HUMANS, MONKEYS, AND THE ROCK: THE ANTHROPOGENIC ECOLOGY OF THE BARBARY MACAQUES IN THE UPPER ROCK NATURE RESERVE, GIBRALTAR

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ABSTRACT

Current perspectives on ecology are increasingly incorporating humans as significant components of dynamic ecosystems. However, these approaches frequently focus on measuring the impact of humans' habitat alteration, degradation and exploitation on animal or plant populations. In many cases non-human organisms and humans co-exist and interact in a myriad of ways, ranging from competitive to commensal to mutualistic. Understanding these interactive complexes can enable us to increase our assessment and understanding of complex ecological systems. The macaque monkeys (*Macaca sylvanus*) living in the Upper Rock Nature Reserve, Gibraltar, have co-existed with humans for centuries and currently engage in frequent interactions with large numbers of people from across Europe. These interactions involve behavioral, nutritional, physiological, and potentially epidemiological factors. Humans are a core part of these macaques' ecology and the ecosystems in the Upper Rock Nature Reserve. In this paper we present an overview of human-monkey interactions in Gibraltar with a focus on the role that anthropogenic elements play in the behavioral ecology of these monkey and consider the implications of these patterns for the ecosystems across the Upper Rock Nature Reserve.

Keywords: Anthropogenic, Humans, Macaca sylvanus, Ecosystems, Stakeholders, Gibraltar.

INTRODUCTION

Current perspectives on ecology are increasingly incorporating humans as significant components of dynamic ecosystems. However, these approaches frequently focus on measuring the impact of humans' habitat alteration, degradation and exploitation on animal or plant populations. In many cases non-human organisms and humans co-exist and interact in a myriad of ways, ranging from competitive to commensal to mutualistic. Understanding these interactive complexes can enable us to increase our assessment and understanding of complex ecological systems.

It is a widely recognized that a substantial portion of the human adaptive success is effectively represented by ecological alteration and niche construction (Fuentes 2004, Odling-Smee *et al.* 2003, Potts 2004). This pattern is described by geographers and anthropologists as the creation of human "place" (*sensu* Richardson 1989). If there are other organisms living in or around this "place", they are impacted by the ecological contexts manipulated, produced, and modified by human action. In other words, anthropogenic engagement with the environment changes selection pressures and ecological contexts for all sympatric organisms. Humans may be seen as competitive dominants or foundation species in many anthropogenic systems. However, humans are not the only stakeholders with agency in ecological systems. Other mammals, plants, and even microorganisms also impact the structure of elements within any given ecosystem. Fuller understanding of the relationships between humans and the other animals with which they share their environments can facilitate a broader and more inclusive view of ecological systems.

As is evident from the rapid and dramatic reduction in numbers and range of many species, most large animals do not do well when they are a part of human "place". However, in many instances some species, members of the monkey genera *Macaca* (the macaques) for example, do quite well around humans (Fuentes *et al.* 2005). In anthropogenic environments, certain organisms play major roles in the structuring of the local ecology. In the Upper Rock Nature Reserve, Gibraltar, the relationship between barbary macaques (*Macaca sylvanus*) and humans (*Homo sapiens*) plays a principle role in the structure of the environment and therefore the ecological system. In this essay we will examine the role of macaque-human interactions in a human "place" in order to gain insight into the anthropogenic ecology of the barbary macaques in the Upper Rock Nature Reserve, Gibraltar.

ECOLOGICAL CHALLENGES, NICHE CONSTRUCTION, AND FACILITATION

The basic ecological challenges faced by organisms include acquiring energy, avoiding predators and successfully mating (Denham 1971). These challenges are shaped by variables such as the structure of the local habitat, the type and number of conspecifics and other organisms in the habitat, the distribution and densities of food sources, and the patterns of climate change across annual cycles. These variables act as the proximate pressures eliciting the behavioral strategies practiced by organisms in a given ecological context. In order to examine organisms that successfully exist in highly anthropogenic habitats (human "place") two additional concepts need to be added to these basic premises.

Niche construction- Among the most salient advances in evolutionary biology and ecology is the recognition of the role of niche construction, resulting in a removing of the traditional organism/environment dichotomy and its replacement with a more integrated and dynamic view of organism/environment interactions and co-evolution. It is becoming increasingly evident that organisms not only impact their immediate environments but also, in part, shape the selection (ecological/environmental) pressures that they face (Laland *et al.* 2001, Stamps 2003). The niche is best characterized as a "multidimensional hypervolume" (Hutchinson 1957), the "way" that organisms make a living and the eco-context in which organisms occur. If organisms exhibit agency in the active construction of their niches there arises a need to discard the

traditional organism/environment dichotomy and replace it with a concept that more accurately reflects the mutually engaged set of changes and patterns in organisms and environments that emerge through the course of time. According to Laland *et al.* (2001) niche construction, per se, can be seen as "when an organism modifies the functional relationship between itself and its environment by actively changing one of the factors in its environment either by physically perturbing these factors at its current address or by relocating to a different address thereby exposing itself to different factors." Of interest for this essay, humans exhibit dramatic patterns of niche construction (cultural practices across human populations certainly attest to this) that can result in significant ecological changes and subsequent behavioral changes in an array of sympatric organisms (Fuentes *et al.* 2005, Odling-Smee *et al.* 2003, Potts 2004). Environmental modification/manipulation is an important part of the human niche and its impact extends to more than just the humans living in that environment.

Facilitation- While competition does occur and is a significant factor for organisms on this planet, facilitation, or positive interactions between species, or groups within an ecosystem, also drives evolutionary change. Research from ecology, especially intertidal and plant ecosystems, demonstrates that the interactions between two or more species co-existing in the same location and ecological space may alter the selective environments such that each does better when the other is also sharing the environment/ecology (Bruno *et al.* 2003). This is seen at the distinction between realized and fundamental niches (Hutchinson 1957). The fundamental niche is the ecological context in which a species can live indefinitely in the absence of negative interspecific interactions. The realized niche is that eco-space actually occupied by a species after exclusion/competition by other species/competitors (Bruno *et al.* 2003). Research has demonstrated that facilitation can expand the realized niche of many organisms in a shared system, thereby expanding the ecological success of the organisms via mutual use of the same environment.

While this research is currently focused on small animals and plants, the theoretical emphasis on examining multi-species, multi-group, population level interactions for patterns of facilitation can have dramatic impact on our models of what ecological pressures were and are acting on organisms that co-exist in anthropogenic habitats. In this context, some organisms currently viewed as engaged in commensal (co-existant) or mutualistic (directly co-beneficial) relationships with humans could be seen as engaged in a facilitated relationship with humans and/or each other. Facilitation is distinct from commensualism or mutualism in that the interactors do not directly assist one another but rather impact the ecological context such that both groups realized niches expand (and they then receive reduced selective pressures resulting from niche constraints). This is different from by-product mutualism in that we are not focusing on single benefits to one organism arising as a by-product of selfish habitat exploitation by another.

Rather than seeing humans and other organisms as exclusively engaging in strict competition with each other over resources, or directly interacting in mutualistic manners, some level of facilitation may be occurring such that by co-existing with humans the overall pressures are reduced compared to living in non-human occupied environments. In a sense this reinforces the conceptualization of human as a foundation species (sensu Bruno *et al.* 2003, box 3). Even if there is some level of competition between the humans and the other species, their communal impact on their "living space" may be enhancing some aspects of survivability. So, rather than seeing other organisms as living alongside humans and simply competing with them for resources we can potentially view the interaction as one that changes the selective pressures for one or both species such that evolutionary benefits, and therefore possibly biological changes, accrue via co-existence. Combining the concepts of facilitation and niche construction allows us to create a template in which to assess the impacts and relationships between humans and other sympatric organisms.

THE UPPER ROCK NATURE RESERVE. AN ANTHROPOGENIC HABITAT

The local habitat of interest for this essay is the Upper Rock Nature Reserve of Gibraltar. The reserve covers 2.5-3 Km of the middle and upper reaches of a Jurassic limestone uplift, called the Rock of Gibraltar or El Peñón, with the highest point in the reserve being approximately 424 meters above sea level. The reserve contains nine floral habitat types with unequal distribution, over 350 plant species, an extensive variety of migratory and some resident bird species, at least 11 mammal species, 12 species of reptile, and a diverse array of invertebrates (Cortés 1979, Pérez and Bensusan 2005). Of the various animal species in the reserve a few seem to be clearly benefiting from the anthropogenic environment; the barbary macaques, the yellow-legged gull (*Larus michahellis*), feral cats (*Felis catus*), the black rat (*Rattus rattus alexandrinus*) and feral goats (*Capra hircus*). Other medium to large mammals including the Spanish Ibex (*Carpa pyrenaeica*), the red fox (*Vulpes vulpes silacea*), the wild boar (*Sus scrofa*) and the small-spotted genet (*Genetta genetta*) all went extinct in the reserve area by the middle on the 20th century. This suggests that specific components of the anthropogenic environment favor certain animals on the Rock.

Currently, the reserve contains an extensive road system, two restaurants, a cable car system, a number of private residences and various tourist attractions ranging from caves, to gun batteries to monkey viewing sites. However, this extensive human modification of the environment is not completely recent. The lower reaches of the Rock have experienced continuous human habitation since at least the early 8th century AD, with numerous indications that human residents used at least part of the upper reaches of the Rock since then. Beginning in the 15th century fortifications, buildings and pathways were constructed and maintained throughout the upper Rock (Pérez and Bensusan 2005). Today, numerous road systems traverse the reserve and create open areas in between patches of high maquis, cliff faces, and the other habitat types. The numerous fire breaks impact the structure and composition of vegetation types and maintenance of electrical and water services also create pathways and blockages amongst the habitat types in the middle and upper reaches of the Rock.

The main tourist attractions and the roads act to consolidate and direct human movement in the reserve, however, foot traffic also diverges from the road and main tourist areas. While there is little direct contact between humans and any animals aside from the macaques (see below), feral cats congregate and are fed at main tourist sites and feral goats take advantage of the extensive cover provided by the maquis vegetation.

With 718, 919 visitors from more than 19 countries to the upper Rock in 2003, including more than 72,000 a month during peaks season (June-September (Pérez and Bensusan, 2005)) a very large number of humans visit the Upper Rock Nature Reserve. Humans can access the Rock with on foot, via automobile/coach or by the cable car service. In 2002 alone, 1,758,460 motor vehicles (including 12,407 coaches) crossed into Gibraltar from Spain and an estimated 60,000 vehicles (taxis, coaches, and private vehicles) passed through the main tourist sites in the Upper Rock Nature Reserve (Pérez and Bensusan, 2005). The volume of human presence on the Rock carries with it a diverse array of habitat influencing contexts. The noise and litter from the daily visits to the reserve create a cyclical pattern of rubbish abundance and ambient noise that varies across the year in intensity (Pérez and Bensusan 2005). The traffic movement throughout the road system also acts as a major source of mortality for the larger mammals and the yellow-legged gulls in the reserve (Pérez and Bensusan 2005). As nocturnal access is limited to those with permission or resident in the reserve, the density and impact of human activity is very low during the hours of darkness. However, as residents of Gibraltar can drive at higher speeds, or less impeded speeds, along the roads at night, the potential risk to animals using those roads may be higher. Currently, there is little evidence of any sustained hunting or capture of animals in the reserve, except for the culling of yellow-legged gulls (Pérez and Bensusan 2005).

AN ABBREVIATED HISTORY OF THE BARBARY MACAQUES

While there is some contention regarding the first appearance of the barbary macaques in Gibraltar, it is generally assumed that macaques have been on the Rock since the Moorish occupation (711-1462 AD) (Perez and Bensusan 2005). The history of the macaques on Gibraltar has been well reviewed by Fa (1984), O'Leary and Fa (1993), and Shaw and Cortés (in press), so we will not attempt to provide a thorough historical overview here. However, a brief summary of the provisioning and interaction history with humans is relevant. From the 19th century until the mid 1990s there were two main groups of macaques in the population on the Rock; one at Ape's Den (formerly Queen's Gate) and another at Princess Caroline's Battery. By 1946 both groups were provisioned by the British military separately, and by 1970 provisioning for the Princess Caroline's Battery group was moved to Middle Hill (a restricted military reservation area) to reduce the macaques incursions into Gibraltar town (Fa 1984). From 1972 onward the Middle Hill group had minimal interactions with non-military humans whereas the Ape's Den group has been regularly visited by tourists at the site since at least 1936 (Fa 1984). Increased human interactions began in 1960 with the promotion of the Gibraltar apes as a tourist attraction. As tourism increased substantially during the 1980s-90s economic pressures came to bear on the taxi drivers and tour guides ferrying tourists to visit the macaques. This may have led to illegal provisioning by some Gibraltarans at new areas on the Rock of Gibraltar (Pérez and Bensusan, 2005). By the late 1990s this had contributed to a fissioning of extant groups which by 2004 had resulted in the permanent presence of approximately 250 macaques in 6 groups on the Rock (Shaw and Cortés in, press). Today the main interaction sites are Ape's Den, Anglian Way/St. Michael's cave, Prince Phillips Arch and the cable car station at the top of the Rock.

It is clear that interactions with humans have been a substantial aspect in the daily lives of the Gibraltar macaques for several generations and that these interactions impact the social behaviour and ecology of the macaques (Fa 1984; Fa and Lind 1996; O'Leary and Fa 1993; Pérez and Bensusan 2005, Shaw and Cortés,in press). Throughout this history of interactions some records on the impact of disease have also been kept. In the period of 1936-1944 gastroenteritis appears to have had a substantial mortality impact on the Gibraltar macaque population and pneumonia caused high mortality amongst infants in the late 1980s (Fa 1984; O'Leary and Fa 1993). Both of these cases may reflect pathogen transmission from humans to macaques. Unpublished observations of intermittent outbreaks of nasal discharge and coughing amongst the macaque groups also suggests that the macaques may be acquiring mild respiratory pathogens from humans (A. Fuentes Pers. Observation and Pers. Communication Staff members of Gibraltar Ornithological and Natural History Society (GONHS)). To date there are no published records of a viral pathogen transmission event from the Gibraltar macaques to humans, however the transmission of *campylobacter* and a macaque louse to humans may be possibilities (Dr. M. Pizarro pers. Comm.).

Currently the feeding, management and care of the macaques is undertaken by the Gibraltar Ornithological and Natural History Society (GONHS) under an agreement with the government of Gibraltar. GONHS provision the macaques at five locations in the reserve providing a selection from 15 or 16 kinds of fruits and vegetables plus grains every day of the year (Pérez and Bensusan 2005). Although no formal dietary study has been conducted across this population it appears that the macaques derive the majority of their annual diet from provisioning, however, they do feed daily on both vegetation and invertebrates in the reserve.

HUMAN-MACAQUE INTERACTIONS

Interactions with humans have been a substantial aspect in the daily lives of the Gibraltar macaques for several generations and that these interactions impact the social behavior and ecology of the macaques (Fa 1984; Fa and Lind 1996; O'Leary and Fa 1993; Pérez and Bensusan 2005, Shaw and Cortés in press). Long-term exposure and subsequent habituation of the macaques to human presence suggests that the macaques are fully acclimatized to being around humans (Fuentes 2006; Shaw and Cortés in press) Fa (1984) suggested that human presence and tourist provisioning may have a negative impact on macaque reproduction and lead to other physiologically stressful outcomes. It may be that the current provisioning strategy of feeding groups a total of over 43,000 kilograms of food annually (Pérez and Bensusan 2005) lessens the impact of humans and that the multi-generational exposure to high numbers of humans in the current population of macaques has altered the perceptions and physiological responses of the macaques relative to earlier times (see Fa 1984 for demographic data 1936-1980).

During 2004 observers collected general data on 5489 human-macaque interactions with 808 of the interactions recorded in full detail during focal follows (Fuentes 2006). Across all of the five interactions sites in the Upper Rock Reserve there are significantly more contact interactions than non contact interactions (X^2=459, p<.001) between humans and macaques. There does not appear to be a simple relationship between the number of humans in proximity to a macaque and the occurrence of contact interactions and/or aggressive interactions. Across the sites 382 (47%) of the 808 focal interactions involved tourist/taxi driver/tour guide provisioned food. However, each site varies substantially in the relative impact of food presence during interactions, and overall presence of food does not appear to have a direct, linear relationship to interaction rates or aggression (Anderson *et al.*unpublished). A comparison of the two main interaction sites in the Upper Rock Reserve (Apes Den and Prince Phillips Arch) was made to examine the participation of taxi/coach drivers in the interactions. Interactions between taxi/coach drivers and the macaques usually involve the taxi driver luring with food, and/or physically assisting, the macaque onto the head and shoulders of a tourist for a photo opportunity. Additionally, many taxi/coach drivers feed the macaques, often placing food items directly into the monkey's mouth. These tourist couriers accounted for 18.1% of all recorded interactions observed during focal follows at Apes Den and 33.8% percent of all interactions recorded during focal follows at Prince Phillip's Arch. As there are usually no more than a few (0-3) of these individuals at a given location during a sample period, they make up a maximum of ~8% of humans at an interaction location (Fuentes 2006). Taxi/coach drivers are significantly overrepresented in interactions with the macaques (Apes Den X^2 = 38.4, p<.001, Prince Phillip's Arch X^2 = 202.8, p<.001).

MODELING AN ANTHROPOGENIC ECOLOGY FOR THE GIBRALTAR MACAQUES

It is obvious that the macaques in the Upper Rock Nature Reserve are doing well. Their population size has grown consistently across the last 20 years. Can this simply be explained by invoking by-product mutualism; that human provisioning has led to increased nutritional intake and increased reproductive rates? Or can we envision these macaques as participants in an anthropogenic ecosystem (along with the other successful animals) and see this scenario as potentially an example of facilitation in a human "place"? What role does assessing the anthropogenic environment play in understanding the ecology of this habitat? To answer these questions we will review aspects of the macaques' behaviour, habitat, ranging and general ecology.

It is fairly clear that, contrary to the assertion of Fa (1984), provisioning and high rates of human interaction are not suppressing the reproductive rate of the population. However, it may be possible that human patterns and provisioned food act as selective pressures and are impacting the behaviour and activity patterns of the macaques. Current research suggests

no linear, or simple, relationship between human density and macaque aggression (Fuentes 2006, Anderson *et al.* unpublished). Preliminary data also suggest that there is not a clear association between the presence of food and aggression between humans-macaques or macaques-macaques (Fuentes unpublished data). However, these data reflect only peak tourist season, when food sources are extremely plentiful and thus may not accurately reflect the overall impact of provisioned food on the levels of aggression in the macaques.

Ranging patterns appear to have shifted over the last decade in response to human activity. Increased feeding at diverse locations by taxi drivers appears to correlate with the break up of multiple groups. This fractioning of two groups into as many as six groups signals a significant shift in the demographic structure of the macaque population. Subsequent management decisions to provision the new groups may have acted to reinforce these entities as social units as did the earlier change in feeding regimes in 1946. In addition to the provisioning impact on ranging two other elements appear to shape the patterns with which macaques use the Rock area. As of 2003 at least one group has begun spending substantial amount of time in the waste dumping site on the Southeast corner of the Limestone uplift. They are tolerated at the site by the local human workers and appear to split their time between the dump area and the habitat around one of the major tourist sites (St. Michael's Cave). They appear to partition the use of the tourist site with another group (from which they may have split off) (E. Shaw pers. comm). The presence of the trash dump combined with the tolerance of the human workers may have opened up a novel ranging and foraging site for this group. Previous to this, the dump site was not a part of any group's range. Another impact on ranging is that the reserve is bounded by urban areas (Gibraltar Town and Caleta Bay Village). While individual macaques have ventured into these areas for centuries, consistent use by groups of fringe areas bordering the reserve such as housing estates and hotels appears to be relatively new. In part this ranging shift by some groups or subgroups may be elicited by human activity. Macaques are highly opportunistic and plastic foragers. As new feeding sites appear in proximity to current ranges, macaques are likely to explore them. Active provisioning by humans and access to uncovered and overflowing rubbish bins may be powerful stimuli eliciting an adaptive foraging response. In both of these cases the shift in macaque ranging must be understood both as a foraging response and in the context of human activity and habitat change.

If we can see that a significant portion of the macaques foraging strategies are being impacted by human patterns of provisioning, trash creation and management then we also must consider the nutritional impact. In general human foods are high in readily utilizable carbohydrates and lipids (fats). If some of the macaques are supplementing their GONHS provisioned foods with a significant percentage of human trash and handouts, then the energetic balance of some groups or individuals will be quite different from that of others. This can impact ranging, daily activity cycles and possible overall health. The site with the longest history of tourist provisioning, Ape's Den, does appear to have the highest rate of overweight animals (as assessed by overt skin folds). Understanding the nutritional ecology of these monkeys requires an assessment of the various foraging opportunities and the diversity of food chemistries in these choices.

The physical structure of the sites where macaques spend much of their time (the tourist interaction sites) also might impact macaque behaviour. Most sites where moneys interact with tourists are along a roadway. However, the highest density interaction sites (Ape's Den and Prince Phillip's Arch) differ dramatically in structure. Ape's Den has a large (~10m x 50m) multi-level area where macaques and humans can interact. The macaques can avoid human interaction by moving over a retaining wall onto the western cliff face (low wind, not a sheer cliff) or by moving to the north or south. Humans cannot follow in any of these cases. This suggests that when macaques are interacting with humans they are doing so explicitly by choice. At Prince Phillip's Arch the road way itself is the main interaction location. With a small (~10m x 5m) interaction area and a small (~1m x 2.5m) raised platform (the arch itself). The eastern cliff face is minimally accessible to due its sheer drop and the frequent high winds that buffet it. To avoid human interactions the macaques must move off of the road to the western slope or north towards the cable car station and restaurant. It is possible that the human manipulation of physical structure (the roads

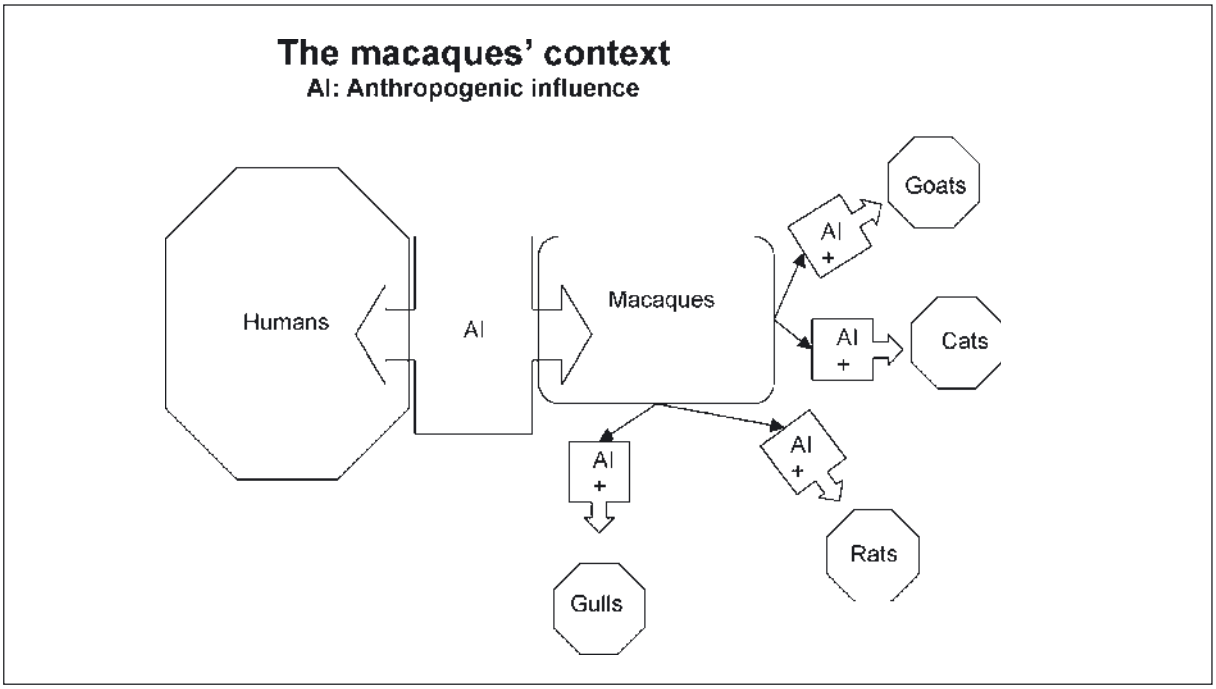

Figure 1

and the existing structures at the two sites) combined with the different micro-habitats on the east (Prince Phillip's Arch)and west (Ape's Den) faces of the Rock create a different set of costs and benefits for interacting with humans.

One final and important component of anthropogenic environments deserves attention: the potential risk of pathogen transfer. The frequent overlap of macaques with human use areas suggests the possibility for the acquisition of human pathogens. Macaques are potentially at risk to an array of human pathogens including measles, influenzas and other respiratory diseases (Jones-Engel, *et al.* 2001). Physical contact and climbing of macaques onto tourists (with encouragement/training from taxi/coach drivers) places human and macaque faces in close proximity and thus respiratory zones into close contact. Pathogens most easily transmitted via mucosal contact or aerosol dispersal may pose a significant danger to this macaque population.

THE MACAQUES IN CONTEXT

Interactions with humans and the structure and patterns within the anthropogenic environment are a core part of the barbary macaque ecology and potentially a reason why these macaques are doing so well. However, the macaques themselves are a major part of upper Rock ecosystem both because they are large mammals and due to the human use of the reserve. One can argue that the Upper Rock Nature Reserve can be viewed as an ecosystem with a few large animals as foundation species in the structure of the habitats and thus selection pressures on all of the inhabitants. In this essay we focused only on the macaques and humans as we see these two primates as main elements in structuring the ecology of the reserve. However, the other successful non-human animals in the reserve also contribute to its structure and context.

Although the barbary macaques are large bodied mammals there are no actual comparative data to address their relative contribution to the overall mammalian biomass in the reserve. However, with approximately 250 individuals in the population

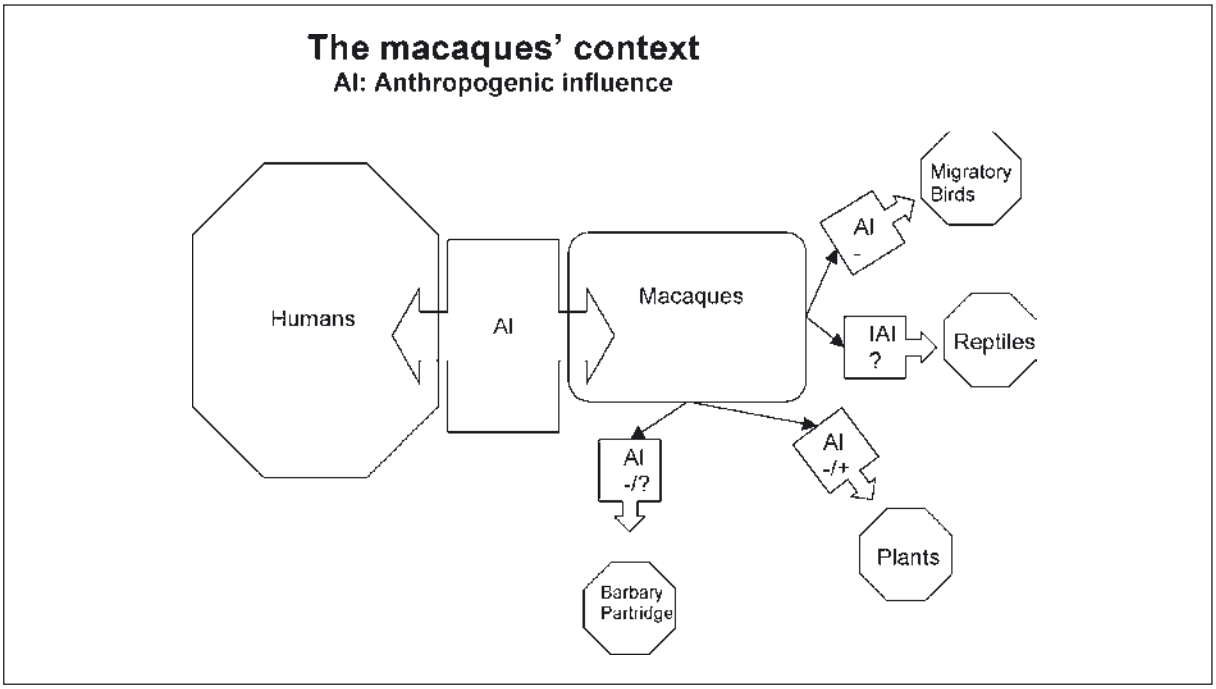

Figure 2

they contribute over 1000 Kg to the overall mammalian biomass, probably significantly more than the feral goats or cats, and potentially any other mammals aside from the black rats and possibly rabbits (*Oryctolagus cuniculus*). However, above and beyond their biomass contribution, the macaques are integrally tied to the human presence in the reserve. At least 20% of tourists visiting the reserve specifically come to see the macaques and a much larger percentage participate on tours that include a visit the macaque sites (Fuentes unpubl. data). Additionally, local taxi drivers market their tours to visitors to Gibraltar with the specific reference to seeing and interacting with the macaques. This suggests that the macaques' presence in the reserve is a major contributor to the human tourist presence and thus contributes to the daily cycle of traffic and rubbish dispersal. The rubbish alone provides forage for many of the other organisms in the reserve including the ubiquitous yellow-legged gulls and the black rats. The continued presence of tourists also stimulates the Gibraltaran government not only to maintain a relationship with GONHS for the continued provisioning of the macaques but also for the support network of road maintenance, water dispersal and fire control crews. This constant use and managing of the reserve, stimulated in part by the economic benefits the macaques provide, acts to maintain relatively static habitat structure and to provide direct human assistance to some species (such as feral cats) and protection to others (feral goats). Even the yellow-legged gulls, who are actively culled in high numbers annually, receive a trade-off in the form of protection for a myriad of predators found in other areas of their breeding range but extinct or non-resident in Gibraltar (figure 1).

Is this more than by-product mutualism? The cats, gulls, rats, goats all benefit from structure and context of roads, macaque tourism, and the trash situation. They benefit from the ongoing relationship between the macaques and the humans and its pattern of impact on the Upper Rock Nature Reserve. This may be seen as, in part, some degree of facilitation resulting from a human impacted habitat and active role that the macaques have within it. Other organisms, such as some of the plant species,

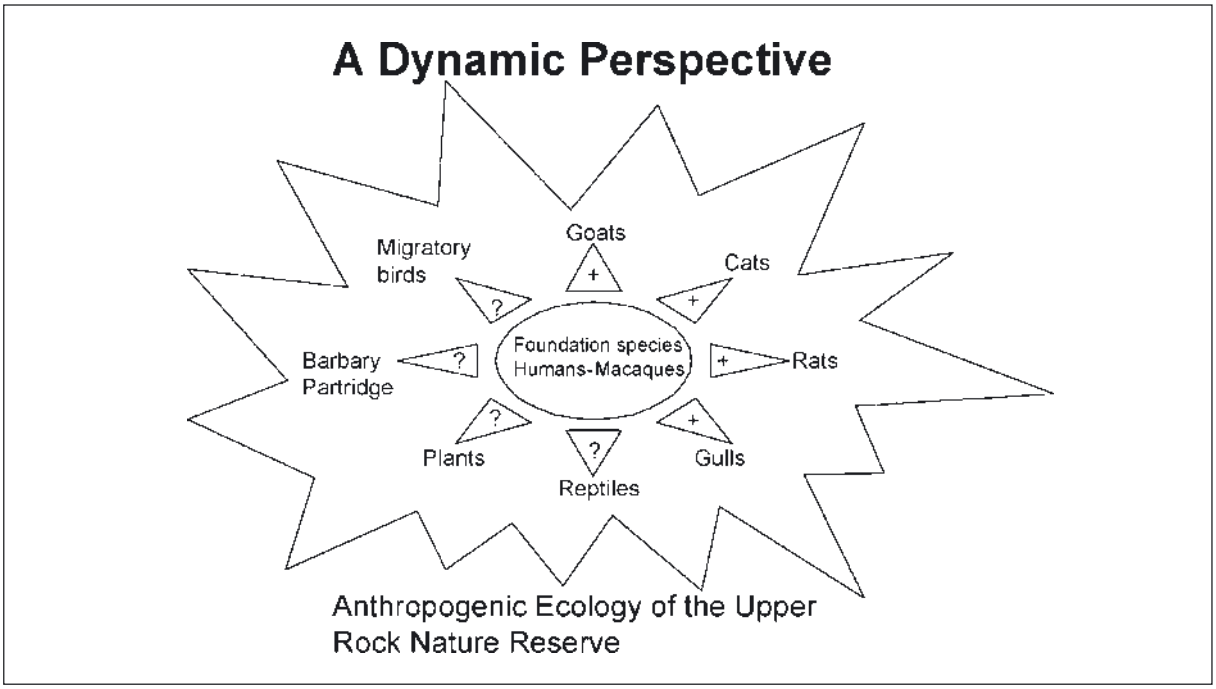

Figure 3

migratory birds, the endemic barbary partridge (*Alectoris barbara*), and some resident reptiles may not benefit, and might in fact suffer from the extensive human use and management. In this case the anthropogenic environment that is in part constructed via interaction with the macaques has created sets of ecological challenges (selection pressure) that are beneficial for some inhabitants and not for others (figure 2). In a sense, we can see a potential expansion of realized niche for a select group of resident species while at the same time a reduction in the realized niche of others. The active and dynamic relationships between the resident organisms and their environment is structured, shaped and changed in an anthropogenic context.

In the broadest sense we can tackle an assessment of the Upper Rock Nature Reserve from the perspective of the macaques by envisioning a dynamic ecosystem with two large mammals as major stakeholders; humans and macaques. The relationships between these two species acts to structure the habitat, provide forage options and opportunities for an array of organisms and maintain a high volume human use of the area. Although other organisms also act as significant components in this ecosystem, the macaques and humans represent two of the major factors (foundation species) influencing the structure of the niches available (figure 3).

WHAT IS THE BENEFIT OF THE PERSPECTIVE PUT FORWARD IN THIS ESSAY?

If niche construction entails an organism modifying "the functional relationship between itself and its environment by actively changing one of the factors in its environment either by physically perturbing these factors at its current address or by relocating to a different address thereby exposing itself to different factors" (Laland *et al.* 2001) then one can argue that we are seeing niche construction by humans as well as the macaques on the Rock. If facilitation entails interactions between two or more species co-existing in the same location and ecological space altering the selective environments such

that each does better when the other is also sharing the environment/ecology (Bruno *et al.* 2003), the possibility remains that in the Upper Rock Nature Reserve we may be seeing some facilitation via niche expansion amongst various animals. Looking at this ecosystem with both an eye towards management and with an evolutionary perspective, our analyses may produce a more comprehensive set of results.

Many researchers would agree that seeing anthropogenic influence as a core component of an environment allows for a more realistic management approach to studying ecosystems. If we take this a step further and include the roles of other significant non-human contributors to the shaping of the anthropogenic environment, such as macaques in this case, we can expand our assessments and move towards a complexity based, multi-stakeholder approach. Thinking about realized niches and their partitioning within an environment in the context of the active management and construction of local ecologies allows for the use of tools from a diverse array of fields. Toolkits from disciplines such as ecology, animal behavior, anthropology, and resource management can be brought to bear on the same questions in the hopes of producing more effective and engaged results. Results that then may be of relevance not just to ecologists or resource managers but also to evolutionary theorists, animal behaviorists, and other researchers trying to understand relationships between organisms in an increasingly anthropogenic world.

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