that attempt to explain occupancy or absence in relation to the landscape. The size of the patch, isolation or difficulty crossing the matrix is rarely analysed resulting in a lack of thorough results and conservation suggestions based on incomplete data. The bias towards analysis of relation to human settlements in Apes could be due to the increasing threat of hunting, however without proper investigation into ecological factors it is difficult to assess what other threats could be causing the declining population.

CONCLUSION

Apes and Howler monkeys face similar habitat fragmentation issues where continuous habitat is split up into patches by increased urbanisation and agriculture. The scale on which fragmentation occurs between the two groups is similar; however the scale on which it affects them is not. Howler monkeys are able to survive in very small home ranges due to their small body size and lower energy requirements. Whereas on the other hand, Apes are large bodied with long generation times, low fecundity and have large home ranges. The stark differences between the two primate groups mean that fragmentation problems are amplified in Apes. Furthermore, any genetic adaptation that might occur in Howler monkeys will be unable to form fast enough in Apes in order to be of any consequence due to their long generation times. Despite these differences, Apes are able to adapt and have been shown to be more ecologically adaptable than first thought and are able to persist in partially logged areas. Therefore, many behavioural adaptations that occur in Howler monkeys are also seen in Apes such as landscape supplementation, increased terrestrial movement and changes in social structure in isolated areas.

Despite the analysis in this essay only taking into account presence and absence data in a few key studies, it is possible to tentatively extract conclusions. Howler monkeys are a common study subject in fragmentation studies and many are for an extended period of time over many patches. However, despite often being carried out at the same site and on the same species, the results are frequently not concurrent. This could be improved by increasing the number of studies that occur on a landscape scale in order to reduce bias at a patch scale. However there is strong evidence suggesting that howler monkeys are better able to survive in larger patches closer to each other, so conservation aims should work towards increase average patch sizes which should then reduce the distance between them. As with the Howler monkeys, some data in the Apes seems repeatedly bias. However, in this case it is towards assessing hunting threat or distance to human settlement instead of ecological factors, and studies often lack detail or thought in regards to matrix composition. Nevertheless, as population density was not analysed, some more subtle effects might be lacking which absence/presence data would not be able to pick up, or there could be a time lag between the effect a factor has, and complete absence in a patch which would not be seen here.

Nonetheless, hunting pressure is extremely detrimental and found in all Apes. It is exacerbated by fragmentation which increases access for hunters and poachers. Hunting and relation to human settlements is the main predictor in the absence of Apes in patches

and can even be the cause of fragmentation. However, it is possible that the threat of hunting is so strong that it means that alternate ecological factors are not being recognised or scientifically investigated. The evolution of fragmentation studies in Apes seems to be lacking when compared with Howler monkeys. Limited information is available in regards to matrix configuration, patch size and connectivity between patches, and both groups lack landscape scale studies and comparisons with continuous habitat. For the Apes, the scaling factor plays a part in that it sometimes is not feasible to carry out research on many patches or landscapes as the areas Apes live in are larger than that of howler monkeys. Ape home ranges can be upwards of 1000ha whilst Howler monkey home range are often a restricted to a 10^{th} or 100^{th} of that size, and due to extremely loud calls they make are much easier to find. Furthermore, population density is frequently low for Apes, and often the only sampling technique available to quantify their population is to count their nests. Despite these complications, it is important that future studies carefully and quantitatively assess the impact habitat fragmentation has on Apes with and without the threat of hunting. Furthermore, conservation efforts should focus on reducing hunting through mitigation and education in order to allow the Apes to have a fighting chance in fragmented habitats.

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