The human-baboon Interface in Laikipia County, Kenya: Implications towards human social evolution and primate/wildlife management strategies.

Introduction

The term "Anthropocene era", first coined in the 1980s by ecologist Eugene F. Stoermer, is an informal geo-chronological term that marks the period during which human activities have had a significant global impact on the Earth's ecosystems. While much of the environmental change on Earth is suspected to be a direct consequence of the Industrial Revolution, it has been proposed that the Anthropocene began approximately 8,000 years ago when humans gradually replaced hunter-gatherer subsistence with farming, animal husbandry, and sedentary lifestyles. These innovations were followed by a wave of wildlife extinctions driven by both the direct activity of humans (e.g. hunting) and the indirect consequences of land-use changes that are still ongoing. The extent of the human impact is further supported by scientific evidence, using global geographic data and advanced GIS technology to map out "The Human Footprint", to illuminate how human activities affect almost every terrestrial system.

It is from this premise I studied the olive baboon's adaptive behavior in contrasting land use systems (i.e., pastoralism and commercial ranching) in Laikipia County. The overarching question for this study was – How do different anthropogenically modified habitats influence primate adaptive social behavior? From an evolutionary perspective, olive baboons are an ideal subject for examining adaptive shifts in behavior in response to short-term ecological changes wrought by anthropogenic impact. This knowledge will provide insights on how humans may have historically induced adaptive behaviors that contributed to both human and nonhuman primate social evolution. More specifically, information on how ecological changes historically contributed to different social systems that ranged from nepotistic or despotic to egalitarian societies.

Laikipia County, in particular, is an ideal scenario in which to evaluate how different anthropogenic impact on the landscape may have influenced how humans evolved socially as a consequence of adaption to ecological changes. First, the different land use systems in Laikipia range from private commercial ranching, communal pastoralism, agropatoralism, all of which are increasingly complemented with ecotourism ventures thus, offering ecological variations that contribute to an overall mosaic landscape scenario. Second, the county is also ideal for studying baboon behavioral response in these varied human modified ecologies for the purposes of improving current management strategies, baboons inhabit and utilize all different land use systems found in Laikipia. Little, however, is known about the nature and flexibility of baboon's responses to human-altered habitats. What has become evident after more than 50 years of primatological research is that, like humans, behavioral flexibility in the face of varying ecological conditions is, in fact, shared by many other primates. The olive baboon (*sensu lato*) is the most widely distributed of all extant *Papio* spp., and an apparently expanding geographical distribution over historical time. This suggests significant behavioral and ecological flexibility in relation to a variety of habitats as well as a possible competitive edge over other baboon morphs. One possible reason for this may be the superior adaptability of the olive baboon to human modified environments. Consequently, olive baboons inhabit diverse human modified habitats that range from semi-arid, thorn scrub to savanna, woodland, gallery forest, and rain forest in arid land use systems.

Theoretical rationale

The potential importance of food availability and predation as selective forces in human social evolution has been hypothesized by the socioecological models. These models are the foundation of our general understanding of social evolution, and the principles derived from them not only help us understand nonhuman primate societies,

but also the evolution of human societies as well as social evolution in general. According to the socioecological models, females compete primarily for resources, and the nature of this competition shapes female social relationships. Competition has two distinct components (i.e., contest or scramble) whose relative strength depends on resource distribution patterns. Contest competition occurs when food resources with high or varying energetic value are relatively discrete ("patchy") allowing some individuals to systematically exclude others from these patches. Consequently, inter-individual distances are predicted to decrease among cohorts of related females who provide coalitionary support to one another for access to these resources. The result is "despotic" social relationships based on female dominance and alliances.

Scramble competition occurs over food resources that are either low in value, highly dispersed, or spread evenly over extremely large areas (relative to the size of the group). In this ecological scenario, inter-individual distances increase and the resulting social pattern is based on weak or non-linear hierarchies (egalitarian). Thus, the nature of female competition and social interaction are hypothesized to reflect these particular patterns of food availability. Additionally, there are trade-offs between foraging efficiency and predation, as increasing group size potentially reduces the risk of predator attack, but simultaneously increases within-group foraging costs. Thus, low predation risk facilitates dispersion of group members (to reduce foraging costs). More importantly, a study of this process can test models of primate social evolution that explicate how solutions to the problems of finding food and minimizing risk of predation influence females social interactions and ultimately social systems.

Traditional socioecological models explain primate social behavior in relation to factors such as the abundance and distribution of food resources as well as the risk of predation - all of which are potentially and substantially impacted by a range of anthropogenic processes. Thus, the significance of my study is the unusual and potentially valuable unique opportunity to exploit a "natural" experiment - human modifications of the habitat to which the olive baboon is well adapted—to test the socioecological model in a manner very rarely executed in the wild. Anthropogenic alteration of habitat vegetation found in Laikipia provided an opportunity to evaluate these models' predictions with respect to variation of food resources and predation on female social interactions. To achieve this goal I conducted ecological surveys a pastoralist land (Thome B) and the other a commercial ranch (Segera) and studied adult females in a baboon group for 18 months, whose home range encompassed these two contrasting land use systems in Laikipia, Kenya.

While it can be argued that incorporating the human dimension to tests socioecological models can be perceived as "noise" that is interfering with the models' predictive powers, some primatologists have argued otherwise. Few primatologist have argued that incorporating the human dimension—beyond the "classic" studies of primate crop raiding and human hunting of primates—is critical for testing socioecological models. It is from this perspective that I argued that conducting primatological studies in a putatively "natural" environment without considering the human dimension implies irrelevance of humans in influencing contemporary primates' socioecology – which also includes humans. This view may not only be ecologically inappropriate in certain cases, but it also overlooks the growing archeological evidence that primates and humans have shared a long evolutionary history and may as a result be coevolving in these shared human modified ecologies as a result.

Major findings

Ecological surveys I conducted within an occupied pastoralist land and a commercial ranch confirmed that these mosaic human modified ecologies with different land used systems contribute to variations in food resources as well as in predation levels for wildlife depending on the management regime in place. I found that differing composition and densities of livestock within two contrasting livestock management regimes (i.e., pastoralism and commercial ranching) influenced the dispersion, abundance, structure, and diversity of local vegetation.

Specifically, food resources were patchier and with increased predator presence on the commercial ranch relative to the pastoralist land.

My findings indicate that humans are key agents in reinforcing the selective pressures of ecological factors (i.e., food availability, predation) that potentially influence primate adaptive behavior and consequently their social evolution. My data revealed that anthropogenic impact on vegetation and predator presence can influence primate feeding and social behavior in a manner consistent with the adaptive socioecological models. More specifically, I confirmed that differing composition and densities of livestock within two contrasting livestock management regimes (i.e., pastoralism and commercial ranching) influenced the dispersion, abundance, structure, and diversity of local vegetation. The anthropogenic influences embodied by the contrasting habitats studied are currently moderate enough to allow baboons (and other wildlife species) to subsist and reproduce, but substantial enough to expose these primates to significantly different ecological settings.

In particular, the overall longer feeding bouts and increased feeding rates observed in the baboons on the commercial ranch suggest that food resources within the commercial ranch were relatively patchier compared to those characterizing the pastoralist land. Of particular interest to this study is the contrary manner in which differing livestock regimes produce differences in woody food availability for baboons in the two land use systems. The pastoralist land had significantly smaller but more abundant woody plants. *Acacia drepanolobium* was the most dominant baboon woody food resources found in the baboons group home range. This *Acacia* species has been documented to increase its thorns and galls (swollen thorns) also known as "compensatory defense mechanisms" in response to increased browsing intensity due to higher livestock densities in the pastoralists' land relative to the commercial ranch. Symbiotic ants are housed within the galls and are also consumed by baboons. These ants attack anything that feeds on these *Acacia* trees as a means of protecting their eggs, larvae and pupae also found in these galls. Thus, the increased number of thorns with galls, combined with the increased numbers of symbiotic ants found in them, limited the ability for baboons to monopolize relatively greater abundance of *Acacia* food resources in the pastoralist land.

Thus, the effective availability of woody food resources on the pastoralist land was therefore more limited than in the commercial ranch despite their relatively higher abundance on the pastoralist land. The ability to monopolize clumped food resources is an attribute of feeding behavior that is predicted to promote contest competition (i.e., increased aggression) as predicted by socioecological models. The scenario on the pastoralist land, thus, appeared to have promoted greater scramble rather than contest competition in the baboons given the limitation to monopolize resources while feeding as a result of increased number of attacking ants, relative to the commercial ranch. These findings also suggest that anthropogenic impact of primate food resources has the potential to influence primate social behavior in a manner somewhat contrary to socioecological predictions.

With respect to socioecological theory, food resources were the most important factor influencing baboon aggressive behaviors across the anthropogenic land use systems in this study. This result reiterates the importance of food availability as an integral selective pressure in the evolution of social behavior in primates. More recently, the validity of socioecological theories has been called into question by primatologists. For example, a few primatologists have reviewed the literature pertaining to the extent, strength, and mode of feeding competition as an influence on female social relationships, as predicted by the socioecological models. Others argue that phylogenetic inertia (the extent of evolutionary relatedness) is the primary force that influences primate social evolution. While it is well documented that parental care, mate guarding, sexual conflict, and phylogenetic inertia are key factors that contribute to the evolution of our social systems, this study re-established the importance of

food as a selective pressure in influencing primate social systems. Baboons in this study also made apparent trade-offs by foraging more efficiently where predation risks was higher, by concurrently potentially decreasing vulnerability to predation by increasing individual vigilance (scanning for predators), as predicted by socioecological theory.

I therefore, reiterate the importance of behavioral plasticity in light of variation of food resources and predator levels in baboons as an attribute of their success in varied human modified ecologies. This study also improves understanding of how (ancestral) humans may have influenced selective pressures that are predicted to have acted on primate social systems – which also includes their own (human) social systems. Such an acknowledgement forces us to reexamine how we humans could, in fact, be coevolving in modified ecologies (both faunal and floral) that we construct to promote our very existence. This study compels us to examine how humans have historically shaped habitats, resource availability, and the presence of predators throughout history. These human modified ecologies consequently influenced the nature of female relationships and ultimately shaping social regimes that ranged from despotic to egalitarian societies. Underlying the use of anthropogenic influence to test socioecological models is an attempt to evaluate *Homo sapiens* (and possibly some of its ancestors) as an important selective force on the evolution of baboon social behavior, beyond simply the effects of baboon predation and crop raiding.

Implications towards primate/wildlife management

Pastoralism is one of the most widespread land use practices in Africa and Asia. It has been going on for thousands of years while commercial ranching was only introduced about two hundred years ago. The comparative approach I used in this study revealed how landscapes are transformed differently under pastoralism versus commercial ranching. Although the potential for indirect competition for terrestrial vegetation between primates and livestock has been recognized for a long time, there are few quantitative data available regarding the influence of livestock grazing on primate social strategies feeding. The rationale for incorporating land use systems in my research is that pastoralism and commercial ranching are more recent anthropogenic phenomena that impose recent, but contrasting, anthropogenic changes to the habitat that can be used to examine behaviorally flexible responses to these ecological changes. The evidence in the archeological record, however, shows that humans have historically shaped habitats, resource availability, and the presence of predators throughout their evolutionary history suggesting a potential coevolutionary relationship between human and primates.

In this study, I provide evidence that a system of adaptive behavioral plasticity operates in response to differences in human modified ecologies. Various anthropogenic processes directly influence the ecological and social challenges that species face. Exactly how wildlife modify their behavior in response to anthropogenic habitats and their associated risks (e.g. during crop raids, livestock predation) is of central concern for the long-term survival of animals whose ranges overlap with humans in shared environments. This approach is a means of testing the socioecological models and not an end in itself. For one, such an approach compels us to examine how humans have historically shaped habitats, resource availability, and the presence of predators throughout history. Further, underlying the use of anthropogenic influence to test socioecological models is an attempt to evaluate *Homo sapiens* (and possibly some of its ancestors) as an additional important selective force on the evolution of primate social behavior which also includes humans. Secondly, the findings from this study are an indication that the humans-primate interface needs be considered while designing primate behavioral field research. It seems very likely that patterns of

primate behavior that we observe today are more often than not a response to human modification of the habitat. Within this Anthropocene era, where man has left his mark virtually everywhere on the globe, it appears almost impossible to tease out which of the behaviors we see in primates today are inherent and which ones are not.

A better understanding of primate behavioral adaptations to human modified habitats is highly warranted as humans are modifying primate habitats at an accelerating rate throughout the world. Some species, including some nonhuman primates, beneficially exploit human modified habitats. Understanding how some wildlife species appear to adapt to human-modified habitats, while others do not, is critically important for implementing conservation and management strategies. Thus, examining the behavioral flexibility of the olive baboon's response to contrasting human modified habitats may therefore also help to clarify why some species of primates, specifically the macaques found in Asia and vervets in Africa, remain exceptionally resilient to anthropogenic disturbance even to the point of thriving in such circumstances. This information will contribute to conservation/management efforts in various regions in in these continents where human-primate interactions are high. Thus, by testing predictions about primate feeding and social behavioral responses to human-modified habitats, this study links theory with practice by evaluating the utility of the socioecological models as practical management/conservations tools based from theoretical information. Such can approach will provide more informed and effective recommendations that will yield tangible and practical contributions to effective wildlife management and conservation practices.