

Methods for Studying the Ecological Physiology of Feeding in Free-Ranging Howlers (*Alouatta palliata*) at La Pacifica, Costa Rica

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Abstract We lack a general understanding of how primates perform physiologically during feeding to cope with the challenges of their natural environments. We here discuss several methods for studying the ecological physiology of feeding in mantled howlers (*Alouatta palliata*) at La Pacifica, Costa Rica. Our initial physiological effort focuses on recording electromyographic activity (EMG) from the jaw muscles in free-ranging howlers while they feed in their natural forest habitat. We integrate these EMG data with measurements of food material properties, dental wear rates, as well as spatial analyses of resource use and food distribution. Future work will focus on incorporating physiological measures of bone deformation, i.e., bone strain; temperatures; food nutritional data; and hormonal analyses. Collectively, these efforts will help us to better understand the challenges that howlers face in their environment and the physiological mechanisms they employ during feeding. Our initial efforts provide a proof of concept demonstrating the methodological feasibility of studying the physiology of feeding in free-ranging primates. Although howlers offer certain advantages to in vivo field research, many of the approaches described here can be

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applied to other primates in natural habitats. By collecting physiological data simultaneously with ecological and behavioral data, we will promote a more synthetic understanding of primate feeding and its evolutionary history.

Keywords Feeding ecology · Jaw-muscle physiology · Mastication · Research methods

A holistic understanding of primate feeding biology requires examination of morphology, behavior, physiology, and the natural feeding environment (Fig. 1a). To date, most research efforts have focused on independently dissecting these different aspects of primate feeding through museum studies of morphology, laboratory studies of physiology, and field studies of feeding behavior and ecology. Although highly beneficial to our general understanding of primate feeding biology, these research agendas require us to make significant assumptions about their potential interrelationships when inferring adaptive and evolutionary patterns in primates (Thompson *et al.* 2011; Vinyard *et al.* 2008; Williams *et al.* 2008). In this contribution, we discuss integrating these various research techniques to study primate behavior, ecology, and physiology while subjects feed in their natural environment. We briefly discuss this work in the broader context of developing an ecological physiology of feeding for primates followed by short descriptions of primary methods we are using in describing the ecological physiology of feeding in mantled howlers (*Alouatta palliata*) at La Pacifica, Costa Rica.

Developing an Understanding of the Ecological Physiology of Primate Feeding

Ecological physiology broadly refers to studying environmentally relevant physiology, allowing researchers to identify how specific physiological processes help an organism cope in their environment (Bradshaw 2003; Karasov and del Rio 2007; Schmidt-Nielsen 1990; Sibly and Calow 1986; Tracy *et al.* 1982;). Essentially, ecological physiology asks “What physiological mechanisms allow animals to live where and how they do?” (Bartholomew 1987, p. 30). Although we recognize the ultimate explanations for feeding in terms of energy and nutrient intake, we generally lack detailed descriptions of how physiological parameters during feeding vary with environmental factors, such as seasonal food availability, spatial distribution of foods, food properties, and temperature, across primates (Fig. 1). Because the evolutionary adaptations of animals are intricately tied to specific environments, understanding how feeding physiology interacts with environmental variables is essential for interpreting variation in masticatory morphology and feeding behavior across primate species.

In platyrrhines, feeding ecology research has described annual diets (Ayres 1986; Di Fiore 2004; Norconk 1996; Norconk *et al.* 2009; Palacios *et al.* 1997; Peetz 2001; Porter 2001; Strier 1991; Wallace 2005) and their mechanical properties (Norconk *et al.* 2009; Teaford *et al.* 2006; Vinyard *et al.* 2009; Wright 2005) in addition to other aspects of feeding and diet such as nutrition. To build on these studies of feeding behaviors and food properties, we are recording jaw-muscle activity during feeding in free-ranging mantled howlers (Williams *et al.* 2008). By linking in vivo

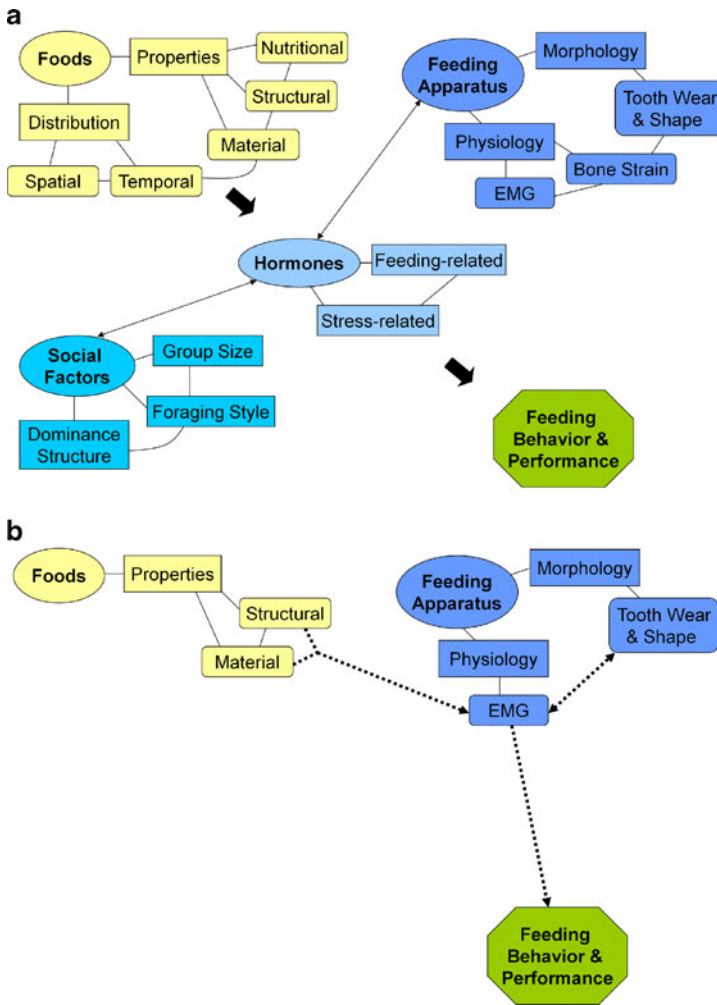


Fig. 1 Some of the factors influencing feeding behavior and performance. **a** Essential flow diagram demonstrating several key variables we are examining that potentially influence feeding behaviors. In this basic diagram, our environmental factor, i.e., food, is depicted in yellow and monkey-related factors in blue. Within each grouping, subcomponents are connected by small black lines reflecting their likely interrelationships. The medium-sized arrows connecting the “feeding apparatus,” “hormones,” and “social factor” groups represent the potential interrelationships among these factors. The large arrowheads demonstrate the basic flow of information where environmental factors influence the animal which based on these interactions generates its feeding behavior and performance. **b** A subdiagram depicting an initial hypothesis relating food properties, jaw-muscle activity patterns, and tooth wear to feeding behavior. The dashed lines represent predicted relationships among variables, with arrowheads providing direction of influence. **c** A subdiagram incorporating the potential influence of spatial distribution of foods on feeding behavior with food properties, jaw-muscle EMGs, and tooth wear. In this case, the spatial and temporal distribution of foods may impact the material and structural properties of foods with consequences for the physiology and morphology of the feeding apparatus. **d** A more realistic example showing the complexity of interrelationships among environmental and monkey-related factors and their joint influence on feeding behaviors. (Arrows are as described in **b**). These diagrams depict only the factors we discuss in this article and are not meant to provide an exhaustive list of influencing factors. For example, gastrointestinal morphology and digestion are not included despite their clear significance for feeding behaviors (Milton 1998). Moreover, connections among components are illustrative rather than complete, as future work will likely demonstrate additional interrelationships as well as suggest that others are less important.

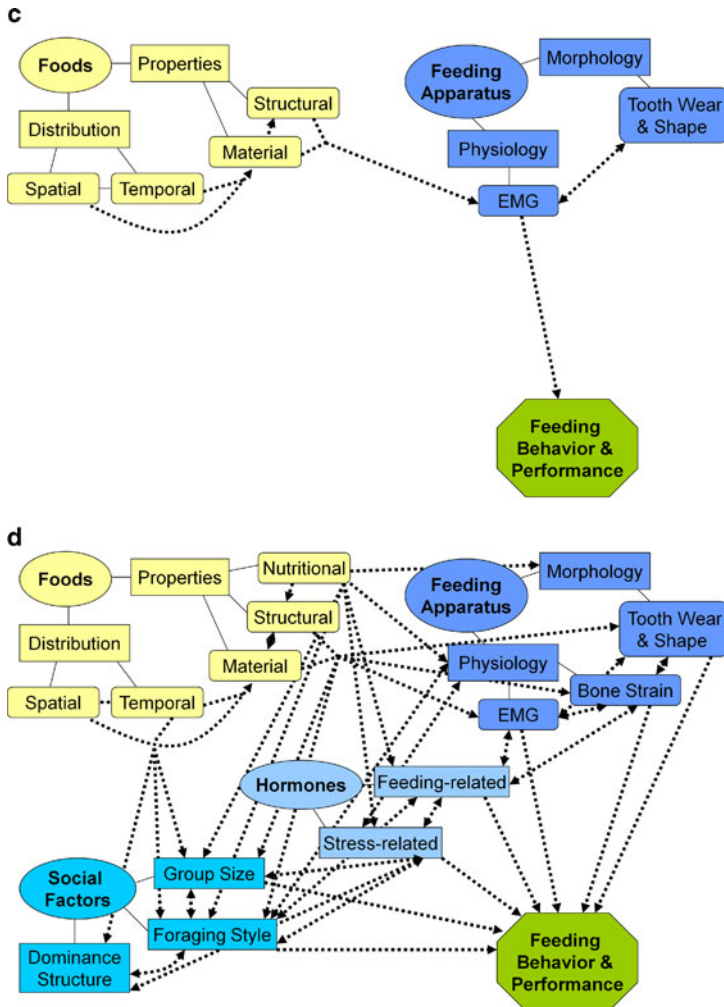


Fig. 1 (continued).

laboratory and field-based ecological research, we can explore how this aspect of feeding physiology relates to both natural feeding behaviors and several environmental factors experienced by the same individuals. Specifically, we have developed approaches that allow us to assess the relationships among jaw-muscle activity patterns during chewing, feeding behaviors, food material and structural properties, dental wear, spatial ranging, and food distribution patterns (Fig. 1). We outline our methods for assessing these variables and their relationships in the text that follows. Our immediate goal in this research is to better understand how howler physiology relates to patterns of feeding behavior and resource use in their natural environment. Over the longer term, we hope to provide a methodological template for future studies of ecological physiology of feeding that ultimately can be applied to other primate species to further our understanding of feeding adaptations.

Jaw-Muscle Activity During Feeding

Question and Background

How do the timing of contraction and relative recruitment of the jaw muscles during feeding relate to ecological variation? Electromyograms (EMGs) recorded from primate jaw muscles during feeding are routinely used to test hypotheses about primate craniofacial adaptations and evolution (Hylander and Johnson 1994; Hylander *et al.* 2000, 2004, 2005, 2011; Ross and Hylander 2000; Vinyard *et al.* 2005, 2006). To date, jaw-muscle EMG data during chewing in primates, as well as other mammals, have been collected only from captive animals in laboratories. Whereas researchers have collected telemetered data from unrestrained individuals (Kawai *et al.* 2007; Langenbach 2011; Langenbach *et al.* 2002, 2004) and humans (Miyamoto *et al.* 1996; Po *et al.* 2011), the primate data were still collected in laboratory settings where subjects were fed and restrained. Previously, we acknowledged the benefits of these laboratory data for understanding masticatory physiology, but also highlighted the importance of collecting ecologically relevant data on jaw-muscle function from free-ranging primates in their natural habitats (Williams *et al.* 2008). Specifically, we argued that naturalistic physiology data are integral for more accurately linking jaw-muscle EMGs to the evolution of primate cranial form and for placing the laboratory data in an appropriate adaptive context (Thompson *et al.* 2011; Williams *et al.* 2008). By determining how the timing and relative magnitude of jaw-muscle recruitment during feeding varies with food mechanical properties and other ecological parameters in free-ranging primates, we gain a better understanding of how diets relate to masticatory function (Fig. 1b).

Methods

Previously, we reported on a telemetry system that transmitted EMG data to a digital compact flash recorder using an FM radio receiver (Williams *et al.* 2008). Although this system continuously transmitted data in real time, we had no ability to power the system on or off to preserve battery life. The available recording time limited our ability to study naturalistic feeding behaviors. Thus, we have modified the prototype telemetry unit described in Williams *et al.* (2008) to extend battery life by allowing remote control of data recording.

The new EMG telemetry system features the ability to control recording duration using Bluetooth technology and on-board storage of EMG data to a MicroSD card. The telemetry unit carried by the subject is attached to a Parani SD100 Bluetooth serial adapter. A similar adapter is attached to the serial port on a laptop computer operated by a researcher (Fig. 2). The Parani units have a communication range of up to 100 m with open line of sight, but this range is reduced by foliage. In our experience, we have routinely communicated between devices at distances of 50 m. We send start and stop commands to the telemetry unit via the Bluetooth adapters. These commands control when data are recorded to the MicroSD card. When data are not being recorded, the telemetry unit defaults to a battery-conservation mode for a chosen duration (typically 3 min) and then “wakes up” for approximately 15 s to search for a command signal from the computer’s Bluetooth adapter. If the remote unit

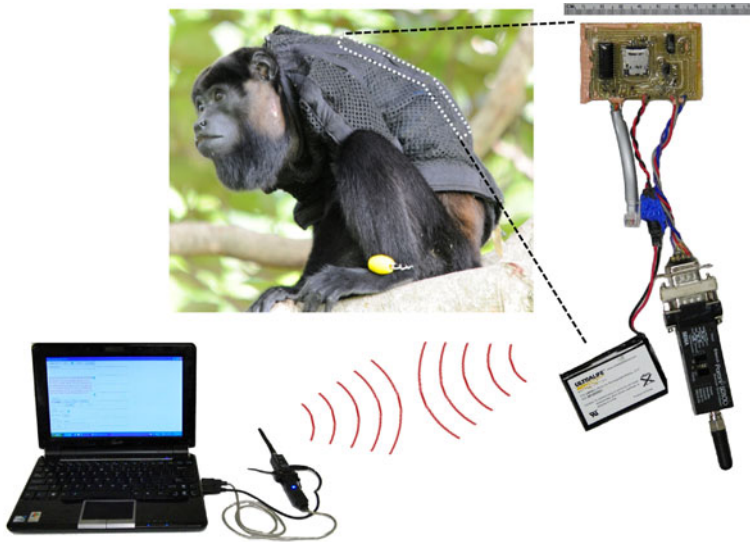


Fig. 2 The EMG telemetry unit. Bipolar indwelling electrodes are inserted into the jaw muscles and attached to the telemetry unit (at right with attached Bluetooth device and battery). The telemetry unit with electrodes attached is placed on the subject's back underneath the jacket worn by the subject (white dotted line on back of jacket). Recording is started and stopped remotely via a Bluetooth connector attached to a computer that must be within 100 m of the Bluetooth connector attached to telemetry unit. We can view EMG traces via the computer software.

does not receive a record command, then it will default to its battery-conservation mode. If instructed to begin recording, the telemetry unit will remain connected to the laptop adapter and record data to the MicroSD card. The telemetry unit will also send subsamples of EMG data to the laptop computer for visual inspection. The transmitted signal includes sector information from the MicroSD card, allowing researchers to use standard field notes to link observed behaviors, e.g., eating leaves in a specific tree, to EMG data stored on the MicroSD card. Once a feeding bout is completed, we remotely stop recording on the telemetry unit, allowing it to return to the battery-conservation mode. Currently, this technology allows 2–3 days of data recording per experiment.

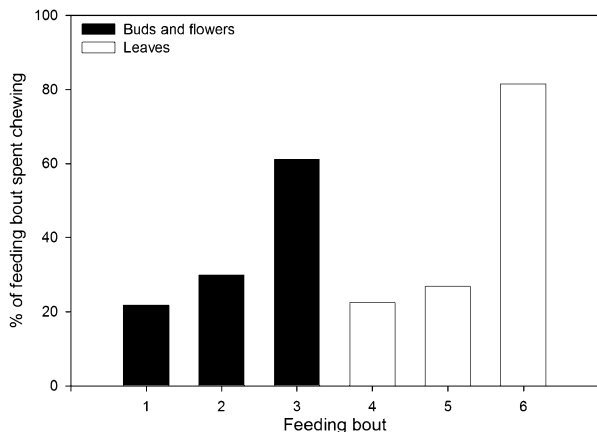
Preliminary Results

We have recorded EMG activity during feeding from the superficial and deep masseter as well as temporalis muscles in several free-ranging mantled howlers at La Pacifica, Costa Rica. These EMG recordings span feeding on leaves, fruits, flowers, and buds from multiple plant species during both wet and dry seasons. The increased recording duration of the new telemetry system has facilitated the characterization of jaw-muscle activity during feeding as primates typically engage in several extended feeding bouts per day with short, opportunistic “snacks” interspersed between these longer bouts. Our preliminary observations unequivocally demonstrate that summed jaw-muscle duty factors, or the percentage of time a muscle is active during a feeding bout, do not necessarily correlate with food

type and can vary markedly within and among individuals (Fig. 3). Moreover, the number of chews per chewing sequence can also differ within and among individuals. We speculate that variation in summed duty factors and number of chews may be related to the patchy distribution of foods within the environment as well as the time required to ingest and evaluate their palatability (Fig. 1c). Although preliminary, these data suggest that summed jaw-muscle duty factors and chewing sequence length may be more variable than anticipated based on expectations from laboratory studies.

Although our primary goal is to document jaw-muscle activity during feeding in natural environments, our findings should benefit other areas in primate feeding research. By directly linking EMG and behavioral data, we can provide novel insights into how behavioral and temporal parameters associated with feeding are related to an animal's physiology in an ecological context (Fig. 1). For example, recent interspecific studies have modeled the relationships among temporal variables associated with feeding, such as chew duration, feeding time; body size; and food properties to understand how the primate feeding system has evolved to meet metabolic requirements (Perry and Hartstone-Rose 2010; Ross *et al.* 2009a,b). By necessity, some of the variables in these models must be estimated from disparate data sets for each species or simplified to constant values. For example, Perry and Hartstone-Rose (2010) recently summarized that primates use a consistent 10 chewing cycles per sequence in their scaling analysis of maximum bite sizes (Ross *et al.*, 2009b). From our EMG data, we can assess the average and, more importantly, the variance in the number of chews per sequence during feeding in natural conditions that will help inform these broader comparative efforts. Thompson *et al.* (2011) also demonstrated that experimental manipulation can result in slightly, but significantly, reduced chewing speeds in laboratory primates. Thus, data on chewing parameters collected in a natural setting will likely generate more realistic estimates of chewing cycle duration as well as other physiological variables for comparative analyses. Finally, we anticipate uncovering novel relationships among jaw-muscle activity and ecological parameters that will benefit a range of research efforts focused on primate feeding (Fig. 1d).

Fig. 3 Percentage of time spent chewing across six different feeding bouts (numbered 1–6) based on jaw-muscle activation patterns. Our preliminary data indicate a fairly high degree of variation in percentage of time the jaw muscles are active, or summed jaw-muscle duty factor, across feeding bouts, suggesting that the time spent chewing may not be closely related to food type.



Food Material Properties and EMG

Question and Background

Is variation in jaw-muscle EMGs correlated with variation in food material properties? Numerous factors influence the physiology of chewing in primates. One of the more important influences on physiology is variation in the material and structural properties of foods. Several laboratory studies have documented changes in jaw-muscle EMGs with variation in food properties (Agrawal *et al.* 1998; Ahlgren 1966; Foster *et al.* 2006; Horio and Kawamura 1989; Hylander and Johnson 1994; Hylander *et al.* 2000; Mioche *et al.* 1999; Møller 1966; Ottenhoff *et al.* 1996; Woda *et al.* 2006). In primates, however, almost all of these laboratory-based studies of chewing physiology have controlled food choice, bite size, and the subjects' environments through various procedures and restraints. One of the key advantages of collecting physiological data on chewing in a natural setting is that each individual has the ability to make its own decisions regarding food type and bite size. Recently, Reed and Ross (2010) hypothesized that animals will modulate their ingested bite size to reduce muscle fatigue by maintaining relatively consistent physiological parameters during feeding. We can evaluate this hypothesis by determining whether jaw-muscle activity patterns correlate with food material properties in free-ranging howlers (Fig. 1b).

Methods

We are measuring mechanical properties of foods eaten by howlers following Teaford *et al.* (2006). Given this repetition, we only outline our methods here. We collect fresh food items similar to those eaten by howlers from marked feeding trees and measure up to five items per tree. We quantify toughness (R), or the energy consumed in propagating a crack of a given area (Ashby 1992), for leaves. We quantify both toughness and the elastic modulus (E), or the ratio of stress to strain during linear deformation (Ashby 1992), for the remaining foods using a portable mechanical properties tester (Darvell *et al.* 1996; Lucas *et al.* 2000). Toughness is measured using "scissors" tests (Darvell *et al.* 1996) at multiple locations for each leaf (Teaford *et al.* 2006). By assessing leaf toughness at multiple locations on a leaf, we can determine whether regional variation in leaf toughness correlates with preferred leaf parts consumed by howlers. Average material properties are compared to average jaw-muscle EMGs observed during chewing of similar food items from the same tree.

A Preliminary Comparison of Leaf Toughness and Masseter EMG

As an illustrative example, we consider the relationship between scaled jaw-muscle EMG activity and food toughness over a 2 d recording period from a single, adult female. During this time period, the female consumed leaves from 11 different trees. We see little association between jaw-muscle EMG activity and leaf toughness ($R=-0.42$, $P=0.2$, $N=11$) among trees over the 2 d recording period. Although highly preliminary, the lack of association may suggest that food material properties are not always closely related to physiological parameters during mastication on a day-to-day basis

in howlers. If this result holds up with additional data analysis, it would support the hypothesis that animals effectively modulate their masticatory physiology to reduce muscle fatigue (Reed and Ross 2010). Whether other primate species follow this pattern, particularly those that may exhibit a larger daily range of variation in food material properties, requires further study. Moreover, this finding would suggest a possible scale effect on the relationship between jaw-muscle activity and food properties. Daily patterns may not be closely correlated with EMG values, but seasonal and longer scale patterns are more likely to be associated, as greater dietary variation would be expected over these longer periods of time. We speculate that the range of foods offered primates in a single laboratory experiment, where stronger correlations between jaw-muscle EMG and food properties are observed, are more likely to capture levels of variation that would typify longer time scales in the wild.

Tooth Wear and Jaw-Muscle EMGs in Mantled Howlers

Question and Background

How is jaw-muscle activity related to patterns and rates of tooth wear in howlers? Since the early 1990s, Teaford and colleagues have been studying the dental morphology and tooth wear of howlers at Hacienda La Pacifica. By adapting laboratory methods for molding teeth of living primates (Teaford and Glander 1991; Teaford and Oyen 1989) as well as collecting molds of selected individuals over multiple annual seasons, they have amassed an extensive data set for studying the relationship between dental functional morphology and feeding ecology. Previously, these data have been used to study 1) the relationship between diet and dental wear (Teaford and Glander 1996), 2) the effects of seasonality and microhabitat on microwear patterns (Teaford and Glander 1991, 1996), 3) long- and short-term wear rates and patterns (Dennis *et al.* 2004; Teaford and Glander 1996), 4) the effects of natural exogenous abrasives on microwear (Ungar *et al.* 1995), and 5) how differential wear among tooth types, i.e., incisors versus molars, correlates with feeding behaviors (Teaford *et al.* 2006). Coupled with data on feeding ecology collected by Glander and colleagues (Glander 1975, 1979, 1981; Glander and Nisbett 1996), this work provides a unique perspective into primate dentitions over their functional lifetime and one of the most detailed views into the functional and ecological morphology of wild primate dentitions.

Recent research on howler teeth at La Pacifica has focused on quantifying topographical changes in occlusal morphology associated with tooth wear over time (Dennis *et al.* 2004). This research demonstrates that although howlers from different microhabitats exhibit varying microwear patterns (Teaford and Glander 1991, 1996), they do not exhibit different wear-related changes in occlusal morphology. Moreover, some aspects of molar topography, e.g., cusp angle, are maintained with wear. These results highlight the importance of understanding how wear affects dental function and suggest that natural selection may promote dental morphologies that maintain functionality with wear (Dennis *et al.* 2004). Similar to other work on wild primate dentitions (Cuozzo and Sauter 2006; King *et al.* 2005; Millette *et al.* 2009), these long-term studies at La Pacifica also help us understand how changes in tooth

function may influence other aspects of primate behavior, ecology, and life history (Fig. 1).

Methods and Approach

We continue to collect dental impressions from howlers at La Pacifica focusing on individuals with concurrent jaw-muscle EMG data. Methods for collecting dental molds follow procedures described in Teaford and Glander (1991, 1996). For several individuals, we have molds of the dentition taken just before and after EMG data collection in both the wet and dry seasons. Comparisons of casts spanning these 2–3 day periods will allow us to calculate short-term wear rates (Teaford and Glander 1991, 1996). Comparisons of casts spanning different seasons will allow us to track rates and patterns of molar wear over the course of several months and potentially years with repeat assessment. Collectively, we will correlate short-term changes in rates and patterns of microscopic dental wear with jaw-muscle EMGs (Fig. 1b). We will consider how variation in average food properties as well as food types, e.g., leaves vs. fruits, across our short-term windows, i.e., 2–3 days, impacts rates of dental wear (at different points along the tooth row) and jaw-muscle activity patterns. Finally, we will evaluate how jaw-muscle EMGs and feeding behaviors vary as a function of tooth wear stages. These temporal comparisons will provide insight into how animals physiologically or behaviorally compensate for decreased chewing efficiency associated with the loss of occlusal topography at advanced stages of wear (M'Kirera and Ungar 2003) (Fig. 1c).

Spatial Analysis Using GPS/GIS and Feeding Ecology

Question and Background

How is spatial variation in ranging behavior, resource distribution and habitat use related to feeding ecology in howlers? Ecologists have provided a wealth of data on primate feeding ecology, documenting many aspects of diet, feeding behaviors, and resource utilization in numerous primate species (Campbell *et al.* 2007; Charles-Dominique 1977; Clutton-Brock 1977; Kappeler and Pereira 2003; Milton 1980; Richard 1985; Smuts *et al.* 1987; Terborgh 1983). Glander was one of the first primatologists to initiate a long-term study on the nutritional ecology of primate feeding, focusing his efforts on the howlers of La Pacifica (Glander 1975, 1979, 1981; Glander and Nisbett 1996). This research documents how howlers optimize the nutritional value of foods by adjusting plant selection and feeding behaviors between seasons. Although these behavioral modifications have clear physiological consequences for energy and nutrient acquisition, additional data on the distribution of available foods and how animal movement patterns relate to this food distribution will benefit our understanding of primate feeding ecology and physiology. By combining with EMG data and tooth wear data, we can begin to assess whether spatiotemporal distribution of foods and travel patterns relate to physiological data, such as increased or decreased jaw-muscle activity, as well as whether advanced dental wear states correlate with travel patterns to potentially identify more easily processed foods throughout a monkey's range (Fig. 1c).

Methods

Our initial goal is to document the spatial distribution of trees throughout the home range of our primary study group, i.e., Forest 1A (Fig. 4). Approximately 10,000 trees were previously tagged by Glander at La Pacifica (Glander 1975; Glander and Nisbett 1996). Between 2008 and 2010, we completed tree tagging in Forest 1A and recorded GPS coordinates for all trees reaching the canopy using a hand-held GPS unit (Garmin, GPSMap 60 CS). We are in the process of species identification of the trees in this home range area. Tree coordinate data will be integrated into geographical information systems (GIS) using ArcGIS 10 for spatial analysis.

We use two methods to document ranging patterns and habitat use of howlers in Forest 1A. First, we conduct focal animal sampling at 5-min intervals to document position in the forest using tree tag numbers as well as several basic behaviors such as feeding, resting, locomotion, grooming, and various social interactions. We also document movement patterns for focal individuals by recording the time a subject enters or leaves a tree. Second, several individuals have been outfitted with a GPS pod (Quantum 4000 Enhanced GPS pod, Telemetry Solution) that logs GPS coordinate data every 20 s for several days. Typically, subjects carrying these GPS units are the same individuals that have been simultaneously outfitted to record EMG data. This allows us to simply place the GPS pod in the jacket that EMG individuals wear during the recording period (Fig. 2).

Preliminary Results

Using the tree GPS data, we have started to document the spatial distribution of several tree species in Forest 1A (Fig. 5). To date, we have observed howlers feeding

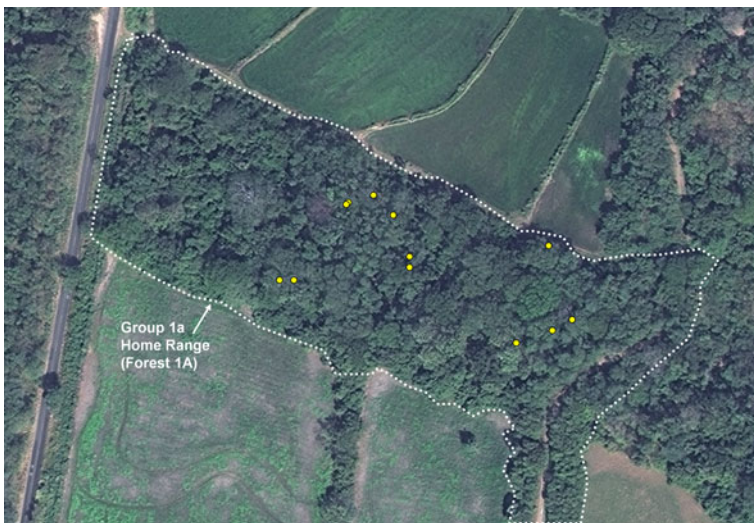


Fig. 4 High-resolution satellite image of Forest 1A showing the approximate home range for howler group 1A at La Pacifica (dotted white line). Within this home range, the yellow dots indicate feeding sites for a female howler over a single day during the wet season (July). The individual traveled *ca.* 545 m throughout that day.



Fig. 5 Aerial photograph of Forest 1A showing the distribution of *Lonchocarpus minimiflorus* (blue), *Myospermum frutescens* (purple), and *Chlorophora tinctoria* (red) trees. Feeding sites for the single female shown in Fig. 3 are overlain (yellow).

in only one (*Lonchocarpus minimiflorus*) of the five most common trees in Forest 1A. This preliminary result matches previous long-term data from at La Pacifica where Glander (1979) observed that howlers spent only 5.1% of feeding time (during 442 h of observation) in the five most common trees (Glander, 1979). In contrast, we observed repeated feeding bouts over multiple days (and years) on the fruit of *Chlorophora tinctoria*, despite the limited number of trees of *C. tinctoria* in Forest 1A (Fig. 5). Collectively, these results support the concept that howlers may not have unlimited food resources in their range.

We have also documented daily path lengths for several individuals using GPS records. As an example, Fig. 4 shows the feeding trees of an adult female during a single day in July 2008. We estimated a daily path length of 545 m using GPS data and ArcGIS 9.2 (Fig. 4). This calculated path length of 545 m is consistent with wet (592 m) and dry (552 m) season averages at La Pacifica (Glander 1979). In this example, the howler's movements appear to be directed toward specific feeding trees. This finding is not surprising given that previous work shows howlers increase their daily travel length to feed from specific trees after deforestation (Clarke 2001). Our preliminary interpretation is that high tree species diversity helps howlers to exist within relatively small home ranges and may allow them to fare particularly well relative to other primates in fragmented habitats. Additional habitat use data and verification of tree species are necessary to address this and related questions fully.

Spatial analysis of feeding ecology may have broader implications for the conservation of mantled howlers. The quality and quantity of food available to primates covaries with deforestation and isolation of forest fragments (Arroyo-Rodriguez and Mandujano 2006; Fahrig 2003). It has even been suggested that populations of primates living in small fragments have higher probabilities of extinction (Hanski 1999). Further, there is research to suggest that many primate species, including howlers, have little probability of occupying forest fragments smaller than 10 ha

(Mandujano and Estrada 2005). At La Pacifica, habitat destruction due to clear-cutting began in the 1950s, but many forest fragments were left to serve as wind-breaks to prevent erosion. In 1990, a government-initiated canal system reduced the forest by an additional 60 ha (4.5%) (Clarke *et al.* 2002; Glander and Nisbett 1996). A previous study at Hacienda La Pacifica on the response of mantled howlers to deforestation demonstrated that although the number of adults per group decreased significantly, the population size remained unchanged due to the increase in immature howlers. This increase in number of young howlers suggests a stable, if not expanding population at La Pacifica (Clarke *et al.* 2002). Spatial analysis of feeding ecology may provide additional insight into how these populations persist at La Pacifica despite the destruction of their habitat.

Future Directions in Studying the Ecological Physiology of Feeding in Howlers

We have outlined several approaches related to studying the physiology and ecology of feeding in howlers. In addition to these ongoing efforts, we are currently incorporating additional research questions into our studies of howler ecological physiology. We briefly describe three of these research areas below related to *in vivo* bone strains during chewing and social as well as hormonal influences on feeding. Although the methods associated with these research questions have been applied to primates in the past, we argue that the synthesis resulting from asking all of these questions simultaneously will benefit our understanding of primate feeding biology (Fig. 1d).

Recording *In vivo* Bone Strains During Natural Feeding

In vivo bone strains in laboratory studies of primate chewing and biting provide much of the empirical basis for identifying which areas of the skull we think experience significant loads during feeding and what types of loads occur in these regions (Hylander 1979a–c, 1984, 1985; Hylander and Johnson 1992; Hylander *et al.* 1987, 1991, 1998; Ross 2001; Ross and Hylander 1996). We routinely translate these *in vivo* data into functional and evolutionary interpretations of morphological variation in primate skull form (Anapol and Lee 1994; Bouvier 1986; Daegling 1992; Hylander 1979b, 1985, 1988; Ravosa 1991; Ravosa *et al.* 2000; Taylor 2002; Vinyard *et al.* 2003). As is true for EMG data, we do not know whether bone strain patterns collected in the laboratory closely match deformations routinely experienced by free-ranging individuals during feeding in their natural habitats. We can utilize the telemetry technology and protocol described earlier for EMG data collection to record *in vivo* bone strains during feeding in free-ranging howlers at La Pacifica. In addition to furthering our understanding of how platyrrhine jaws are loaded during mastication, we can calibrate laboratory data on bone deformation patterns as well as understand how naturalistic feeding impacts the skull in these primates.

Social Impacts on Feeding Behavior in Howlers

The influence of food distribution on social behavior has been extensively documented in primatology (Isbell 1991; Koenig 2002; Terborgh and Janson 1986; van

Schaik 1989; Wrangham 1980) as socioecological models have formed the dominant paradigm for understanding primate social behaviors over the last 30 years. Social pressures can also influence feeding behavior, as evidence exists that humans modify feeding behavior in response to social stimuli (Meyer and Waller 1999; Raspopow *et al.* 2010; Waller and Mijatovich 1998) and that social rank can affect food intake in nonhuman primates (Janson 1988; van Noordwijk and van Schaik 1987; Vogel 2005). Studies assessing food choice often compare an individual's exploited food species to either a random sample of potential foods or a census of available resources. If social factors, such as dominance, feeding competition, or intragroup alliances, restrict the feeding options available to an individual, then the observed feeding behavior may not necessarily reflect the optimized food preference in an environment, but rather the equivalent of a "realized feeding niche." In this case, the individual may attempt to optimize feeding resources within a situation constrained by both ecological and social variables. It is easy to envision instances in which social factors could constrain feeding behavior: 1) a dominant individual may exclude one of lower rank from a preferred feeding tree, forcing it to consume a lower quality resource or 2) an individual may choose to forage independently on low-density, dispersed resources rather than compete with group members feeding in a larger, clumped food resource (Fig. 1). Incorporating these social interactions with research on the ecological factors influencing feeding will provide a more holistic understanding of feeding behaviors in socially complex primates (Fig. 1d).

Hormones as a Proximate Mechanism for Feeding Decisions

Hormone pathways provide a proximate physiological mechanism through which environmental and social conditions can directly influence an animal's behavior. Thus, it is likely that changes in certain hormone levels serve as functional cues for an animal to modify its food selection or foraging strategy (Fig. 1d). For example, multiple studies have correlated changes in the stress hormone cortisol to seasonal changes in food availability (Behie *et al.* 2010; Cavigelli 1999; Muller and Wrangham 2004). A metabolic function of cortisol in mobilizing glucose is also well established (Sapolsky 2002), suggesting that cortisol may act as a physiological signal for changes in feeding behavior (Fig. 1d). In captive rhesus macaques, low-rank individuals consumed more calorically dense foods relative to high-rank ones. The increased consumption of these foods by low-rank individuals reduced their cortisol levels, suggesting associations exist among hormones, social environment, and feeding behavior (Arce *et al.* 2010). Finally, cortisol is feasibly measured noninvasively in free-ranging primates through urine and feces (Whitten *et al.* 1998; see Hodges and Heistermann 2011 for methodological considerations related to field endocrinology).

Hormones that play a functional role in signaling nutritional status, such as leptin, are also promising physiological mechanisms for triggering feeding modifications (Fig. 1d). Leptin can serve as a direct indicator of an animal's caloric deficits as well as predict future food intake (Chin-Chance *et al.* 2000; Friedman and Halaas 1998; Margetic *et al.* 2002). We hypothesize that relative leptin levels, taken from urine samples of free-ranging howlers will correlate with temporal changes in food choice, masticatory activity, foraging and ranging patterns (Fig. 1d). Once appropriate

methodological validations are completed, potential associations would implicate variation in this nutritional hormone as an important factor influencing feeding behaviors.

Finally, quantifying thyroid hormones (triiodothyronine [T_3] and thyroxine [T_4]) provides an avenue for investigating how thermoregulation impacts feeding behaviors in free-ranging primates. T_3 and T_4 act to generate body heat by increasing an animal's metabolism. For example, Basal Metabolic Rate (BMR) in humans can decrease by 30% in the absence of these hormones (Silva 2003). By changing BMR, T_3 and T_4 can significantly alter an animal's caloric needs. Interestingly, excess T_3 and T_4 , i.e., hyperthyroidism, generate not only increased food consumption, but also preferential consumption of carbohydrates over protein or fats (Pijl *et al.* 2001). This finding provides intriguing evidence that environmental variation, mediated through hormones, may impact food choice in primates (Fig. 1d). Expanding our knowledge of the role hormones play in feeding behavior is necessary to holistically understand an organism's ecological physiology.

Prospects for an Ecological Physiology of Feeding in Primates

Mantled howlers offer a useful primate model for initiating an ecological physiology of primate feeding because of their relatively large size and diurnality, and our ability to observe feeding behaviors in their habitat. Other primate species and their environments may pose added challenges related to smaller body sizes, increased ranging of animals, and inhabiting higher canopy levels or denser habitats. Despite these challenges, we argue that many of the approaches described here can be adapted effectively to collect similar physiological, ecological, and behavioral data in other primate species. Many of these methods require an improved field station including power and sufficient space for primate manipulation and minor surgery. An additional significant challenge is the ability to capture wild primates effectively and safely without subsequent debilitation. Specifically, capture will require expertise commensurate with the challenges posed by the animal's size, ranging patterns, and habitat density (Glander *et al.* 1991). Although certainly challenging, the effective capture and manipulation of species from dwarf lemurs to baboons demonstrates the feasibility for capture of multiple primate species across a range of habitats (Brain and Mitchell 1999; Cuzzo and Sauther 2006; Dausmann *et al.* 2004; Glander *et al.* 1991; King *et al.* 2005; Vinyard *et al.* 2008). We argue, based on this assessment, that it is possible to expand this research to other primate species and further document how physiological processes during feeding help primates cope with the ecological and social challenges posed by their environments.

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References

- Agrawal, K. R., Lucas, P. W., Bruce, I. C., & Prinz, J. F. (1998). Food properties that influence neuromuscular activity during human mastication. *Journal of Dental Research*, *77*, 1931–1938.
- Ahlgren, J. (1966). Mechanism of mastication. *Acta Odontologica Scandinavica*, *24*, 1–109.
- Anapol, F., & Lee, S. (1994). Morphological adaptations to diet in platyrrhine primates. *American Journal of Physical Anthropology*, *94*, 239–261.
- Arce, M., Michopoulos, V., Shepard, K. N., Ha, Q. C., & Wilson, M. E. (2010). Diet choice, cortisol reactivity, and emotional feeding in socially housed rhesus monkeys. *Physiology & Behavior*, *101*, 446–455.
- Arroyo-Rodriguez, V., & Mandujano, S. (2006). Forest fragmentation modifies habitat quality for *Alouatta palliata*. *International Journal of Primatology*, *27*, 1079–1096.
- Ashby, M. F. (1992). *Materials selection in mechanical design*. Oxford: Pergamon.
- Ayres, J. M. (1986). *Uakaris and Amazonian flooded forest*. Cambridge: Cambridge University Press.
- Bartholomew, G. A. (1987). Interspecific comparison as a tool for ecological physiologists. In M. E. Feder, A. F. Bennett, W. W. Burggren, & R. B. Huey (Eds.), *New directions in ecological physiology* (pp. 11–35). Cambridge: Cambridge University Press.
- Behie, A. M., Pavelka, M. S. M., & Chapman, C. A. (2010). Sources of variation in fecal cortisol levels in howler monkeys in Belize. *American Journal of Primatology*, *72*, 600–606.
- Bouvier, M. (1986). A biomechanical analysis of mandibular scaling in Old World monkeys. *American Journal of Physical Anthropology*, *69*, 473–482.
- Bradshaw, D. (2003). *Vertebrate ecophysiology: An introduction to its principles and applications*. Cambridge: Cambridge University Press.
- Brain, C., & Mitchell, D. (1999). Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *International Journal of Primatology*, *20*, 585–598.
- Campbell, C. J., Fuentes, A., MacKinnon, K. C., Panger, M., & Bearder, S. K. (2007). *Primates in perspective*. New York: Oxford University Press.
- Cavigelli, S. A. (1999). Behavioural patterns associated with faecal cortisol levels in free-ranging female ring-tailed lemurs, *Lemur catta*. *Animal Behaviour*, *67*, 935–944.
- Charles-Dominique, P. (1977). *Ecology and behaviour of nocturnal primates*. New York: Columbia University Press.
- Chin-Chance, C., Polonsky, K. S., & Schoeller, D. A. (2000). Twenty-four-hour leptin levels respond to cumulative short-term energy imbalance and predict subsequent intake. *Journal of Clinical Endocrinology and Metabolism*, *85*, 2685–2691.
- Clarke, M. R. (2001). Responses to deforestation in a group of mantled howlers (*Alouatta palliata*) in Costa Rica. *International Journal of Primatology*, *23*, 365–380.
- Clarke, M. R., Crockett, C. M., Zucker, E. L., & Zaldivar, M. (2002). Mantled howler population of Hacienda La Pacifica, Costa Rica, between 1991 and 1998: Effects of deforestation. *American Journal of Primatology*, *56*, 155–163.
- Clutton-Brock, T. H. (1977). *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes*. London: Academic.
- Cuzzo, F. P., & Sauther, M. L. (2006). Severe wear and tooth loss in wild ring-tailed lemurs (*Lemur catta*): A function of feeding ecology, dental structure, and individual life history. *Journal of Human Evolution*, *51*, 490–505.
- Daegling, D. J. (1992). Mandibular morphology and diet in the genus *Cebus*. *International Journal of Primatology*, *13*, 545–570.
- Darvell, B. W., Lee, P. K. D., Yuen, T. D. B., & Lucas, P. W. (1996). A portable fracture toughness tester for biological materials. *Measurement Science and Technology*, *7*, 954–962.
- Dausmann, K. H., Glos, J., Ganzhorn, J. U., & Heldmaier, G. (2004). Hibernation in a tropical primate. *Nature*, *429*, 825–826.

- Dennis, J. C., Ungar, P. S., Teaford, M. F., & Glander, K. E. (2004). Dental topography and molar wear in *Alouatta palliata* from Costa Rica. *American Journal of Physical Anthropology*, *125*, 152–161.
- Di Fiore, A. (2004). Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest. *International Journal of Primatology*, *25*, 767–801.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 487–515.
- Foster, K. D., Woda, A., & Peyron, M. A. (2006). Effect of texture of plastic and elastic model foods on the parameters of mastication. *Journal of Neurophysiology*, *95*, 3469–3479.
- Friedman, J. M., & Halaas, J. L. (1998). Leptin and the regulation of body weight in mammals. *Nature*, *395*, 763–770.
- Glander, K. E. (1975). Habitat description and resource utilization: A preliminary report on mantled howling monkey ecology. In R. H. Tuttle (Ed.), *Socioecology and psychology of primates* (pp. 37–57). The Hague: Mouton.
- Glander, K. E. (1979). Howling monkey feeding behavior and plant secondary compounds: A study of strategies. In G. G. Montgomery (Ed.), *The ecology of arboreal folivores* (pp. 561–574). Washington, DC: Smithsonian Institution Press.
- Glander, K. E. (1981). Feeding patterns in mantled howling monkeys. In A. C. Kamil & T. D. Sargent (Eds.), *Foraging behavior: Ecological, ethological, and psychological approaches* (pp. 231–257). New York: Garland Press.
- Glander, K. E., & Nisbett, R. A. (1996). Community structure and species density in tropical forest associations in Guanacaste Province, Costa Rica. *Brenesia*, *45–46*, 113–142.
- Glander, K. E., Fedigan, L. M., Fedigan, L., & Chapman, C. (1991). Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatologica*, *57*, 70–82.
- Hanski, I. (1999). *Metapopulation ecology*. New York: Oxford University Press.
- Hodges, J. K., & Heistermann, M. (2011). Field endocrinology: Monitoring hormonal changes in free-ranging primates. In J. M. Setchell & D. J. Curtis (Eds.), *Field and laboratory methods in primatology: A practical guide* (pp. 353–370). Cambridge: Cambridge University Press.
- Horio, T., & Kawamura, Y. (1989). Effects of texture of food on chewing patterns in the human subject. *Journal of Oral Rehabilitation*, *16*, 177–183.
- Hylander, W. L. (1979a). Mandibular function in *Galago crassicaudatus* and *Macaca fascicularis*: An in vivo approach to stress analysis of the mandible. *Journal of Morphology*, *159*, 253–296.
- Hylander, W. L. (1979b). An experimental analysis of temporomandibular joint reaction force in macaques. *American Journal of Physical Anthropology*, *51*, 433–456.
- Hylander, W. L. (1979c). The functional significance of primate mandibular form. *Journal of Morphology*, *160*, 223–240.
- Hylander, W. L. (1984). Stress and strain in the mandibular symphysis of primates: A test of competing hypotheses. *American Journal of Physical Anthropology*, *61*, 1–46.
- Hylander, W. L. (1985). Mandibular function and biomechanical stress and scaling. *American Zoologist*, *25*, 315–330.
- Hylander, W. L. (1988). Implications of in vivo experiments for interpreting the functional significance of “robust” australopithecine jaws. In F. E. Grine (Ed.), *Evolutionary history of the “robust” australopithecines* (pp. 55–83). New York: Aldine de Gruyter.
- Hylander, W. L., & Johnson, K. R. (1992). Strain gradients in the craniofacial region of primates. In Z. Davidovitch (Ed.), *The biological mechanisms of tooth movement and craniofacial adaptation* (pp. 559–569). Columbus: Ohio State University.
- Hylander, W. L., & Johnson, K. R. (1994). Jaw muscle function and wishboning of the mandible during mastication in macaques and baboons. *American Journal of Physical Anthropology*, *94*, 523–547.
- Hylander, W. L., Johnson, K. R., & Crompton, A. W. (1987). Loading patterns and jaw movements during mastication in *Macaca fascicularis*: A bone-strain, electromyographic, and cineradiographic analysis. *American Journal of Physical Anthropology*, *72*, 287–314.
- Hylander, W. L., Picq, P. G., & Johnson, K. R. (1991). Masticatory-stress hypotheses and the supraorbital region of primates. *American Journal of Physical Anthropology*, *86*, 1–36.
- Hylander, W. L., Ravosa, M. J., Ross, C. F., & Johnson, K. R. (1998). Mandibular corpus strain in primates: Further evidence for a functional link between symphyseal fusion and jaw-adductor muscle force. *American Journal of Physical Anthropology*, *107*, 257–271.
- Hylander, W. L., Ravosa, M. J., Ross, C. F., Wall, C. E., & Johnson, K. R. (2000). Symphyseal fusion and jaw-adductor muscle force: An EMG study. *American Journal of Physical Anthropology*, *112*, 469–492.

- Hylander, W. L., Vinyard, C. J., Ravosa, M. J., Ross, C. F., Wall, C. E., & Johnson, K. R. (2004). Jaw adductor force and symphyseal fusion. In F. Anapol, R. Z. German, & N. G. Jablonski (Eds.), *Shaping primate evolution: Papers in honor of Charles Oxnard* (pp. 229–257). Cambridge, UK: Cambridge University Press.
- Hylander, W. L., Wall, C. E., Vinyard, C. J., Ross, C., Ravosa, M. R., Williams, S. H., & Johnson, K. R. (2005). Temporalis function in anthropoids and strepsirrhines: An EMG study. *American Journal of Physical Anthropology*, *128*, 35–56.
- Hylander, W. L., Vinyard, C. J., Wall, C. E., & Johnson, K. R. (2011). Functional and evolutionary significance of the recruitment and firing patterns of the jaw adductors during chewing in Verreaux's sifaka (*Propithecus verreauxi*). *American Journal of Physical Anthropology*, *145*, 531–547.
- Isbell, L. A. (1991). Contest and scramble competition: Patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, *2*, 143–155.
- Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. *Behaviour*, *105*, 53–76.
- Kappeler, P. M., & Pereira, M. E. (2003). *Primate life histories and socioecology*. Chicago: University of Chicago Press.
- Karasov, W. H., & del Rio, C. M. (2007). *Physiological ecology*. Princeton: Princeton University Press.
- Kawai, N., Tanaka, E., Langenbach, G. E. J., van Wessel, T., Brugman, P., Sano, R., van Eijden, T. M. G. J., & Tanne, K. (2007). Daily jaw muscle activity in freely moving rats measured with radio-telemetry. *European Journal of Oral Science*, *145*, 15–20.
- King, S. J., Arrigo-Nelson, S. J., Pochron, S. T., Semprebon, G. M., Godfrey, L. R., Wright, P. C., *et al.* (2005). Dental senescence in a long-lived primate links infant survival to rainfall. *Proceedings of the National Academy of Sciences of the USA*, *102*, 16579–16583.
- Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, *23*, 759–783.
- Langenbach, G. E. J. (2011). The physiology and ontogeny of daily oral behaviors. *Integrative and Comparative Biology*, *51*, 289–296.
- Langenbach, G. E. J., van Ruijven, L. J., & van Eijden, T. M. G. J. (2002). A telemetry system to chronically record muscle activity in middle-sized animals. *Journal of Neuroscience Methods*, *114*, 197–203.
- Langenbach, G. E. J., van Wessel, T., Brugman, P., & van Eijden, T. M. G. J. (2004). Variation in daily masticatory muscle activity in the rabbit. *Journal of Dental Research*, *83*, 55–59.
- Lucas, P. W., Turner, I. M., Dominy, N. J., & Yamashita, N. (2000). Mechanical defenses to herbivory. *Annals of Botany*, *86*, 913–920.
- M'Kirera, F., & Ungar, P. S. (2003). Occlusal relief changes with molar wear in *Pan troglodytes troglodytes* and *Gorilla gorilla gorilla*. *American Journal of Primatology*, *60*, 31–41.
- Mandujano, S., & Estrada, A. (2005). Detection of area thresholds and isolation distance for forest fragment occupation by howler monkeys, *Alouatta palliata*, Los Tuxtlas, Mexico. *Universidad y Ciencia*, *11*, 11–21.
- Margetic, S., Gazzola, C., Pegg, G. G., & Hill, R. A. (2002). Leptin: A review of its peripheral actions and interactions. *International Journal of Obesity*, *26*, 1407–1433.
- Meyer, C., & Waller, G. (1999). The impact of emotion upon eating behavior: The role of subliminal visual processing of threat cues. *The International Journal of Eating Disorders*, *25*, 319–326.
- Millette, J. B., Sauther, M. L., & Cuozzo, F. P. (2009). Behavioral responses to tooth loss in wild ring-tailed lemurs (*Lemur catta*) at the Beza Mahafaly Special Reserve, Madagascar. *American Journal of Physical Anthropology*, *140*, 120–134.
- Milton, K. (1980). *The foraging strategies of howler monkeys: A study in primate economics*. New York: Columbia University Press.
- Milton, K. (1998). Physiological ecology of howlers (*Alouatta*): Energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology*, *19*, 513–547.
- Mioche, L., Bourdiol, P., Martin, J. F., & Noel, Y. (1999). Variations in human masseter and temporalis muscle activity related to food texture during free and side-imposed mastication. *Archives of Oral Biology*, *44*, 1005–1012.
- Miyamoto, K., Yamada, K., Ishizuka, Y., Morimoto, N., & Tanne, K. (1996). Masseter muscle activity during the whole day in young adults. *American Journal of Orthodontics and Dentofacial Orthopaedics*, *110*, 394–398.
- Møller, E. (1966). The chewing apparatus: An electromyographic study of the action of the muscles of mastication and its correlation to facial morphology. *Acta Physiologica Scandinavica*, *69* (Supplement 280), 1–229.

- Muller, M. N., & Wrangham, R. W. (2004). Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology and Sociobiology*, 55, 332–340.
- Norconk, M. A. (1996). Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 403–423). New York: Plenum.
- Norconk, M. A., Wright, B., Conklin-Brittain, N. L., & Vinyard, C. J. (2009). Mechanical and nutritional properties of food as factors in platyrrhine dietary adaptations. In P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. Heymann, & K. Strier (Eds.), *South American primates: Testing new theories in the study of primate behavior, ecology, and conservation* (pp. 279–319). New York: Springer.
- Ottenhoff, F. A. M., van der Bilt, A., van der Glas, H. W., Bosman, F., & Abbink, J. H. (1996). The relationship between jaw elevator muscle surface electromyogram and simulated food resistance during dynamic condition in humans. *Journal of Oral Rehabilitation*, 23, 270–279.
- Palacios, E., Rodriguez, A., & Defler, T. R. (1997). Diet of a group of *Callicebus torquatus lugens* (Humboldt 1812) during the annual resource bottleneck in Amazonian Colombia. *International Journal of Primatology*, 18, 503–522.
- Petz, A. (2001). Ecology and social organization of the bearded saki *Chiropotes satanas chiropotes* (Primates: Pitheciinae) in Venezuela. *Ecological Monographs*, 1, 1–170.
- Perry, J. M. G., & Hartstone-Rose, A. (2010). Maximum ingested food size in captive strepsirrhine primates: Scaling and the effects of diet. *American Journal of Physical Anthropology*, 142, 625–635.
- Pijl, H., de Meijer, P. H. E. M., Langius, J., Coenegracht, C. I. G. M., van den Berk, A. H. M., Chandie Shaw, P. K., et al. (2001). Food choice in hyperthyroidism: potential influence of the autonomic nervous system and brain serotonin precursor availability. *Journal of Clinical Endocrinology and Metabolism*, 86, 5848–5853.
- Po, J. M. C., Kieser, J. A., Gallo, L. M., Tesenyi, A. J., Herbison, P., & Farella, M. (2011). Time-frequency analysis of chewing activity in the natural environment. *Journal of Dental Research*, 90, 1206–1210.
- Porter, L. M. (2001). Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *International Journal of Primatology*, 22, 961–992.
- Raspopow, K., Abizaid, A., Matheson, K., & Anisman, H. (2010). Psychosocial stressor effects on cortisol and ghrelin in emotional and non-emotional eaters: Influence of anger and shame. *Hormones and Behavior*, 58, 677–684.
- Ravosa, M. J. (1991). Structural allometry of the prosimian mandibular corpus and symphysis. *Journal of Human Evolution*, 20, 3–20.
- Ravosa, M. J., Vinyard, C. J., Gagnon, M., & Islam, S. A. (2000). Evolution of anthropoid jaw loading and kinematic patterns. *American Journal of Physical Anthropology*, 112, 493–516.
- Reed, D. A., & Ross, C. F. (2010). The influence of food material properties on jaw kinematics in the primate, *Cebus*. *Archives of Oral Biology*, 55, 946–962.
- Richard, A. F. (1985). *Primates in nature*. New York: W. H. Freeman.
- Ross, C. F. (2001). In vivo function of the craniofacial haft: The interorbital “pillar”. *American Journal of Physical Anthropology*, 116, 108–139.
- Ross, C. F., & Hylander, W. L. (1996). In vivo and in vitro bone strain in the owl monkey circumorbital region and the function of the postorbital septum. *American Journal of Physical Anthropology*, 101, 183–215.
- Ross, C. F., & Hylander, W. L. (2000). Electromyography of the anterior temporalis and masseter muscles of owl monkeys (*Aotus trivirgatus*) and the function of the postorbital septum. *American Journal of Physical Anthropology*, 112, 455–468.
- Ross, C. F., Reed, D. A., Washington, R. L., Eckhardt, A., Anapol, F., & Shahnoor, N. (2009). Scaling of chew cycle duration in primates. *American Journal of Physical Anthropology*, 138, 30–44.
- Ross, C. F., Washington, R. L., Eckhardt, A., Reed, D. A., Vogel, E. R., Dominy, N. J., et al. (2009). Ecological consequences of scaling of chew cycle duration and daily feeding time in primates. *Journal of Human Evolution*, 56, 570–585.
- Sapolsky, R. M. (2002). Endocrinology of the stress response. In J. B. Becker, S. M. Breedlove, D. Crews, & M. McCarthy (Eds.), *Behavioral endocrinology* (2nd ed., pp. 409–450). Cambridge: MIT Press.
- Schmidt-Nielsen, K. (1990). *Animal physiology: Adaptation and environment* (4th ed.). Cambridge: Cambridge University Press.
- Sibly, R. M., & Calow, P. (1986). *Physiological ecology of animals: An evolutionary approach*. Oxford: Blackwell.
- Silva, J. E. (2003). The thermogenic effect of thyroid hormone and its clinical implications. *Annals of Internal Medicine*, 139, 205–213.

- Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. (1987). *Primate societies*. Chicago: University of Chicago Press.
- Strier, K. B. (1991). Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *American Journal of Primatology*, *23*, 113–126.
- Taylor, A. B. (2002). Masticatory form and function in African apes. *American Journal of Physical Anthropology*, *117*, 133–156.
- Teaford, M. F., & Glander, K. E. (1991). Dental microwear in live, wild-trapped *Alouatta palliata* from Costa Rica. *American Journal of Physical Anthropology*, *85*, 313–319.
- Teaford, M. R., & Glander, K. E. (1996). Dental microwear and diet in a wild population of mantled howlers (*Alouatta palliata*). In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of Neotropical primates* (pp. 433–449). New York: Plenum Press.
- Teaford, M. F., & Oyen, O. J. (1989). Live primates and dental replication: New problems and new techniques. *American Journal of Physical Anthropology*, *80*, 73–81.
- Teaford, M. F., Lucas, P. W., Ungar, P. S., & Glander, K. E. (2006). Mechanical defenses in leaves eaten by Costa Rican howling monkeys (*Alouatta palliata*). *American Journal of Physical Anthropology*, *129*, 99–104.
- Terborgh, J. (1983). *Five New World primates: A study in comparative ecology*. Princeton: Princeton University Press.
- Terborgh, J., & Janson, C. H. (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics*, *17*, 111–135.
- Thompson, C. L., Jackson, E. M., Stimpson, C. D., Horne, W. I., & Vinyard, C. J. (2011). The influence of experimental manipulations on chewing speed in vivo laboratory research in tufted capuchins (*Cebus apella*). *American Journal of Physical Anthropology*, *145*, 402–414.
- Tracy, C. R., Turner, J. S., Bartholomew, G. A., Bennett, A., Billings, W. D., Chabot, B. F., Gates, D. M., Heinrich, B., Huey, R. B., Janzen, D. H., King, J. R., McClure, P. A., McNab, B. K., Miller, P. C., Nobel, P. S. & Strain, B. R. (1982). What is physiological ecology? *Bulletin of the Ecological Society of America*, *63*, 340–347.
- Ungar, P. S., Teaford, M. F., Glander, K. E., & Pastor, R. F. (1995). Dust accumulation in the canopy: A potential cause of dental microwear in primates. *American Journal of Physical Anthropology*, *97*, 93–99.
- van Noordwijk, M. A., & van Schaik, C. P. (1987). Competition among female long-tailed macaques, *Macaca fascicularis*. *Animal Behavior*, *35*, 577–589.
- van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology* (pp. 195–218). Oxford: Blackwell.
- Vinyard, C. J., Wall, C. E., Williams, S. H., & Hylander, W. L. (2003). Comparative functional analysis of skull morphology of tree-gouging primates. *American Journal of Physical Anthropology*, *120*, 153–170.
- Vinyard, C. J., Williams, S. H., Wall, C. E., Johnson, K. R., & Hylander, W. L. (2005). Jaw-muscle electromyography during chewing in Belanger's treeshrews (*Tupaia belangeri*). *American Journal of Physical Anthropology*, *127*, 26–45.
- Vinyard, C. J., Wall, C. E., Williams, S. H., Johnson, K. R., & Hylander, W. L. (2006). Masseter electromyography during chewing in ring-tailed lemurs (*Lemur catta*). *American Journal of Physical Anthropology*, *130*, 85–95.
- Vinyard, C. J., Yamashita, N., & Tan, C. (2008). Linking laboratory and field approaches in studying the evolutionary physiology of biting in bamboo lemurs. *International Journal of Primatology*, *29*, 1421–1439.
- Vinyard, C. J., Wall, C. E., Williams, S. H., Mork, A. L., Armfield, B. A., Melo, L. C. O., *et al.* (2009). The evolutionary morphology of tree gouging in marmosets. In S. M. Ford, L. C. Davis, & L. M. Porter (Eds.), *The smallest anthropoids: The marmoset/Callimico radiation* (pp. 395–410). New York: Springer.
- Vogel, E. R. (2005). Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: The effects of contest competition. *Behavioral Ecology and Sociobiology*, *58*, 333–344.
- Wallace, R. B. (2005). Seasonal variations in diet and foraging behavior of *Ateles chamek* in a southern Amazonian tropical forest. *International Journal of Primatology*, *26*, 1053–1075.
- Waller, G., & Mijatovich, S. (1998). Preconscious processing of threat cues: Impact on eating among women with unhealthy eating attitudes. *The International Journal of Eating Disorders*, *24*, 81–89.
- Whitten, P. L., Brockman, D. K., & Stavisky, R. C. (1998). Recent advances in noninvasive techniques to monitor hormone-behavior interactions. *Yearbook of Physical Anthropology*, *41*, 1–23.

- Williams, S., Vinyard, C., Glander, K., Deffenbaugh, M., Teaford, M., & Thompson, C. (2008). Telemetry system for assessing jaw-muscle function in free-ranging primates. *International Journal of Primatology*, *29*, 1441–1453.
- Woda, A., Foster, K., Mishellany, A., & Peyron, M. A. (2006). Adaptation of healthy mastication to factors pertaining to the individual or to the food. *Physiology & Behavior*, *89*, 28–35.
- Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, *75*, 262–299.
- Wright, B. W. (2005). Craniodental biomechanics and dietary toughness in the genus *Cebus*. *Journal of Human Evolution*, *48*, 473–492.