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EDITORIAL/INTRODUCTION TO SYMPOSIUM

Bridging Gaps Between Experimental and Naturalistic Approaches in the Study of Primate Behavior

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Experimental approaches are a mainstay in the study of primate behavior and functional morphology, particularly those conducted in the laboratory setting where researchers can employ a myriad of sophisticated techniques to precisely and accurately document locomotion (Demes *et al.* 1994, 2001; Larson and Stern 1989; Schmitt and Larson 1995; Schmidt 2005), feeding (Hylander *et al.* 1987; Ross *et al.* 2007; Vinyard *et al.* 2008a), and cognitive behaviors (Tomasello and Call 1997). Experimental techniques permit the isolation of extrinsic variables, allowing us to explore their effects upon primate behaviors separately as well as in combination (D'Août *et al.* 2004; Vereecke *et al.* 2005). A tradeoff occurs in that the laboratory setting restricts choices available to study subjects. Dietary and habitat complexity in laboratory studies (by design) rarely approach those available in the natural environment (Thorpe *et al.* 2007). Captive animals might not be motivated to move at a pace equivalent to the pace of their free-ranging counterparts during naturalistic predator, competitor, or potential mating situations; they may never reach quite as far to select a ripe fruit. Moreover, experimental subjects are often confined to small areas, and rarely have access to natural supports and enclosures extensive enough to recreate daily path lengths, complexity of dietary choices, and overall activity levels that reflect their free-ranging counterparts (Chang *et al.* 1999).

Natural stressors also are likely to differ from those in captivity. Food provisioning replaces the need for hours of physical activity and travel related to foraging, and may render captive animals less active, and generally less inclined or unable to behave in a way representative of conspecifics in the wild. In contrast, captive animals experience the benefits of veterinary care and their survival is less influenced by predator avoidance, seasonal food stress, parasite load and strong

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competition relative to their wild counterparts. As a result, captive animals may exhibit better health at a given age relative to wild individuals, and likely experience longer life spans overall (Morbeck 1999; Morbeck *et al.* 2002). Although these are not necessarily undesirable outcomes of captivity, researchers must recognize the potential bias in performance data collected on animals with seasonally regular diets, lower parasite loads and from those that are geriatric. Indeed, aspects of the captive setting have demonstrated influences upon locomotor/feeding behavior and skeletal morphology (Szalay and Dagosto 1980; Sarmiento 1985; Isler and Thorpe 2003; O'Reagan and Kitchener 2005; Williams *et al.* 2005). Not surprisingly, authors have long promoted caution in generalizing from results obtained solely from indirect measurements of primate behavior in the captive laboratory setting (Altmann 1974).

Collecting behavioral data on wild primates offers advantages mainly in being able to capture the dietary and locomotor strategies that primates actually use in order to survive in nature (Fleagle 1979). Field studies can be as challenged as lab-based studies in several ways. Visibility of study subjects in a complex natural setting can limit the scope of behavioral data sets to a subset of what subjects are actually doing. Behaviors of interest may occur infrequently during the observation period, may be performed out of view of the observer or may not be observed at all. Inaccessibility of parts of home ranges to cumbersome laboratory equipment reduces the types of data that can be assembled, as does the unavailability of electricity that many sophisticated data capture methods require. Experimental approaches conducted in the wild often require live animal capture, commonly including manipulation, placement, and removal of recording devices directly upon subjects. Although certain behavioral variables remain fairly robust to the limitations of field data collection (Stevens *et al.* 2006), even in the best of natural conditions, the dispersion of free-ranging study subjects tends to vary more than in the laboratory. Because experimental field data are difficult to obtain and may not be prerequisites for answering certain primate biology/behavior questions, the following 5 papers in this issue emphasizes the interface of laboratory and field approaches when combined approaches are imperative to collect precise and accurate data for research questions that cannot be addressed solely in the laboratory. Given the limitations in collecting experimental and naturalistic data, using a combined approach can produce significant advantages because questions can be addressed that cannot realistically be answered via either approach in isolation.

The authors of the following 5 papers share perspectives, tools and solutions for integrating experimental and naturalistic data in primatological research on a broad range of feeding and locomotor questions across a diversity of primate species. Collectively, they demonstrate how combined laboratory and field approaches offer new insights into the study of primate behavior.

- Vinyard and colleagues (2008b) apply novel experimental approaches in understanding the ecomorphology of feeding in strepsirrhine primates. They quantify mandibular metric data and maximum bite force in three sympatric bamboo lemur species at Ranomafana National Park, Madagascar. They compare these data with the material properties of food items in the species' respective diets in order to relate jaw morphology and bite performance to differences in diet and feeding behavior. Using portable force transducers in a field setting, they record bite forces on 17 individuals. They demonstrate that the largest of the species examined, the greater bamboo lemur, both exhibits the highest bite forces and also routinely consumes the most mechanically challenging foods.

- B. Wright and colleagues (2008) quantify the material properties of leaves eaten by 4 species of captive primates in Vietnam in order to examine biomechanical requirements of food choice and folivory. They also present a field method for quantifying chewing rates to describe feeding behavior in the subjects. Whereas some chewing variables appear fairly consistent across leaf monkey species, e.g., average toughness of chosen leaves and duration of chewing cycle, other variables differ between *Trachypithecus* species and *Pygathrix* species, e.g., feeding rate. Wright and colleagues suggest this is consistent with distinctive attributes of digestive anatomy reflecting greater emphasis on food breakdown by chewing in *Trachypithecus* and by the stomach in *Pygathrix*. In this way, they integrate digestive morphology, food material properties and feeding behavior to understand feeding in highly specialized folivorous primates.
- Williams and colleagues (2008) examine the use of portable telemetered electromyographic approaches in order to provide unprecedented quantification of jaw muscle activity during feeding in wild primates. They note that the vast majority of research on primate jaw muscle function has been conducted in the laboratory setting, upon restrained animals consuming objects that typically would not constitute natural dietary items. In order to obtain naturalistic chewing data by extending EMG techniques into the wild, they designed a portable system to measure and transmit data on muscle activity. They recorded bilateral activity of superficial and deep masseter muscles and anterior and posterior temporalis muscles in mantled howler subjects at Hacienda La Pacifica in Costa Rica. They provide the first field data on jaw muscle activity in any primate, and provide proof-of-principal for the feasibility of collecting detailed muscle physiology data from wild primates selecting and consuming natural food items.
- Carlson and colleagues (2008) draw upon behavioral observations and bone morphology of free-ranging chimpanzees in order to investigate form-function relationships in their proximal limb segments. They compare structural properties of 28 chimpanzees from communities in Gombe, Mahale Mountains, and Taï Forest National Parks. They find evidence for age-related bone loss among community females, but less so among community males. They also discuss age-related and community-related trends in diaphyseal shape differences in the context of habitat variability among the 3 communities.
- K. Wright and colleagues (2008) quantify limb postures and locomotor behaviors of 3 species of Asian primates in a semi-natural setting, focusing in particular on the relative proportion of suspensory behaviors within their positional repertoires. They document frequent use of suspensory postures and arm-swinging behaviors not only in the white-cheeked gibbons, but also in both red-shanked and gray-shanked doucs. They note that during bimanual locomotion in doucs, forelimb angles at initial contact and release of the branch are similar to those observed in the gibbons filmed in a similar semi-natural setting, but that trunk posture is quite variable, and often less orthograde in the monkeys. They conclude that although suspensory postures and arm-swinging behaviors are

common in doucs relative to other Old World monkeys, continuous bimanual locomotion is less common than in gibbons because doucs also frequently engage in quadrupedal and leaping behaviors.

To ensure a cohesive theme across the papers, each research team considered the following questions: 1) How are experimental and naturalistic data integrated into a single research program? 2) What are some of the challenges in bridging the gaps between these approaches, and what solutions are generated in addressing such challenges? 3) What prospects are envisioned for combined laboratory and field approaches in primate behavior? Taken together, they offer perspectives for primatologists in bridging gaps between experimental and natural approaches in order to offer additional insights into the adaptations and abilities that characterize the Primates.

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