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The Abundance, Geographical Distribution and Habitat Use of an Introduced Patas Monkey (Erythrocebus patas) Population in Southwest Puerto Rico

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To the Dean of the Graduate School:

We are submitting a thesis written by Magaly Massanet entitled The Abundance, Distribution and Habitat Use Patterns of a Patas Monkey (*Erythrocebus patas*) Population in Southwest Puerto Rico.

We recommend acceptance in partial fulfillment of the requirements for the degree of Master of Biology.

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THE ABUNDANCE, GEOGRAPHICAL DISTRIBUTION AND HABITAT USE OF AN INTRODUCED PATAS MONKEY (*ERYTHROCEBUS PATAS*) POPULATION IN SOUTHWEST PUERTO RICO

A Thesis

Presented to the Faculty

Of the

College of Art and Sciences

In Partial Fulfillment

Of the

Requirements for the Degree

Of Master of Science

In

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By

Magaly Massanet

ABSTRACT

The southwest portion of Puerto Rico is home to introduced free-ranging populations of patas (*Erythrocebus patas*) and rhesus macaque (*Macaca mulatta*) monkeys. The rhesus macaque population originated from a colony established in 1961 on the islands of Guayacán and Cuevas off the southwest coast of Puerto Rico as part of the La Parguera Primate Research Center, which was administered by the Caribbean Primate Research Center. The descendants of these escapees have established free-ranging introduced monkey populations in mainland southwest Puerto Rico and the only previous study done on their ecology was conducted from 1990 to 1993 by González-Martínez (1995). Since that study, these populations had not been surveyed to determine their status and detect changes, if any, in their ecology and population biology. I carried out a reassessment of patas monkeys in southwest Puerto Rico. In this study I estimated current population abundance for the patas monkeys in southwest Puerto Rico, as well as the geographic areas and habitats that are utilized by the different groups, and the patterns by which they use them. I chose to focus only on the patas and not the rhesus macaques because the majority of crop raiding events in southwest Puerto Rico are attributed to patas monkeys. I collected data from 22 May to 20 September 2006 in the southwest portion of Puerto Rico. My population estimate for the patas monkeys in southwest Puerto Rico, shows that the population had a 328% increase in size over a period of 13 years ranging from 1993 to 2006. In addition, I calculated the population density for the patas in Puerto Rico taking into account the entire study area; this estimate gave me one of the highest population

densities reported for a patas monkey population anywhere, with 2.99 individuals/ km², roughly three times what González-Martinez reported (1995). I also found that the mean group size also increased in the 13-year period between 1993 and 2006 from 26 to 52 individuals. The patas monkeys in southwest Puerto Rico increased their geographical distribution over the 13 years from 1993-2006 by 38%, expanding in an east direction. In 2006 I found that the patas monkeys were utilizing the same habitats as Gónzalez-Martínez had found in 1993 (1995); however, they had begun to exploit developed urban areas that were avoided by the monkeys in 1993 (Gónzalez-Martínez, 1995). In my study, the activity performed at a significant higher proportion than other activities in grazing lands was resting. A possible explanation for this finding is that this type of habitat provides the monkeys with important sources of water, and when they are less active during the middle of the day because of high temperatures they stay close to these water sources. The patas population in Puerto Rico is abundant and can be characterized as a successful colonizer of the area. Different factors, such as a lack of non-human predators and the presence of rich, abundant, food sources in the area, could have favored a continued increase in the size of the population since González-Martínez's 1993 study (Gónzalez-Martínez, 1995).

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INTRODUCTION

Introduced Species: Establishment and Colonization

The southwest portion of Puerto Rico is home to introduced free-ranging populations of patas (*Erythrocebus patas*) and rhesus macaque (*Macaca mulatta*) monkeys. The rhesus macaque population originated from a colony established in 1961 on the islands of Guayacán and Cuevas off the southwest coast of Puerto Rico as part of the La Parguera Primate Research Center, which was administered by the Caribbean Primate Research Center. Throughout the 1970's new rhesus macaque individuals were added to the existing colony, while from 1971 to 1981 a colony composed of patas monkeys was introduced to the islands (González-Martínez, 1995). Shortly after the La Parguera Primate Research Center started operations, it became evident that individuals from both species were able to disperse to the mainland; multiple emigration events occurred throughout the period that the research center was open for operation up until 1984 when La Parguera was closed. The descendants of these escapees have established free-ranging introduced monkey populations in mainland southwest Puerto Rico and the only previous study done on their ecology was conducted from 1990 to 1993 by González-Martínez (1995). Since that study, these populations had not been surveyed to determine their status and detect changes, if any, in their ecology and population biology.

The phenomenon of humans introducing new species into ecosystems for a variety of reasons, including the use of introduced species as a potential food source, for pest control and for transportation purposes has been occurring for thousands of years (Long, 2003). However, the rate of new species introductions into ecosystems by humans has increased, especially in the past few decades, due to the globalization of economic activities and an increase in international travel; this increase in species introduction includes both accidental and intentional introductions (Kolar and Lodge, 2001; Mooney, 2005). Recent intentional introductions include the use of exotic species as a food source, for aesthetic purposes, for biological control, as pets, and for commercial purposes such as the fur trade (Long, 2003; Lockwood et al., 2007). Accidental introductions include instances where animal species, such as rodents, and plant species are brought inadvertently in commercial cargoes, especially ships, as an unintended byproduct of the transportation of commercial goods; thus, these accidentally introduced species are commonly referred to as “hitchhikers” (Lockwood et al., 2007). In turn, the potential for negative effects on ecosystems from these introductions has also increased significantly.

Introduced species are regarded as one of the principal factors causing human-induced global environmental change, along with increasing carbon dioxide concentrations in the atmosphere, changes in the cycling of nitrogen and other elements throughout the ecosystem, the production and release of persistent organic compounds, habitat loss and disturbances, and poaching (Vitoseuk et al., 1997). One focus of the scientific research on introduced species has been to document the effects of invasion on the native fauna and flora within the introduced species’ range. One of the most documented negative effects that introduced species can have on an ecosystem is biodiversity reduction. Through the introduction of new species to various habitats, the biogeographical barriers that promote biodiversity are broken and the homogenization of animal and plant species can occur at a local and a global scale (Vitoseuk et al., 1997; Mooney and Cleland, 2001). Homogenization events can be produced through various pathways, including the hybridization of introduced species with resident species, competitive exclusion of resident species in the introduced species' range, niche displacement of native species by the introduced species, and the extinction of resident species driven by the introduction of new species in the area (Mooney and Cleland, 2001). In turn, the alteration of biodiversity at local and global scales can have a degrading impact on the processes of an ecosystem. The degradation of an ecosystem as a consequence of the alteration of the species composition of an area can take place when the cycling of energy and materials through the ecosystem is disturbed by a change in the availability of resources and the disturbance regime of the habitat with the introduction of a new species (Chapin et al., 2000).

Introduced species can also have a negative impact on the economy of the affected area. In the United States alone, damages associated with the activities of invasive species were estimated to be around 79 billion dollars in the period between 1906 to 1991 (Pimentel et al., 2000). Economic damages induced by invasive species can be especially detrimental to the public health, forestry industry and agriculture activities of a country (Pimentel et al., 2000).

Contingent upon the success of an invasive species in a certain area, control and eradication management plans can take a considerable amount of money and labor. Simberloff (2003) argues that a successful early intervention in eradicating an invasive species does not always require a thorough knowledge of the population biology and ecology of the introduced species. Simberloff proposes the example of the Caribbean black-striped mussel (*Mytilopsis sallei*), which was introduced at Cullen Bay, Australia in 1999. Within six months of the mussel's arrival, a successful eradication plan was conducted without the necessity of gathering scientific information on the invader’s patterns (Simberloff, 2003). However, once the introduced species has established itself and expanded its range within the introduced area, eradication plans can fail without the appropriate knowledge about the population biology and ecology of the species. The expansion of the introduced species can occur rapidly, especially if the population is not restricted to just one region or habitat type within the introduced range. Often, the information gathered about the population biology and ecology of an introduced species can aid in identifying the traits and conditions that made the invader successful; this information can be vital in the preparation of control and eradication management plans (Sakai et al., 2001; Allendorf and Lundquist, 2003).

Investigations into the biology and ecology of introduced species in their new range have identified at least three stages an introduced species has to go through successfully before causing both economic and ecological damage (Forsyth et al., 2004; Lockwood et al., 2007). The first stage is the introduction of the species into a new ecosystem. The second stage is the establishment of a viable population in the introduced range. The third and final stage is the spread of the species in the introduced range (Sakai et al., 2001).

Another focus of research on introduced species has been the study of the biological and ecological factors that make an exotic species a successful invader. Factors such as the exotic species’ ability to affiliate with humans, absence of natural predators in the introduced range, broad geographical native range and life-history characteristics of the exotic species have been suggested as having an influence on the propagation of the introduced species. However, the degree to which each of these factors influence invasive success across different taxonomic groups is difficult to determine (Jeschke and Strayer, 2006). The only factor reliably associated with invasion success across different taxonomic groups and considered key in understanding why some introduced species can establish and expand their populations while others do not, is propagule pressure, or introduction effort (Lockwood et al., 2005; Jeschke and Strayer, 2006; Kolar and Lodge, 2001). It is hypothesized that the higher the number of individuals that are introduced in an area and the greater the number of times that the species is introduced, the higher the probability that at least one population of the introduced species will become established in the introduced range (Duncan et al., 2003; Forsyth et al., 2004). Multiple introductions of a species to an area can give the introduced population higher genetic diversity, which is believed to aid in the establishment and success of the species (Stepien et al., 2002). The introduction effort required for success will also depend on a minimum population threshold size which differs across taxa (Forsyth et al., 2004).

The ability of introduced species to use human altered landscapes gives them access to rich microhabitats, supplying the individuals with varied resources for the establishment and growth of the population (Jeshcke and Strayer, 2006). A study that analyzed the effect of 20 variables on several introduced species of mammals and birds determined that ability to affiliate with humans has a strong correlation with the population expansion of an introduced species (Jeschke and Strayer, 2006). It has been argued that species with a history of affiliation with human altered landscapes in their native range have a higher probability of successfully establishing a population when introduced to a new range (Elton, 1958). But it has also been argued that the level to which an introduced species will succeed because of an affiliation with human-altered landscapes is contingent upon how the native species can adapt to these altered landscapes (Lockwood et al., 2007). Human-induced disturbances in a landscape, of which urbanization and agriculture are two of the most documented, and their consequent effects, fall outside the realm of natural disturbances to which native species are accustomed; thus, native species may not yet have evolved mechanisms which would enable them to take advantage of human-induced disturbances in a landscape (Lockwood et al., 2007). By contrast, several of the exotic species that have succeeded in their introduced range had a history of adapting to human-caused disturbances taking place in the areas they utilize within their native range (Hierro et al., 2005). Areas that are not utilized by native species because these species have not adapted to the human disturbances taking place in them can represent empty niches and microhabitats rich in resources that the introduced species can exploit (Parker et al., 1999).This factor influencing the success of introduced species is the premise for the empty niche hypothesis, which states that the presence in the introduced range of empty niches unused by the native species of the area can provide the introduced species with resources to establish and spread in the new location (Levine and D'Antonio, 1999).

The enemy release hypothesis (ERH) is also commonly used to explain invasion success of introduced species' populations. The ERH postulates that the abundance of an introduced species in an ecosystem is influenced by the scarcity or absence of natural predators in the introduced range compared with the native range of the species (Elton, 1958; Keane and Crawley, 2002; Colautti et al., 2004). The presence of a predator can influence the population dynamics of a species in an area. For example, studies of the effects of predation risk on the population dynamics of Old World primates indicate that the level of predation risk influences factors such as group size and group composition in several species (Hill and Lee, 1998). The scarcity or lack of predators can also affect the life-history patterns that confer a fitness advantage on invaders, which conspecifics in the native range of the species do not have because of predator pressures. As a result of this release from natural enemies in its new environment, resources previously allocated towards predator defense mechanisms in its native range can now be allocated towards life history traits such as reproductive output and growth (Blossey and Notzold, 1995). This hypothesis derived from the ERH is known as the evolution of increased competitive ability hypothesis, or the EICA (Blossey and Notzold, 1995).

Models of antipredator behavior predict that as species' group size increases, organisms allocate less time to antipredator behaviors and more time to activities such as foraging because of an increase in vigilance by others in the group with the increase of individuals; this phenomenon is known as the "group size effect" (Krause and Ruxton, 2002). In a study comparing tammar wallaby (*Macropus eugenii*) populations that had experienced some kind of predator pressure or no predator pressure at all, populations that had some predator pressure over 9,500 years showed a "group size effect" on the time spent in foraging and vigilance behaviors, while an introduced population that did not have any predator pressure in a period of 130 years had lost the "group size effect" on foraging and vigilance behaviors (Blumstein et al., 2004). The introduced population that had no predator exposure was located at Kawau Island, New Zealand, where they were introduced approximately 130 years prior to the study and where they had virtually no threat or pressure from predators (Blumstein et al., 2004). Blumstein and colleagues concluded that modifying time allocation and the "group size effect" was costly to the individual if the predation stimulus was not there. Group size increases competition and so affects foraging and vigilance behaviors. As group size increases in a food limited environment, so does the feeding rate because of competition for the limited resources available for use to the group (Krause, 1994; Saino 1994). The Ecological Constraints Model states that a faster depletion of available foods for larger groups leads these groups to have to travel larger distances to obtain needed resources for all the individuals (Waser, 1977; Chapman et al., 1995). If resources are not limiting to a group or a number of groups in an area, then as the various groups increase in size there will also be an increase in group density for the area.

Introduced species may not only escape from their natural predators and competitors in their introduced range, but may also escape pathogens and parasites. Parasites and pathogens can reduce the population density of a species in an area, as well as reduce the body size of the individuals in the population (Torchin et al., 2003). Studies of a wide range of animal taxa including mollusks, crustaceans, fishes, birds, mammals, amphibians, and reptiles concluded that introduced species contained half the number of parasites in their new range when compared with their native range (Torchin et al., 2003).

Other factors that have been proposed as influential to the success of introduced species are the presence of appropriate climatic conditions and suitable habitats in the new environment, resembling the ecological conditions in the native range of the species (Blackburn and Duncan, 2001). The suitability of certain habitats for the establishment of a particular species in the introduced range can be affected by the similarity between the latitudes of the points of origin and introduction for the species (Blackburn and Duncan, 2001; Forsyth et al., 2004). In addition, large regions that have a diversity of habitats and altitudes are more than likely to provide a suitable habitat for the establishment of the introduced species

Introduced Primate Populations

Several free-ranging introduced primate populations have been studied over the past decades. Most of these populations were introduced 300 to 400 years ago by European settlers to various sites in Asia and the Caribbean. The majority of these populations share key characteristics, including the absence of natural predators in their introduced range and very little, if any, non-human competition for resources.

One such population which has been extensively studied is that of long-tailed macaques (*Macaca fascicularis*) on the island of Mauritius in the southwest Indian Ocean. It is not clear exactly when these monkeys were introduced to the island, but by the early 1900 they were abundant, causing major agricultural damages (Sussman and Tattersall, 1981). Long-tailed macaque are widespread throughout the islands of Southeast Asia and mainland Asia, and they possess a behavioral flexibility that permits them to utilize a wide variety of habitat types, a behavioral characteristic which has contributed to the species' establishment and success in Mauritius. A study of the Mauritius long-tailed macaques' daily activities found that they spent a high amount of time on the ground except when feeding, and all travel was terrestrial; this differs from what has been reported for long-tailed macaques in their native range where they are less terrestrial (Sussman and Tattersall, 1981). Sussman and Tattersall (1981) hypothesized that because of the lack of primate competitors in their introduced range, long-tailed macaques are able to exploit a more terrestrial niche in Mauritius. Another aspect of long-tailed macaques' ecology in Mauritius is their exploitation of habitats that are disturbed or secondary, thus they are a "weed" species that is able to use vegetative areas that have been disturbed by humans (Sussman and Tattersall, 1986). The availability of open niches in these areas on the island of Mauritius has provided the species with resources to exploit. Long-tailed macaques have one of the widest geographical ranges of any monkey in southeast Asia; this factor seems likely to have aided in the adaptation and the establishment of the species in Mauritius. The last documented count of the Mauritius population estimated between 25,000 and 35,000 monkeys in an area of 1,865 km^2 (Sussman and Tattersall, 1986). Because of the large population size for the long-tailed macaques in Mauritius, a culling program has been developed in the island to annually export a portion of the population for biomedical research. The long-tailed macaques of Mauritius also have a high reproductive rate, with almost every adult female trapped either lactating or pregnant (Sussman and Tattersall, 1986).

The ability of primate populations to succeed in introduced ranges has also been documented on Caribbean islands. On the islands of Barbados, St. Kitts and Nevis, populations of vervet monkeys (*Chlorocebus aethiops)* were introduced by European settlers around 300 years ago. Like long-tailed macaques, vervet monkeys in their native Africa also use a variety of habitat types, and have a wide geographical range. The population dynamics of the vervet monkeys on St. Kitts has been analyzed in terms of their colonization patterns in the area of St. Timothy Hill, located in St. Kitts. Censuses of the population spanning the ten-year period from 1971 to 1981 revealed a population growth of over 300% (Fedigan et al., 1984). In this period from 1972 to 1981 the natality levels declined, butFedigan and her colleagues pointed out that the monkeys had enough resources available that the population was still not near carrying capacity (Fedigan et al., 1984). The authors hypothesize that the population patterns of the vervets in St. Timothy Hill follow a model for a species colonizing an area with a slow-down in population growth after an initial rapid growth, conforming to demographic theories that populations growth will stabilize in environments where they are not limited by the resources available (Fedigan et al., 1984). Again like the long-tailed macaques in Mauritius, the vervets on St. Kitts use areas of secondary growth more often than other habitat types mainly because of the food resources available in these areas and the vervets on St. Kitts have little or no competition for the resources in these areas (Chapman, 1987).

On Barbados vervet monkeys are trapped and hunted annually. In the 14-year period from 1980 to 1994, however, the population of vervets in Barbados remained stable even though around 10,000 were trapped or hunted (Boulton et al., 1996). Barbados vervets are considered agricultural pests due to their extensive crop raiding (Boulton et al., 1996).

Patas Monkeys: Behavior and Ecology

Patas monkeys (*Erythrocebus patas*) occupy a wide geographical range in Africa and thrive in seasonal arid habitats (Hall, 1965). However, because of their vulnerability to habitat modifications they are being extirpated from much of their original range mainly due to the conversion of the natural habitats they occupy into agricultural lands (Isbell and Chism, 2007). Thus, more information on any patas monkey populations that are able to adapt to disturbed habitats is potentially important to efforts to protect the species. In one of the few long term studies done on the ecology and behavior of the patas monkeys, in the Lakipia District of Kenya, they were shown to be selective about their habitat choice; the main habitat that they occupied was open acacia woodland, which they preferred over open grasslands, riverine woodlands, and dense woodlands (Chism and Rowell, 1988). Patas monkeys at this site utilized the margin of the acacia woodlands as a mean of exploiting the resources of both open grassland and woodland habitats, because, the authors suggest, this strategy allowed the monkeys to stay near trees for predator defense while having access to a rich ecotone for foraging. Also attributed to the monkeys' predator defense strategy was the observation that the Laikipia patas monkeys did not occupy the same sleeping site two nights in a row, and that each individual (except mothers with dependent infants) in the group slept in an individual tree (Chism and Rowell, 1988). Patas population density in Kenya is low, while their home and day ranges are large. It has been hypothesized that this is a function of their exploitation of foods which are high quality but scattered in their distribution in their habitat (Chism and Rowell, 1988; Isbell, 1998). In other areas of Africa, specifically in Uganda, patas population density is also low (Hall, 1965). In Laikipia District of Kenya the patas' diet consisted mainly of berries, fruits, beans and seeds, gum and insects. Of special interest at this site is the high proportion of tree parts from the *Acacia drepanolobium* consumed by the patas monkeys, including gum (Chism and Rowell, 1988; Isbell, 1998). Also of special interest is the large number of insects consumed (Chism and Rowell, 1988; Isbell, 1998), which is usually considered a characteristic of the high quality diet more typical of small bodied primates (Isbell, 1998). A possible alternative explanation for the patas monkey's large home and day range is need for access to water sources. Isbell hypothesized that by including several water sources in their extensive home ranges they could take advantage of the scattered food sources without depleting them (Isbell, 1998).

The role of water sources in the ranging behavior of other primates has been established in studies of the redfronted lemurs (*Eulemur rufifrons*) in Madagascar, where the investigators found the seasonal availability of food and water sources caused the migration of lemur groups, and their day range length behavior increased as the distance to the water sources increased (Scholz and Kappeler, 2004).

Patas monkeys in their native range have a polygynous mating system usually with one resident adult male per group, although in the breeding season heterosexual groups can receive an influx of non-resident males (Chism and Rowell, 1988; Chism and Rogers, 1997). Patas monkeys are strongly seasonal breeders and the group sizes in different areas in Africa range from 9 to 61 individuals, with typical group size ranging from 15 to 30 individuals (Hall, 1965; Chism and Rowell, 1988).

Patas Monkeys in Puerto Rico

The southwest portion of Puerto Rico serves as the location for populations of introduced free-ranging patas and rhesus macaque monkeys that have inhabited the area for around 25 to 30 years (Gonzalez-Martinez, 1995). As briefly described earlier, members of these populations are descendants of groups of monkeys that escaped from captive colonies on the small islands of Guayacán and Cuevas, off the coast of southwest Puerto Rico. The rhesus macaque captive colony was established in 1960 for the purpose of scientific research by the National Institute of Health (NIH) as part of the La Parguera Primate Breeding Colony (See Figure 1). Starting in 1970 the Caribbean Primate Research Center, through a NIH contract, administered the La Parguera facilities (González-Martínez, 1995). In 1971 a group of 26 patas monkeys originating from

Nigeria were added to the rhesus macaque colony in La Parguera, to study their social behavior and reproduction. By 1977 the patas colony in La Parguera consisted of approximately 56 individuals. Over the next years several new patas individuals were added to the colony, and by 1981 the patas population in La Parguera consisted of 149 individuals (González-Martínez, 1995).

Figure 1. Cueva and Guayacán Islands off the southwest coast of Puerto Rico.

When the La Parguera Primate Breeding Colony commenced operations in the early 1960s, it soon became apparent that rhesus macaque individuals were dispersing from the islands to the mainland. Since the islands are not far from the mainland, the mangrove forests surrounding the islands formed “bridges” that the monkeys utilized to move from the islands to the mainland and vice versa; this was also the case for patas monkey individuals after their arrival in 1971. In 1982 the La Parguera Primate Breeding Colony operations were terminated, and all the monkeys of both species were relocated. When final census lists were reviewed, it was discovered that approximately 54 patas monkey individuals were missing from the islands (González-Martínez, 1995). The only previous study of the ecology and behavior of the free-ranging patas and rhesus macaque population in Puerto Rico was conducted from 1990 to 1993 by Dr. Janis González-Martínez. González-Martínez (1995) found a population consisting of around 120 patas monkeys divided into four heterosexual groups, four to five all male bands and various lone males. The heterosexual groups ranged from 20 to 38 individuals, with an average group size of around 26. This study concluded that the habitats preferred or used more frequently than expected based on their availability by the patas monkey groups were secondary scrub, semideciduous woodland, and mesquite woodland (González-Martínez, 1995). González-Martínez (1995) also indicated that even though livestock pastures were widely available in the study area, this habitat type was utilized less frequently than expected. The study also found that patas monkeys in southwest Puerto Rico completely avoided urban areas, mangrove forests, sugar cane areas and saltflats. Their diet consisted mainly of seed pods, seeds, and fruits from trees and shrubs of *Tamarindus indica*, *Melicoccus bijugatus*, *Mangifera indica*, *Prosopis juliflora*, and *Leucaena leucocephala* (González-Martínez, 1995). They supplemented their diet with insects by foraging for them in the grass when moving from one location to the other (González-Martínez, 1995). The study also indicated that the patas monkey groups had available and utilized both natural and anthropogenic water sources within their home ranges.

González-Martínez (1995) reported for patas monkeys a population density of 0.96 individuals per km² within the entire study area, but within their combined home ranges, the population density was 4.47 individuals per km². She concluded that the distribution and amount of the resources available to the monkey groups was able to sustain that density. The study also reported that crop raiding was carried out by some of the patas groups in the area, and the use of agricultural fields was proportional to their availability within a group's home range (González-Martínez, 1995).

The only potential predators of the patas monkeys in southwestern Puerto Rico at the time of the study were humans and domestic dogs (González-Martínez, 1995). In addition, the only potential competitors for the patas monkeys in southwest Puerto Rico were the rhesus macaques that range over the area. During her study, González-Martínez (1995) reported that the differences in the habitat use by patas and rhesus macaques groups resulted in infrequent encounters between the two species. The result of these encounters of the patas monkeys with the rhesus macaque groups was always the displacement of the patas groups by the rhesus macaques. These encounters took place mostly during the fruiting period of mangoes (*Mangifera indica*) from May to July (González-Martínez, 1995).

Since that study the number of complaints from farmers in Puerto Rico about the incidences of crop raiding on their properties by patas monkey groups has steadily increased. Local residents claim that the monkeys in southwest Puerto Rico cause damage to cantaloupes, watermelons, pumpkins, and vegetables (USDA et al., 2008).

Approximately 1.9 million dollars of actual economic losses in crop damage has been attributed to patas and rhesus monkeys by agricultural producers in the period between2002 to 2007 (USDA et al., 2008). A survey conducted by the National Wildlife Research Center (NWRC) in cooperation with the Puerto Rico Department of Agriculture (PRDA) in 2007 in southwest Puerto Rico on agricultural producers concluded that 62% of those properties surveyed reported monkeys in their properties; of those agricultural producers that reported monkeys on their properties, 16% attributed crop damage to them (USDA et al., 2008). In addition, biologists from the Puerto Rico Department of Natural Resources claim that there is anecdotal evidence of monkeys depredating nests of endangered yellow-shouldered blackbirds (*Agelaius xanthomus*) (USDA et al., 2008). However, during her study González-Martínez (1995) did not observe either monkey species using areas of coastal mangrove, which is the main nesting habitat for the yellow-shouldered blackbird.

Goals and Purpose of Study

In light of the increases in crop raiding events attributed to the monkeys and the general public's impression that the monkey population has increased significantly in the last decade, I carried out a reassessment of of patas monkeys in southwest Puerto Rico. In this study I estimated current population abundance for the patas monkeys in southwest Puerto Rico, as well as the geographic areas and habitats that are utilized by the different groups, and the patterns by which they use them. I chose to focus only on the patas and not the rhesus macaques because the majority of crop raiding events in southwest Puerto Rico are attributed to patas monkeys. Also, the majority of the sightings of groups of monkeys crossing roads and utilizing urban areas are described as belonging to patas monkeys. This research aims to provide baseline population data needed as a basis for a management plan for this introduced species. Given the large population growth observed at other locations with introduced primate populations, and the fact that the last census for the patas monkeys in Puerto Rico was done 13 years earlier, it was imperative to reassess this population.

I examined the population abundance through the following four parameters: population size, population density, group size and group density. Based on González-Martínez (1995) findings that the resource distribution and availability within their immediate environment in 1993 was relatively abundant and able to sustain the density of the patas population within its range at that time, I predicted that, compared with the 1993 data, a) the population size would have significantly increased, and b) the population density would have significantly increased. By contrast, González-Martínez (1995) found that in 1993 the mean group size for the patas monkey population in southwest Puerto Rico was comparable to average group sizes in African patas populations, I predicted that compared to the 1993 data, c) the mean group size would not have increased significantly, and d) the group density would have increased significantly.

For the population's geographic distribution, and based on González-Martínez (1995) findings that their resource distribution in 1993 was able to sustain the density of the patas population within their home range, I predicted that e) the patas monkeys in Puerto Rico would not have a significant expansion of their geographic distribution when compared with the 1993 data. Based on González-Martínez (1995) predictions that any geographic expansion of the patas population distribution would occur to the east of their

1993 geographic distribution because that area would provide more suitable habitats for the population, I predicted that e) if any geographic distribution expansion of the patas monkeys in southwest Puerto Rico occurred, it would be to the east of the 1993 distribution.

To provide information on how the patas monkey population uses the areas they occupy, I examined the habitat use patterns of the population by analyzing the activities performed within and between the different habitats. Finally, based on hypotheses stating that one of the factors that influences the success of an introduced species population is their association with human-disturbed habitats and on González-Martínez's (1995) beliefs that at the time of her study the area was under urban development pressure, I predict that g) the patas monkeys would preferably be utilizing areas of human-disturbed habitats in the area.

MATERIALS AND METHODS

I conducted the study from May to September of 2006 on the current abundance, geographic distribution, and habitat use patterns of the patas monkeys in southwest Puerto Rico. I collected data on one of the monkey species introduced in the area. The other introduced primate species present in the area is the rhesus macaque, but I did not collect systematic data on it.

Study Area and Subjects

Before I started the data collection for my study, I established a survey area in southwest Puerto Rico composed of locations that I had earlier visited in the search for patas monkey groups. The survey area included the municipalities of San Germán, Sabana Grande, Lajas, Cabo Rojo and Guánica (See Figure 2). The locations visited within the survey area were chosen based on four criteria:

1) Information conveyed to me directly by major landowners in the area who had observed patas monkeys on or near their land;

2) Media reports of landowners' monkey sightings within their properties;

3) Personal communications with personnel from the Puerto Rico Department of Natural Resources and the Caribbean Primate Research Center about monkey sightings in the Southwest area of Puerto Rico by the general public and the locations of these sightings;

4) Indirect evidence in the form of monkey tracks and feces.

Within this survey area I defined a study area which included all the locations where I found patas monkey groups or individuals with direct evidence of the patas monkeys in the form of group or individual visual sightings. This area encompassed the municipalities of Lajas, Cabo Rojo and Guánica in southwest Puerto Rico and was approximately 306km² (17 59.680’N 066 56.359’W, 18 02.764’N 06705.691’W) (See Figure 2). At all the locations where I had visual sightings of patas individuals or groups, I took Geographical Positioning System (GPS) readings using a Magellan eXplorist 210 North America handheld GPS unit.

Figure 2: Blackened area in map denotes study site in southwest Puerto Rico

A study undertaken in the 1960s by the United States Forestry Service and the United States Department of Agriculture to characterize the ecological life zones of Puerto Rico classified the southwest portion of the island as Subtropical Dry Forest (Ewel and Whitmore, 1973). The study described the vegetation in the region as composed mainly of species that contain thorns and spines. Typical tree species found in the area include *Tamarindus indica, Acacia farnesiana, Melicoccus bijugatus, Prosopis juliflora, Bucida burseras,* and *Leucaena glauca* (Ewel and Whitmore, 1973). A more recent characterization of forest type and land cover on the island of Puerto Rico classified the woody vegetation in the southwest portion of the island as lowland dry semideciduous forest or woodland and shrubland (Helmer et al., 2002). Portions of the land in the area are utilized for hay production, livestock pasture, cultivated crop fields and urban development.

I took climatological data for the area for the period from 1986 to 2006 from the Southeast Regional Climate Center webpage, (http://www.sercc.com), maintained by the University of North Carolina, Chapel Hill, NC. I extrapolated the climatological data from the Lajas Substation, the nearest reporting station to the municipalities of Lajas, Cabo Rojo, Guánica and Sabana Grande. The average annual temperature in the area for the period from 1986 to 2005 was 25.2˚C, while in 2006 the average annual temperature was 25.8˚C (See Table 1, Figure 3).

Table 1. Maximum, minimum and mean monthly temperature (Cº) for the 1986-2005 period and the year 2006 in Lajas, Puerto Rico

Period from 1986 to 2005												
	Jan	**Feb**	**Mar**	**April**	**May**	**June**	**July**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Min	15.65	15.87	16.71	16.56	19.78	20.36	20.18	20.33	20.18	19.59	18.37	19.84
Mean	22.83	23.16	23.78	24.82	25.95	26.67	26.82	26.83	26.60	26.01	25.11	23.68
Max	29.97	30.43	30.85	31.38	32.12	32.98	33.46	33.33	33.02	32.42	31.86	30.85
Year 2006												
	Jan	**Feb**	**Mar**	**April**	**May**	**June**	**July**	**Aug**	**Sept**	**Oct**	**Nov**	**Dec**
Min	17.15	16.01	17.19	19.30	20.95	21.87	21.02	21.04	21.24	21.35	19.89	18.23
Mean	24.06	23.02	23.70	25.11	26.42	27.26	26.97	27.15	27.32	27.34	25.98	25.15
Max	30.98	30.02	30.22	30.91	31.90	32.65	32.92	33.26	33.41	33.14	32.07	32.06

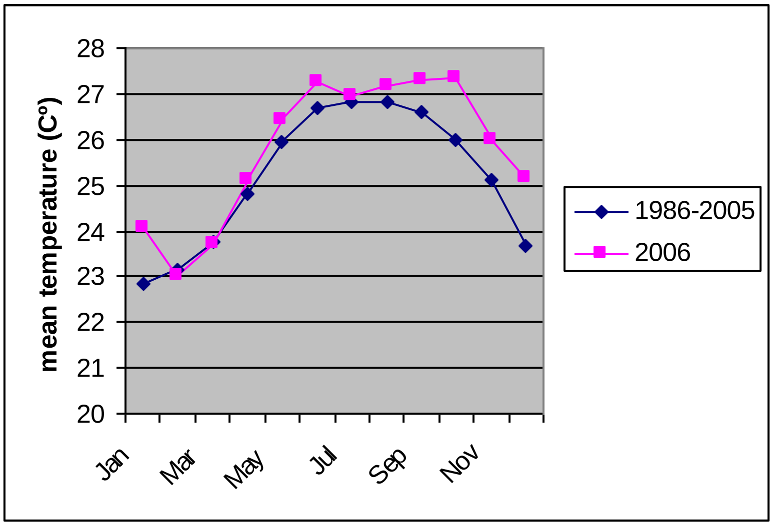


Figure 3. Mean monthly temperature (Cº) for the 1986-2005 period and the year 2006 in Lajas, Puerto Rico

The dry season runs from December to March, with an average of 58.23 millimeters of rainfall per month. During May there is a brief rainy period followed by another dry period during June and July. The main rainy season runs from August to November with an average of 149.60 millimeters of rainfall per month in the area. The average total rainfall per year for the period from 1986 to 2005 in the area was 1199.39 millimeters, while in 2006 it was 1231.39 millimeters (See Table 2, Figure 4).

Table 2. Monthly total rainfall (mm) for the 1986-2005 period and the year 2006 in Lajas, Puerto Rico

Period from 1986-2005												
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
monthly total	59	57.7	55.1	96.5	135.1	77	68.1	135.4	148.3	181.4	142.8	52.8
Year 2006												
	Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
monthly total	121.2	42.2	154.4	120.4	126	81.5	95	98.8	81.5	96.8	136.9	76.7

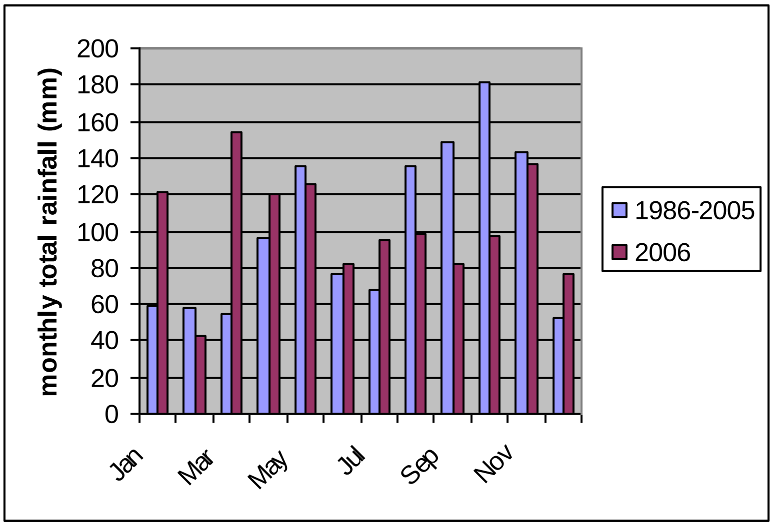


Figure 4. Mean monthly rainfall (mm) for the 1986-2005 period and the year 2006 in Lajas, Puerto Rico

Data Collection

I collected data from 22 May to 20 September 2006 in the southwest portion of Puerto Rico. Initially, I visited several locations that were included in the survey area. Once I established that one or more patas monkey groups were utilizing a site within the survey area, I monitored the location to collect data on the group. A site within the survey area that yielded direct evidence of patas monkey activity was considered part of the study area for the research.

Group Follows

I collected data on 9 to 11 patas monkey groups. A typical day of data collection began at 0630 and ended at 1800 hours. If I knew the location of a group's sleeping area based on observations from the previous day I would return to the sleeping site between 0600 and 0630 the next morning and begin observing and following the group as soon as I located it. If a monkey group could not be located at its sleeping site during the morning, I would search the area until I found a patas monkey group. As soon as I found a patas monkey group, I would begin following the group and collecting data on it. I stopped data collection on the monkeys when the group moved out of sight, but as soon as the group was relocated or another group was found, data collection would resume. When possible, I followed a group until it reached its sleeping site in the evening. There were several groups for which I was able to collect all-day data on several days. Due to the cryptic behavior of patas monkeys (Chism and Rowell, 1988) and since groups were not habituated to my presence, the group (or groups) to be observed on a given day were selected opportunistically, depending on the level of difficulty in finding certain groups and the reports I received from the local people in the area about the whereabouts of groups that had not been previously detected.

Identifying Groups

To distinguish and characterize the different patas monkey groups inhabiting southwest Puerto Rico I utilized two criteria. The first criterion was the age/sex composition of each group, as well as unique physical characteristics of individuals in each group that would aid in the identification process. Of special interest was recording detailed descriptions of the individual characteristics of the adult male(s) in each group encountered. The second criterion utilized was the best group counts for each area visited to identify individual groups in each location. Best group counts are defined as groups for which there was a higher probability that all the individuals belonging to the group were counted after the individual male (s) or other known individuals in the group were identified. Usually the best group counts were obtained in open areas with higher visibility, or from higher elevation locations.

To complement these group identification techniques whenever possible I utilized field assistants to help me detect and follow the individual groups in the area. Field assistants were trained in the observations methods utilized for this research, as well as in the identification of patas monkey individuals according to demographic age stage and gender. When field assistants were available, I coordinated our activities using cellular telephones so that I could spend time collecting data from one patas monkey group, while the field assistants collected data at the same time on a different group sharing the same area. By keeping in touch with field assistants via cellular telephones and comparing the groups' locations and directions of travel I was able to differentiate among groups sharing the same resources and lands with overlapping home ranges. I also established a telephone network with local residents who would alert me when they sighted a monkey group. This network aided me in tracking monkey groups for which observation had been difficult either because of the elusive behavior of the monkeys or because of poor visibility in the groups' habitat.

Instantaneous Scan Sampling

I spent a total of 91 days tracking monkey groups, out of which I spent 64 days in direct observation of groups. To collect the data I used the instantaneous scan sampling method (Altmann, 1974) with a ten-minute interval between scans. During the study I collected a total of 610 scans (Table 3). During an individual scan I collected data on each visible individual utilizing Bushnell Falcon™ binocular and Bushnell Laser Rangefinder Yardage Pro Sport 450. For all scans I recorded the time of the scan, the group's location and direction of movement (using GPS coordinates), distance of the closest monkey to the observer in meters (utilizing the rangefinder), habitat type, the number, age-sex class and activities of all visible individuals in the group. Before the data collection started, I practiced visual approximations of distances ranging from 5 to 200 meters utilizing a measuring tape. This allowed me to estimate the spread of the group to the nearest meter.

Activity data categories utilized in scans were based on those used by González-Martínez (1995) in her earlier study and included: 1) **social behavior**, defined as maternal interactions, aggression, play, allogrooming, and mating; 2) **resting**, defined as sitting while inactive, sleeping, and selfgrooming; 3) **locomotion**, defined as walking, running, and jumping; 4) **feeding/foraging**; 5) **drinking water**; 6) **vigilance**, defined as scanning the environment, being alert to its surroundings (González-Martínez, 1995). Following González-Martínez's (1995) activity characterizations, **feeding** was defined as a monkey collecting a food item or putting food in its mouth, whereas foraging was defined as clearly moving and searching for food, e.g. looking under leaves, searching the grass, or searching under cattle dung. The data collected on their daily activities enabled me to examine how the monkey groups utilized the different habitats.

In order to be able to compare my data on this population's habitat utilization as directly as possible with that collected in the 1993 study, I also used the same habitat characterizations defined by González-Martínez (1995). These habitat categories were:

1) **Semideciduous woodland**, which included small patches of deciduous or semideciduous trees mainly *Bucida burseras, Tamarindus indica, Melicoccus bijugatus,* and *Mangifera indica*;

2) **Mesquite woodland**, which included an uninterrupted expanse of woodland containing *Prosopis juliflora, Pithecellobium dulce,* and *Boureria succulenta* with an understory of grasses;

3) **Secondary climax scrub**, which included large trees of *Hymanea courbaril, Boureria succulenta, Capparis baducca* and *Leucaena leucocephala* surrounded by a dense shrub layer;

4) **Savannah**, which included unfenced patches of large trees interspersed within large tracts of grassland;

5) **Grazing land**, which included fenced areas that were primarily used as pasture for cattle, horses and/or sheep, and natural and non-natural water source for the grazing animals;

6) **Agricultural fields**, which included areas utilized for the cultivation of crops;

7) **Urban**, which included areas that contained structures such as residential and commercial buildings.

In addition, I added a new habitat category which I named "**Edges**". I defined this as a distinct tract of space that serves as a border between different habitat types, including fence lines and some dirt roads. I added this category because the patas monkey populations in Africa are characterized as utilizing habitat margins frequently (Chism and Rowell, 1988). In addition, I observed the patas monkeys in Puerto Rico using habitat margins during my study on more than one occasion throughout the area.

Following Chism et al. (1984) age/class characterizations and González-Martínez's (1995) age/class and weight characterizations, the age/sex classes recorded included:

1) Adult Male: This is the largest individual in the group, with a bright blue scrotum, and a bright mahogany-red coat that stands out against the white hind legs. On his face the adult male has white hair covering the upper lip and chin, as well as a black patch over the nose and black hair covering the brows. Adult males usually weight 7 to 13 kg (almost twice the size of the adult females) and are at least 5 years old.

2) Adult Female: Females have a paler sandy-red coat, usually weight 4 to 7 kg and are at least 2.5 years old. The adult female face has white hair covering the upper lip and chin, as well as a black patch over the nose and black hair covering the brows.

3) Subadult Male: These individuals are smaller in size and have a paler blue scrotum when compared to the adult male, but they are approximately larger in size than the adult female.

4) Juveniles: These are nutritionally independent from and are not carried around by the mother. Patas monkeys reach the juvenile stage at one year of age. The juvenile can be distinguished from the adult female by the facial hair color, which is almost entirely black on the cheeks, moustache area, chin and brows. Juveniles weight up to 4 kg, approximately, and are smaller in body size than adult females.

5) Red infants: These animals have achieved the paler or red phase of the pelage which occurs at around 4 months of age but are still dependent on mothers for transport and nutrition.

6) Black infants: These individuals have the dark phase of pelage (natal coat) which is shown from birth to around 3 months of age.

Table 3. Summary of locations visited and effort[1]

Location	**Group/s Utilizing the Location**	**Number of Scan Samples Collected**	**Number of Days Spent in the Location**
Cattle Hill, Lajas	Parguera	65	10
JB House, Lajas	Parguera	34	5
Parguera 305 Street, Lajas	Parguera	17	3
304 Road, Lajas	323, 116, Parguera	24	6
324 Road, Lajas	323, 116, Parguera	62	16
Museum House, Lajas	323, 116, Parguera	9	4
Combate, Cabo Rojo	Carreras,Tony's, Boqueron	10	3
Carreras Property, Cabo Rojo	Carreras,Tony's, Boqueron	14	4
Pitahaya, Cabo Rojo	Carreras, Boqueron	76	7
Costa Bermeja, Cabo Rojo	Carreras	2	1
Tony's Property, Cabo Rojo	Carreras, Tony's	34	4
301 Road, Cabo Rojo	Blimp	5	1
Cabo Rojo NWR, Cabo Rojo	Carreras	1	1
Arturo Acosta Property, Lajas	116	12	2
116 Road	116	38	3
306 Monte Interior, Lajas	Pineapple	6	2
323 Street, Lajas	323, 324	63	13
Abras Fuig, Guánica	116	2	1
Blimp Road, Lajas	Blimp	9	1
Km 6.0, Lajas	Blimp	9	1
Sierra Bermeja, Cabo Rojo	Tony's, Boqueron	88	9
Viándon, Cabo Rojo	Tony's, Boqueron	12	4
Peñones de Melones, Cabo Rojo	Boqueron	10	2
Total	**9**	**602**	**103**

[1] The locations included in this table are all within the study area. Locations in the survey area where I did not find any monkey groups or individuals were not included in the study area.

DATA ANALYSIS

I used the data collected to determine size and density, geographic distribution, and habitat use patterns for the population in the area. The alpha level used for all statistical tests in my study was ≤0.05.

Population Size and Density

To obtain an estimate of the current size of the population of patas monkeys in my study area, I utilized two methods of estimation. In the first one I summed together the best group count for each individual group for the whole patas population, which gave me an estimate of population size. The best group count utilized for data analysis was the count which gave me the maximum number of individuals sighted for each identified individual group during the duration of the study. In the second method I summed together all the counts for each group, and calculated from these counts a mean. This mean was utilized to determine a second estimate for population size and the ranges of group size. Group counts were obtained mainly when monkey groups crossed roads or open areas or came out of a sleeping site, as I performed group follows. I obtained at least two group counts on each identified group; these group counts occurred after having followed the group on successive days and being able to obtain repeated counts on the group as it crossed open areas. During the study I encountered two potentially new groups for which I was only able to obtain one group count each. Although I did not observe these groups often enough to be certain they were actually different groups, to account for the possibility that they were different groups, I reported a range estimate for both the population size and the number of groups. I utilized the minimum number and the maximum number of the population size range to compare my 2006 data with those of González-Martínez (1995) to examine percentage change of the population size in the last 13 years.

To determine population density for the 2006 study, I utilized the minimum number from the population size range based on best group count means and the estimated geographic distribution area for the patas monkeys in Puerto Rico, and applied the formula:

$$D = \text{Number of Individuals}/\text{km}^2$$

I compared the population density estimates for 1993 and 2006, and calculated the change over the intervening 13 years.

By pooling together, the mean size for each recognized individual group and utilizing the minimum number of groups counted (n=9), I calculated the overall mean group size for the population. To test for a significant difference between the mean group size for 2006 and 1993, I used a two tailed Student t-Test (Moore and McCabe, 1989) using Microsoft® Excel 2003. Utilizing the minimum number of groups counted (n=9) and the estimated geographic distribution area for the patas monkeys in Puerto Rico, I calculated group density in the area with the formula: $D = \text{Number of Groups}/\text{km}^2$. I compared the 1993 group density with the 2006 estimates and calculated the percentage of change in the intervening 13 years.

Population Distribution

Utilizing the GPS coordinates of the patas monkeys' locations, as well as a 2004 Ikonos digital aerial photograph provided by the Puerto Rico Department of Transportation, and ArcGIS (version 9.2), I produced a geographic range map of the species' current distribution in southwest Puerto Rico following the Minimum Convex Polygon method (Boitani and Fuller, 2000). Once the GPS coordinates were projected onto the Ikonos digital aerial photograph of the area, and the geographic range map was created, utilizing the ArcGIS program, I calculated the area of the distribution in km². To determine whether a change in the patas monkeys' distribution had occurred over the 13 years since González-Martínez's study, I compared my geographic distribution map with the map from González-Martínez' 1993 study area (1995). By comparing both patas monkey population geographic distribution maps, I was able to determine if there had been an expansion of the species range in km² and the direction of such a geographic expansion in the area over the 13 years since González-Martínez's study.

Habitat Use

With the GIS program I was able to estimate the area available in km² for each type of general habitat category within the patas monkeys' geographic range. These areas were then converted into percentages. A Chi-squared goodness of fit test (Moore and McGabe, 1989) was used to compare the monkeys' proportional use of these two habitats with the expected use for each habitat based on its proportion of area.

To determine how the patas monkeys utilized the different habitats available to them I examined the activities performed by the monkeys in each habitat at two scales. First, I examined the percentage of each activity performed in each habitat, analyzing the data utilizing a single factor ANOVA (Moore and McGabe, 1989) performed on a Microsoft® Excel 2003 program on the arcsine transformed proportion of the habitat type data from the instantaneous scan samples, examining the proportions at which the monkeys utilized each habitat type between each activity performed. By performing this analysis, I was able to detect differences in the monkeys' behavior according to habitat type. Secondly, I examined the percentage each habitat contributed to an activity. By comparing the activities performed in each habitat I was able to detect whether activities occurred in different proportions in different habitat types. I analyzed the data utilizing a single factor ANOVA (Moore and McGabe, 1989) performed with Microsoft® Excel 2003 on the arcsine transformed proportion of the activities data from the instantaneous scan samples, examining the proportions at which the monkeys performed each activity between each habitat type. For both the activity performed between each habitat type analysis and the habitat type utilized between each activity performed analysis, I utilized a Scheffé post-hoc test (Lomax, 2007) for each single factor ANOVA test where the null hypothesis was rejected.

Because the success of various introduced species has been correlated with their associations with human-disturbed habitats (Lozon and MacIsaac, 1997)). I examined the human-disturbed habitat usage of the patas monkeys in Puerto Rico. To examine the occurrence of patas monkeys in different habitats, I created two general habitat categories: **human-disturbed** habitats, which included agricultural lands, grazing lands and urban development; and **semi-natural** habitats, which included semideciduous woodland, mesquite woodland, savannah and secondary climax scrub. I used ArcGIS (version 9.2) program and the 2004 Ikonos digital aerial photograph, plotting all my GPS coordinates onto the aerial photograph. The GPS coordinates not only contained information about the locations of patas monkey groups, but they also contained the habitat type classification for all the locations visited. Utilizing these GPS coordinates and additional information I had on the area collected while surveying for patas monkey groups, I adopted a classification strategy, for which prior knowledge about an area was used as training polygons within the image that I used to identify other polygons with spectrally similar characteristics.

RESULTS

With the data collected I made comparisons with González-Martínez's 1993 study (1995) of the patas population in southwest Puerto Rico, which contains the only previous data collected on this population. By making comparisons with the 1993 data I was able to examine whether the population had changed significantly over the 13 years between the two studies, as well as to examine the possible future impacts of the patas monkeys in the area. I also examined the habitat use patterns of the population to try to determine whether these had altered detectably in the years since the previous study.

Over the 13 year period between 1993 and 2006 the number of individual patas monkeys increased by 328%, while the population density increased by 212% and the mean group size increased from 26 to 52 individuals In contrast, the group density only increased by 66% and the geographic range only increased by 38%. Below, I discuss the details of these changes.

Population Abundance

In 1993, González-Martínez (1995) found a population of around 120 patas monkeys including 4 heterosexual groups and several all-male bands. The population size estimate range for my study had a minimum of 514 individuals and a maximum of 621 individuals, for a mean of 567.5 individuals. When I compared the minimum estimate of the population size range in 2006 with data collected by González-Martínez (1995) in 1993, there was a 328% increase in the population over the 13-year period, while there was a 418% increase in the population when the maximum estimate of the population size range was compared with González-Martínez's (1995) data (See Figure 5). Because I did not observe any all-male bands or solitary males in my study, my counts only included heterosexual groups in the area whereas González-Martínez's (1995) population estimate also included all-male bands and solitary males.

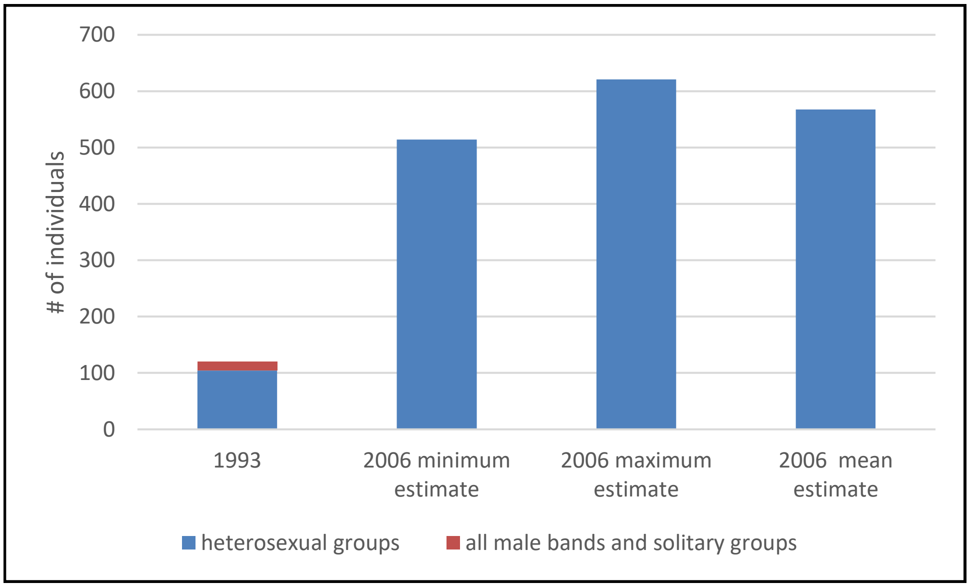


Figure 5. Population size in 1993 versus 2006 population size estimates

Population Density

Utilizing the minimum estimate of the population size range based on best group counts (n=514) and the calculated geographic distribution area of 172 km², the population density for patas monkeys in the study area in 2006 was 2.99 individuals per km². When I compared this density with González-Martínez's population density calculations of 0.96

individuals per km² based on her study area (1995), I found a 212% increase in population density for the population over the 13-year period (See Figure 6).

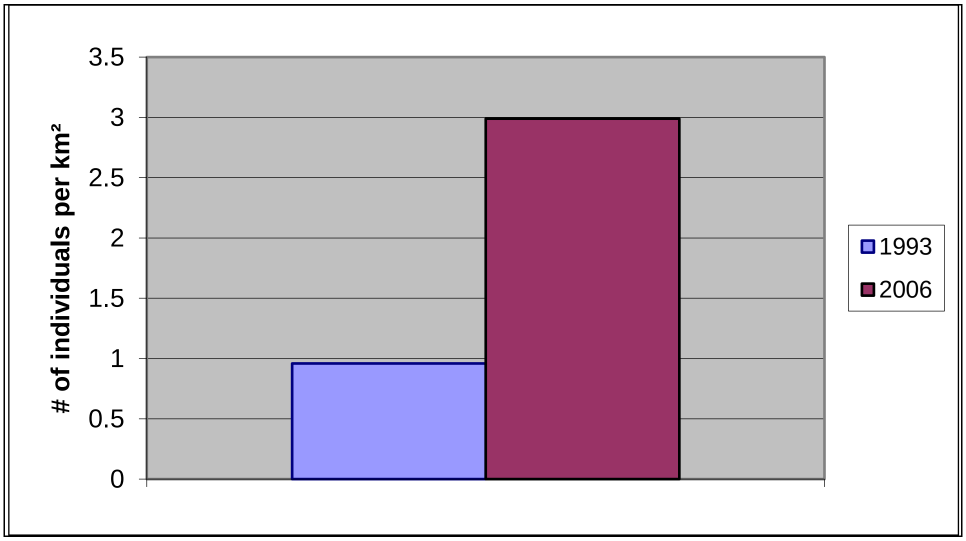


Figure 6. Patas monkey population density increase from 1993 to 2006

Group Size and Number

In 1993 González-Martínez (1995) found 4 heterosexual patas monkey groups that ranged in size from 20 to 35 individuals, with a mean group size of 26.23 (SD=±7.06, n=4). Based on best group counts, I found 9 to 11 heterosexual patas monkey groups in my study area which ranged in size from 19 to 91 individuals (See Table 4). Utilizing the minimum number of groups counted (those for which I had at least two group counts) yielded a mean group size for the population of 57.11 individuals (SD=±27.97, n=9). Utilizing a two-tailed, unpaired *t*-test (Moore and McCabe, 1989), I found a significant difference in the mean group size between González-Martínez's 1993 data (1995) and my 2006 data (*t*=-2.69109, d.f.=11, *P*=0.020988) (See Figure 7).

Table 4. Patas monkey group counts for the 2006 study

Group ID	Range Number of Individuals	Mean Group Size ±SD	Number of Counts
323	**30-36**	**34±2.5**	6
324	**54-91**	**73±14.1**	5
116	**54-63**	**58.5±6.4**	2
Parguera	**62-71**	**66.2±3.5**	10
Blimp	**74-76**	**75±1.4**	2
Carreras	**17-19**	**18.5±1.0**	4
Pineapple	**44-45**	**44.5±0.7**	2
Tony	**43-50**	**46.2±2.9**	4
Boquerón	**50-63**	**54±8.9**	6
SB1[1]	**48**	**NA**	1
SB2[1]	**59**	**NA**	1

[1] Potential new group for which only one group count was obtained. The group was not observed on a sufficient amount of time in order to be identified as a separate group from the ones already observed in the area.

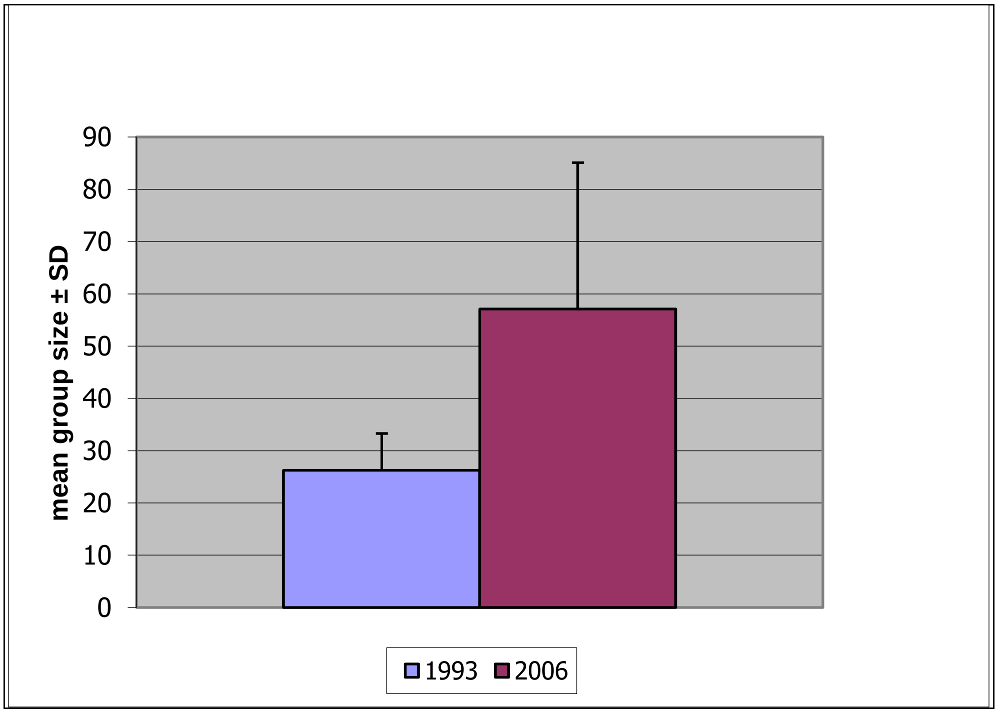


Figure 7. Mean size of patas monkey groups in 1993 (26.23, n=4) versus 2006 (57.11, n=9)

Group Density

Using the minimum number of groups identified (n=9) and the calculated geographic distribution area of 172 km², I found that the group density for the study area was 0.053 groups per km². When I compared the group density of the patas monkey population in 2006 with their group density in 1993 of 0.032 groups per km² (n=4 groups in 125 km²), I found a 66% increase in group density over the 13-year period (See Figure 8).

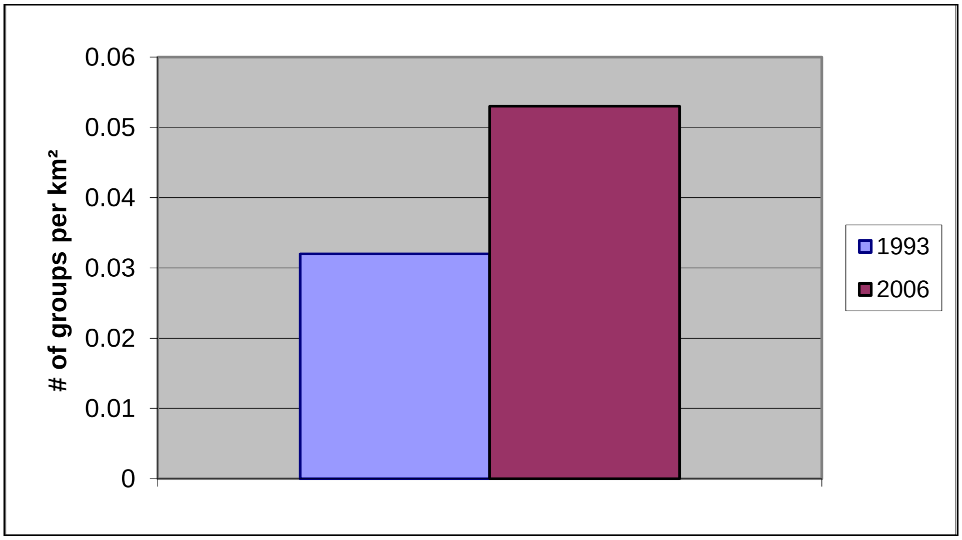


Figure 8. Patas monkey group density of 1993 (n=4) versus 2006 (n=9)

Geographic Distribution

Over the course of my study I recorded the GPS coordinates for all of my sightings of patas monkeys in southwest Puerto Rico (See Figure 9), and produced a geographic range map of the population using the Minimum Convex Polygon method (Boitani and Fuller,

2000) (See Figure 10). Based on these locations, I calculated a distribution for this population of approximately 172 km² (17° 59.680’N 66° 56.359’W, 18° 00.575’N 67˚07.539’W). All the localities included in the map of geographic distribution for the population in 2006 had confirmed direct evidence of monkey groups. The only monkey group sighting not included in the geographic distribution map was one observed near Route 306 at the north side of the municipality of Lajas. Because this location was outside of the apparent distribution range for the population and I observed only one group at this location over a period of two days, I treated this sighting as an outlier (See Figure 10). In addition, it was apparent from the GIS digital aerial photograph that the majority of the areas separating the main distribution range from the outlier patas monkey sighting location could be classified as human-disturbed habitats. I observed the outlier group in two habitat types; these were semideciduous woodland and agricultural field. The majority of the observations recorded for the outlier group were in semideciduous woodland, but because this woodland area was surrounded almost on all sides by pineapple fields and residential houses, the monkeys had to use the pineapple fields to enter or exit the woodland area. During the duration of the study I did not observe the outlier group feed in the pineapple fields; the only activity recorded for the outlier group in these fields was of a locomotive nature.

When I compared the geographic distribution of the population in 2006 with González-Martínez’s 1993 geographic distribution of approximately 125 km² (1995), I found a 38% increase in geographic distribution area over the 13-year period. The patas population’s geographic distribution for the 2006 data included the municipalities of Lajas, Cabo Rojo and Guánica. Among these municipalities, Guánica constituted a new area utilized by the monkey groups in 2006 compared with the 1993 study (González-Martínez, 1995). The monkeys' geographic range for the 2006 data was bounded on the north side by secondary state roads 101 and 116, as well as by the Loco River, and on the east side by the Loco River. To the south and west the patas monkey population was bounded by the sea. In 2006 the monkeys were utilizing all the areas that Gonzalez-Martinez reported them as using in her 1993 study. Furthermore, the patas in 2006 were also utilizing areas that were located to the east of tertiary state road 323 in the Parguera (Lajas) and Ensenada (Guánica) areas, whereas in 1993 the monkeys maintained their range to the west of this road.

In comparing the 2006 geographic distribution of the population against González-Martínez's 1993 data (1995), I found that their expansion has occurred in an easterly direction in the area (See Figure 10).

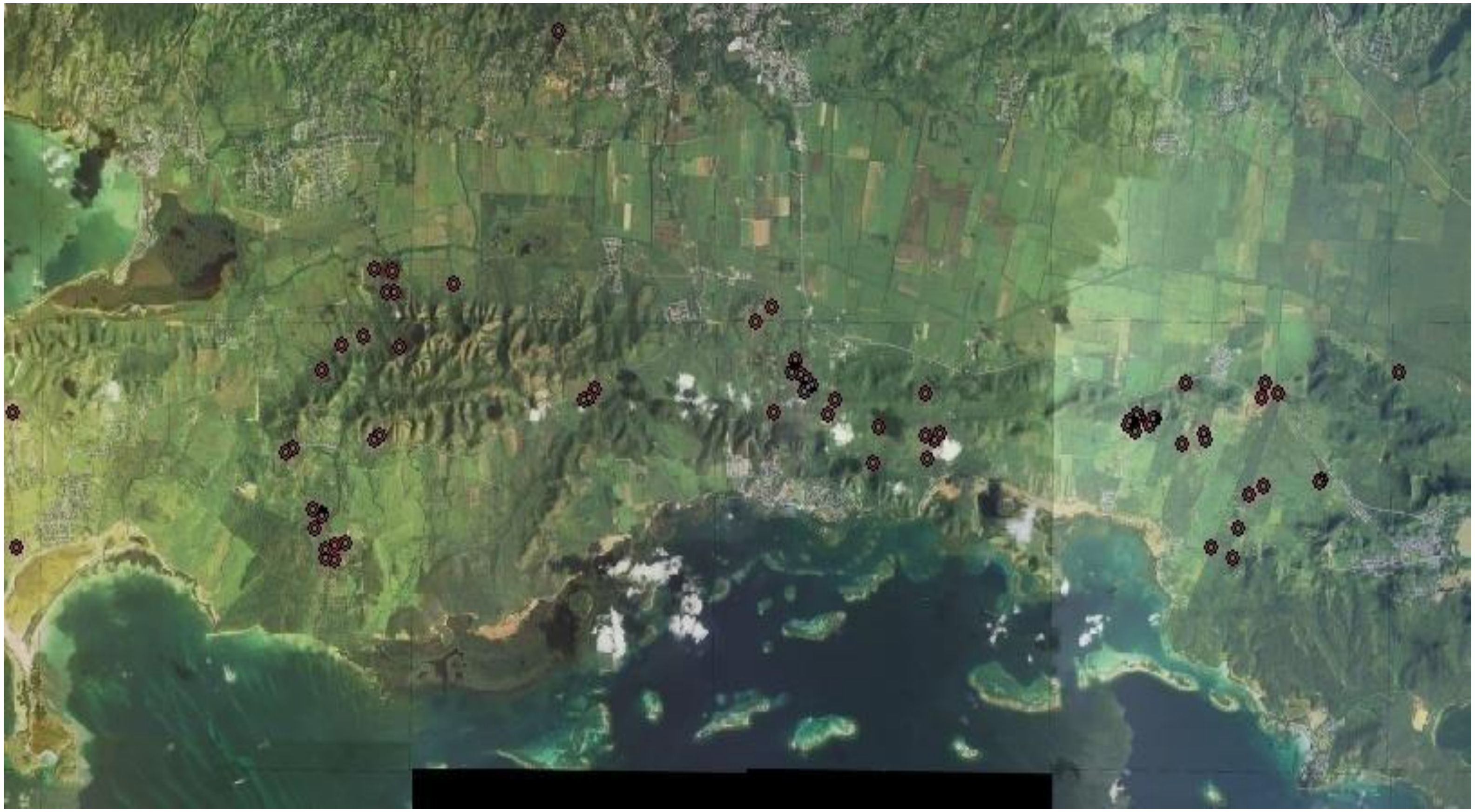


Figure 9. Locations of patas monkey group sightings in southwestern Puerto Rico, 2006.

Figure 10. 2006 Geographic range and distribution expansion of the patas monkey population from 1993 to 2006

Habitat Use Patterns

Activities Performed in Different Habitat Types

I analyzed the distribution of four different patas monkey activities, feeding and foraging, social, rest and locomote over the eight habitat types identified. With two exceptions the patas distributed their feeding and foraging evenly across the habitat types. A single factor ANOVA (Moore and McCabe, 1989) revealed no significant difference among the different habitat types in the proportion of the feeding and foraging by the monkeys (F=1.04; Fcrit=2.20; d.f.=7, 49; *p*=0.417) (See Table 5a, Fig. 11). I never saw any feeding or foraging by the patas in the agricultural fields during the entire length of the study and the instances of feeding and foraging in urban areas took place in the backyard of houses that had wild fruit trees such as mango (*Mangifera indica*) and Spanish lime (*Melicoccus bijugatus*).

Table 5a. Feeding and Foraging in Different Habitats[a]

Grazing Land	**Mesquite Woodland**	**Semideciduous Woodland**	**Savannah**	**Secondary Climax Scrub**	**Urban Development**	**Agricultural Field**	**Edge**	**ANOVA**
30%±22	42%±41	57%±31	48%±36	25%±0	67%±29	0	51%±34	**F**=1.04 **Fcrit**=2.20 **d.f.**=7,49 ***p***=0.417

[a]Mean±SD percentages of scans for the activity of feeding and foraging by habitat type in which at least one visible group member was engaged in the activity. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously.

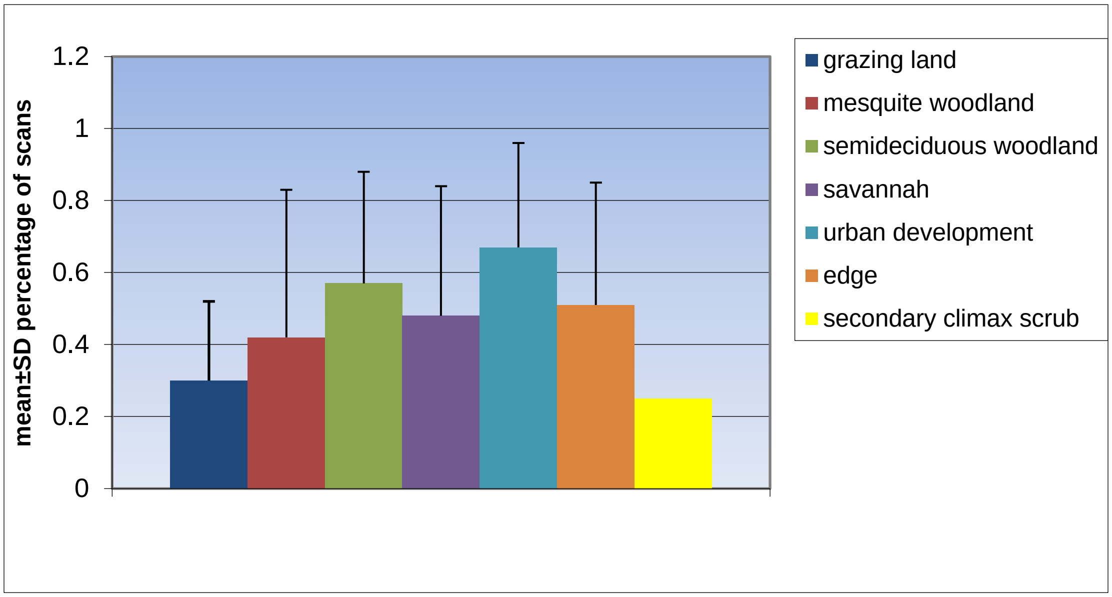


Figure 11. Mean percentage and standard deviation of feeding and foraging activities by habitat type

The proportion of scans with social activities also did not differ across habitats; a single factor ANOVA (Moore and McCabe, 1989) revealed no significant difference among the different habitat types in the proportion of the social activities by the monkeys (F=0.21; Fcrit=2.36; d.f.=7, 28; *p*=0.981) (See Table 5b, Fig.12). The monkeys were never observed to engage in social activities in secondary climax scrub areas, agricultural fields or urban development areas.

Table 5b. Social Activity by Habitat Type[a]

Grazing Land	Mesquite Woodland	Semideciduous Woodland	Savannah	Secondary Climax Scrub	Urban Development	Agricultural Field	Edge	ANOVA
39%±22	35%±31	54%±32	43%±40	0%	0%	0%	56%±39	**F**=0.21 **Fcrit**=2.36 **d.f.**=7, 28 *p*=0.981

[a] Mean±SD percentages of scans for social activities by habitat type in which at least one visible group member was engaged in the activity. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously.

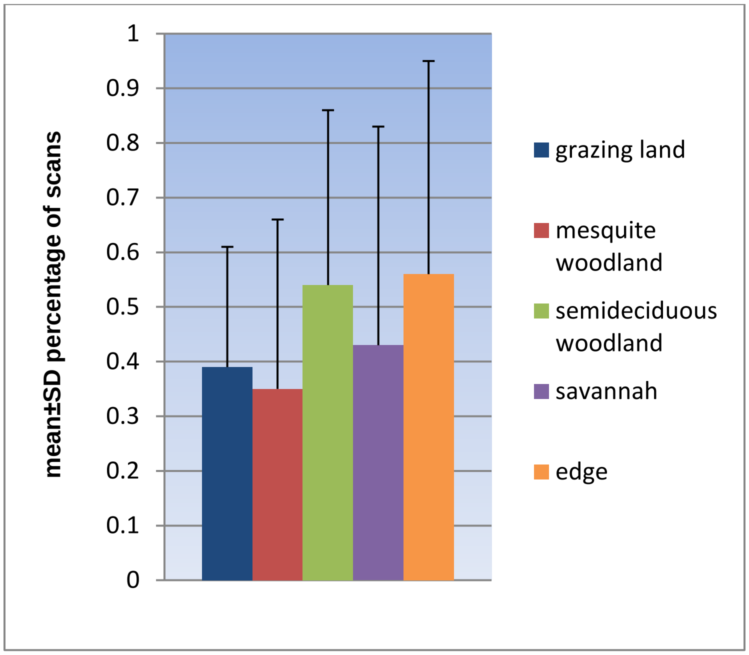


Figure 12. Mean percentage and standard deviation of social activities by habitat type

The patas monkeys were equally likely to rest in all habitats. A single factor ANOVA did not yield a significant difference among the various habitat types utilized by the monkeys for the activity (F=0.69; Fcrit=2.11; d.f=7, 89; *p*=.682) (See Table 5c, Fig. 13). All habitat types available in the area had at least one scan in which one or more monkeys were engaged in resting behavior.

Table 5c. Resting Activity by Habitat Type[a]

Grazing Land	**Mesquite Woodland**	**Semideciduous Woodland**	**Savannah**	**Secondary Climax Scrub**	**Urban Development**	**Agricultural Field**	**Edge**	**ANOVA**
74%±26	82%±20	74%±26	76%±22	50%±0	70%±19	50%±0	55%±39	**F**=0.69 **Fcrit**=2.11 **d.f.**=7,89 *p*=0.682

[a]Mean±SD percentages of scans for resting activities by habitat type in which at least one visible group member was engaged in the activity. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously.

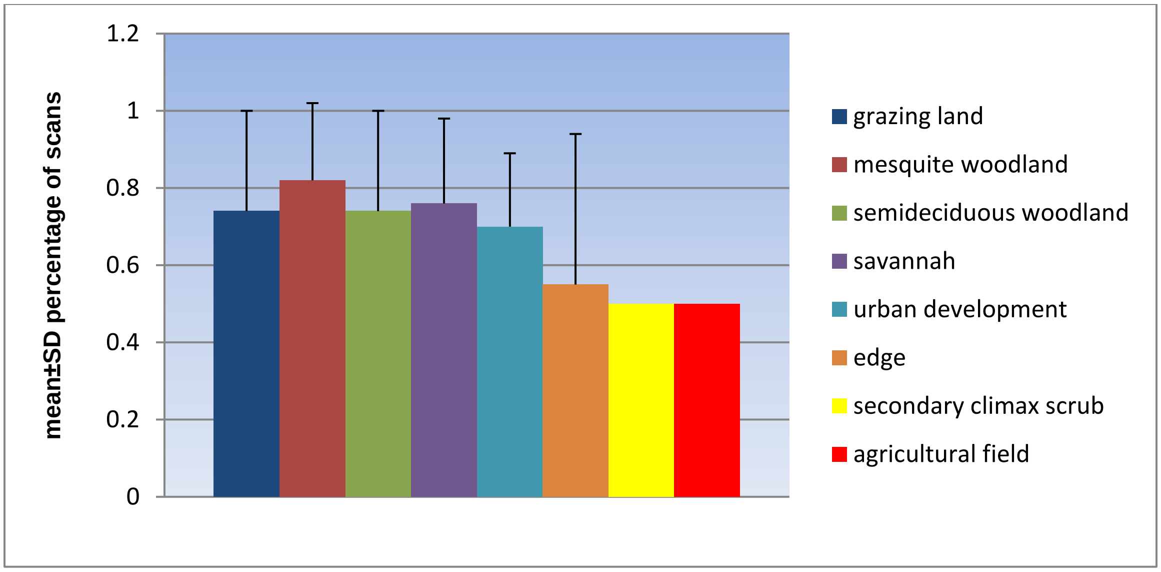


Figure 13. Mean percentage and standard deviation of resting activities by habitat type

A single factor ANOVA on locomotor activity yielded a significant difference among the habitat types for the proportions for this behavior (F=2.89; Fcrit=2.09; d.f.=7, 111; *p*=0.008) (See Table 5d, Figure 14). Because secondary climax scrub had only one record for locomotor activities, which was considered to be too small a sample to be included in the post hoc test, it was excluded from further analysis. In a Scheffé post-hoc test (Lomax, 2007) on locomotion activities between habitat types, mesquite woodland was shown to be used least for locomotor activities while edges were used the most and these two habitats differed significantly for this measure (F=2.63; Fcrit=2.18; d.f.=6, 111, p=.05). None of the pairwise comparisons between the other habitat types in the area for locomotive activities were significantly different.

Table 5d. Locomotive Activity by Habitat Type[a]

Grazing Land	**Mesquite Woodland[1]**	**Semideciduous Woodland**	**Savannah**	**Urban Development**	**Agricultural Field**	**Edge[1]**	**ANOVA**
70%±31	57%±31	68%±27	62%±27	63%±41	75%±35	93%±17	**F**=2.89 **Fcrit**=2.09 **d.f.**=7,111 *p*=0.008

[a]Mean±SD percentages of scans for locomotive activities by habitat type in which at least one visible group member was engaged in the activity. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously.

[1]Scheffé post-hoc test denotes a difference at the 0.05 level of significance

***Secondary Climax Scrub habitat is omitted from this table because sample size is too small**

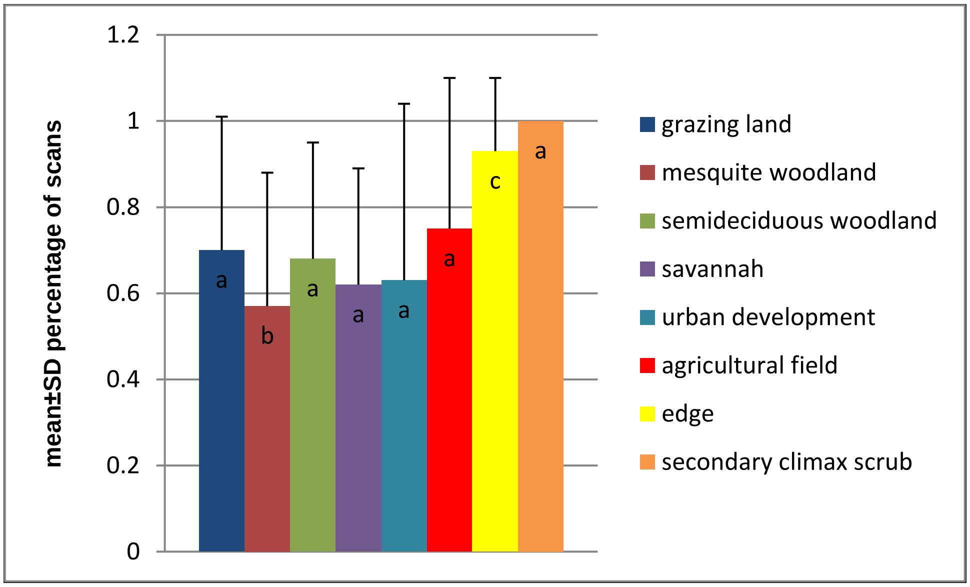


Figure 14. Mean percentage and standard deviation of locomotive activities by habitat type. Letters b and c denote a difference at the 0.05 level of significance.

Activities Performed Within Habitat Types

An analysis of each habitat type by the main four activities (feeding and foraging, locomotion, resting, and social) performed by the monkeys revealed significant differences in the activities performed in the mesquite woodlands, grazing lands and edges. The secondary climax scrub habitat type was excluded from this analysis because of the low frequency of the activities within this habitat type (n=1), which was insufficient to perform a single factor ANOVA.

A single factor ANOVA test for the urban development areas did not reveal a significant difference among the activities performed at this habitat type by the monkeys (F=0.04; Fcrit=3.86; d.f.= 3, 9; *p*=0.987) (See Table 6a, Fig. 15).

Table 6a. Activities in Urban Development Habitats[a]

Feeding	**Locomotion**	**Social**	**Resting**	**ANOVA**
67%±29	56%±41	0	64%±14	**F**=0.04 **Fcrit**=3.86 **d.f**.=3, 9 ***p***=0.987

[a] Mean±SD percentages of scans for urban development habitats by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously

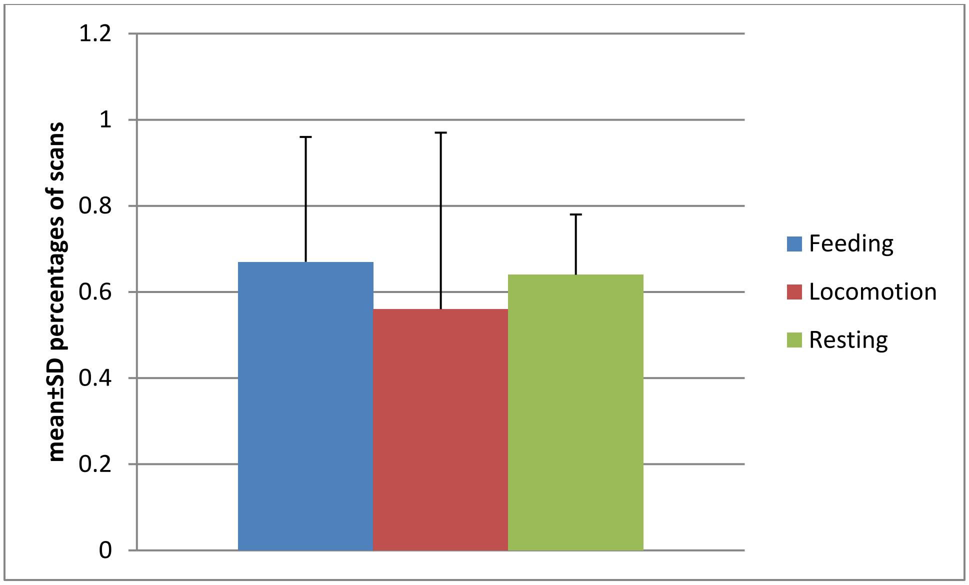


Figure 15. Mean percentage and standard deviations of scans for activities which occurred in urban habitats

A single factor ANOVA test did not reveal significant differences in proportions of activities performed in the savannah (F=1.18; Fcrit=2.93; d.f.=3, 29; *p*=0.335) and semideciduous woodland (F=1.27; Fcrit=2.77; d.f.=3, 57; *p*=0.292) habitats (See Table 6b and 6c, Figures 16 and 17).

Table 6b. Activities in Savannah Habitats[a]

Feeding	**Locomotion**	**Social**	**Resting**	**ANOVA**
48%±36	62%±27	43%±40	76%±22	**F**=1.18 **Fcrit**=2.93 **d.f.**=3,29 ***p***=0.335

[a]Mean±SD percentages of scans for savannah habitats by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously

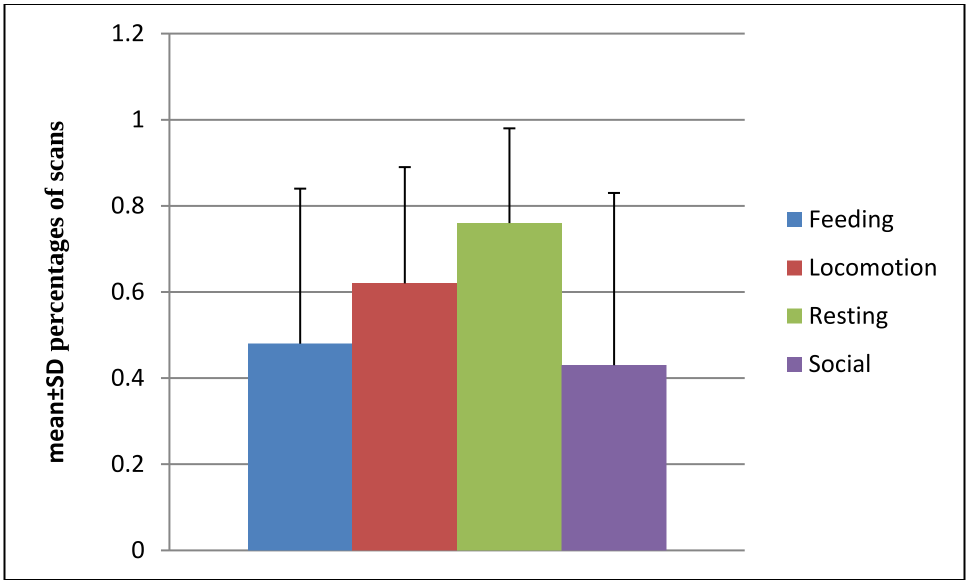


Figure 16. Mean percentage and standard deviations of scans for activities which occurred in savannah habitat

Table 6c. Activities in Semideciduous Woodland Habitats[a]

Feeding	Locomotion	Social	Resting	ANOVA
57%±31	68%±27	54%±32	74%±26	**F**=1.27 **Fcrit**=2.77 **d.f**.=3,57 *p*=0.292

[a] Mean±SD percentages of scans for semideciduous woodland habitats by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously

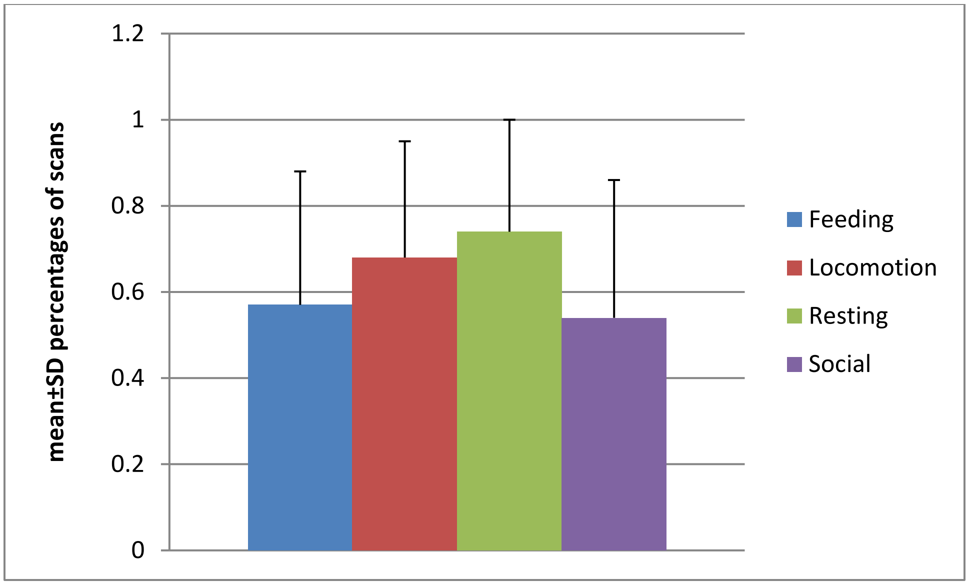


Figure 17. Mean percentage and standard deviations of scans for activities which occurred in semideciduous woodland habitat

For the edges habitats, a single factor ANOVA test yielded a significant difference among the different activities performed by the monkeys (F=8.16; Fcrit=2.99; d.f.=3, 25; *p*=0.0006) (See Table 6d). Using a Scheffé post-hoc test I found that the proportion of locomotive activities was significantly higher than the proportion of social activities in edges habitat (F=4.38; Fcrit=2.99; d.f.=3, 25, α=.05) (See Figure 18). None of the other pairwise comparisons for activities in edge habitat yielded a significant difference.

Table 6d. Activities in Edge Habitat[a]

Feeding	**Locomotion[1]**	**Social[1]**	**Resting**	**ANOVA**
51%±35	93%±07	31%±28	55%±39	**F**=8.16 **Fcrit**=2.99 **d.f**.=3,25 *p*=0.0006

[a]Mean±SD percentages of scans for habitat edges by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously

[1]Scheffé post-hoc test denotes a difference at the 0.05 level of significance

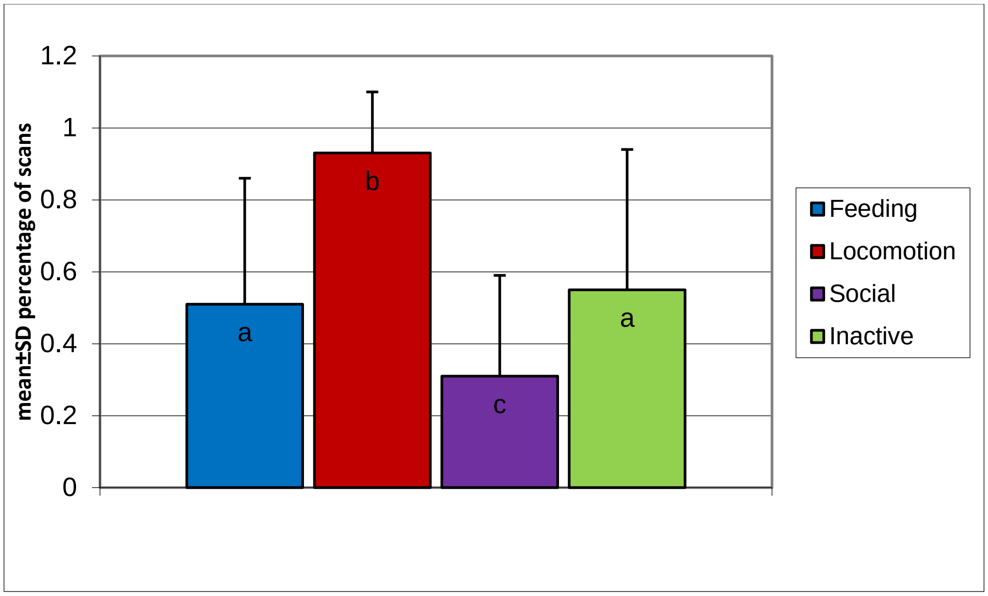


Figure 18. Mean percentage and standard deviations of scans for activities which occurred in edge habitat. Letters b and c denote a difference at the 0.05 level of significance.

For grazing land habitats, a single factor ANOVA test yielded a significant difference among the different activities performed in this habitat by the monkeys. Feeding and foraging were the least frequent and social behavior the most (F=11.18; Fcrit=2.69; d.f.=3, 108; *p*=0.000002) (See Table 6e). A Scheffé post-hoc test showed that the monkeys were inactive in a significantly higher proportion of samples than those in which they engaged in feeding activities (F=7.78; Fcrit=2.69; d.f.=3, 108; p=.05), and they were observed in locomotive activities at a significantly higher proportion than in social activities in the grazing lands (F=3.36; Fcrit=2.69; d.f.=3, 108; α=.05) (See Figure 19).

Table 6e. Activities in Grazing Lands[a]

Feeding (a)*	**Locomotion (b)***	**Social (b)***	**Resting (a)***	**ANOVA**
32%±22	69%±31	74%±25	43%±26	**F**=11.18 **Fcrit**=2.69 **d.f**.=3,108 *p*=0.000002

[a]Mean±SD percentages of scans for grazing lands by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously

***Scheffé post-hoc test denotes a difference at the 0.05 level of significance**

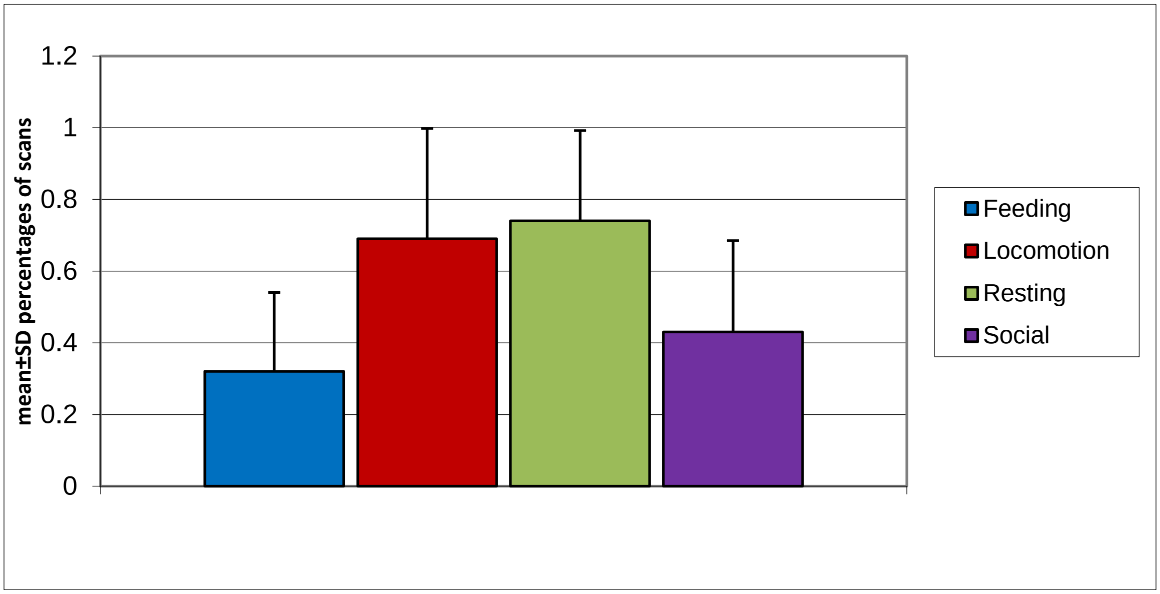


Figure 19. Mean percentage and standard deviations of scans for activities which occurred in grazing lands habitat

For mesquite woodland habitat, a single factor ANOVA test yielded a significant difference among the different activities performed in this habitat by the monkeys with social activity being the most frequent and resting the least (F=4.85; Fcrit=2.78; d.f.=3, 53; *p*=0.005) (See Table 6f). Utilizing a Scheffé post-hoc test I found that the monkeys performed a significantly higher proportion of resting activities than social activities in this habitat (F=3.77; Fcrit=2.78; d.f.=3, 53; α=.05) (See Figure 20). None of the other pairwise comparisons of activities in mesquite woodland showed a significant difference.

Table 6f. Activities in Mesquite Woodland Habitats[a]

Feeding	**Locomotion**	**Social***	**Resting***	**ANOVA**
42%±41	59%±32	35%±31	82%±20	**F**=4.85 **Fcrit**=2.78 **d.f.**=3,53 *p*=0.005

[a]Mean±SD percentages of scans for mesquite woodlands by activity performed in which at least one visible group member was in the habitat type. Percentages will not add to 100% because different group members may be engaged in different behaviors simultaneously
***Scheffé post-hoc test denotes a difference at the 0.05 level of significance**

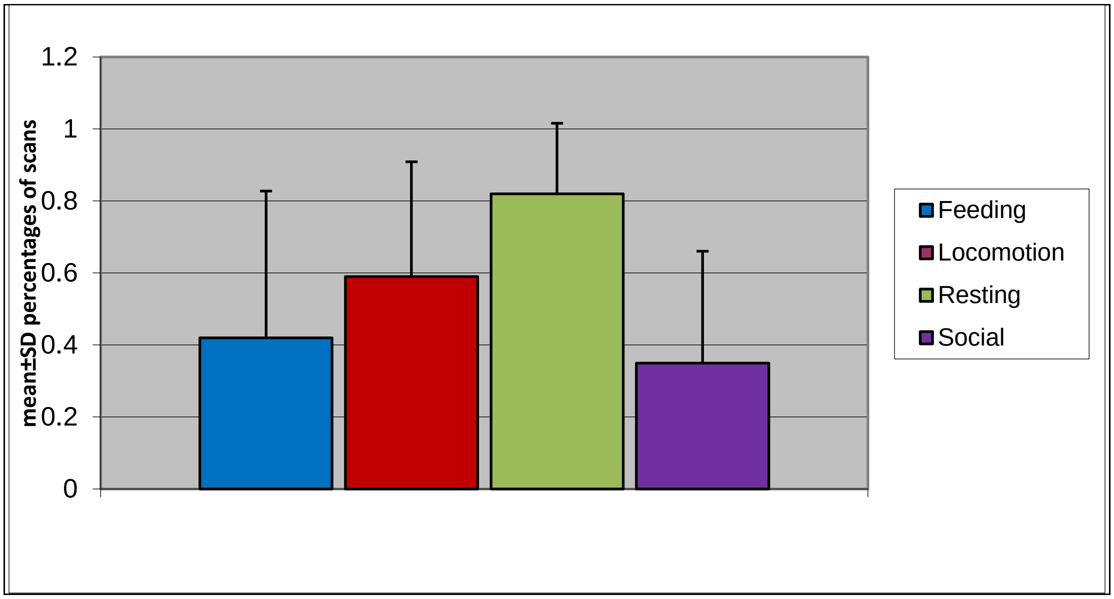


Figure 20. Mean percentage and standard deviation of scans for activities which occurred in mesquite woodlands habitat

Use of Seminatural vs Human-disturbed Habitats

To further probe the way that the patas monkeys were using available kinds of habitat, after analyzing their use of each habitat separately I grouped habitats into two categories, human-disturbed versus seminatural habitats. I compared the number of instantaneous scan samples that the patas monkeys spent in habitats that could be classified as either human-disturbed or seminatural to the proportion of these habitat types in the area. A GIS analysis of the area using an aerial survey photograph showed that human-disturbed lands made up 49% of the area while seminatural lands made up 51% of the available habitats (See Figure 21). The percentage of patas monkey group sightings in human-disturbed lands was 41.9%, while the percentage in seminatural lands was 49.5% and in edges was 8.5% (See Figure 22). Because the area contributed by the habitats' edges could not be quantified utilizing the GIS program, this habitat type was excluded from this analysis. A Chi-squared goodness of fit test (Moore and McGabe, 1989) showed that sightings of the monkey groups did not differed significantly from the expected total for each habitat type ($X^2=2.30$, Xcrit=3.84, d.f.=1, $p=0.14$), showing that the monkey distribution throughout the human-disturbed and seminatural habitat types was proportionate to their availability in the area (See Figure 23).

Figure 21. Percentage of habitat type in the area

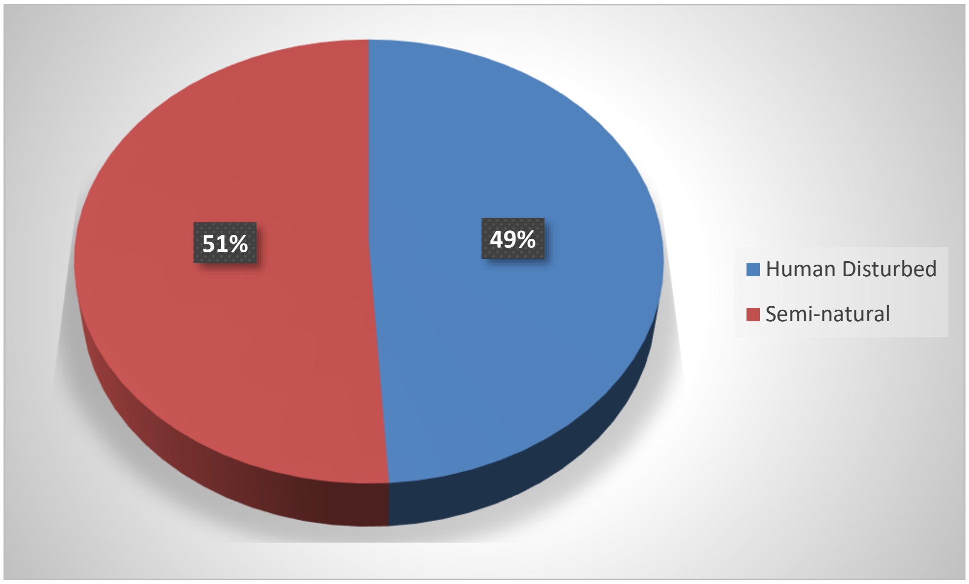
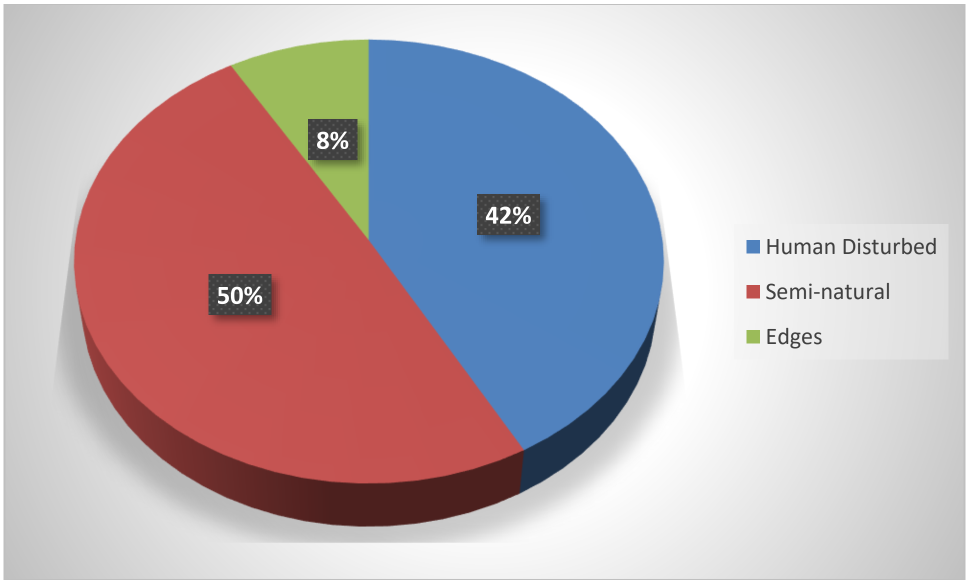


Figure 22. Percentage of monkey group sightings in each habitat type



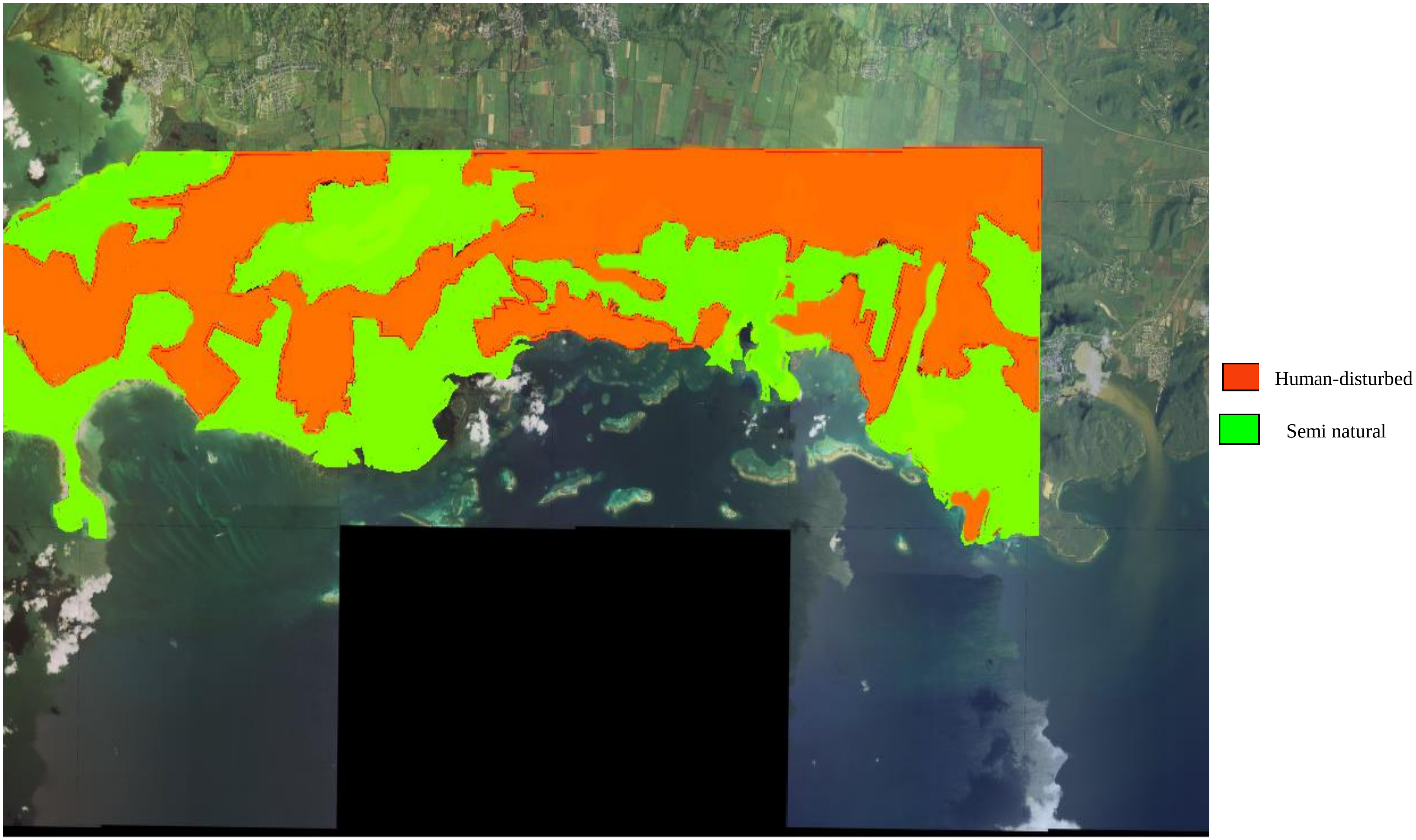


Figure 23. Distribution of human-disturbed and seminatural habitats in the geographic range in southwest Puerto Rico

DISCUSSION

Population Abundance

One of the principal aims of this study was to assess changes in population abundance and density for the patas monkeys in southwest Puerto Rico, an introduced, non-native species living in a highly human-altered environment, over the 13-year period. I predicted that the population size and density in 2006 would have significantly increased since it was surveyed in 1993.

My population estimate for the patas monkeys in southwest Puerto Rico, shows that the population had a 328% increase in size over a period of 13 years ranging from 1993 to 2006. Various factors could have influenced this significant population growth. One factor is the lack of non-human predators for the monkeys in the area. Although the influence of predation on the dynamics of any primate populations has been difficult to quantify in the past, predation events can exert ecological pressures on the life-history traits, behavior of individuals and community structure of a prey population. These ecological pressures can also influence the distribution and density of the prey population within a defined territory or home range (Korpimaki and and Norrdahl, 1998; Sinclair and Arcese, 1995). In African populations, patas monkeys are under the pressure of predation risk from various avian and terrestrial predators, and their behavioral response to encounters with predators has been characterized as one of avoidance (via vigilance, evasion, crypticity) instead of confrontation in the majority of the observed encounters (Chism et al., 1983; Isbell and Enstam, 2002;). Patas monkey predators in Africa include leopards (*Panthera pardus*), wild dogs (*Lycaon pictus*), rare spotted hyenas (*Crocuta*

crocuta), lions (*Panthera leo*), black-backed jackals (*Canis mesomelas*) and martial eagles (*Polemaetus bellicosus*) (Chism and Rowell, 1988; Nakagawa, 1999; Enstam and Isbell, 2002). Research on the ecology of various patas monkey populations suggests that predation risk has an influence on their habitat use. For example, in locations where predation risk is lower patas monkeys utilize open grasslands more frequently (Nakagawa, 1999; Enstam and Isbell, 2004). Furthermore, a study on patas monkeys' microhabitat preferences showed that they preferentially use taller microhabitats, or taller trees within the habitat used; the authors speculate that this preference could be due to the fact that taller microhabitats provide greater protection from predators (Enstam and Isbell, 2004).

Recognizing the influential role of predation in the regulation of prey population dynamics and growth, studies investigating the factors that contribute to the success of introduced populations have suggested that lower numbers or absence of natural predators for the species in the introduced range as one of the contributing factors for their success. The enemy release hypothesis (ERH) states that the release from pathogens, parasites or predators in the new range can explain the proliferation of introduced species (Keane and Crawley, 2002; Colautti et al., 2004). The majority of the evidence for the ERH has come from studies of different plant populations that had a reduced number of, if any, predators in the introduced range when compared to their counterparts in the native range. The general trend in these studies is that plant populations in the introduced range had less damage produced by herbivores, a higher population density, and a smaller mortality rate compared with populations from the native range (Vila et al., 2005; Cincotta et al., 2009). In addition, studies comparing invasive introduced species, less invasive introduced species, and non-invasive introduced species concluded that the less invasive and the non-invasive introduced species suffered more herbivore damage and had more pathogens in the introduced range than the invasive introduced species, which had fewer pathogens in the new environment (Mitchell and Power, 2003; Cappuccino and Carpenter, 2005). In addition to release from natural predators, evidence for the ERH has also been found in introduced populations that contain a lesser load, if any, of the parasites found in their native counterparts (Torchin et al., 2003; Kvach and Stepien, 2008). One particular population of Barbary ground squirrel (*Atlantoxerus getulus)* introduced to the Canary Islands was found to have a less diverse load of parasites when compared with its native counterparts in Morocco (López-Darias et al., 2008). In Puerto Rico, the significant population increase of the patas over the 13-year period from 1993-2006 may signal that the release from non-human predators in their introduced range constitutes one of the biotic factors that is contributing to the proliferation of the species in this new habitat. However, the only studies done on the topic of Puerto Rico's free ranging monkey populations and parasites comes from the island of Cayo Santiago, which is part of the Caribbean Primate Research Center and it harbors an introduced free ranging rhesus macaque population. In these studies the authors concluded that the monkeys in the island

Another factor that may be playing a role in the significant population increase of the patas monkeys in Puerto Rico is the abundance and distribution of the available resources in the area. The population density of the patas monkeys in Puerto Rico in 1993 was 0.96 individuals/km^2, which was comparable to population densities of patas in different areas in Africa (González-Martínez, 1995). However, González-Martínez (1995) arrived at this number by taking into account the entire study area. When González-Martínez (1995) calculated the population density taking into account only the estimated home ranges for the different groups, the population had an overall density of 4.47 individuals/km²; this represents a high population density for a patas monkey population. In my study I calculated the population density for the patas in Puerto Rico taking into account the entire study area; this estimate gave me one of the highest population densities reported for a patas monkey population anywhere, with 2.99 individuals/ km², roughly three times what González-Martinez reported. In Laikipia, Kenya, the population density reported for eight heterosexual groups was 1.4 individuals/km² (Chism and Rowell, 1988), while a recent reassessment of the population in the entire Laikipia area calculated the density for the population at 1.0 individuals/ km² over a 25-year period (Isbell and Chism, 2007). Thus, the Puerto Rico patas population density is two-and-a-half to three times the densities reported for the species in Kenya. The densities of the various patas monkey populations studied in Africa are considered one of the lowest for a monkey species. The principal explanation proposed for their low population densities, along with their large home ranges and day ranges, is that it is a result of the quality and distribution of the resources that they exploit. In contrast with the food sources exploited by the various species of guenon monkeys, which are closely related and sympatric in many areas in Africa with patas monkeys, said patas monkeys utilize less abundant, relatively small food items, that are widely dispersed throughout the habitat (Chism and Rowell, 1988; Isbell, 1998; Nakagawa, 2003). In Puerto Rico, the types and distribution of food sources available to the patas monkeys may decrease the necessity for them to range over large areas to meet their nutritional requirements, thus resulting in a higher population density when compared with populations in the native range. In her study, González-Martínez (1995) characterized the food sources exploited by the patas monkeys in southwest Puerto Rico as relatively abundant rich resources and primary food items were mostly tree fruits (González-Martínez, 1995). Also, at that time, the patas monkeys appeared to coordinate their movement patterns according to the locations of these ripe fruits and seed pods (González-Martínez, 1995). Thus the high population density of the patas monkeys observed in my study could be a result of the abundance of the main fruits and fruit parts that they exploit in southwest Puerto Rico, as well as the lack of non-human predators. This increase in population density correlating with an abundant food supply within the used territory is consistent with the previously tested model of the optimal feeding-territory size (Imre, et al., 2004).

I found that the mean group size also increased in the 13-year period between 1993 and 2006 from 26 to 52 individuals. In African populations of patas monkeys, group size usually ranges between 15 to 30 individuals, with 61 individuals in a group being one of the highest group sizes reported for this species (Hall, 1965; Chism and Rowell, 1988). A recent reassessment of the patas monkey population in Laikipia, Kenya, found that large groups were rare with no more than 3 to 4 having more than 50 individuals in the group, out of approximately 13 to 17 reliably-censused groups (Isbell and Chism, 2007). In contrast to these findings, in Puerto Rico five out of nine groups surveyed in 2006 had more than 50 individuals in the group. Not only did group size increase over the 13-year in the Puerto Rico population, but several of the groups observed in the population represent some of the largest group sizes reported for any population of patas monkeys.

Several hypotheses have been proposed with regard to primate group size and the ecological variables that can affect it. One of the most prominent is that group living is highly influenced by a species' predation risk: the greater a population's predation risk, the greater the probability that groups will increase in size to augment antipredator mechanisms such as vigilance and predator defense (Hill and Lee, 1998; Stanford, 2002). As increased group size provides increased vigilance against predators, it may allow more time to be dedicated to activities such as feeding and foraging, since the individuals in the group do not have to spend as much time watching out for predators in a large group versus a smaller group (Stanford, 2002). However, there are tradeoffs to increased vigilance and predator protection in a larger group, including more competition for mates and an increase in intragroup feeding competition (Grand and Dill, 1999). In Puerto Rico I found the opposite situation occurring, in which the patas monkeys have no non-human predatorsin the area but the group sizes in the population are relatively larger than the group sizes in the native range and the mean group size has increased since 1993. Thus, some other factors may be influencing group size.

Increase in mean group size for the patas monkeys in Puerto Rico may signify that the amount of food available for the population in the different habitats utilized at the time of my study was not limiting. Group size for a population has been correlated with the density of the food available to the individuals in the occupied area (Wrangham et al., 1993). Depending on the abundance and distribution of the available resources, there will be a maximum group size above which the costs of living in a larger group size can outweigh the benefits as a result of feeding competition (Knopff and Pavelka, 2006). This "ecological constraint model" proposes that, if the food source is limited, the costs of living in a large group can outweigh the benefits above a certain group size. These costs include a higher amount of energy spent by individuals in the group because of increased intragroup feeding competition (Chapman and Chapman, 2000). Ecological constraints on group size include the amount of food available in the habitat, as well as the energy requirements for the species (Chapman and Chapman, 2000). For the patas monkeys in Puerto Rico the mean group size continued increasing significantly over a period of 13 years. Since the resources available to the population in the introduced range have been characterized as abundant, the patas monkey groups in Puerto Rico, when compared with groups in the native range, have a higher potential for maintaining a larger size without depleting the resources available in the area. In addition, the group density of the monkeys in the area had a 66% increase during the 13 years between 1993 and 2006. When compared with the 328% increase in population size, the 212% increase in population density, and the significant increase in mean group size over the 13-year period, the increase in group density was less significant. My findings on group density may signify that, instead of fragmenting into smaller groups as the population size increases, the patas monkey groups in Puerto Rico are expanding in size because the abundant resources in the area can support larger groups.

Geographic Distribution

The patas monkeys in southwest Puerto Rico increased their geographical distribution over the 13 years from 1993-2006 by 38%, expanding in an east direction. Similar to the results in group density, the increase in geographic range, when compared with the increase in population size, population density and group size over the 13 years, was smaller. In 2006, patas monkeys in Puerto Rico were occupying inherently the same areas as in 1993, with only a small geographic range expansion to the east over the previous 13 years. In 1993 Gonzalez-Martinez, utilizing GIS and radio-tracking data, analyzed the areas surrounding the patas population's range to determine which areas had similar characteristics to those preferred by the monkeys. Based on this analysis she predicted that the patas monkeys were more likely to expand their territory size in an easterly direction rather than to the north direction. As she predicted, in the 13 year period that followed her study the patas monkey population expanded their geographical distribution in southwest Puerto Rico in an easterly direction, occupying areas that possessed similar characteristics to the areas that they occupied in 1993.

One of the groups found during my study was observed in a location to the north of the municipality of Lajas, outside of the main geographic range for the patas population. A review of aerial photography suggested that the areas separating this outlier location from the population's geographic range are in the majority composed of human-disturbed habitats. A plausible explanation for the absence of the remaining groups in this locality on the north side of Lajas is the lack of vegetation corridors within human-disturbed habitats separating the outlier locality from the main geographic range; such corridors would enable the monkeys to utilize or disperse into the area while avoiding contact with humans.

Habitat Use Patterns

Several primate species provide examples of how the quality of a habitat and the richness of the resources it provides can affect the density and group size of a population.

One such case is the vervet population at Amboseli, Kenya, where population density was the highest when the habitat was composed of diverse food sources that had a high density (Struhsaker, 2008). In addition, a hypothesis proposed to explain the success of introduced species in areas where they have established and spread rapidly is that these locations contain a diverse array of habitats that provide the exotic species with a higher probability of finding a suitable location with abundant resources (Smallwood, 1994). In Puerto Rico, the geographic range that the patas monkeys occupied at the time of González-Martínez's study in 1993 had rich food sources composed mainly of fruit trees and abundant water available from natural sources or cattle water troughs in grazing lands throughout the area. These resources were found in a variety of habitats that were utilized by the patas monkeys in 1993. At the time of her study González-Martínez (1995) found that the monkeys were preferentially using semideciduous woodland, secondary scrub and mesquite woodland. Other areas that they used were grazing lands and mesquite savannahs. González-Martínez (1995) also found that only all-male bands would occasionally raid agricultural fields. In 2006, I found that the patas monkeys were utilizing the same habitats, however, they had begun to exploit developed urban areas that were avoided by the monkeys in 1993. Even though the proportions of the various activities measured did not differ significantly, the activity that was most frequently performed in urban areas was feeding and foraging, and the largest proportion of feeding and foraging events was performed in urban areas. These feeding and/or foraging events took place mainly in the front and back yards of people's houses that contained fruit trees such as mango and Spanish lime; these food sources are also typical of the resources that patas monkeys exploit in semideciduous woodlands. In her study González-Martínez

(1995) stated that the study area was under intense development pressure, and this continued in 2006. My observations suggest that the patas monkeys are increasingly utilizing urban areas as other habitats that provide them with food sources, such semideciduous woodlands, vanish as a result of development.

Other habitats provided the monkeys with protection to perform other activities. I found that they utilized edges at a significantly higher proportion for locomotion than any of the other habitats present. This behavior is similar to that of African patas populations, where they exploit the resources of the grassland and the woodland, while gaining the predator protection from the woodland by remaining at the edge where the two habitats meet (Chism and Rowell, 1988). Clearly, in Puerto Rico the patas exploit the edges of the various habitats to move through the area and gain access to cover and resources.

In my study, the activity performed at a significant higher proportion than other activities in grazing lands was resting. A possible explanation for this finding is that this type of habitat provides the monkeys with important sources of water, and when they are less active during the middle of the day because of high temperatures they stay close to these water sources. Patas monkeys in Laikipia, Kenya showed a similar pattern and Isbell and Chism (2007) stated that the monkeys' association with large-scale ranching provided them with important sources of water that were vital for their survival in the semi-arid conditions of the Laikipia area. Portions of the area that the patas monkeys utilize in southwest Puerto Rico are considered some of the most arid in the island. Even though the monkeys can acquire water from natural sources in the area, the association of the population with grazing lands containing cattle water troughs may be a factor influencing their survival and increase in southwest Puerto Rico.

In mesquite woodlands resting was also performed at a significant higher frequency than any other activity. In addition, even though there was not a significant difference, the proportion for mesquite woodland was the highest among the habitats where resting was performed. This habitat was preferentially used by the monkeys at the time of González-Martínez study (1995), and my findings suggest that it could be providing the monkeys with protection from high temperatures and human detection, while they are resting. I must add that, although I did not collect systematic data on sleeping site habitat features, the majority of the sleeping site locations where I found the patas monkeys were in mesquite woodlands.

Another proposed factor that influences success of introduced species is their ability to use human-disturbed habitats (Sakai et al., 2001; Evans et al., 2005; Jeschke and Strayer, 2006). Human-disturbed habitats give the introduced species the opportunity to occupy empty niches with rich microhabitats in their new geographical range with little or no competition from the native species of the area (Byers, 2002). The patas monkeys have no competitors in their new range except for the introduced rhesus macaque monkeys; however, groups of these two species utilize different areas in southwest Puerto Rico. Opportunistic sightings of rhesus macaque groups in my study were limited mainly to the Sierra Bermeja hills and adjacent areas. In addition, in the areas that are occasionally utilized by both species the patas groups or individuals were displaced by the rhesus. My analysis of the patas monkeys' use of human-disturbed versus semi natural habitats found that the monkeys use human-disturbed habitats in proportion to their availability in the area, not preferentially. I conclude from these findings that a general association with human-disturbed lands is not the main factor contributing to the abundance of patas monkeys in Puerto Rico. The monkeys exploit resources from some human-disturbed areas, such as grazing lands and urban development areas, but also highly important for the population's survival are the resources the monkeys obtain from semi natural lands and their ability to take refuge there. For the patas monkeys in Puerto Rico, the resources that they obtain from certain human-disturbed habitats may not be worth the risk of detection by humans. Other primate populations provide examples of how this perceived risk of detection from human and non-human predators can influence the habitat use patterns of the population. An investigation of the crop raiding patterns of an introduced vervet population in the Caribbean island of Barbados concluded that the monkeys' distribution throughout the island was more influenced by the availability of cover in the area than the availability of food and the human population density (Horrocks and Baulu, 1994). However, in certain species that dwell in urban areas, and have become adapted to them, behaviors for crypticity when crop raiding and/or foraging may have been selected for. A prime example of this type of behavioral adaptation can be observed in urban dwelling large predators that exhibit temporal avoidance in response to human stress (Ditchoff, S.S. et al., 2006). For the patas monkeys in southwest Puerto Rico, the reward in the form of the resources obtained from raiding fruit trees in urban habitats could be a driving factor for the development of cryptic behaviors in the population. Additionally, could be a factor in their non-detection when crop raiding in urban areas southwest Puerto Rico.

CONCLUSIONS

The area where I performed my study is under development pressure. Various outcomes will more than likely occur if these urban areas continue to be developed, provoking the loss of more seminatural habitats: the patas population will continue expanding to the east of their current geographic range; a slowdown in population size increase, or a rapid population collapse that will halt the population size increase and drive the population to either extinction or to size stabilization. Several introduced species have undergone documented population collapses, and a portion of these collapses are attributed to the overuse of the available resources in the area by the introduced species (Simberloff and Gibbons, 2004). Of special interest are introduced populations that inhabit small isolated areas and islands, where the opportunity for recovery is affected by the restricted character of the habitats and resources that compose the species' new range (Simberloff and Gibbons, 2004). After analyzing the activities performed by the patas monkeys within and between different habitats in Puerto Rico I can conclude that the seminatural habitats in the area are vital for the continued existence of the population. Not only do these areas provide the monkeys with resources, but seminatural habitats provide the patas with cover to perform other activities while avoiding detection. If the geographic area they currently occupy continues to be developed, the resources and cover that the monkeys get from seminatural habitats could easily be depleted by an increasing population; thus, a population collapse of the patas monkeys in southwest Puerto Rico could take place. In addition, the urban development that is taking place in the area could be negatively affecting the local native fauna; thus, at least some of the negative affects attributed to the presence of the patas monkeys in southwest Puerto Rico may be a result of development pressures.

The patas population in Puerto Rico is abundant and can be characterized as a successful colonizer of the area. Different factors, such as a lack of non-human predators and the presence of rich, abundant, food sources in the area, could have favored a continued increase in the size of the population since González-Martínez's 1993 study. Not only had the population grown considerably in the 13 years between her study and mine, but by 2006 it was well-established in different areas in southwest Puerto Rico. In the year 2007, the Puerto Rico Department of Natural and Environmental Resources initiated a population control program for the monkey populations in southwest Puerto Rico. This program was established in cooperation with the U.S. Department of Agriculture, and is an ongoing project.

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