

An analysis of primate behavioral responses to environmental change

An anthropological and neurobiological approach

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Abstract:

This thesis explores the relationship between stress, measured by glucocorticoid levels, and parasites in primate taxa to evaluate physiological and behavioral responses to human-induced and environmental change. By conducting an in-depth literature review, data was collected from relevant studies and compared in novel ways to try and create a primate behavioral template. Fragmented and disturbed habitats were compared to intact environments. In general, across taxa primates living in anthropogenically disturbed sites exhibited elevated parasite loads and glucocorticoid levels, as was expected. Notable exceptions to this trend indicate that a more detailed consideration of the kind of anthropogenic influence primates are experiencing is an important factor. In disturbed sites, reduced food availability, increased population, and increased terrestriality all contributed to the risk of parasite infection. Where these indicators are present, there is also a high likelihood of observing chronically elevated levels of glucocorticoids. However, if resources are supplemented, either through human provisioning or crop raiding, elevated glucocorticoids is less likely. In these situations there may be more parasite diversity, but not necessarily a rise in density or degree of infection. These results indicate that parasite measures coupled with glucocorticoid analysis is an important and novel method for monitoring the health of primates and particularly their responses to environmental change. Such analyses may also facilitate conservation efforts.

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Introduction:

Environmental degradation and anthropogenic influences are major threats to the health and conservation of primate species. Primates across taxa are being threatened by many of the same stressors. This analysis aims to identify patterns of behavioral responses to anthropogenic influences such as forest fragmentation, degradation, and direct human interactions and the potential health consequences.

Glucocorticoid and parasite studies were used as foci because of the relationship between stress and immune response. Based on preliminary research and trends, the expectation was to find that the general effect of anthropogenic influence would be adverse, with parasite loads and measures of glucocorticoid (CORT), or fecal glucocorticoid (fGC), levels being elevated in disturbed habitats.

There were exceptions to the general trends that could be attributed to the innate plasticity of primates. However, the patterns identified the roles of nutritional stress that may also explain why certain primates do not show a negative response to anthropogenic change. Specific kinds of exposure, such as tourism, have a more disruptive effect on primate health causing an exaggerated stress response while food availability, specifically fruit, has a significant role in the length and severity of a primate stress response. Relationships between anthropogenic stimuli, stress, and primate health were uncovered and the relevance of this is discussed in this thesis.

Background and Methodology:

The decision to focus on glucocorticoid (CORT) and parasite research was driven by the potential relationship between them, the availability of published data, and the novelty of the

connection. As parasite loads and CORT have become popular measures and recognized indicators of primate health, research has been conducted on a variety of primate populations and provided the most pervasive data.

Glucocorticoids are the general class of steroid hormones the body releases in response to stressful stimuli. The specific hormone in primates is cortisol, colloquially named the “stress hormone.” CORT virtually has receptors in all tissue, with roles in: arousal and sleep, metabolism, growth, reproduction, and the immune system (Chrousos 2009). At pathological levels CORT’s normal role becomes aversive, stunting growth, causing immunosuppression, and disrupting metabolic function (Chrousos 2009). The effect CORT has on the immune system, causing cell death at elevated levels, increases the susceptibility of individuals to infection, such as parasites (Chrousos 2009). Similarly parasites have been used as a measure of the overall health of ecosystems and primate populations. If parasite load, referring to parasite species density and diversity, increases then primates are assumed to be at risk. This potential correlation encouraged the direction of this project, as it seems likely that anthropogenic disruption is a stressor.

Data was collected from studies on strepsirrhine, platyrrhine, cercopitheine, and hominoid primates, which explored CORT and parasite load in response to environmental and human-induced change. Research on a variety of mammals indicates the cost of high, long-term stress is a reduction in primate fitness, increases in mortality, and decreases in survival probability. Ultimately stress places the primate population at a risk of decline.

Summary of Trends and Exceptions:

A survey was performed considering a wide range of primate taxa. The charts (**Table 1-4**) summarize the results of numerous studies conducted in the field. Focus was given to results

that considered parasitology of impacted primates and CORT levels. Other results were included to show that the influence of anthropogenic change is diverse and manifests in numerous ways.

Comparison across taxa revealed a potentially expected outcome: in general, anthropogenic change has an adverse effect on nonhuman primates. Studies that compared fragmented habitats to their undisturbed counterparts found differences in health: higher parasite loads and higher levels of CORT were measured. While there are exceptions to the trend, such as the Balinese Macaques, which have successfully habituated to a human-dominant area, the overall pattern stands.

Strepsirrhine Primates

Species Findings	Parasitology	CORT	Other Findings
Blue-eyed black lemur (<i>Eulemur flavifrons</i>)	Parasite prevalence was higher in secondary than in primary forest. Prevalance was also high when compared to other studies of parasite load in wild lemurs.		Suggests <i>E. flavifrons</i> were generally under pressure, possibly due to high degrees of fragmentation and degradation of the remaining forest habitat (Schwitzer et al. 2010).
Red-bellied lemur (<i>Eulemur rubriventer</i>)		Fecal glucocorticoid metabolite levels (fGCs) were higher in the males but was also higher in the most undisturbed habitats, contrary to expectation. fGCs were invariable in the disturbed site, despite lower and less fruit availability.	Two hypotheses suggested: it is possible that disturbed population's display of muted hormonal and behavioral responses is indicative of chronic stress. It is also possible that stress-sensitive individuals have been selected out of the group (Tecot 2013).
Indri (<i>Indri indri</i>)	Multiple parasite infections and higher parasite prevalence was observed in primates in disturbed habitat compared to undisturbed.		Fragmented site findings may reflect poor nutrition due to lower quality secondary forest (Junge et al. 2011).
Ring-tailed lemur (<i>Lemur catta</i>)	Ring-tailed lemurs in anthropogenically disturbed forests have novel parasites possible due to corophagy or contact with local domestic animals.		Degraded habitats are correlated with lower body weight, reduced body fat, increased incidence of tooth damage, and smaller body size (Fish et al. 2007).
	Ring-tailed lemurs that use camps, and have regular interactions with humans, house more endoparasites.		Lemur "camp" groups engaged in coprophagy of human, dog, and zebu fecal matter. Ring-tailed lemurs supplement their diet by consuming human foods, refuse, and waste (Loudon et al. 2006; Loudon 2009).
		Lemurs with high fGC levels had a significantly higher mortality rate.	Glucocorticoid levels among individuals in a wild population predicts their chance of survival (Pride 2004).

Gray mouse lemur (<i>Microcebus murinus</i>)	In good quality, small forest fragments lemurs had higher prevalence of infection of gastrointestinal nematodes and protozoans. In large forest fragments, excretion of eggs from Ascarididae and tapeworms was higher.		Lemurs from larger fragments had lower parasite loads than animals from corresponding smaller one, but more parasites were found in the larger fragment as a whole (Raharivolona et al. 2009).
Diademed sifaka (<i>Propithecus diadema</i>)			Fragments have higher population density than continuous forest. Possible that fragment resources are denser but of poorer quality (Irwin 2008a).
			Fragment groups utilized mistletoe heavily compared to continuous forest (Irwin 2008b).
			Habitat disturbances has an impact on physiological health within the population: altered diet, slower juvenile growth, reduced activity in fragments (Irwin et al. 2010).
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Few endoparasite species: three species types compared to nine total species found in ring-tailed lemurs at Beza Mahafaly.		Verreaux's sifaka are specialized arboreal vertical clinger and leapers, consequently they minimize time on the ground, where they would directly encounter humans (Loudon2009).

Table 1: A survey of studies on strepsirrhine primates focusing on parasite and CORT research.

Platyrrhine Primates

Species Findings	Parasitology	CORT	Other Findings
Howler Monkey (<i>Alouatta palliata</i>)	Parasite richness was lower, but prevalence and density were higher in fragmented forests compared to intact ones.		Endoparasite species richness did not vary across fragmented landscapes but prevalence and egg density differed (Valdespino et al. 2010).
Howler Monkey (<i>Alouatta palliata mexicana</i>)	Parasitic prevalence was generally higher in fragmented forests than continuous and/or protected ones.		Males tended to have higher parasite prevalence values than those of adult females. Parasite prevalence was associated to average group size (Trejo-Macias et al. 2007).
Black Howler Monkeys (<i>Alouatta pigra</i>)	Parasitic prevalence was generally higher in fragmented forests than continuous and/or protected ones.		Males tended to have higher parasite prevalence values than those of adult females. Parasite prevalence was not associated to average group size but population density (Arroyo-Rodriguez et al. 2010).
Black Howler Monkeys (<i>Alouatta pigra</i>)		CORT was higher in howler monkeys living in forest fragments.	The CORT levels were variable with time. Patterns of locomotion varied (fragment-occupying monkeys travelled more). No difference between frequencies of feeding, resting, social interaction (Martinez-Mota et al. 2007).
Black Howler Monkeys (<i>Alouatta pigra</i>)		CORT increased as fruit availability decreased. Presence of tourists also contributed to high CORT (Behie et al. 2010).	
Geoffroy's Spider Monkey (<i>Ateles geoffroyi</i>)			Spider monkeys spent less time feeding and less time resting in forest fragments. Leaf consumption is also higher and exhibit lower levels of energy (Gonzalez-Zamora et al. 2011).

Yucatan Geoffroy's Spider Monkey (<i>Ateles geoffroyi yucatanensis</i>)		Higher CORT levels noted in fragmented forest populations and in captive individuals. In fragmented habitats CORT remained high throughout the year.	CORT was higher in males than females, and variable among seasons (higher during dry compared to wet) (Rangel-Negrin et al. 2009).
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Table 2: A survey of studies on platyrrhine primates focusing on parasite and CORT research.

Cercopithecine Primates

Species Findings	Parasitology	CORT	Other Findings
River Mangabey (<i>Cercocebus galeritus</i>)	Higher, but not statistically significant, number of observed parasites. Parasite load increases and fecundity decreases with increased habitat disturbance.		Degraded habitats correspond to larger home ranges (Mbora et al. 2009).
Redtail guenons (<i>Cercopithecus ascanius</i>)	Higher prevalence of parasites (and 3 kinds not observed in unfragmented forest) in fragmented forest.		Larger home ranges-guenon home range increased due to forestation. Diet mostly fruit, in disturbed habitat may shift to potential parasite-host intermediary foods (Gillespie et al. 2005).
Vervet monkeys (<i>Chlorocebus aethiops</i>)		Monkeys experiencing high human interaction show elevated basal CORT (Fourie 2003).	
Black-and-white colobus (<i>Colobus guereza</i>)	Prevalence of parasite infection did not differ between fragmented than unfragmented forests.		It's not clearly understood why these colobines are not being infected, at least from red colobus, by parasites considered generalists (Gillespie et al. 2008).
Gray-cheeked mangabey (<i>Lophocebus albigena</i>)		Mangabeys in disturbed areas had higher CORT levels.	In undisturbed forests mangabeys exhibited diurnal patterns of CORT while those in disturbed did not (Jaimez et al. 2012).
Balinese macaques (<i>Macaca fascicularis</i>)	Anthropogenic environment mitigated the prevalence and intensity of specific gut parasites.		Non-anthropogenically driven landscape had no significant effect on the intensity of the community gut parasites in Balinese macaques (Lane et al. 2010).
Olive/Hamadryas babboons (<i>Papio anubis/hamadryas</i>)	Crop-raiding group had better overall health (strength, physical fitness, lower infant mortality), but did seem to have increased parasite prevalence (Fourie 2003).		

Chacma baboons (<i>Papio ursinus</i>)		High CORT due to nutritional stress in male hybrid baboons and Hamadryas; Female <i>anubis</i> had higher CORT in response to drought.	Light weight juvenile males had elevated CORT compared to heavy-for-age juveniles--implies maternal effect (Fourie 2003).
Red Colobus (<i>Piliocolobus tephrosceles</i>)			Human-modified habitats provide predictable food sources, allow survival in marginal habitats (Hoffman et al. 2012)
Red colobus (<i>Pliocolobus tephrosceles</i>)	Increased degradation and human presence increased parasite prevalence; infection risk was also higher in fragments with highest stump density (Gillespie et al. 2005).		
Red Colobus (<i>Procolobus rufomitratu</i> s)	No difference in parasite prevalence or species type observed between fragmented and unfragmented habitats.		Ranging patterns did not differ between habitats, neither did day ranges (associate with increased parasitism). Equal size groups in both forests (Gillespie et al 2005).
Red Colobus (<i>Piliocolobus tephrosceles</i>)	Prevalence of parasite infection was greater in fragmented than unfragmented forests.		Greater infection risk for fragmented population corresponds with changes in host population size. Humans and livestock may be reservoirs carrying observed parasites (Gillespie et al. 2008).
	Increased parasite prevalence in fragmented forests, potentially related to nutritional stress/food availability.	CORT not related to population change, but potentially nematode prevalence. Also seemed that declining populations had most variable CORT levels.	Change in colobus population size was correlated with food availability and incidences of parasite infection (Chapman et al. 2006).

Table 3: A survey of studies on cercopithecine primates focusing on parasite and CORT research.

Hominoid Primates

Species Findings	Parasitology	CORT	Other Findings
Gibbon (<i>Hylobates lar</i>)	Characterized parasite richness of Gibbon population at Khao Yai National Park and found 10 parasite species.	Found no relationship between parasite load and physiological state (fGC levels).	Suggests that competition is low and gibbons cooperative defensive may mitigate the impact of stress and reduce susceptibility to infection (Gillespie et al. 2013).
Western Gorilla (<i>Gorilla gorilla</i>)	Found seasonally (dry) higher levels of parasite prevalence and intensity of infection (Masi et al. 2012).		
Gorilla and Chimpanzees (<i>Gorilla gorilla</i> ; <i>Pan troglodytes</i>)			The Minkebe Forest area does not experience a high degree of anthropogenic influence, but was greatly affected by the Ebola outbreaks of 1994. The population decline persisted and has reduced gorilla and chimpanzee density in the area (Huijbregts et al. 2003).
Chimpanzee (<i>Pan troglodytes</i>)			Chimpanzees had a higher occurrence of diarrhea and wound records--perhaps made more intense by their greater levels of social interaction (Masi et al. 2012).
	At Fongoli: Chimpanzee parasitology was compared to baboon's (<i>Papio hamadryas papio</i>) and was shown to have low prevalence of pathogenic species.		Baboons presented with high parasite prevalence compared to chimpanzees surveyed at the site suggesting chimpanzee health may be at risk (Howells et al. 2011).
	Found higher prevalence of parasite (Nodular worm) infection in higher-ranking male chimpanzees than other individuals.		Ecotourism and forest fragmentation is increasing the amount of human-great ape contact; public health is becoming a major concern as nodular worm infections can be cross transmitted (Kreif et al. 2010).
	Elevated levels of leaf swallowing could indicate that chimpanzees at Bulindi are especially vulnerable to parasite infections.		Suggests that susceptible to infection because of environmental changes and/or increased contact between apes and people. This also increases the chance of cross-transmission between apes and humans (McLennan et al. 2012).

	At Kibale parasite infections of chimpanzees was investigated and found instances of unique infections among the population.	Tested fGC levels in chimpanzees and found a positive correlation to parasite load.	Suggests that there is a positive correlation between fGC, and testosterone, and infection load due to immunosuppressive effect of steroidal hormones (Muehlenbein 2006).
Chimpanzee (<i>Pan troglodytes schweinfurthii</i>)	Found potential zoonotic parasites both in close proximity living chimpanzees and humans, suggesting cross-transmission.		Risk of cross-transmission likely associated with increasing levels of human interaction with the habituated free-ranging chimpanzees (Mugisha et al. 2003).

Table 4: A survey of studies conducted on Hominoid primates focusing on parasite and CORT research.

Strepsirrhine Primates:

A survey of strepsirrhine primate studies showed a mix of results. In blue-eyed black lemurs, indri, and ring-tailed lemurs parasite intensity and prevalence were greater in primates living in fragmented and disturbed forests (Schwitzer et al. 2010; Junge et al. 2011; Fish et al. 2007, Loudon 2009). Raharivololona et al. observed gray mouse lemurs in varying sized forest fragments and found smaller patches housed lemurs with higher prevalence of parasites despite being “good quality” sites (Raharivololona et al. 2009). Long-term field studies of diademed sifakas have not focused on parasites but have documented that habitat disturbance impacts the population’s physiological health (Irwin et al. 2010). Previous studies suggested nutritional stress, which may directly cause altered diet, reduced activity of primates, and slowed the growth of juveniles at the site (Irwin 2008b; Irwin et al. 2010).

Despite sharing habitat with ring-tailed lemurs at Beza Mahafaly sympatric Verreaux’s Sifaka had few endoparasites; a stark difference compared to the elevated parasite loads of the ring-tailed lemurs (Loudon 2009). Loudon (2009) also noted that ring-tailed lemurs carried novel parasites that did not appear in other primate species at the site, but did occur in domestic animals.

Unfortunately, there was a lack of glucocorticoid research relating habitat degradation to lemur health. Pride’s investigation of fecal glucocorticoids (fGC) showed these levels were an indicator of survival probability: ring-tailed lemurs with high fGC levels had a significantly higher mortality rate (Pride 2004). Tecot (2013) performed the first study in Madagascar investigating the relationship between fGC levels and habitat disturbance. In red-bellied lemurs, contrary to expectation, fGCs were higher in undisturbed sites. Disturbed sites showed no variability in fGC levels despite lower and less fruit availability (Tecot 2013).

Taken together, these studies indicate that parasite infections increase with the amount of degradation and terrestriality, and suggest that population density may mask or impact the parasite loads of primates. While CORT research is not extensive among these species, Pride's (2004) study emphasizes the cost of stress for primates. Tecot's (2013) study while seemingly against the trend also found increased mortality and decreasing population, signifying that red-bellied lemurs in fragmented habitats may be at greater risk for harm than the raw data suggests.

Platyrrhine Primates:

Studies of howler monkeys support that primates living in disturbed, fragmented forests have higher parasite loads compared to those in protected, continuous forest. In addition, studies of both howler and spider monkeys indicate that primates in fragmented sites have elevated glucocorticoid (CORT) levels. Behie et al. (2010) found that CORT increased as fruit availability decreased in black howler monkeys, somewhat surprising given the species ability to use leaves as a primary resource. In line with their observations, Gonzalez-Zamora et al. (2011) noticed that spider monkeys have a more folivorous diet in fragmented forests. Their observations fit with earlier notes of elevated CORT in fragments. Interestingly, spider monkeys in fragmented forests not only had elevated CORT, but the high levels persisted throughout the year (Ranger-Negrin et al. 2009).

There is a lack of parasite studies to compliment the CORT research performed on spider monkeys. Parasitology and CORT data has been collected from howler monkeys though. The studies together suggest a pattern: monkeys living in disturbed forest have both elevated parasite loads and CORT levels. Research conducted on platyrrhine primates has most extensively catalogued both CORT and parasite studies. The relationship between elevated CORT and parasite loads is likely the result of chronic stress. Elevated CORT may be the cause of immunosuppression and increased susceptibility to parasite infections (Chrousos 2009).

Cercopithecine Primates:

The response to habitat degradation and anthropogenic influence is variable in cercopithecine monkeys. Generally, river mangabeys, red tail guenons, olive baboons, and red colobus showed increased parasite loads in disturbed, fragmented forests (Mbori et al. 2009; Gillespie et al. 2005; Weyher et al. 2006; Gillespie et al. 2008; Chapman et al. 2006). Black-and-white colobus monkeys did not differ in parasite load intensity between forest types (Gillespie et al. 2005). Olive baboons' overall health benefited from crop-raiding and human influence despite variation in parasite infection (Weyher et al. 2006). Contrary to the generalized trend, Balinese macaques actually benefited from anthropogenically altered environments, exhibiting decreased prevalence and intensity of gut parasite infections (Lane et al. 2010). The macaques were home to a temple; it is most likely that adverse anthropogenic influences on macaques were mitigated by the food supplementation from temple-visiting humans provided (Lane et al. 2010). In this case, these primates were not subject to nutritional stress.

Interestingly, Gillespie et al.'s 2005 study shows red colobus monkeys have no statistical difference in parasite load between fragmented and unfragmented habitats. However, in 2008 not only had parasite prevalence increased in fragmented forests, but the red colobus population had suffered a 20% decline (Gillespie et al. 2005, 2008). In the few years separating studies the forest had been further fragmented and the red colobus' primary food sources were further compromised, placing them under significance nutritional strain (Gillespie et al. 2008).

Vervet monkeys that experienced high levels of human interaction presented with elevated basal CORT due to environmental stress and possibly hybridization (Fourie 2003). Vervet monkeys are viewed as pests by local humans, consequently their encounters with humans are disruptive and potentially violent (Fourie 2003). High CORT due to nutritional stress

was observed in male hamadryas baboons; female olive baboons also showed elevated CORT in response to environmental stress. Most significant from these studies was the potential maternal effect on the juvenile's stress response and smaller body mass of affected offspring (Fourie 2003). The effects seen in male juveniles suggest that the mother's stress may be altering the stress responsiveness in offspring; long-term, elevated CORT levels may also be responsible for the decrease in body weight (Chrousos 2009).

Chapman et al. (2006) investigated parasite load and CORT levels simultaneously on red colobus. They found higher parasite prevalence in fragmented forests as well as elevated CORT. They suggest a correlation between population decline and CORT levels: primate groups with the most variable CORT levels suffered most from population declines (Chapman et al. 2006). This observation is reminiscent of Pride's mortality study in ring-tailed lemurs.

Overall, these studies support the trend. Disruption and anthropogenic change will lead to elevated CORT levels and increased incidence of parasite infections. Lane et al. (2009) and Gillespie et al.'s (2008) studies repeat sentiments seen in the platyrrhine studies: food availability can mitigate anthropogenic stress or exaggerate it.

Hominoid Primates:

The foci of hominoid primate research has been directed more towards disease and potential for cross transmission. Unfortunately, there is a general absence of applicable CORT data. Despite this, there were enough studies to suggest that observed patterns are applicable in hominoid primates.

A study of western gorillas revealed that forest fragmentation exacerbated natural fluctuations in parasite load, worsening the health consequences of infection (Masi et al. 2012). The same study observed increased instance of diarrhea in chimpanzees though parasites were

not directly implicated; disease spread quickly throughout the chimpanzee group, likely the result of sociality (Masi et al. 2012). Conversely, at Fongoli, chimpanzees did not show elevated parasite levels (Howells et al. 20011). Used as a control in Howells et al.'s (2011) study was a baboon population sharing the site; baboons there presented with elevated parasite loads. The researchers suggest that, even though the Fongoli chimpanzees currently exhibit good health, the high infection rate in baboons foreshadows future threats. Further research about cross-transmission is needed (Howells et al. 2011). It is also important to note that Fongoli baboons are known to crop raid. Increased interaction and trips to the edge of the forest, where villagers defecate, may be responsible for the elevated parasite loads found in baboons (Krief et al. 2010).

At Bulindi chimpanzees have been observed leaf-swallowing. McLennan et al. (2012) found performance of this behavior indicated vulnerability to parasite infection. They noted that the leaf swallowing behavior [leaf ingestions causes increased expulsion of nematodes] had a positive relationship to incidence of anthropogenic disturbance (McLennan et al. 2012). Increased anthropogenic influence increases the potential for cross-transmission and disease infection; the leaf-swallowing behavior is likely an adaptive mechanism for mitigating the effect (McLennan et al. 2012).

Cross-transmission has become a focal point of hominoid research in response to disease outbreaks that effect humans and apes, such as the Ebola outbreaks of 1994. The risk of zoonotic disease is greater because of the genetic similarity between humans and chimpanzees. This is especially of concern given studies such as Mugisha et al.'s (2003), which found zoonotic parasites in chimpanzees and humans living in close proximity.

Muehlenbein (2006) was the only study to investigate the interaction between fGC levels and parasite load; they found a positive correlation between the two indicators that supports the

general trend. In order to fully include hominoid primates in the pattern of behavioral responses to anthropogenic change further research exploring CORT responsiveness to disruption is needed. Additionally, parasite studies which examine if infection increases in individuals that travel to the edge or interact more with humans would help solidify the suggested pattern.

Discussion:

There are inherent problems with making generalizations across taxa. Searching for patterns must be done carefully and with consideration for differences in species characteristics, for example is the primate arboreal or terrestrial? Most generally, anthropogenic influence has a negative impact on primate health. Primates react variably to anthropogenic change; however, if interactions are considered more specifically it may be possible to predict a response. In **Figure 1**, the patterns have been visually synthesized. Primates living in a fragmented habitat are at a greater risk of developing parasite infections. If these primates also experience nutritional stress beyond the natural fluctuations that follow seasonal changes, they are at risk of having elevated CORT levels. CORT at chronic elevation can lead to numerous health consequences and exaggerate the risk of infection (**Table 1-4**).

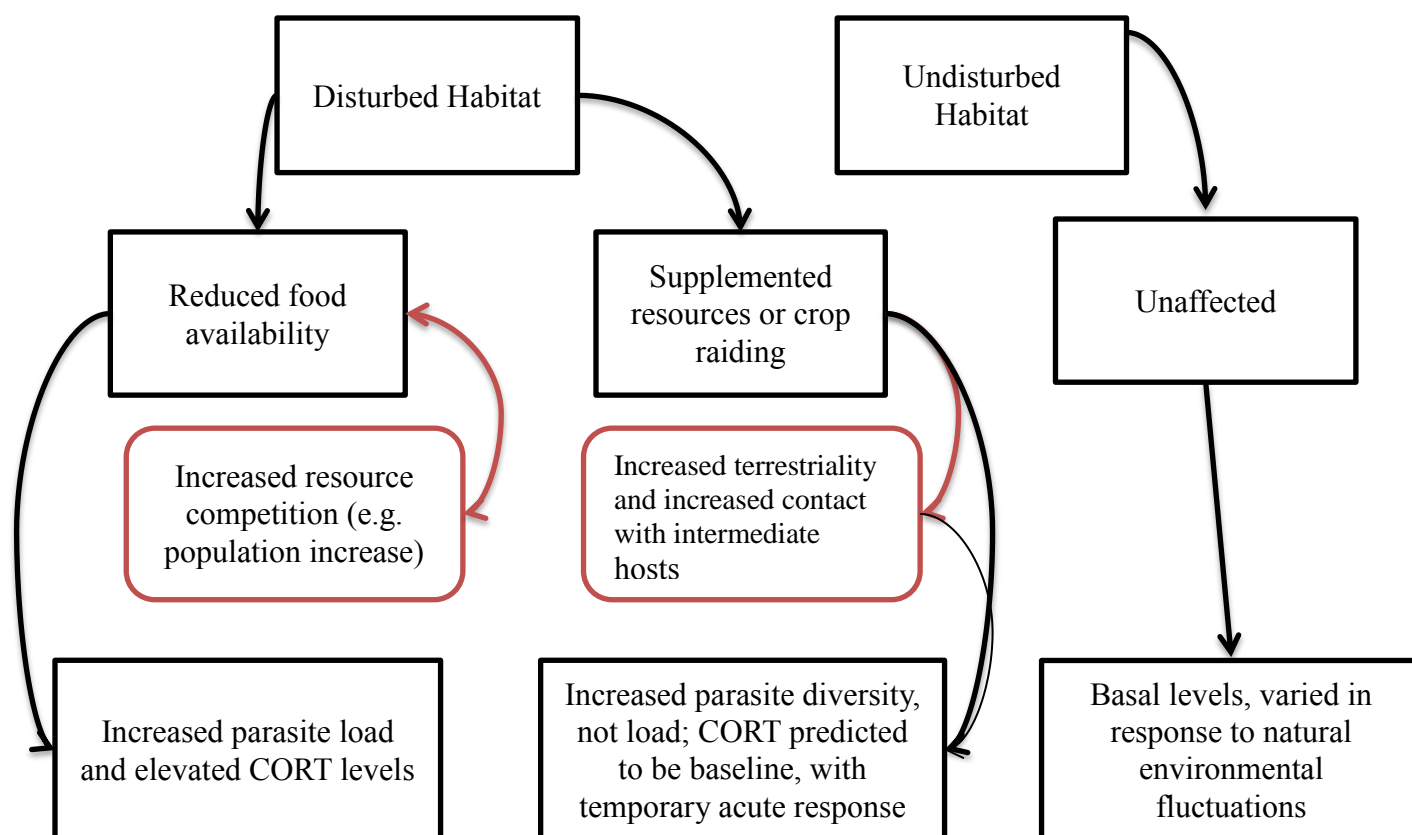


Figure 1: A visual summary of the trends and expectations based on the findings of this study. The first row refers to the state of the forest, “disturbed” referring to environmental degraded and anthropogenically influenced forest; “undisturbed” refers to intact habitats. Row two references the availability of food; specifically of concern is fruit however, if any primary resource is diminished, there will be an effect of nutritional stress. Row three, in red, are “other” factors that influenced the measures of CORT and parasites. The final row predicts the result based on the relationship of the above factors.

Parasite loads, both parasite richness and species diversity, tends to increase in primates experiencing high levels of human impact. This is evidenced in ring-tailed lemurs and Verreaux’s sifakas at Beza Mahafaly Special Reserve. Ring-tailed lemurs engage in several behaviors, such as spending extensive time on the ground and engaging in corophagy, that increases their vulnerability to infection (Loudon 2009; Fish et al. 2007). Their risk is not idle as ring-tailed lemurs not only had an elevated parasite load but novel parasites suggesting cross transmission or an increasing susceptibility within the population (Loudon 2009).

Comparatively, Verreaux's sifakas at the site presented with few endoparasite infections (Loudon 2009). These primates are primarily arboreal, using vertical clinging and leaping for locomotion rather than movement on the ground. By limiting time on the ground, the chance of encountering humans and infected feces is greatly reduced.

Evidence that contact with humans led to increased parasite loads is also found in primates occupying forest edge habitats and/or crop-raiding groups (Krief et al. 2010; Mugisha et al. 2003). This suggests that exposure or contact with humans and their products (e.g. waste, domestic animals, crops) increases nonhuman primate risk of infection, and that this susceptibility is exaggerated for primates most likely to travel on the ground. It is important to note that highly arboreal species, such as howler monkeys, may be forced to travel on the ground due to deforestation. This was seen in Trejo-Macias et al.'s (2007) study where howler monkeys live in fragmented habitats. The researchers observed that this resulted in increased contact with humans and parasitic intermediate hosts, becoming a possible cause for the increased parasite load measured (Trejo-Macias et al. 2007).

Multiple studies also highlighted a causal relationship between nutritional stress and primate health. The effects of nutritional stress were observed differently in species. In diademed sifakas nutritional stress was suspected as their resources were reduced to using mistletoe as a primary nutrient (Irwin 2008b). Consequently, male adults and juveniles in fragments were lighter than their undisturbed counterparts. A similar observation was made in *Hamadryas* baboons, where nutritional stress led to stunted growth (Fourie 2003). Indri, red-tailed guenons, and red colobus responded to nutritional stress with increased parasite loads (Junge et al. 2011, Gillespie et al. 2005, 2008). The effect of nutritional stress was also seen in relation with CORT levels and variation among populations. Primarily observed in the platyrrhine primates, reduced

availability of fruit for black howler and Yucatan Geoffroyi's spider monkeys led to elevated levels of CORT (Mota et al. 2007; Behie et al. 2010; Rangel-Negrin et al. 2009). This is supported by grey-cheeked mangabeys, hamadryas baboons, and red colobus, all of which resided in disturbed habitats and presented with elevated CORT levels (Jaimez et al. 2011; Fourie 2003; Chapman et al. 2006). Behie et al. (2010) highlight cortisol's role in metabolic function as the elevated CORT levels are part of the stress response in which it mobilizes glucose. Primates, even the highly folivorous howler monkey, consume sugar from fruit. Restrictions on its availability may directly stimulate a rise in CORT as the body depends on different energy sources until proper nutrients are found. In part, this is why CORT fluctuates during the seasonal year, on average higher during periods of dryness and drought (Rangel-Negrin et al. 2009; Fourie 2003). When nutritional stress persists beyond seasonality, the likelihood of chronic, or pathological levels of stress, increases. Chronic stress mutes responsiveness to stimuli meaning CORT levels will be elevated and steady during the year, as was seen in Yucatan Geoffroyi's spider monkeys (Rangel-Negrin et al. 2009).

CORT's role in metabolic function may explain why food supplemented groups were exceptions to the trend: Balinese macaques, olive baboons, and black-and-white colobus (Lane et al. 2010; Fourie 2003; Gillespie 2005, 2008). While there is no CORT data in these studies, given CORT's metabolic role normal, basal levels would be expected. The provisioning that macaques and baboons receive due to their close proximity to humans mitigates nutritional stress. Black-and-white colobus at Kibale are spared nutritional stress as their primary food sources are not threatened by logging (Gillespie 2005, 2008). It is interesting to note that resource competition increases, due to immigration from threatened sites, caused temporary, but high rates of infection. The stressor was not lasting for black-and-white colobus monkeys which

returned to basal levels and maintained steady population (Gillespie 2008). Red colobus however did not recover; it would be beneficial to have a CORT profile to see if the stress response of these primates has been affected by anthropogenic disturbances (Gillespie et al. 2008).

A secondary contributing factor to elevated levels of CORT was human presence. Tourists and human traffic led to increased stress in black howler monkeys (Behie et al. 2010). Forest edge populations may also exhibit increased levels of CORT but there is no current data to support the prediction. Such studies could be beneficial to conduct especially in crop-raiding populations to see if the food benefits outweigh the stress of interaction. It is possible that the farm and villager interactions experienced by chimpanzees at Kibale, where they presented higher prevalence of parasites, and olive baboons do not elicit the same stress response as tourism traffic does in new world monkeys, where long-term stress is likely (**Table 3, 2**). A recent study showed that the CORT response in wild habituated orangutans showed an acute stress response following tourist visitation, but was not indicative of long-term stress (Muehlenbein et al. 2012). Based on animal temperament and habituation of the group, the impact of human visitation could have a vastly different impact.

The standing expectation of CORT response is that elevated levels will be seen in disturbed, fragmented forest when compared to undisturbed, continuous forest. However, studies have yielded confounding results such as Tecot's (2013) investigation of fGCs in red-bellied lemurs. Her study consisted only of fragments, but of varying sizes. The smallest, but least disturbed fragments contained lemurs with the highest fGC levels. Tecot (2013) explains the unexpected results by suggesting stress-sensitive individuals may have been selected out of the group or that the stress response of these lemurs has become muted. She also notes there is a high infant mortality rate and a declining population (Tecot 2013). Recalling Pride's (2004)

study, which showed high levels of fGC were an indicator of individual survival probability, the results are most likely the byproduct of a disrupted, long-term stress response (Tecot 2013).

Observations of reduced size and weight in ring-tailed lemurs and diademed sifakas are likely the result of chronic or long-term stress, which has been known to stunt growth, effect bone density, and cause redistribution of fat (Chrousos 2009).

Long-term stress has the ability to impact individual survival, impact mortality rate of the population by decreasing fertility and damaging the overall health of primate group, and it can also impact the development and behavior of later generations (Clarke et al. 1996; Coe et al. 2003). Prenatal stress, such as food restriction upon pregnant primates can lead to neurodegenerative effects that have lasting impacts in offspring (Clarke et al. 1996). Clinical studies of rhesus monkeys have found that prenatally stressed (PNS) primates show increased locomotion [an indicator of nervousness/anxiety], abnormal and disturbance behavior, and a significant decrease in juvenile's play behavior (Clarke et al. 1996). These results ultimately led to decreased adaptive and social behavior in offspring, alterations that were still observed when the primates reached four years of age (Clarke et al. 1996). Coe et al. (2003) found PNS primates had reduced hippocampal volume [roles in spatial memory and learning] and inhibition of neurogenesis in the dentate gyrus [role in memory formation]. The changes were associated with increased activity in the hypothalamic-pituitary-adrenal (HPA) axis, causing an increase in CORT in affected individuals (Coe et al. 2003).

Coe et al. (2003) lessened the impact of their results on humans by pointing out that macaque infants are born with approximately 60% brain development, compared to human's 24%. In humans, the result of prenatal stress may not be permanent because the stressful environment experienced in utero can be corrected after birth. This allows for neural

development to occur in a favorable environment. For primates born with a mostly developed brain and into a disturbed environment, the impact may be more severe. This means the consequences of the stressful uterine environment will have significant and lasting impact on individual fitness. The disruption of the HPA axis will increase the baseline level of CORT. It may either mute a stress response, as seen in red-bellied lemurs, or contribute to a persistent elevation, as seen in Yucatan Geoffroyi's spider monkeys (Tecot 2013; Rangel-Negrin et al. 2009).

It is also important to note the relationship between CORT and the immune response. Elevated levels of CORT causes immunosuppression in individuals, compromising individual ability to fight infection. In this way, it is likely there is a causational relationship between CORT and parasite load. Chapman et al. (2006) investigated parasite load and CORT levels in parallel; they found that CORT variation was related to parasite prevalence rather than the population size. They did note that the groups with declining populations had the most variable levels of CORT (Chapman et al. 2006). Unfortunately, this study was the only one to investigate CORT and parasite load together. It is possible the indicators of long-term stress will be masked in a population because overall fitness is compromised and does not allow for accurate measure in comparative studies. As well, if baseline activity of the HPA axis is already up-regulated in the population at the time of study, the "baseline" characterized may already be elevated and camouflage the influence of stress.

Further exploration of the relationship between anthropogenic change, stress, and parasites is needed to fully understand the complex interplays. There are numerous factors that contribute to primate stress, a virtually undefinable concept. However, there is a definite pattern: disturbances in habitat cause a stress response which weakens primate health. More research

looking at the relationship between parasite load and CORT could establish a causal link. While they can be described physiologically as affecting each other, together they have not been used as a measure of primate health or as a means to predict population stability. Variable CORT levels and heavy parasite loads are likely indicative of a waning population with decreasing survival probability. These measures could benefit conservation research. Deeper investigation could clarify primate stress responses and the limitations of the plasticity of primate behavior.

Conclusion and Future Directions:

Ultimately, the universality of primate physiological responses to stress, here in the forms of environmental degradation and direct human involvement, emphasizes the importance of holistic conservation efforts. Fragmentation and tourism have noted adverse effects on an array of primate species. It may be possible to minimize disruption or help primates by removing nutritional stress. It becomes vital to mitigate the impact of reduced fruit availability, or any essential food source. Crop-raiding groups' overall health benefitted from the proximity of humans. The increased parasitism, or appearance of novel parasites for the primate population, should be expected in anthropogenically-influenced primates either from exposure to human activity or immunosuppression resulting from stress.

There was some evidence of cross-transmission of parasites, specifically between chimpanzees and close villagers (Mugisha et al. 2003). The risk of cross-transmission to humans from other, less closely related nonhuman primates appears low, as genetic differences become more substantial. However, there are parasites that are considered generalists and zoonotic disease, such as Ebola, that have been identified in domestic animals, nonhuman primates (howler monkeys), and humans (Valdespino et al. 2010; Huijbregts et al. 2003).

While it is impossible to account for the variety of factors that impact behavioral and physiological responses, it was found that contact with humans in the form of disruptive tourism, domestic animals and use of forests as latrines all increases the risk of parasite infection in nonhuman primates. Increasing time spent on the ground, a result of fragmentation in many areas, exaggerates disease susceptibility. Additionally, reduction in food availability can cause acute and long-term stress (**Figure 1**). If the latter occurs it feeds back negatively on primate health, weakening fitness, immune response and ultimately decreasing the probability of primate survival.

By monitoring the relationship between glucocorticoid's fluctuating levels and responsiveness and parasite loads of primate populations, primate health may be better monitored and conservation efforts adjusted to changing needs. As follow up to this project, we will be measuring cortisol levels in ring-tailed lemur hair samples in reference to the parasite data on hand. Furthermore, the hair samples have been collected over the course of a long-term field project. This will allow us to see fluctuations, or potentially lack, in cortisol providing an insight to the effect of seasonality on primate health and show a progressive response of primates to human-induced changes.

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