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# THESIS

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#### SUMMARY

Herbivores invest time and energy searching for food. Additionally to the risk of predation, food quality and availability may represent a challenge for herbivores in specific environments like deserts, where annual precipitation often limits the plant growth and productivity. While social foragers have the benefits of shared vigilance and safety in numbers, the cost of exploiting the same resource may limit group size when food is scarce and widely dispersed.

Dolichotis patagonum (Rodentia: Caviidae) inhabits the central and southern desertic plains of Argentina and can weigh up to 10 Kg as an adult. Commonly called mara or Patagonian cavy, this large rodent is a unique model to address foraging/ predation questions in relation to social behavior. Mara's social system shifts between pair bonding and communal rearing. These large rodents live in environments considered of low relative productivity and food availability together with the female's short receptive period are thought to be the drivers of its mixed social system.

This study examines the foraging dynamics of maras, to begin to understand the role of predation risk on habitat selection and sociality in maras and took place in the Sierra de las Quijadas National Park, Central Argentina. The park is a critical conservation unit at the boundary of the Monte and Chaco regions. Here, maras feed mainly on grasses from two distinct habitats: creosote flats, mesquite woods and hillside bajadas. These habitats vary in opportunities and challenges for vigilance, food availability, and cover from predators.

I provide a brief background on the scientific information available for *Dolichotispatagonum* regarding foraging and social behavior (Chapter 1) in the wild and in captivity. I also looked into the spacial and temporal habitat use by maras in Sierra de las Quijadas National Park. I counted fecal pellets along transects to assess habitat use (presence/ absence) by maras (Chapter 2).

Artificial food patches provide a reliable method for measuring animals' perception of risk within a specific landscape. The food left behind in a feeding patch should reflect the point at which individuals give up foraging to engage in a different activity (vigilance, resting, or seeking another food patch). I conducted a study offering maras a set of artificial food patches with different levels of sight lines to measure their perception of safety/danger and their preference for open spaces in Sierra de las Quijadas national Park. I examined maras' habitat preference and response to vegetation structure in two ways: a) food patches in clearly distinguishable open or covered areas, and b) food patches as a grid with equal feeding opportunities at each station (Chapter 3). In order to evidence the use of the patches by maras or other herbivores, motion sensor camera traps were installed at the different stations throughout the period of the study. The activity in front of these cameras was then analyzed as part of maras' temporal habitat use section (Chapter 2).

Maras foraged significantly more in open than in covered bushy habitats when pumas are present in the area on the triplets experiment (P<0.001). Maras also displayed a complex set of behaviors regarding territory defense (marking, aggression) in response to artificial food patches at the microhabitat level. Data showed that not only maras seem to prefer habitats with low vegetation cover and good sightlines but also visit artificial food patches during hours of light more often than during the night. These findings suggest that predation plays an important role on maras' habitat selection and use. Individuals foraging in pares alternated foraging and vigilance such that one member of the pair was vigilante at all times. In addition, results on the landscape of fear for maras supported the species' sensitivity to poor sightlines. There was a significant difference between food left behind in patches with a higher removal for patches with lower plant cover. This research makes a contribution on the understanding of *Dolichotis patagonum's* interaction with the features on its environment under the risk of predation and the importance of the latter in habitat selection decisions by the species. Future directions should include a detailed analysis of the presence and boundaries of the predation/foraging trade off while revealing how the flexible social system in relation to foraging needs contributes to the evolutionary ecology of this unique large rodent.

### CHAPTER I: AN OVERVIEW OF THE PATAGONIAN CAVY

# **1.1 - INTRODUCTION**

The patagonian cavy or mara (*Dolichotis patagonum*) inhabits arid and semi-arid regions of central and southern Argentina (Redford and Eisemberg, 1992; Taber, 1987). Among the large variety of body sizes, morphologies and behaviors present in the rodent world, maras represent a rather unique study animal where questions in evolutionary ecology arise from the interplay of sociality, predation and foraging.

*Dolichotis patagonum* (Zimmerman, 1870) is a remarkable member of the Caviidae family. With an average body mass of 9 Kg, maras share characteristics with both small ungulates (deer) and large lagomorphs (rabbits and hares). It has the most distinct morphology of all of the cavies (FIGURE 1). The mara's unusual social organization combines communal breeding with monogamous pair bonding (Taber, 1987), something not observed in other species of Caviidae (Maher and Burger, 2011). Foraging constraints might play a role in the expansive and mobile territories that maras defend. Yet, these same low productivity environments may be preferred from the perspective of avoiding predation (Macdonald *et. al.*, 2007).

Here, I offer an overall description of the mara's natural history, ecology and behavior. By reviewing what is known about *Dolichotis patagonum*, I hope to show how the interplay of sociality, predation and foraging have shaped the evolution of this unique mammal.

FiG. 1: Facts sheet for Dolichotis patagonum (from Campos et. al., 2001)



#### Dolichotis patagonum:

Habitat: Arid and Semi-Arid plains of Central and South Argentina.

Body Mass: 8-9 Kg. average in the wild (17-19Lb.)

**Behavior:** Maras are cursorial and mainly diurnal. Males maintain a floating large territory around a female promoting a monogamous social system that alternates with a communal breeding colony.

**Reproduction:** Occurs through the year in captivity and shows some kind of seasonality in the wild (spring-summer). Twins are the most common litter size (70%).

**Diet:** Strictly herbivores. Grasses, forbs and shrubs vary in their proportion in the diet depending on the area.

## 1.2 - CLASSIFICATION AND ORIGIN:

Maras belong to the Family Caviidae that is part of the Caviomorphs also known as Hystricognaths of the New World. This infraorder is related to the Old World Hystricognaths that includes old world porcupines and mole rats among others (Phiomorphs) (FIGURE 2). Researchers agree that caviomorphs comprise a monophyletic group (Huchon and Douzery, 2001; Blanga-Kanfi et al., 2009) that arrived in South America from a solitary and unique colonization event.

Caviomorphs emerge in the fossil record around 31.5 Mya (Flynn and Wyss, 1998) during the Eocene/Oligocene boundary. The Tinguiririca Fauna of the Chilean Andes represents the first fossil record of rodents in South America and includes specimens of caviomorphs (Chinchillidae and Dasyproctidae) together with marsupials and notoungulate mammals that overall depict a primarily grassland fauna (Flynn et. al., 2003). Two main alternative hypotheses for explaining the appearance of these Caviomorphs in South America include the African origin and the Asian origin hypotheses.

An African-South American migration has been suggested by different authors (Lavocat, 1969; Martin, 1994; Flynn and Wyss, 1998). This transatlantic migration could have occurred during a period of convulsive climatic changes like the one at the end of the Eocene and the beginning of the Oligocene (Pascual and Ortiz Jaurguizar, 1990; Flynn and Wyss, 1998). Contributors to this colonization may have been oceanic currents, stepping stone islands, vegetation mats, and/or paleowinds (Poux *et. al.*, 2006).

FIG 2: Phylogeny based on the analysis of six nuclear genes (modified from Blanga-Kanfi *et. al.*, 2009).



Caviomorphs share with Phiomorphs the hystricognathus mandible, dental morphology and the structure of the bony ear (Martin, 1994). Molecular data supports the relatedness of Phiomorpha and Caviomorpha as Hystricognathi but suggests that the common ancestor may have originated in Asia (Huchon and Douzery, 2001).

Fossils recovered in Southern Asia (Pakistan) strengthen the Asian origin of Caviomorphs and Phiomorphs. The new fossil found in the Bugti Hills takes the name of *Bugtimys zafarullahi* and may represent the first Hystricognathi from the early Oligocene (Marivaux *et. al.* 2001). Based on dental structure, and comparing dates of the fossil records in Asia, Africa and South America, the relationship between these three faunas seems to indicate a branching event from a common 'ctenodactyloid' ancestor situated in Asia (Marivaux *et. al.* 2001). Molecular data also adds support to the Asian origin of Hystricognathi. The phylogenetic analysis of a nuclear marker estimates, divergence dates between caviomorphs from South America, phiomorphs from Africa and hystricomorphs from Asia indicating an Asian origin for these groups (Huchon and Douzery 2001).

Even though these findings strongly support an Asian origin of Hystricognath rodents, the migration of the South American group that gave rise to caviomorphs remains unclear. The spread and colonization could still have been from Asia to Africa to South America. There are no fossil remains of Caviomorpha in North America that would suggest a migration via northern land bridges (Huchon and Douzery 2001).

A spread from Asia would have required a much longer rafting event across the Pacific. A rafting event from Africa remains the most likely route for the spread of rodents and primates into South America.

While the monophyletic origin of caviomorphs is well supported, there remains debate over how the group diversified into the different families and species (Cabrera, 1961; Honeycutt *et. al.*, 2003; Rowe and Honeycutt, 2002). The Caviidae family (Gray, 1821), includes at least five different genera from both the Caviinae and Dolichotinae subfamilies (Mckenna and Bell, 1997). Recent studies have incorporated the subfamily Hydrochoerinae into Caviidae as well (Rowe and Honeycutt, 2002). Thus, the Caviidae family comprises the subfamilies Hydrochoerinae (capybaras and rocky cavies), Caviinae (true cavies) and Dolichotinae (patagonian and dwarves cavies) (Rowe *et al*, 2010). Both the patagonian cavy and the dwarf mara or dwarf cavy that lives in the north-central region of Argentina share the same genus (*Dolichotis patagonum and D. salinicola*, respectively). They differ from each other in body size, habitat range and habitat type (Campos *et. al*, 2001a) (FIGURE 3).

FIG. 3 :Distribution of *Dolichotis patagonum* and *D. salinicola* in Argentina (modified from IUCN Red List of Threatened Species, 2010).



## 1.3 - MARAS (Dolichotis patagonum, Zimmerman, 1870)

In 1870 Zimmerman formally described maras based on one specimen from the Leever Museum of natural curiosities in London. The text depicts the mara as a short eared rodent as big as the european hare with black thick whiskers and no tail. The legs were described as long with four toes in the front and three toes in the back. Zimmerman also reports on the digging behavior of the mara and the properties of its meat (Zimmerman, 1870). Among the first descriptions made on the mara we also find the one provided by the English naturalist Charles R. Darwin. During the H.M.S. Beagle's trip to South America, Darwin described maras as the equivalent of European hares emphasizing the difference in body shape and size. Darwin called the maras Agoutis (a name at present given to a different type of cavy), and talks about a possible decrease in their population at the ports of San Julian and Desire (Darwin, 1845). This "friend of the desert" (in Darwin's words) that stots like a deer and looks like a hare has been studied in the wild and in captivity by a number of authors.

### 1.3.1- <u>Behavior</u>:

Dolichotis patagonum exhibits one of the most intriguing social systems among rodents and mammals in general. During the breeding season, groups of maras can often be seen rearing young in communal dens. During the rest of the year monogamous pairs seem to be the most common social unit (Taber and Macdonald, 1992). As unusual as this combination is in nature, both communal rearing and monogamy may be understood by a set of complementary hypothesis (See Taber and Macdonald, 1992). In 1974, Dubost and Genest analyzed the mara's behavior over a period of two years at Branféré Park in Brittany (France). This represents one of the first detailed studies on Dolichotis' social structure and activity patterns. The authors remark on the strength of the monogamous pair bond and the ability partners to communicate. Partners show a high degree of fidelity. Even though monogamy is not a frequent mating system in mammals being present in 3 to 5% of the species (Mock and Fujioka, 1990), several rodent and lagomorph species, like prairie voles and pikas, have served as models for the study of genetic and social monogamy (Sommer *et. al.*, 2002). In captivity, male maras showed an intense defense of their females and their respective territories, the male mara marks the ground with an anal gland and reacts aggressively to approaching males (Dubost and Genest, 1974). Interestingly, male maras may tolerate the proximity of another male if the latter is courting a young female in the family (usually the offspring of the pair) waiting for her to sexually mature (*op. cit.*). Dubost and Genest's study describes a monogamous system where partners show behaviors of mutual assistance throughout the year and beyond just reproductive activities.

The first complete behavioral study in the wild (Taber, 1987) showed that the pair was the most common family unit (65% of the time). Maras can also be solitary and form small family groups of more than two members. Taber studied maras in Patagonia (Valdes Peninsula) between 1981 and 1984, where he observed a colony at a distance and radio-collared some individuals. From Taber's ethological scans, grazing was the main activity when no pups where being reared and this pattern was stronger for females than for males.

Analyzing maras' movements through radio-collars, Taber observed the seasonal changes in territory for the pairs and the occasional formation of larger groups. Here he describes the mara's food resource as patchily dispersed with a slow recovery time following depletion. Following the local depletion of food Maras move somewhere else to keep foraging. This is one of the possible explanations for why maras have drifting territories with large spacing between different family units. Maras seem to keep a distance of at least 100 mts between family units. In suggesting a hypothesis based on resource depletion and predation, Taber and Macdolad (1992) suggest that maras den communally and form large groups when the resource (mainly food and water) is clumped. In combination, open areas with resources are favored for building dens. Such open areas facilitate vigilance against predators. Thus, due to the restrictions on the mara's foraging supply, the pair might be the perfect unit to survive and assure reproduction. At he same time, the presence of a richer patch and the need for more protection during the breeding season may explain the formation of large groups around several dens (Taber and Macdonald, 1992).

In a more recent study, Baldi (2007) investigated the maras' preference for open areas when constructing dens for offspring-rearing. Baldi observed failed hawk attacks on maras at dens in Patagonia and he measured the maras' reproductive potential depending on den size. The use of communal warrens by maras may be a function of higher predation pressure during early age, common in precocial rodents and lagomorphs. Because maras are diurnal and cursorial they fit the expectation of using visual detection to avoid predators.

The maras' predators include pumas (*Puma concolor*), grison (*Galictis cuja*), Patagonian red fox (*Dusicyon griseus*) and red-backed hawk (*Buteo polysoma*) (Baldi, 2007).

## 1.3.2 - Foraging:

Different diets have been reported for *Dolichotis patagonum* at different locations. Despite the apparent variability/flexibility of its diet, maras live in close association with creosote bush flats (Larrea spp.) a plant not present in its diet (Campos *et al*, 2001b; Sombra and Mangione, 2005). Given the species' body mass it is possible that maras cannot tolerate the high concentrations of secondary metabolites (SMP's) found in the creosote bush. Maras seem to prefer the high fiber content of grasses instead (Foley and McArthur 1994). Maras have been categorized as opportunistic herbivores taking advantage of seasonally abundant resources at each location (Campos *et al*, 2001a). While its diet occasionally overlaps with cattle and exotic species (Kufner and Pelliza de Sbriller 1987; Bonino et al., 1997), different species of grasses comprise the bulk of a mara's diet (TABLE I).

In Nacuñán, Mendoza, dietary overlap between the mara and the local domestic cattle (bovine) showed that maras turn to dicots when the cattle exerts pressure on seasonal grasses (Kufner and Pelliza de Sbriller, 1987). Overall the diet reported in Nacuñán leans towards a high proportion of shrubs and forbs compared to grasses. Maras, however, seem to respond to seasonal variability in food availability and competition by increasing the diversity of items in their diet whenever the abundance of preferred foods decline.

The diet in Península Valdés does not include actual frequencies but observations of the type of plants (monocot and dicot) consumed by maras during the researchers' scans (Taber, 1987).

While scattered and occasionally unavailable, grasses were highly favored by maras. Their observations supports the hypothesis that this kind of environment promotes the monogamous family unit that defends and utilizes shifting territories (Taber, 1987; Taber and Macdonald, 1992). Maras consumed primarily grasses in most locations in Argentina (TABLE I). Considering the maras' efficiency at digesting fiber due to their body size and physiology (Sakaguchi *et.- al.*, 1992; Sakaguchi, 2003), a mainly grass based diet would not represent a challenge for the species. In a comparative study of the different diets described for *Dolichotis patagonum* in Argentina, Puig *et al.* (2009) found that maras will incorporate shrubs and forbs in their diet when drought conditions restrict the availability of seasonal grasses.

In general *Dolichotis patagonum* is considered a grazer with the flexibility to expand its diet to a variety of dicotyledon species when grasses are scarce. Additionally, in every diet reported for maras, there is an absence and avoidance of plant species with high concentrations of secondary metabolites (like creosote bush) (Sombra and Mangione, 2005).

TABLE I: Diet of *Dolichotis patagonum* for several locations in Argentina.

Diet*		Location	Authors
Grasses Shrubs and Forbs	30% 70%	Reserva de la Biósfera de Ñacuñán (Mendoza)	Kufner and Pelliza de Sbriller, (1987)
<i>Observations</i> Eating grasses Eating shrubs	4702 8	Península Valdés (Chubut)	Taber A. B. (1987)
Grasses	40%	Río Negro province	Bonino et al.
Shrubs and Forbs	60%		(1997)
Grasses Shrubs and Forbs	70 % 29.9%	Reserva de la Biósfera de Ñacuñán (Mendoza)	Campos C. and Ojeda R. (2001)
Grasses	70 %	Sierra de las Quijadas National	Sombra M., and Mangione A. (2004)
Shrubs and Forbs	30 %	Park.	
Grasses aprox	66%	South East of Monte Pampeano	Rodriguez and Dacar, (2008)
Shrubs/Forbs aprox	(. 34%	(La Pampa Province)	
Grasses	80%	Northern Patagonia	Puig et. al. (2009)
Shrubs and Forbs	20%	(Mendoza Province)	

## 1.4 - ECOLOGICAL AND EVOLUTIONARY CONVERGENCE

Maras are diurnal cursorial rodents in the Argentinean deserts. As desert rodents, maras have been categorized, for practical reasons, as diurnal, folivorous, and quadrupedal. They share this categorization with other rodents like degus and viscachas, the asian lemming and the african dassie rat (Shenbrot et. al., 1999). Within this group and mainly due to its body size, maras do not converge morphologically with any other desert rodent. Except for sociality (one of the aspects shared with most folivorous and cursorial desert rodents), maras are considered , ecologically convergent with artiodactyls and lagomorphs (Shenbrot et. al., 1999, Macdonald et. al., 2007).

On the "rodent side" of *Dolichotis*, sociality represents an aspect that has been strongly analyzed for the New World Hystricognaths. For rodents in general, factors affecting or driving sociality and group living are associated with philopatry, parental care, and the costs and benefits that rise from it (Wolff and Sherman, 2007; Lacey and Sherman, 2007; Ebensperger and Hayes, 2008). For South American hystricognaths, Ebensperger and Cofre (2001) tested hypotheses for the influence of burrowing, habitat-specific predation risk, and the need for extended parental investment on sociality. Interestingly, only the cost of digging burrows had a significant effect on group size (op. cit.). Thus, this concept would be true for maras considering that they only dig burrows for breeding purposes which also corresponds with periods of maximum aggregation (Taber, 1987; Baldi, 2007).

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Among desert caviomorphs with herbivorous diets, the southern mountain cavy (*Microcavia australis*) is social, with groups ranging from 4-38 individuals (Rood, 1970). The Chilean chinchilla (*Chinchilla laniger*) forms large colonies of more than 100 individuals (Spotorno et. al., 2004) and the degus (*Octodon degus*) lives in colonies where communal care of the young is provided (Hayes et. al., 2009). In general, caviomorphs show a wide variety of social interactions across species, highly flexible social behaviors within species (Maher and Burger, 2011) and *Dolichotis patagonum* is a good example for both.

South American deserts do not differ greatly in flora and landscape from the North American deserts (Shenbrot *et. al.*, 1999). However, there is no ecological equivalent to maras among the rodents of the North. Instead, the North American deserts have medium-sized herbivores like the black-tailed jackrabbit (*Lepus californicus*). This lagomorph weights around 2 Kg and eats mainly grasses and forbs in the desert areas of Western North America (Best, 1996). Just like the South American maras, jackrabbits prefer open areas inside their home ranges due to predation risk (Marin *et. al.*, 2003). In the Mapimi Biosphere Reserve (Chihuahuan desert, Mexico), black-tailed Jackrabbits were more abundant in areas with both open grassland patches and shrub cover despite the low availability of high quality food in the grassland area (Laundre *et. al.*, 2009). Maras are also ecologically convergent on some medium and small body-sized deer (artiodactyla) (Macdonald et al., 2007, Taber, 1987). But, unlike the monogamous dikdik's or kilpspringers, maras defend larger drifting territories around their partner (Taber and Macdonald, 1992).

An additional point of strong similarity between maras and small-sized deer is their antipredatory behavior. Tail flashing as a means for the prey to alert the predator that it has been detected represents a typical artiodactyl behavior found in species like white-tailed deer, Thomson's gazelle and in *Dolichotis patagonum* (Smythe, 1970).

In conclusion, maras can be considered typical cavies, but maybe not typical rodents. Maras are ecologically similar to large lagomorphs and small deer. Maras possess social flexibility in the face of dry, unproductive and unpredictable desert environments. Being endemic to just one country and habitat type, questions about the mara's perception and use of this habitat are not only interesting but also crucial for the preservation of this species and its ecological relationships.

## CHAPTER II: HABITAT USE BY MARAS

### 2.1 - INTRODUCTION

Defining and describing the habitat of a species has been one of the central issues for ecologists. The habitat of a species can refer to the physical aspects (structure) of the environment (Shenbrot, 2007), or, as a more inclusive definition, to a specific patch with a set of resources in addition to the physical conditions chosen by individuals to inhabit and reproduce (Morrison *et. al.*, 1992). Some of the most commonly addressed questions in this regard include, what kind of patch to select in a specific habitat, what kind of food to consume from the patch, and how much time to allocate to each patch (Pike *et. al.*, 1977). In addition to foraging, certain habitats and microhabitats decrease in value for a species as a result of the species' perception of danger (Brown, 1988; Brown *et al.*, 1999; Lima and Dill, 1990).

Here, I analyze the mara's (*Dolichotis patagonum*) habitat using the pellet count method in Sierra de las Quijadas National Park. Maras seem to prefer open environments (Taber, 1987; Baldi, 2007). In Sierra de las Quijadas National Park, maras have been observed to rest and forage around open areas with bare soil and along or around the Park's roads (pers. obs.). In addition, the Park provides at least two different types of landscapes that differ in plant cover and elevation. Here, I will apply a pellet count method to measure the use of these areas by maras. I will also analyze temporal patterns of activity in relation to motion sensitive cameras placed around the park and associated with experimental food stations. I expect more evidence of maras in open areas and around roads (bare soil and less than 40% plant cover) than in sites with closed vegetation (more than 60% plant cover).

#### 2.2 - WHAT WE KNOW

## 2.2.1 - Maras' Habitat Use in the Wild:

Maras inhabit the dry plains of central and south Argentina and have been studied primarily for their unique social system (Redford and Eisemberg, 1992). Some work has been done on their feeding habits in different locations distributed across four different areas of Argentina (FIGURE 4).

In Mendoza province, maras have been observed and studied in two different locations (Ñacuñán Biosphere Reserve and La Payunia) belonging to the phytogeographical regions of Monte and Patagonia, respectively (Cabrera, 1976). Ñacuñán can be described as xerophytic woods dominated by mesquite (*Prosopis flexuosa*) and layers of shrubs (mainly creosote bush) and herbs like *Atriplex sp.* (Campos *et. al.,* 2001b). La Payunia is located in the south of the geographical province of Mendoza with open shrublands, grasslands and sandy grasslands. Species include the verbenaceae *Neosparton aphyllum* and grasses like *Panicum* and *Sporobolus* (Puig *et. al.,* 2009). Despite the difference between these areas, both locations have maras that show diet flexibility (Campos *et. al.,* 2001b; Kufner and Sbriller, 1987; Puig *et. al.,* 2009) and preference for open patches with bare soil versus covered bushy areas (Kufner and Chambouleyron, 1991).

FIG 4: Map with the areas where maras have been studied. Modified from SIAM (Sistema de Información Nacional Argentina).



The Rio Negro province belongs geographically to the Patagonia region. It displays typical Monte vegetation (Cabrera, 1976). Here, maras inhabit shrublands of evergreen species like *Chuquiraga avellanedae* and Creosote bush (*Larrea sp.*) with a few herb species, grasses like *Stipa tenuis* and patches of bare soil (Bonino *et. al.*, 1997). Annual precipitation is approximately 270 mm and the percent of plant cover ranges from 40 to 60 % (Baldi, 2007). Based on Taber's (1987) extensive behavioral study in Patagonia, males maras defend shifting territories around the females. Taber estimated home range sizes from 33 to 197 Ha for eight radio collared maras. Also, home ranges between pairs of maras overlapped and all of them included a communal rearing area used almost exclusively during breeding periods. Maras in Peninsula Valdés favored temporary wetlands and clearings (open areas with little vegetation) (Taber and Macdonald, 1992).

During the reproductive season, several breeding pairs come together and construct communal warrens. These may enhance safety from the higher predation pressure experienced by pups during their first months (Baldi, 2007). Baldi (*op. cit.*) established that maras prefer open environments for building these warrens (FIGURE 5). Closed habitats may obstruct sightlines for spotting predators. In both Patagonia studies, different pairs of adult maras were observed working cooperatively to defend the warren. These warrens were used only by the offspring (Taber, 1987; Baldi, 2007). Mara predators include pumas (*Puma concolor*), grison (*Galictis cuja*), Patagonian red fox (*Dusicyon griseus*) and red-backed hawk (*Buteo polysoma*) (Taber, 1987). Failed hawk attacks on maras at dens have been reported in Patagonia (Baldi, 2007).

FIG. 5: Evidence of maras' activity. a) warren in the open at Sierra de las Quijadas National Park. b) fecal pellets with urine.



Finally, in the central region of Argentina both diet and habitat use were studied (Rodriguez and Dacar, 2008; Rodriguez, 2009; Sombra and Mangione, 2005). On the ecotonal zone between Monte and Espinal deserts, maras preferred low vegetation and barren areas over covered areas. These areas exhibited a high degree of human activities with 94% of the area experiencing some anthropogenic degradation (Rodriguez, 2009). This study site consists of open shrublands dominated by creosote bush (*Larrea divaricata*) and grasslands dominated by *Stipa sp*. Home range data for this area agreed with that found by Taber (1987) in Patagonia (Rodriguez, 2009).

### 2.2.2 - Maras' Habitat Use in Captivity:

Maras seem to maintain their diurnal behavior in captivity as observed by Dubost and Genest (1974) and Pankhurst (1998). In both cases, maras were enclosed in a flat grassland. At Branféré Park in France a large colony of maras was observed to move daily to a woody area inside the Park where food was distributed by humans (Dubost and Genest, 1974). Most births and nursing activities occurred around noon when the females returned to the burrows to feed their offspring. On sunny days, maras spent more time resting. Foraging activities would increase in the evening (FIGURE 6). Dubost and Genest noted that maras had two foraging peaks per day, from 7:00 am to 12:00 pm and from 6:00 pm to 10:00 pm. Animals sought shelter and ceased other activities during rain showers.





At Whipsnade Wild Animal Park in Great Britain, Pankhurst (1998) analyzed the mara's social system in an area of about 256 Ha. The population had an average of 150 free ranging maras. The maras exhibited overlapping territories of more than 90% overlap due to a common area in the park where food was provided. Also, pairs of maras would change their distribution from one year to the next, with new areas added and other areas abandoned (Pankhurst, *op cit*). Regarding the temporal activity at Whipsnade Wild Animal Park, Pakhurst found that grazing and resting were the most common behaviors. Peaks in grazing occurred in the morning and from late afternoon to dusk (Pankhurst, *op cit*).

# 2.3 - SUTDY SITE: SIERRA DE LAS QUIJADAS NATIONAL PARK

Using pellet count and direct observations I measured patterns of habitat use for maras in Sierra de las Quijadas National Park (32°47' S and 67°10' W, 800 m elevation). The Park is located 116 km north of San Luis City in Central Argentina. It is a protected area with a low level of human modification, surrounded by highly modified areas. Annual precipitation averages 350 mm, with a dry season in fall and winter (May to September) and a rainy season in spring and summer (October to April). The Park represents an ecotonal system between the Monte Desert (xerophytic, resinous and thorny shrubs) and the Chaco (hardwood forests) (Cabrera, 1976). There are three clearly distinguishable habitats, creosote bush flats dominated by *Larrea cuneifolia* (10-20% shrub cover, grass, and firm loess soils), dense mesquite (*Prosopis* sp.) woodlands of short, thorny trees and gravelly soil along hillside drainages, and the typical Monte desert hillside bajadas of rocky slopes with shrubs, grasses and xerophytic thorny woods (FIGURE 7).

The unique ecotones and vegetation types of this geographical region serves as a refuge for many species from both the Monte and Chaco deserts. Among the vertebrates present in the Park, we can find several species of reptiles (40 approximately), more than 200 species of birds, and more than 40 species of mammals (National Park Administration, unpublished data). The three habitat types offer different opportunities and challenges in terms of vigilance, food abundance, cover and escape from predators. The Park encompasses 150,000 Ha. Approximately 50 % of the total area is covered by creosote flats and halophyte steppes, 30% by Monte bajadas, and 20% by the mesquite woods. I limited my sampling area inside the Park to approximately 15 Km<sup>2</sup>.

Based on the available literature and personal observations I predicted that maras would avoid the most densely covered areas in the Park. Maras should favor the creosote bush flats at the entrance of the Park as this area offers better sight lines and open spaces mixed with short bushes and herbs. FIG 7: Different vegetation units in Sierra de las Quijadas National Park. a) Creosote bush flat; b) Mesquite woods; c) Hills bajadas.



## 2.4 - HABITAT USE IN SPACE: Pellet Count

Among indirect methodologies, fecal-pellet counts along transects is a simple and straightforward way to estimate presence/absence and general habitat use by mammals (Krebs et. al., 2001; Mills et al., 2005). Pellet count methodologies have been used for numerous species and with diverse research objectives. In populations of African elephants, dung surveys provide an accurate estimate of population size that compares favorably with direct counts and observation (Boafo et. al., 2009; Olivier et. al., 2009). Similarly, comparing pellet count techniques to two other methods with snowshoe hares provided similar results of habitat use (Litvaitis et. al., 1985; Mills et al., 2005). On the other hand, pellet counts may not be appropriate for studies on the population sizes of animals with large herd size or species with changing defecation rates (Fuller, 1991). For estimating population sizes, pellet counts can be biased when feces do not belong to the season of the study or when animals use defecation to mark territories. However this method works well when animals defecate incidentally or haphazardly with respect to space and time. When pellet counts are used to estimate presence/absence or relative space use of a species, these assumptions do not pose a problem or significant bias (Laundré, 2009). Such is the case for the present study.

I removed pellets from two transects in both creosote bush flats and the transition area with mesquite woods. Each transect consisted of 20 squares of 2x2 meters each. Squares were five meters apart. Pellets were removed on two occasions (May and August 2009). Mara's fecal pellets are easily recognizable for its elongated shape (see FIGURE 5 b).

The total number of pellets per square were counted for each transect. The mean number of fecal pellets removed was higher for the creosote bush flat than for the hill transect ( $35 \pm 9.2$ ;  $0.65 \pm 0.9$ , respectively) (FIGURE 8). More pellets were removed from the first visit than from the second visit to the transects, but this difference was not significant. The difference between the creosote bush and the hill area was significant (F = 14.74, P< 0.001) (TABLE II). The plains were also used by cattle, peccary, gray fox, wild donkey and the introduced european hare. In Sierra de las Quijadas National Park, maras have been observed resting and foraging by the roads around and inside the park (pers. obs.). Both transects intersected the road. However the transect in the plains showed areas of resting and heavy use (pellets, foot prints and hair) not found at any point in the mesquite area. Additionally, personal encounters with maras were more frequent around open areas where the animals kept their distance from people relatively constant.
	df	Mean-Square	F-ratio	Р
DATE	1	2486.450	7.724	0.008
SITE	1	5297.512	14.74 (adj.)	0.001
SQUARE (SITE)	38	359.177	1.116	0.369
Error	38	321.913		

Table II : Analysis of variance for transects of pellet count in Sierra de las Quijadas NP.

FIG 8: Pellet count transects and habitat use by maras in Sierra de las Quijadas National Park.



## 2.5 - HABITAT USE IN TIME: (Camera Traps Around Artificial Food Patches)

Avoiding the hottest hours of the day can be crucial for large mammals in deserts. Maras are the second largest rodent in South America and the largest one living in arid and semi-arid areas in the continent. Several studies have addressed maras' preference for open areas with good sightlines (Baldi, 2007; Rodriguez, 2009; Taber, 1987). However, there has been no studies on the temporal activity of maras in the wild. I installed motion sensor cameras to provide evidence of maras' foraging activity in Sierra de las Quijadas National Park. The cameras were positioned in front of artificial food patches over a period of seven weeks. Cameras and food patches were checked daily. The pictures were analyzed for species, time of the day, activity or behavior of maras on the picture (feeding, vigilant, moving,etc.) and the number of maras per picture.

The cameras were activated more often during day light than during the night, with a peak between four and six in the afternoon (FIGURE 9) with a smaller peak in the morning between 8 and 10AM. Even though the study took place during winter, when temperatures are rarely above 20°C (data provided by Park Administration), maras seem to avoid the high midday temperatures (12 to 14 hs). There is a significant difference between the hours of the day with higher frequency of photos (evening hours), compared to the rest of the day (P< 0.001, X<sup>2</sup> =  $9.7 \times 10^{-200}$ , df= 11). A Chi-square test compared the observed frequency of photos with maras on them in two hours intervals against a theoretical frequency.

FIG 9: Number of pictures with maras on it at different hours of the day in Sierra de las Quijadas National Park. Colors represent day light and night.



Regarding maras' activities, foraging was the most common behavior seen on the pictures. We can assume some bias as the cameras were specifically associated with an experimental food patch (FIGURE 10). However Taber (1987) finds similar results on the study at Peninsula Valdes where maras spent more than 60% of their time feeding in the wild. In our case, over a total of 698 pictures analyzed, 76 % showed maras foraging, 17 % walking, 6.4 in vigilance and 1.3 resting.

I categorized maras' behavior into five different activities: a) foraging with the head down inside the food patch or taking alfalfa pellets from the ground (pic 1, APPENDIX; b) walking (pic 2 APPENDIX; c) keeping vigilance, sitting with the head up (pic 3 APPENDIX); d) resting with the stomach touching the ground (pic 4 APPENDIX) and e) cecotrophy, taking fecal pellets from its own anus (pic 5 APPENDIX) (maras may have hindgut fermentation like rabbits and hares).

FIG 10: Activities / Behavior: Number of photos analyzed with single maras (a), and groups of two or more maras (b).





Maras appeared on the pictures in groups not larger than five (FIGURE 11). The majority of the photos show only one mara, although this can mean that another nearby mara is keeping watch while invisible to the camera (pic 6 APPENDIX). This can be verified by photo sequences showing a second mara appearing and disappearing from consecutive frames over a continuos period of time.

To gain insights into how the artificial food patches were being used, I analyzed the appearance of other species of animals on the photos (FIGURE 12). The second most common species after the maras were cattle. Cows (Bovidae family) are illegally kept inside the Park in groups of more than 15 individuals. Following cattle the most common species occurring in the photos were grey foxes (*Pseudalopex griseus*), the Chacoan cavy (*Dolichotis salinicola*), small birds possibly identified as the common hornero (*Furnarius rufus*), skunks (Conepatus sp.), pumas (*Puma concolor*) which is the main predator for maras, peccary (*Pecari tajacu*), tinamous (*Eudromia elegans*) and the invasive European hares (*Lepus europaeus*). In spite of the cattle dominating specific locations inside the Park, maras were the predominant specie visiting and feeding from the food patches, with more than 80 % of the photos showing maras, 11 % showing cattle and less than 2 % showing other species .(FIGURE 13).

FIG. 11: Most commonly observed group size in camera trap photos for Sierra de las Quijadas National Park.



FIG 12: Species caught in camera traps other than mara for Sierra de las Quijadas National Park.



FIG 13: Number of photos with maras and other species of animals out of a total analyzed in Sierra de las Quijadas National Park.



2.6 - DISCUSSION:

The way herbivores use their environment is a crucial question in ecology. In Sierra de las Quijadas National Park, maras live in close association with creosote bush flats and prefer areas with low vegetation cover like roads. Early detection of possible predators is a common anti-predatory behaviors present in some deer and medium-sized herbivores (Altendorf *et. al.*, 2001; Shrader *et. al*, 2008). Maras belong to this group and show a high preference for areas with good sightlines (Masse and Cote, 2009).

Accordingly, the mara's need for good sightlines can also be seen in their daily activity patterns. When foraging, maras preferred daylight over darkness. Maras foraging from artificial food patches showed a typical diurnal behavior with peaks of activity in the morning after sunrise and in the afternoon before sunset. Even though maras show some level of activity along the day, like other desert mammals, high temperatures around midday are avoided and show the lowest level of activity.

Overall, in Sierra de las Quijadas National Park, maras use the environment in a manner comparable to studies of other populations in Argentina and studies of captivate populations. The mara's relationship to its habitat, and an understanding of the environmental components that contribute to its habitat suitability can help us manage and preserve this unique species.

## CHAPTER III: FORAGING UNDER PREDATION RISK

#### 3.1 - INTRODUCTION:

Herbivores invest time and energy in avoiding predators. At the same time, food quality and availability may limit feeding rates and pose a challenge to herbivores inhabiting environments such as deserts, where annual precipitation strongly restricts the timing and productivity of plants (Gutman *et. al.*, 2007). Brown (1999) characterizes how time allocation and vigilance may be used by animals coping with such foraging/ predation-risk tradeoffs. For desert rodents, the perception of safety plays an important role in determining the quality of a food patch (Kotler, 1984).

Maras, *Dolichotis patagonum* (Rodentia: Caviidae), provide a unique model for addressing foraging/predation questions in relation to social behaviors. Maras live in environments with low productivity (Kufner and Prelliza de Sbriller, 1987) and food availability. This together with the female's short receptive period may influence the maras' unusual social structure. Maras have a mixed social system that shifts from monogamous pair bonding for much of the year to communal rearing of young during the nursing and weaning periods (Taber and Macdonals, 1992). While many rodents and some larger mammals find safety in vegetated covered areas, maras may prefer open spaces with good sightlines for early predator detection. Openness may be crucial for those herbivores benefitting from shared vigilance and group living (Altendorf *et. al.*, 2001; Jarman, 1974; Shrader *et al.*, 2008).

The mara's breeding season seems to respond to this latter pattern of open sightlines and group vigilance. One partner of the pair may serve as sentinel while the other feeds. As in klipspringers (Druce *et al.* 2009), maras may switch these roles frequently during a feeding bout. A preference for open habitats for feeding and communal breeding, as well as the use of sentinels outside of burrows or as others feed, has been hypothesized as a response to predation pressures (Baldi, 2007; Taber and Macdonald, 1992). The young maras may be particularly vulnerable to predation. Interestingly, humans hunting maras have taken advantage of their affinity for open areas. Human modified landscapes with more open areas may become ecological and behavioral "traps" for maras (Rodriguez, 2008).

Food dispersion and the low productivity of environments inhabited by maras may cause females to disperse widely with males remaining in close proximity, defending a territory for their partner (Taber and Macdonald, 1992). Thus, monogamy could be advantageous in a poor environment as long as one member is vigilant while the other forages. Here, we aim to test maras' preference for open areas. What is the maras' perception of danger in relation to sightlines at different spatial scales (micro and macrohabitat levels)? We also examine how percent shrub cover and shrub height influence the maras' perception of predation risk. We did this by measuring the mara's landscape of fear (sensu Laundre *et. al.*, 2001), a topographic map of giving-up densities (GUDs) where lines of equal GUD correspond to lines of equal fear.

Unlike some rodents inhabiting creosote bush flats in North America, maras do not feed from this plant because of creosote's high concentration of toxins (Dearing *et al.*,2002). Jackrabbits in the Chihuahuan Desert prioritize sightlines and open spaces spending more time in the safer grassland with fewer food resources than in the shrublands (Marin *et. al.*, 2003). Maras are morphologically convergent with small ungulates, but unlike the monogamous dik-dik's or kilpspringers, maras defend larger drifting territories around their partner (Taber and Macdonald, 1992). Food availability in the mara's habitat seems to drive this special mating system. However, during the breeding season, maras show a system familiar for social rodents and lagomorphs. They nest communally once the young are born. Whether mimicking the niche of a small ungulate or large lagomorph, mara's are an excellent model for examining approaches and for testing hypotheses about trade-offs between foraging and predation.

Artificial food patches provide a reliable method for measuring animals' perception of risk within a specific landscape (Brown, 1988). The food left behind in a feeding patch should reflect the point at which individuals give up foraging to engage in a different activity (vigilance, resting, or seeking another food patch) (Brown, *op.cit*). We used artificial food patches in Sierra de las Quijadas National Park to asses maras preference for open spaces in response to predation risk. We examined mara habitat preference and response to vegetation structure in two ways: a) By setting patches in clearly distinguishable open or covered areas (FIGURE 14a) and b) by placing arrays of food patches as a grid with equal feeding opportunities at each station (FIGURE 14b).

The first arrangement of food patches tests the response of maras to distinct habitats varying in vegetation cover and height (creosote flat versus mesquite woodland). The second arrangement provides a smaller scale of resolution within creosote flats by measuring the mara's landscape of fear. How does the vegetation in the immediate vicinity of a food patch influence perceived predation risk? At the larger scale, we expect maras to prefer and exhibit lower giving-up densities in the creosote flats as compared to the denser vegetation of the mesquite woodland. At the fine scale, we expect the landscape of fear to exhibit lower GUDs where shrubs are sparse, shrubs are short, and sightlines and escape routes are good.

FIG.14: Different arrangements of artificial food patches for maras in Sierra de las Quijadas National Park

a) Arrange of GUD's in triplets.



b) Arrange of GUD's in the 5x5 grid.



### 3.2 - METHODS

# 3.2.1 - <u>Study site</u>:

Sierra de las Quijadas National Park (32°47' S and 67°10' W, 800 m elevation) is located 116 km north of San Luis City in Central Argentina. Annual precipitation averages 350 mm, with a dry season in fall and winter (May to September) and a rainy season in spring and summer (October to April). The Park is an ecotonal system between the Monte Desert (xerophytic, resinous and thorny shrubs) and the Chaco (hardwood forests) (Cabrera, 1976) and encompasses 150,000 ha. The study took place in two clearly distinguishable environments, creosote bush flats dominated by *Larrea cuneifolia* (10-20% shrub cover, grass, and firm loess soils) and the dense mesquite woods (Prosopis sp.) of short, thorny trees and gravelly soil along hillside washes and drainages.

These habitats offer different opportunities and challenges for maras in terms of food availability, vigilance, cover and escape from predators. We limited our sampling area to approximately 15 Km<sup>2</sup> of the park. In both creosote flats and mesquite woods we were able to differentiate patches of lower and higher vegetation cover allowing us to test for microhabitat features in each environment.

#### 3.2.2 - Giving up densities:

Giving up densities (GUD's) are the amount of food that a forager or group of foragers leave behind as dregs within a depletable food patch.

GUD's provide a surrogate for quitting harvest rates i. e. the rate of harvest within a patch at which it is no longer worthwhile for the forager to remain at the patch. Hence, the remaining food in a food patch after the animal has left is a broadly used and highly efficient way to test for the foragers' perceptions of predation risk (Brown and Kotler, 2004). We used depletable food patches to test which areas in the Park are perceived as high or low predation risk. The remaining food should correspond to a harvest rate that just balances the sum of metabolic (C), predation (P), and missed opportunity costs (MOC) of foraging (Eq.1) (Brown, 1988).

$$H=C+P+MOC \qquad (Eq. 1.)$$

We used artificial food patches consisting of rectangular wooden trays (400 x 600 x 180 mm) to test for the maras' preference for open environments. A feeding "station" consisted of three triplets of food patches for a total of nine patches per station. Within a station one triplet was placed in each of three microhabitats: open (below 30% plant cover), edge (30 to 60% plant cover), and covered (above 60% plant cover). Triplets of a station were arranged as a transect with 20 meters spacing between the open and edge microhabitats, and the edge and covered microhabitats.

We established a total of nine stations: three in the creosote habitat, and six in the mesquite habitat. Stations were spaced at least 200 m apart and up to 1.2 km apart.

The total number of food patches was 81. We used the presence of tracks at all food patches and nine camera traps distributed at each one of the stations to indicate foraging by maras and the presence of other species including potential predators such as grey foxes and pumas. Data were collected for three weeks (July 15th-2009 to August 4th-2009). Each tray contained 100 gr. of alfalfa pellets that were collected daily for a total of 13 days. Cameras put in position during the second week of June prior to formal data collection during the pre-baiting period. Cameras remained in place through the second week of August for a total of eight weeks of daily camera data.

Predation risk was also investigated by mapping the maras' landscape of fear across three representative 0.25 Ha grids of creosote flat. Spatial variability in predation risk can either be sampled by stratifying across habitats or by creating regular grids that encompass a diversity of factors that might influence predation risk (Altendorf et al., 2001; Hochman and Kotler, 2007; Kotler et al., 1994; Van Der Merwe and Brown, 2008). We made three 5 x 5 (25 food patches) arrays of food patches spaced at 10 m intervals. The three grids were between 200m and 800m apart from each other. This study required a total of 75 food patches. Data were collected over two weeks (August 6th to August 15th) with two sessions of three data collection days each. During the first three days, GUD's were collected every 24 hours and during the last session GUDs were collected every 48 hours. For species that may be somewhat nomadic or less frequent in their return to a particular site, it can be more effective to leave food patches out for more than a single day to insure thorough foraging (Whelan and Maina, 2005).

This provided six days of sampling for estimating the maras' landscape of fear setup. Two cameras per grid documented the timing and presence of maras at food patches.

For both the transects and grids we surveyed vegetation features around either the triplet of trays (first study) or at the stations of each grid (second study). Within a 5m diameter around each point, we estimated percent cover, distance to the closest shrub, and height of the tallest shrub. To estimate the average percent cover around each point we walk along both north/south and east/west axes noting the presence/absence of plant cover every 50cm. The distance to the closest shrub and tallest shrub was also measured within each of the four "wedges" along the four cardinal directions.

# 3.3 - RESULTS

From the transect data, maras forage significantly more in the open and edge areas than in the cover habitat (P< 0.001) (FIGURE 15). There was no day effect (P= 0.882) or box effect (P=0.979) but GUDs among sites varied significantly (P< 0.001 df = 8)(TABLE III).

The vegetation cover measured as a percent plants present around each triplet for all nine sites differed markedly for open, edge and covered habitats having a clear effect on the food left behind in the patches ( $R^2$ =0.8, P< 0.001). The average cover for the open, edge and cover microhabitats were 15.7 %, 38.6% and 71.6%, respectively.

FIG 15: Giving up densities for maras in Sierra de las Quijadas National Park. O= Open habitat, E = Edge habitat and C= Covered habitat.



TABLE III: Anova test with the	e results for the	effect of food	patches in	the three	different
habitat types: Covered, Edge	and Open.				

	df	Mean-Square	F-ratio	Р
Day	12	123	0.396	0.882
Box	2	6.6	0.022	0.979
Habitat (open/cover)	3	16665	53.673	0.000
Site	8	7003	22.557	0.000
Error	547	310		

When food patches were arranged as 5 x 5 station arrays on three grids, there were large and significant differences in GUDs among stations. There was no significant differences between the grids themselves, just between the stations within grids. For the ANOVA, there was a significant difference between the sessions (P< 0.001). It seems that 48 hour sessions were successful at determining the mara's landscape of fear. GUD's were significantly lower when patches were left for 48 hours rather than 24 hours. More importantly, almost all patches were foraged when left for 48 hours rather than for 24 hours. (Table IV).

TABLE IV: Anova results for the landscape of fear. Here we can see the effect of the different sessions as well as the difference between the three stations involved in the studio.

	df	Mean-Square	F-ratio	Р
Session	1	26484	19.9	0.000
Grid	2	455	1.08	0.051
Station(Grid)	72	418	2.749	0.000
Day(Session)	4	1325	8.699	0.000
Error	370	152		

Stations within grids varied significantly in their GUDs, whereas there was little difference between the three grids in overall GUDs (P = 0.001; F = 2,204) (FIGURE 16).



FIG. 16: Least square means for the station effect on the foraging habits of maras.

A portion of the station effect on the grids could be attributed to plant cover. GUDs increased significantly with percent cover of vegetation at a station ( $R^2$ = 0.56; P= 0.011). This was the only vegetation metric that seemed to influence the foraging behavior of maras. To obtain a visual representation of the vegetation cover and the giving up densities for the three different grids we used contour graphs (FIG 4). The lines for high vegetation cover in the contour plots coincide with the lines for high GUD's (FIGURE 17). These contour maps were formed by using least square interpolation using the means of either GUDs or percent vegetation cover as the metric for each station.

FIG 17 a : Lines show cover for grids 1, 2 and 3. The numbers represent percent of plants present around each point.



b : Lines show Giving up Densities for grids 1, 2 and 3 in 24 hs treatment . The numbers represent food left behind in grams.



c : Lines show Giving up Densities for grids 1, 2 and 3. The numbers represent food left behind in grams. 1 2 3



Pumas (*Puma concolor*) were the main predator of maras detected in the camera traps. We obtained six photos of two different individuals, on two different grids (Grids 2 and 3), on four different dates. Even though gray foxes were the most frequent carnivore (*Pseudalopex griseus*) shown on the pictures for all the stations, foxes are likely lethal only for mara pups around warrens (Baldi, 2007) (FIGURE 18). Around 40 pictures with solitary foxes were captured during the eight weeks of the field season. It is possible that the presence of foxes poses a non-lethal effect on adult maras. In response to foxes, maras may need to be wary and take appropriate evasive actions to render foxes harmless. In this way, foxes may represent a harassment cost (see Brown and Alkon 1990 for an example where porcupines seem to experience a harassment cost from their potential predators.)

FIG. 18 : Pumas at the food patches visited by maras at the Sierra de las Quijadas National Park



## 3.4 - DISCUSSION

Predators affect the prey's foraging behavior. The compromise between feeding and safety shapes habitat selection in herbivores (Jarman, 1974). Maras foraged significantly more in open than in covered brushy habitats. The pumas in this area may pose the greatest predation risk to the maras, while foxes may be the more ubiquitous non-lethal effect. Even though the maras' preferences for open areas has been reported before (Baldi, 2007; Rodriguez, 2009), the use of depletable food patches to test for risk perception shows that predation risk is likely the most important factor affecting maras' choice of habitats for feeding.

Experimental trials with the triplets of food patches, showed a high sensitivity to openness and sightlines by maras. As part of the non lethal effects of predators on its prey (Brown 1999; Lima, 1998), the selection of safer patches to feed has been reported by several authors (most desert rodents most of the time,Brown and Kotler, 1988; Brown and Alkon, 1990; Kotler, 1984). Risk from specific predators could determine which habitat will be perceived as safer for maras. Some rodents from the Heteromyidae family show a strong response to predation by barn owls. In an enclosure experiment such rodents favored foraging under bushes in response to the presence of owls (Brown et al. 1988). Gerbils in the Negev Desert respond in a similar way when faced with owls and snakes, limiting the use of open microhabitats when owls are present, but increasing it when bushes are occupied by vipers or other snakes (Kotler et al, 1992). In the case of the gerbils, predator facilitation between snakes and owls can later relative preferences for the bush or open microhabitats. We found no indication that the different predators of maras facilitate each other via their presence in different habitats. Rather, even as maras may be quite flexible when foraging in the presence of different predators, the risk they perceive is consistently higher where shrub cover is higher and sightlines reduced.

For example, crested porcupines avoid open spaces that make it more difficult to use quills for protection and leave the individual more vulnerable to attack (Brown and Alkon, 1990; Sweitzer, 1996). On the other hand, some species perceive open spaces as safer than covered ones. Shrader et al. (2008) found that goats preferred to feed in more open habitats where feeding trays at different stations were visible from each other. Some animals with flexible group dynamics or alarm calls prefer open environments that allow for early detection of predators (Kotler, 1984; Lingle and Finbarr Wilson, 2001; Rosenhoover and Bailey,1985).

By using manipulated food patches, we were able to equalize feeding opportunities between stations, transects, grids and habitats. By controlling for other factors, the differences in GUDs from these food patches estimates habitat and microhabitat-specific differences in the mara's foraging cost of predation. We could see where maras felt comfortable or safe. Foraging activity was negatively related to shrub cover for the three grids under study. Even though vegetation height and proximity to the food patch seemed to be an important factor for sightliness, it was percent vegetation cover that most influenced foraging. Of course, these other components of vegetation correlate positively and rather closely with percent cover. Maras exhibit escape behavior similar to some ungulates and hares (Caro, 1986; Fizt Gibbon and Fanshawe, 1988) combines stotting and trotting alternately (Smythe, 1970). While we might expect vegetation height of the most proximate plants to be of some importance to the maras' foraging behavior, given that vegetation height is thought to only influence the proportion of stotting and trotting while escaping, we could expect cover to be a better or more general indicator of habitat selection and foraging behavior in response to predation (Stankowich and Coss, 2006).

This research advances our understanding the role of predators on habitat preferences and selection for *Dolichotis patagonum* including the influence of vegetation features. Future research directions could include a detailed analysis of the presence and boundaries of the predation/foraging trade-off while revealing how the flexible social system in relation to foraging needs contributes to the evolutionary ecology of this unique large rodent.

# APPENDIX I:

PICTURE 1: Mara feeding from the tray.



PICTURE 2: Maras walking.



PICTURE 3: Maras en vigilant position (left) and foraging (right).



PICTURE 4: Maras en resting position (right) and foraging (left).



PICTURE 5: Mara performing cecotrophy (extracting fecal pellets from anus).



PICTURE 6: Maras foraging. Notice the third individual keeping watch at a distance (left).



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VITA:

### Education:

**2006** - MS. candidate University of Illinois at Chicago (UIC), "Foraging, predation and sociality in *Dolichotis* 

patagonum"

**1996 - 2003** - Licensed in Biological Sciences (Licenciada en Ciencias Biológicas), National University of San

Luis, Argentina.

Thesis: "Diet Description for Maras (*Dolichotis patagonum*) (Caviidae), in Sierra de las Quijadas National Park."

#### Teaching Experience:

**2008 - 2010** - Teaching assistant for BIOS 101 (Adventures in populations and communities). University of

Illinois at Chicago (UIC), U.S.A.

**2002 - 2005** - Teaching assistant for the biological chemistry course, College of Chemistry, Biochemistry and

Pharmacy, Universidad Nacional de San Luis (UNSL), Argentina.

**2003 - 2004** - Teaching assistant for the courses of general and cellular biology, introduction to biology, and

advanced course in biology, College of Chemistry, Biochemistry and Pharmacy, (UNSL).

# Participation in Research Projects:

**2009 - present** - Ecología nutricional y fisiológica de vertebrados de zonas semiáridas: Nutritional and

Physiological Ecology of Semi-arid Vertebrates, Principal Investigator: Ph.D. Antonio Mangione.

**2009** - Project on sexual behavior and hormonal estrus cycles in captive female lowland gorillas (*Gorilla gorilla*)

at Lincoln Park Zoo (volunteer on ethological observations), Principal Investigator: Ph.D. Susan Margulis.

**2001-2005** - Project: Plant-Animal Interactions: Nutritional Ecology and Ecophysiology of San Luis Vertebrates,

Principal Investigator: Ph.D. Antonio M. Mangione.

### Grants and Scholarships:

**2010** - Sigma-Xi (Grant-in-Aid of Research Program): "Food and Safety Trade offs in the Socially Complex

Dolichotis patagonum."

2006 - Fulbright Student Program (Grant to pursue PhD/MS studies in United States).

**2004** - Graduate Fellowship in Aid for Research. Nutritional Ecology of Maras (*Dolichotis patagonum*) National

Scientific and Technologic Research Council, Argentina.

**2001 - 2002** - National Program of University Fellowships (National Ministry of Education).

**2001** - Sigma-Xi (Grant-in-Aid of Research Program): "Characterization and quantification of coprophagy in mara

(*Dolichotis patagonum*): Roll of this mechanism in the utilization of diets with low nutritional value."

**1996 - 1998** - Undergraduate awards (financial help to best grades, Universidad Nacional de San Luis).

# **Publications:**

**2005** - Sombra, Moira S. and Mangione, Antonio M. Obsessed with grasses? : The case of mara *Dolichotis* 

patagonum (Caviidae: Rodentia). Rev. chil. hist. nat. 2005, vol.78 (3) 401-408.

# Graduate Level Courses of Specialization:

- 1. University of Illinois at Chicago:
- Mud wrestling with statistics, 2008.
- BIOS 594, Evolutionary Game Theory, 2008.
- EAES 480, Statistical Methods in Earth and Environmental Sciences, 2007.
- BIOS 530, Population Ecology, 2007.
- BIOS 532, Introduction to Ecology and Evolution II, 2007.
- BIOS 490, Topics in Ecology and Evolution, 2007.
- BIOS 531, Introduction to Ecology and Evolution, 2006.

#### 2. Universidad Nacional de San Luis:

- Animal-Plant Interactions: A Nutritional Ecology Approach, 2005.
- Synthesis of Plants Natural Compounds, 2004.
- Evolutionary Ecology: Concepts and Examples, 2004, CONICET (Comahue National University). Nutritional Ecology of Vertebrates, 2003.
- Ecology, Physiology and Animal Nutrition: An Integrative Approach, 2002.

# **Outreach Activities:**

- Cooperation with DNA analysis to identify hybridization levels in squirrel populations of Chicago city, IL.

- Cooperation on plant roots competition at the University of Illinois Greenhouse.

- Member of the Laboratory Security Commission. May 2005-2006.

- Assistant Producer of the radio Program on popularization of science La Búsqueda, 97.9 FM San Luis

National University, 2003 - 2006.