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Getting Humans Off Monkeys' Backs: Using Primate Acclimation as a Guide for Habitat Management Efforts

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Abstract

Wild primates face grave conservation challenges, with habitat loss and climate change projected to cause mass extinctions in the coming decades. As large-bodied Neotropical primates, mantled howling monkeys (*Alouatta palliata*) are predicted to fare poorly under climate change, yet are also known for their resilience in a variety of environments, including highly disturbed habitats. We utilized ecophysiology research on this species to determine the morphological, physiological, and behavioral mechanisms howlers employ to overcome ecological challenges. Our data show that howlers at La Pacifica, Costa Rica are capable of modifying body size. Howlers displayed reduced mass in warmer, drier habitats, seasonal weight changes, frequent within-lifetime weight fluctuations, and gradual increases in body mass over the past four decades. These within-lifetime changes indicate a capacity to modify morphology in a way that can impact animals' energetics and thermodynamics. Howlers are also able to consume foods with a wide variety of food material properties by altering oral processing during feeding. While this capability suggests some capacity to cope with the phenological shifts expected from climate change and increased habitat fragmentation, data on rates of dental microwear warns that these acclimations may also cost dental longevity. Lastly, we found that howlers are able to acclimate to changing thermal pressures. On shorter-term daily scales, howlers use behavioral mechanisms to thermoregulate, including timing activities to avoid heat stress and utilizing cool microhabitats. At the seasonal scale, animals employ hormonal pathways to influence heat production. These lines of evidence cumulatively indicate that howlers possess morphological, physiological, and behavioral mechanisms to acclimate to environmental challenges. As such, howlers' plasticity may facilitate their resilience to climate change and habitat loss. While habitat loss in the tropics is unlikely to abate, our results point to a potential benefit of active management and selective cultivation to yield large, interconnected forest fragments with targeted phenology that provides both a complex physical structure and a diversity of food sources. These steps could assist howlers in using their natural acclimation potential to survive future conservation threats.

Keywords: acclimation, primates, climate change, habitat management, *Alouatta*

Primates face a grim future

Primates face a range of severe conservation challenges in their natural habitats. Climate change and habitat loss/fragmentation are the most significant of these threats, predicted to cause mass extinctions and substantial range reductions in the coming decades (Schloss et al. 2012; Graham et al. 2016; Estrada et al. 2017; Carvalho et al. 2019). While models predicting the effects of climate change vary widely in extinction rates (Urban 2015), a large number of individuals and entire species will realistically perish.

Primates' options for survival are few. Animals' pathways to cope with climate change (which are applicable to habitat loss as well) are commonly described as "move, adapt, acclimate, or die" (Corlett 2011: p. 608). As long-lived mammals with slow reproductive rates, it is unlikely that primates will adapt via natural selection to the conservation threats posed by humans (Kalbitzer & Chapman 2018). Compared to other tropical mammals, primates are predicted to be less capable of migrating to suitable environments as tropical habitats move poleward, based on models incorporating climatic changes, species' dispersal velocity, and generation time (Schloss et al. 2012; Sales et al. 2019). Primate ranges are significantly impacted by geographic dispersal barriers such as rivers and forest discontinuities (Beaudrot & Marshall 2011; Harcourt & Marshall 2012), and increasing deforestation is expected to further limit their ability to track habitat changes poleward (Korstjens & Hillyer 2016; Estrada et al. 2017). However, primates are also animals that demonstrate high degrees of plasticity (van Schaik 2013). This capacity for acclimation could be an important mechanism allowing them to adjust to environmental pressures posed by climate change and habitat loss (Beever et al. 2017; Kalbitzer & Chapman 2018).

A growing primate ecophysiology

The burgeoning of ecophysiology research over the past few decades has placed an increased emphasis on understanding animals' physiology within their natural environments. For primatology, a discipline with a wealth of lab-based literature, this new focus has enabled researchers to better integrate our understanding of physiological principles within the niches animals inhabit (Thompson & Vinyard 2019). This shift in focus has yielded numerous scientific developments, for instance the origin and evolution of field endocrinology (Higham 2016), as well as energetic and thermoregulation studies on primates (Blanco et al. 2018). Our enhanced understanding has been invaluable in developing knowledge of primate biology under ecologically-relevant settings. Yet, as these natural systems and the primates in them are under increasing threat, ecophysiology is newly tasked with applying these insights to aid conservation and management efforts.

Howling monkeys as a model for applied ecophysiology

Our long-term field work on mantled howling monkeys (*Alouatta palliata*) at La Pacifica (LP), Costa Rica provides an opportunity to examine primate responses to current and possible future conservation threats. Mantled howling monkeys are relatively large bodied (at LP, adult males: \bar{x} =5.79 kg; adult females: \bar{x} =4.73 kg: Glander 2006), arboreal primates that feed mostly on leaves (63.6%), flowers (18.2%) and fruits (12.5%) (Glander 1979). Mammals of this size, as well as inhabitants of the warm Neotropics, are among those expected to fare worst under climate change (Sherwood & Huber 2010; Graham et al. 2016; Carvalho et al. 2019). Despite this, howlers are renowned for their ability to tolerate a variety of habitats, including those heavily impacted by anthropogenic changes (Arroyo-Rodríguez & Dias 2010; Kowalewski et al. 2015).

As a field site, LP presents advantages for studying primate conservation threats. First, it is a highly mosaic environment that includes fragments of dry deciduous upland tropical forest as well as wetter riparian habitats. This heterogeneity facilitates comparisons of animals in differing habitats, modeling the shifts expected to occur with climate change and deforestation. Second, LP has a strongly seasonal climate, with distinct wet (cooler) and dry (hotter) seasons. This provides a useful comparison for how animals adjust to hotter, drier conditions. Lastly, LP is an anthropogenic habitat, serving as a commercial ranch with forest patches surrounding cattle pastures, rice fields, and fish-rearing ponds. Over the past few decades, LP has also become increasingly fragmented, and longitudinal monitoring of howlers at this site spans the timeline of these ongoing conservation threats (Clarke et al. 2002). Unfortunately, this fragmentation represents the increasing reality of many primate habitats (Carvalho et al. 2019), providing a template for the types of modifications that may prove feasible for animals under such environmental changes.

Understanding how howlers utilize morphology, physiology, and behavior to thrive at LP can provide insight into the conservation and management of primates facing anthropogenic changes. Phenological changes with habitat loss and climate change will impact animals' food sources and physical environment. Warming temperatures will likewise have a direct impact on animals' ability to thermoregulate. As body size is intrinsically linked to both heat regulation and nutritional requirements, we examine the ecomorphology of body size along with the physiology of feeding, and thermoregulation in the howlers at LP. By better understanding how animals respond to current stressors at LP, we can help shape management applications that support animals' natural coping mechanisms to face future challenges.

Ecomorphology of body size as a tool to decipher acclimation potential

Body size changes have been strongly linked to climate change in birds, mammals, and ectotherms across a number of continents (Gardner et al. 2011; Sheridan & Bickford 2011). These size changes are generally attributed to thermoregulatory and/or energetic benefits in warmer environments (Gardner et al. 2011). Climate-related body size shifts may be evolutionary, but they can also result from change within a lifetime, for instance due to developmental processes or adult weight changes (Gardner et al. 2011). We assessed whether howlers display body size differences related to habitat (cooler wetter riparian habitats vs. drier, warmer upland habitats) and season (wet vs. dry). Body mass comparisons are from adult mantled howlers at LP encompassing 1972-2014, including 203 males (with N=371 total weights) and 364 females (N=756 weights). Methods followed Glander et al. (1991), with further details provided in Supplemental Material. We performed a general linear mixed model (GLMM) to test the effect of season (wet vs. dry) and habitat (riparian vs. upland) (fixed variables) on body mass. We also conducted a GLMM to test for changes in body mass over years (fixed variable). Both models included the identity of individual animals as a repeated random effect. The sexes were tested separately as males are significantly heavier than females (Glander 2006).

Habitat

Males in cooler riparian habitats were significantly heavier than those in hotter upland habitats (GLMM: $F=7.17$, $P=0.008$), with riparian males weighing on average $229.2g \pm 85.6(SE)$ (3.9% of body mass) more. Similarly, females in the riparian forest had significantly greater body mass than females in upland forest habitats (GLMM: $F=7.51$, $P=0.006$), with riparian females weighing on average $164.2g \pm 59.9(SE)$ (3.5% of body mass) more. Howler group home ranges at LP do not span both habitats, and groups use only their range throughout the year. For

our sample, individuals in upland and riparian habitats were mutually exclusive. However, given the overall proximity of riparian and upland forests, there is expected to be gene flow between habitats as animals disperse from their natal group (Glander 1992). As such, body mass differences between habitats could represent within-lifetime changes, as well as among-generation effects. These habitat-level shifts in howlers mirror population-level differences seen for other primates such as marmosets and mouse lemurs, in which animals living in hotter, drier environments display lower body mass (Lahaan et al. 2006; Garber et al. 2019).

Season

Males showed a significant difference in weight between seasons (GLMM: $F=4.35$, $P=0.038$), with animals in both habitats weighing less in the wet than the dry season (riparian: $119.1\text{g}\pm 83.4(\text{SE})$ [1.9% of body mass]; upland: $189.1\text{g}\pm 36.6(\text{SE})$ [3.2% of body mass]). The direction (loss from dry to wet) is unexpected since both habitats appear to have more leaves available during the wet season. The upland forest trees are essentially leafless from mid-November to early May with 85 of 113 tree species shedding most or all of their leaves (Frankie et al. 1974; Glander 1979). However, flowers and fruit are more available in both habitats during the dry season (Frankie et al. 1974; Glander 1981). While howlers eat fewer overall flowers and fruit (18.2% and 12.5% of the diet, respectively) than leaves (63.6%), these items have higher energetic value than leaves and are easier to digest (Glander 1981). It is possible that the lack of energy-rich flowers and fruit during the wet season may lead to decreased male body mass, either through consumption of a lower quality diet or potentially as an adaptive response, since reducing body mass during periods of scarcity will lower animals' absolute energetic requirements.

For females, there was a significant effect of season on body weight (GLMM: $F=15.06$, $P<0.001$). This was mostly attributable to a significant interaction between habitat and season (GLMM: $F=6.44$, $P=0.011$), in which riparian females weighed considerably less in the dry season than wet ($207.4\text{g}\pm 54.4(\text{SE})$; 4.2% of body mass), while upland females weighed only nominally less in the dry season ($46.0\text{g}\pm 28.1(\text{SE})$; 1.0% body mass). This weight loss from wet to dry season is opposite from that of male weight loss. As aseasonal breeders (Glander 1980), there is not an obvious reproductive reason why female weight would shift seasonally for riparian females, although the relationship could be mediated through differential effects of seasonal changes in food supply for reproductive females. While the cause of seasonal body mass changes may be difficult to determine for howlers, these within-lifetime alterations in mass nonetheless demonstrate a capacity for plasticity with possible consequences for both nutrition and heat dispersion.

Long-term monitoring

Longitudinal, long-term monitoring of individual howlers shows that body mass can fluctuate considerably within an animal's lifetime (Fig. 1a). We assessed within-lifetime changes for individual howlers ($N=14$) with ≥ 10 years of weight monitoring. On average, animals' weights were sampled every $1.6 (\pm 0.4\text{SD})$ years; the length of sampling intervals did not show a significant relationship with body mass changes (further details in Supplemental Material). For individual males ($N=4$), body mass changed on average 5.4% (± 1.4 SD) (range of individual means: 3.9-6.9%) between consecutive samples, with both high maximum ($\bar{x}=13.4\%\pm 2.2\text{SD}$) and low minimum ($\bar{x}=0.3\%\pm 0.4\text{SD}$) consecutive-sample mass shifts observed. Not surprisingly, lifetime female body mass fluctuated more than males. Females ($N=10$) on average altered body mass by $9.3\%\pm 3.3\text{SD}$ (range of individual means: 5.2-15.6%) between

consecutive samples, with higher maximum ($\bar{x}=19.7\%\pm 6.2\text{SD}$) and minimum ($\bar{x}=1.6\%\pm 1.8\text{SD}$) mass changes than males. Greater changes in female than male body mass are likely due to intermittent pregnancy, although part of this difference may also be driven by the higher magnitude seasonal body size shifts for females in riparian habitats. Overall, these data directly demonstrate howlers' plasticity in body mass within a lifetime.

At the population level, howlers have demonstrated changes in body mass over 42 years of monitoring at LP. From 1972-2014, male body mass significantly increased (GLMM: $F=52.91$, $P<0.001$), on average $27.5\text{g}(\pm 3.8\text{SE})$ per year, or the equivalent of 4.7% of mean male body mass per decade (Fig. 1b). Female body mass also significantly increased over this period (GLMM: $F=30.46$, $P<0.001$) displaying a slightly weaker trend than males, with an average increase of $16.4\text{g}(\pm 3.0\text{SE})$ per year, but still the equivalent of 3.3% of mean female body mass per decade (Fig. 1c). As howler life spans range from 20-30 years (Glander 2006), these changes may reflect both within-lifetime, as well as some between-generation shifts in body size, potentially due to changes in climate or increased human impacts on the site. Across vertebrates, more species have demonstrated body size reductions than increases under recent climate change. Nonetheless, a number of mammals, including shrews, rodents, otters, and martens, have also increased body size under a warming climate (Gardner et al. 2011; Sheridan & Bickford 2011). Larger animals have been proposed to be less vulnerable to dehydration and overheating under short-term extreme temperatures, while gradual, less extreme temperature increases may favor smaller body size (Gardner et al. 2011). Alternatively, body size increases have occurred in animals with broad ecological niches able to inhabit disturbed environments as climate changes, potentially due to increased access to (or less competition for) food (Sheridan & Bickford 2011). While howlers are capable of exploiting such disturbed habitats (Kowalewski et

al. 2015), a wide array of ecological factors can impact body size and our correlational study is admittedly unable to pinpoint the cause of body size changes for howlers at LP. Regardless, these body size differences between specific habitats, across seasons, within individuals, and over decades demonstrates a capacity for morphological acclimation that could influence howlers' ability to cope with future climate changes in both heat load and phenology.

Using dietary studies to inform conservation efforts: potential impacts of dietary choice on oral processing, food material properties and tooth wear

Phenological changes are expected across primate habitats with climate change (e.g., Korstjens & Hillyer 2016). As a result, dietary flexibility will likely play an important role in the success or demise of primate species in these changing habitats. Primates, including howlers, are often described as having relatively flexible diets (e.g., Chapman 1987; Silver & Marsh 2003; Marsh & Chapman 2013; Behie & Pavelka 2015; Dias & Rangel-Negrin 2015). Within howlers, dietary choice is impacted by both environmental factors, such as rainfall and habitat size, as well as social influences (Dias & Rangel-Negrin 2015). Given the expected environmental change, we can anticipate that dietary shifts and flexibility will be necessary for animal survival. By examining relationships among dietary mechanical properties, oral physiology, and rates of dental microwear, we can help inform management decisions related to how potential changes may impact howler success.

We recorded electromyographic (EMG) activity from the superficial masseter muscles of four free-ranging howlers at LP while these animals consumed their natural diets (Fig. S1) following Williams et al. (2008) and Vinyard et al. (2012). We collected data from N=1,529 chewing cycles across nine extended feeding bouts. We compared scaled EMG recruitment levels to dietary toughness measured with a Lucas tester following previous methods used at LP

(Teaford et al. 2006). Finally, we analyzed rates of microscopic dental wear in two animals over the 2-3 day feeding recording sessions following previous methods used on howlers at LP (Teaford & Glander 1991, 1996; Dennis et al. 2004) (detailed methods in Supplemental Material). These estimates of dental wear rates were related to oral physiology and dietary properties. The small sample sizes for these combined datasets dictate caution in interpreting results as additional data are needed to bolster our preliminary observations.

Food toughness and oral processing

Across the nine feeding bouts, we observed an overall, qualitative tendency for scaled superficial masseter activity to increase with dietary toughness (Fig. 2a). This relationship was not statistically significant (Pearson's correlation: $R=0.53$, $P=0.15$). While at most suggestive, these results demonstrate a potential for variation in food material properties to impact oral physiology during individual feeding bouts. Additional field data upholding this interpretation would agree with numerous lab-based studies demonstrating that food properties impact oral physiology during chewing (e.g., Agrawal et al. 1998; Hylander et al. 2000; Woda et al. 2006; Vinyard et al. 2008). An alternative extenuating factor that may reduce an association between recruitment levels and food properties focuses on the ability of free-ranging animals to behaviorally modulate bite sizes to maintain relatively similar oral processing parameters during chewing (Reed & Ross 2010; Vinyard et al. 2011, 2012). Unfortunately, we do not have the capacity to measure intake volumes in free-ranging primates.

Averaging across individuals shows a similar potential pattern where individuals' mean EMG activity increases with dietary toughness, but this relationship is not statistically significant (Pearson's correlation: $R=0.77$, $P=0.23$) (Fig. 2b). Regardless of any potential association, the variation among individuals in diet choice, oral processing (i.e., relative EMG recruitment) and

rates of dental microwear (see below) suggests the possibility of dietary selection stemming from environmental change. The extent to which this capacity is plastic versus evolutionary and whether this ability can keep pace with habitat shifts remain to be seen.

Rates of dental microwear

Interestingly, the two individuals with measures of dental microwear rates set the extremes of EMG recruitment among our sample and are at separate ends of the dietary toughness range. The nearly 30-fold difference in percent appearance of new features (59.5% in Kolby versus 1.9% in Jamaica) is a striking anecdote for the potential impact of dietary change on dental wear. Given the small sample size, and the fact that impressions were only taken on the left mandibular teeth for each individual (see Supplemental Material), these results could also reflect individual differences in oral processing (see, for example Teaford et al. 2020 for the first documented case of dramatic differences between rates of dental microwear for right and left side reflecting unusual chewing patterns in one experimental animal). However similarly high levels of inter-individual variation have also been found in capuchin and vervet monkeys under experimental conditions in which they were consuming different foods (Teaford & Oyen 1989; Teaford et al. 2020). In wild koalas, which are folivores like howlers, high levels of macroscopic dental wear were correlated with increases in activity patterns, particularly time spent feeding (Logan & Sanson 2002a,b). While analyses of larger sample sizes are clearly necessary, if dental wear can significantly impact howler longevity (see King et al. 2012), then even the suggestion of dramatic differences in rates of wear associated with differences in food material properties raises the possibility that changes in diet that demand increased oral processing may have a significant impact on howler survival. Exploring this potential association may yield significant insights into management decisions related to howlers and other endangered primates.

Applying thermoregulation studies to conservation: can howlers acclimate to a warming climate?

The effects of rising global temperatures will directly impact animals' ability to maintain thermal homeostasis, with a number of climate change models forecasting sharp increases in mortality risk from heat stress (Sherwood & Huber 2010; Mora et al. 2017). Information gathered from ecophysiological thermoregulation studies may provide insight into how animals might cope with rising temperatures. Despite regularly experiencing warm temperatures in their natural environment, howlers do not possess any known specialized adaptations to avoid heat stress. Mantled howlers at LP experience dry season temperatures ranging from 25.3-44.9°C, with a mean daily high of 38.5°C, and wet season temperatures ranging between 22.3-42.6°C, with a mean daily high of 36.4°C (Thompson et al. 2014). Upper limits of the thermoneutral zone (TNZ) vary widely in other primates (28-35°C), but TNZ estimates do not exist for howlers (Thompson et al. 2014). Zoo-housed *Alouatta* sp. generally display core body temperatures from 37.5-39.0°C (Pastor-Nieto 2015); wild black howler monkeys (*Alouatta pigra*) in degraded habitats had core temperatures from 36.7-40.5°C (\bar{x} =38.5) (García-Feria et al. 2017). Although both these estimates may be impacted by anesthesia, they still generally fit within the range of subcutaneous temperatures for mantled howlers at LP (Thompson et al. 2014).

Unlike Old World monkeys and apes, howlers possess a minimal number of eccrine sweat glands on their body, and most New World monkeys have none (Best & Kamilar 2018). Similarly, howlers have not been observed to visibly perspire, pant, or salivate on themselves, and potentially have a low capacity for evaporative cooling. As such, we sought to examine the behavioral and physiological mechanisms that howlers use to cope with changing temperatures. To do so, we fitted mantled howlers at LP with temperature sensors to monitor subcutaneous

temperatures, as well as ambient temperature at the animal's location (Thompson et al. 2014, 2016; Supplemental Material).

Prevalence of warm thermal pressures

Our data indicate that howlers occasionally experience acute warm thermal pressures. At LP, environmental conditions with ambient temperatures exceeding howler body temperatures occurred during 10.4% of the dry season (vs. 0.06% of the wet season). During these heat bouts, which included all ambient temperatures above $\sim 41^{\circ}\text{C}$, howlers' subcutaneous temperatures held steady near 40°C , despite increasingly warm conditions (up to 45°C) (Thompson et al. 2014). By comparison, ambient temperatures $>44^{\circ}\text{C}$ and core body temperatures of 42.5°C lead to deadly heat stroke in baboons (Bouchama et al. 2005), while human skin temperatures $>37^{\circ}\text{C}$ and core temperatures $>42^{\circ}\text{C}$ can be lethal (Sherwood & Huber 2010). Equivalent measures of temperature stress are not known for howlers. Nonetheless, these animals were able to maintain a stable temperature despite facing apparent short-term warm thermal challenges. With increasing climate change, these heat bouts will become more frequent and severe (Buckley & Huey 2016; Mora et al. 2017). However, having sufficient cool recovery periods can limit mortality from heat stress (Sherwood & Huber 2010). Nighttime is the most frequent source of cool thermal pressures for howlers, with subcutaneous temperatures remaining elevated at night, despite dropping ambient temperatures (Thompson et al. 2014). Nighttime lows experienced by howlers, particularly in the wet season, can fall below $\sim 25^{\circ}\text{C}$, which is the lower limit of the TNZ for many primate species (Thompson et al. 2014). Howlers have not been reported to shiver, but are rarely observed at night. Nonetheless, the current prevalence of cool nighttime thermal pressures provides a potential optimistic note for mantled howler conservation, as it

indicates that animals, at least in the short-term, may possess regular cool temporal refugia to aid recovery from acute heat.

Use of microhabitats

Understanding how howlers respond to these thermal stressors can predict future responses to rising temperatures and inform conservation strategies. Howlers at LP inhabit a dynamic and mosaic thermal environment; temperatures can differ substantially across locations within a single square kilometer. Additionally, temperatures consistently vary across canopy heights, with lower forest levels being cooler (Thompson et al. 2016). We found that howlers are adept at using their heterogeneous environment to seek out the relatively cooler microhabitats during the hottest periods of the day: for each 1°C increase at a stationary location, the temperature in the microhabitat chosen by animals increased only 0.25-0.70°C (Thompson et al. 2016). Likewise, howlers selected shaded locations under the forest canopy when their subcutaneous body temperature was highest, with an average 0.35°C(±0.1SE) difference in subcutaneous temperature when in shade vs. sun (GLMM: $F=20.86$, $P<0.001$; methods in Supplemental Material), indicating that microhabitat selection varies with respect to thermal variables beyond temperature. This mimics findings from other primates that cope with heat by exploiting the three-dimensional nature of their habitat, spending time in the lower, cooler forest strata (Takemoto 2004; Gestich et al. 2014). Indeed, the ability to utilize vertical microhabitats may provide crucial buffers that limit the impact of climate change on a number of tropical species (Scheffers et al. 2013, 2014).

Activity timing

Beyond the spatial diversity of temperatures, howlers may also utilize temporal heterogeneity in thermal microhabitats to cope with acute heat. Warm thermal pressures are

highest at midday, while cooler conditions are prevalent at night, early morning and evening. We found that ambient temperature, solar radiation, and relative humidity significantly negatively impacted the amount of time animals spent feeding and locomoting in the wet season (GLMM: temperature: $\beta=-0.169\pm0.04$, $F=19.74$, $P<0.001$; solar radiation: $\beta=-0.002\pm0.0003$; $F=34.40$, $P<0.001$; relative humidity: $\beta=-0.089\pm0.09$, $F=52.16$, $P<0.001$; Fig. S2; methods in Supplemental Material). A similar significant negative relationship between ambient temperature and time spent feeding and locomoting existed during the dry season ($\beta=-0.151\pm0.03$, $F=20.14$, $P<0.001$) although equivalent non-temperature variables are not available for this period. However, during the dry season only 2.6% of activity bouts (feeding and locomotion) occurred between 9:00-14:00 (the hours of the day with the highest temperature and solar radiation) compared to 40.2% during the wet season. This suggests that animals may time activities to avoid warmer midday thermal pressures seasonally, although we cannot rule out other confounding factors that follow daily or seasonal cycles such as digestion time, changes in food resources, day path length, etc. There is also an interaction between temporal and spatial thermal pressures in howler habitats. For example, the top of the forest canopy will be a warm microhabitat at midday, yet cooler at nighttime relative to other locations (Thompson et al. 2016). Thus, timing of activities presents a potential avenue for animals to avoid heat stress (Levy et al. 2019) and an intact forest structure further facilitates this thermoregulatory strategy.

Thyroid hormones

On the seasonal scale, howlers face greater warmer thermal pressures during the dry than wet season. Beyond the behavioral mechanisms mentioned above, howlers also employ physiological alterations that impact heat loss between seasons. Thyroid hormones are an integral component of thermoregulatory and energetic pathways, with exposure to cold

increasing thyroid hormone levels, leading to increased metabolic rate and heat production (Silva 2006). We found that howlers had higher thyroid hormone levels during the cooler wet season, and lower levels during the hotter dry season (Thompson et al. 2017). Thyroid hormones have a number of functions in the body, yet lower hormone levels at warm temperatures leads to reductions in heat production and metabolism in a wide variety of mammals, from wallabies, llamas, and ground squirrels to other primates (Silva 2006; Behringer et al. 2018). This plasticity in howlers demonstrates a potential for physiological, in addition to behavioral, acclimations to changing environments.

There is preliminary evidence that endotherms may vary considerably in their capacity to behaviorally and physiologically tolerate warming temperatures (Boyles et al. 2011), with some mammals being limited or unable to acclimatize to warmer conditions (e.g., Sassi & Novillo 2015). Our data indicate that howlers are among those species able to tolerate warm thermal challenges. In the short-term, howlers accomplish this with behavioral flexibility, primarily utilizing the spatiotemporal complexity of their environment, while longer term thermal challenges may be met through altering physiology to better cope with heat. With climate change, the overall warmth of howlers' environment will increase. However, the current relatively low frequency of warm thermal pressures for howlers at LP is an encouraging sign that their temporal and microhabitat refugia may remain sufficient to avoid (or recover from) the direct effects of extreme heat events. As such, the presence of an intact forest structure with a variety of microhabitats is integral to howlers' thermoregulatory strategy and should be a component of future management efforts.

Implications for habitat management

Howlers' resilience to anthropogenic changes is likely attributable to their high capacity for acclimation. A number of ecological factors may influence within-lifetime changes in body size, physiology, behavior, and habitat use for howlers. Regardless of the impetus for these modifications, such plasticity may ultimately allow them to cope with changing local environmental conditions. This flexibility points to a potential path for survival as primate habitats experience climate change and increased habitat loss (Table 1). However, several models posit that long-term survival will be based on species' ability to track tropical habitats as they move toward higher latitudes (Schloss et al. 2012). While the predictive accuracy of such models remains to be seen, primates are an order whose dispersal ability is expected to lag behind the predicted velocity of climate change (Schloss et al. 2012; Sales et al. 2019). Yet, the presence of suitable, interconnected habitats could allow animals to overcome increasingly common barriers such as agricultural fields, and provide livable habitat in the near term. Over the long term, this may ultimately enable dispersal to possible refugia, such as localized habitat patches (e.g. high-altitude areas) or increase the probability that animals on the limits of their species' range could move sufficiently poleward to find viable long-term habitats. Our data indicate that howlers are capable of within-lifetime changes that facilitate their ability to survive in these marginal fragments, refugia and corridors. Increasing forest size and connectivity are management actions that, despite continually revised models of climate change, would nonetheless benefit the conservation of many tropical species by increasing species movement, gene flow, and restoring/preserving vegetation (Corlett 2011).

However, our results also imply that simply preserving forests may not be enough. Howlers utilize forest and habitat complexity in a way that aids their ability to cope with environmental changes. Actively cultivating forest structure complexity may benefit the survival

of animals such as howlers. This can be achieved in the short term through selective plant and tree management, or as climate change proceeds in the longer term, by constructing novel forests with introduced plants that can cope with emergent environmental conditions. This ‘habitat engineering’ has the added benefit of preserving plant biodiversity as well, as many plants (particularly trees) have fewer options in the face of habitat loss and climatic shifts. This emphasis on cultivating forest complexity mirrors findings that mixed-species forests display multiple advantages over more easily implemented monoculture forests (Wills et al. 2017). Despite the benefits, balancing forest complexity and biodiversity with competing aims such as alleviating local poverty and financial feasibility of reforestation projects has proven challenging (Lamb et al. 2005), and will continue to do so in the face of climate change.

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Figure Captions

Fig 1 Body mass changes for mantled howling monkeys (*Alouatta palliata*) at La Pacifica (LP), Costa Rica. (A) Within-lifetime body mass changes for four representative individuals from each sex and habitat, calculated as the percent body mass change between consecutive samples, (B) Male and (C) Female body mass from 1972-2014. (B) and (C) include data points for animals with repeated samples over time; individual effects are statistically controlled for analyses presented in the text. Linear trendline is shown.

Fig 2 Plot of average scaled superficial masseter recruitment versus dietary food toughness across feeding bouts (A) and individuals (B) for howlers at La, Pacifica (LP), Costa Rica. EMG and food toughness are not statistically correlated across feeding bouts ($R=0.53$, $P=0.15$) or individuals ($R=0.77$, $P=0.23$). The two individuals with available dental wear estimates during EMG recording (B) show the highest and lowest percentage of new wear features and EMG recruitment levels, respectively.

Fig S1 The EMG telemetry unit for measuring jaw-muscle activity in mantled howlers. We inserted bipolar indwelling electrodes into the masseter muscles. Electrodes are attached directly to a telemetry unit (right) and muscle activity is recorded to an onboard microSD card. The telemetry unit is attached to the animal's back underneath a jacket (center, white dotted line). The unit is turned on an off remotely using a Bluetooth connection (<100m communication distance) and a laptop computer (left) in the field based on observed feeding activities. Battery life generally lasts about two to three days. (Adapted from Vinyard et al. 2012)

Fig S2 Mantled howling monkey (*Alouatta palliata*) activity timing across the day, in relation to temperature and solar radiation. Activity (black bars) on the primary axis are the mean % of time feeding and/or locomoting per hour. Temperature (orange) and solar radiation (grey) are depicted as the difference from the daily mean value of that variable.

Table 1 Summary of acclimations found in mantled howling monkeys (*Alouatta palliata*) at La Pacifica (LP), Costa Rica.

Acclimation Variable	Changes With...	Time Scale	Potential Conservation Implications
Morphology^a			
Body size	Habitat	Years, Months	Alter heat loss dynamics to cope with a warming climate
	Season	Months	
	Long-term monitoring	Decades, Years	Alter nutritional needs to cope with phenology shifts from climate change and habitat degradation
Rate of dental microwear	Time	Days, Months, Years	Alter costs of phenology shifts
Physiology^b			
Masticatory muscle recruitment	Food toughness	Days, Hours, Minutes	Alter oral processing to cope with phenology shifts from climate change and habitat degradation
Thyroid hormones	Season	Months	Alter heat production & metabolism to cope with a warming climate
Behavior^c			
Microhabitat selection	Temperature	Days, Hours, Minutes	Alter heat stress to cope with a warming climate
Activity timing	Temperature	Days, Hours, Minutes	
	Solar radiation	Days, Hours, Minutes	
	Relative humidity	Days, Hours, Minutes	

^aMeasurements for morphological acclimations: body size=kg, measured via in-field captures: Glander et al. 1991; dental wear=% of new features, via scanning electron microscope; habitat=upland/riparian; Season=wet/dry; long-term monitoring=1972-2014

^bMeasurements for physiological acclimations: masticatory muscle recruitment=scaled superficial masseter EMG activity: Supplemental Material; thyroid hormones=urinary fT3: Thompson et al. 2017; food toughness=energy consumed in crack propagation, measured via Lucas tester: Supplemental Material

^cMeasurements for behavioral acclimations: microhabitat selection: animal presence in sun vs. shade, on-animal vs. stationary ambient temperatures: Thompson et al. 2016); activity timing: minutes spent feeding and locomoting; temperature: implanted subcutaneous logger, on-animal ambient logger placed on ankle: Thompson et al. 2014; solar radiation, relative humidity: via HOBO weather station at LP

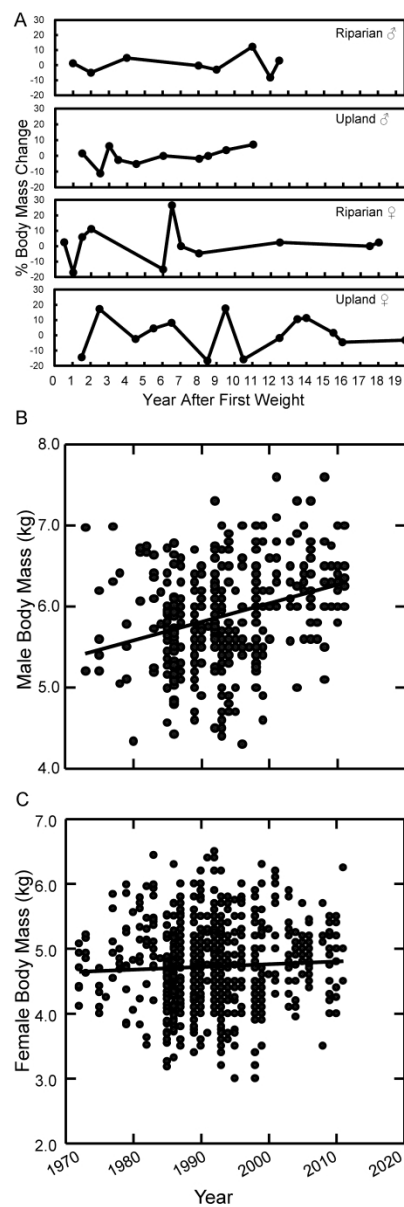


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87x264mm (600 x 600 DPI)

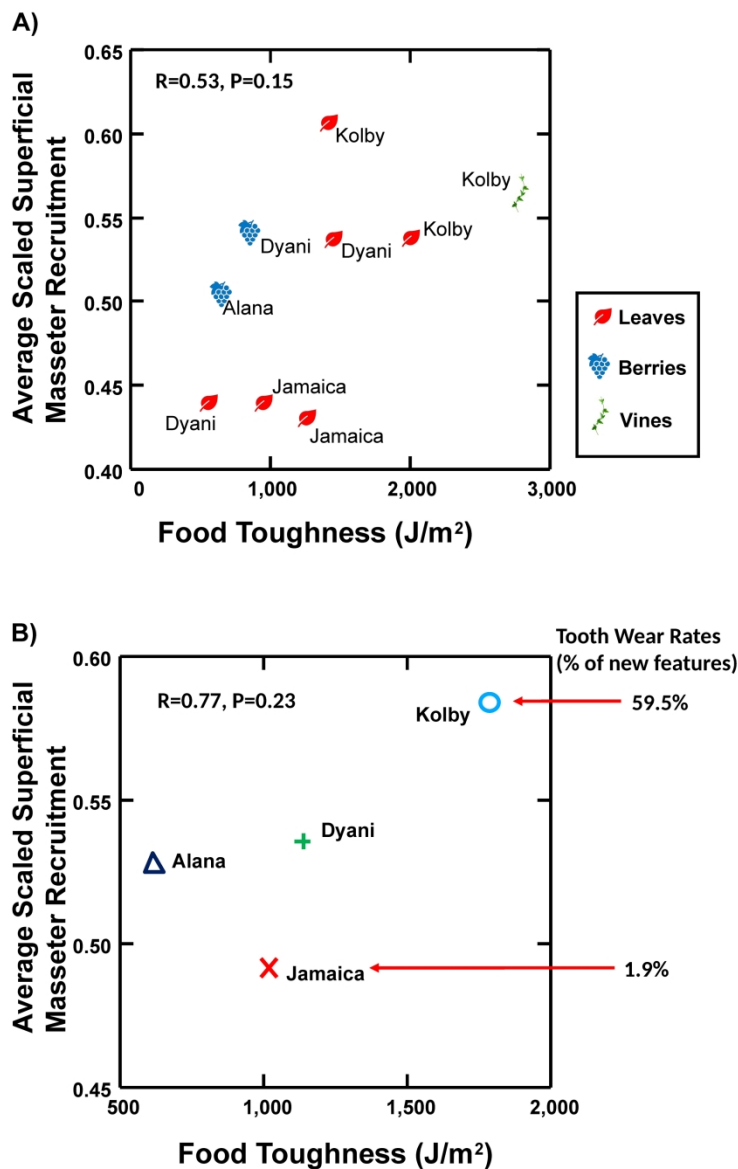


Fig 2 Plot of average scaled superficial masseter recruitment versus dietary food toughness across feeding bouts (A) and individuals (B) for howlers at La, Pacifica (LP), Costa Rica. EMG and food toughness are not statistically correlated across feeding bouts ($R=0.53, P=0.15$) or individuals ($R=0.77, P=0.23$). The two individuals with available dental wear estimates during EMG recording (B) show the highest and lowest percentage of new wear features and EMG recruitment levels, respectively.

208x338mm (300 x 300 DPI)