BEHAVIORAL RESPONSE OF THE MARA (*Dolichotis patagonum*) TO FOOD DENSITY IN ARGENTINA

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ABSTRACT

Optimal foraging models predict animals will consume more food from patches of higher initial densities. They also predict that when food is scarce in the environment, animals will have greater foraging efforts in the patch and hence shorter vigilance times. As an anti-predator behavior an increase in group size is correlated with a reduction of individual vigilance time. We evaluated *Dolichotis patagonum's* (mara) behaviors: feeding, vigilance, walking, and others (sniffing, grooming, resting) in relation to different food densities (100 g, 70 g and 40 g of alfalfa pellet, mixed with 5 kg of sifted soil, offered in wooden box) in a field experiment by using camera traps. As a novelty, maras showed nocturnal activity. They also showed an increase in vigilance time when they were in pairs compared to when they were alone, by alternating feeding and vigilance behaviors. When food density changed, no variation in vigilance was observed and food intake only changed between 100 g and the other two food densities offered. We propose that: first, maras are cathemeral animals. Second, mara's knowledge about patches is critical to assess patch quality; and that alternating feeding and vigilance when in pairs, could be and efficient anti-predator strategy in environments with high predator pressure.

Key words: activity pattern, camera traps, *Dolichotis patagonum*, food consumption, San Luis, vigilance.

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RELEVANCIA

En este trabajo se presentan los patrones de actividad de las maras (*Dolichotis patagonum*) en Argentina. Emplean el método de foto-trampeo para conocer sus diferentes actividades de comportamiento. El empleo de las cámaras-trampa permite conocer el comportamiento y uso del hábitat que tienen las especies en vida silvestre.

RESUMEN

De acuerdo con los modelos de forrajeo óptimo, los animales consumirán más alimentos en los parches con mayor densidad inicial. Además, predicen que cuando el alimento sea escaso, los animales tendrán mayores esfuerzos de forrajeo en cada parche y por tanto menores tiempos de vigilancia. La vigilancia individual también disminuirá al aumentar el tamaño de grupo. En este experimento de campo evaluamos, a través de cámaras trampa, el comportamiento de: alimentación, vigilancia, desplazamiento y otros (ej.: olfatear, acicalarse, descansar) de *Dolichotis patagonum* (mara) en relación a diferentes densidades de alimento (100 g, 70 g y 40 g de pellets de alfalfa mezclado con arena cernida dentro de cajones de madera). Como dato novedoso se observó actividad nocturna. También se observó un aumento en la vigilancia cuando estaban en pareja que al estar solas, dado que alternaban la vigilancia y la alimentación. Entre las densidades de alimento no se observó variación en la vigilancia y la ingesta de alimento cambió solo entre 100 g y las otras dos densidades ofrecidas. Por lo cual proponemos que, primero, la mara es un animal catemeral. Segundo, el conocimiento que las maras tienen de los parches es crítico para evaluar su calidad. Finalmente, la alternancia de comportamientos en la pareja podría ser una estrategia anti-predatoria en ambientes con altas presión de depredación.

Palabras clave: cámaras trampas, consumo de alimento, *Dolichotis patagonum*, patrón de actividad, San Luis, vigilancia.

INTRODUCTION

Animals face a trade-off between anti-predator vigilance, feeding and other activities in order to obtain energy and maintain their level of vigilance (Sirot and Pays, 2011). Vigilance is generally defined as the time spent with the head up during foraging periods. Although the periods with the head up allow for additional functions like looking for co-specifics and handling food, in all anti-predator vigilance models it is assumed that during periods when animals have their heads up they can detect predators more quickly than when they have their head down looking for food or feeding (Whittingham *et al.*, 2004).

The increased vigilance and protection against predators have been suggested as one of the main evolutionary advantages of group foraging (Clark and Mangel, 1986). When animals are alone, they tend to be more vigilant than when they are with co-specifics, since there are more eyes available for vigilance ("many eyes effect"; Lima, 1995), therefore individual vigilance is lower (Periquet *et al.*, 2011; Vásquez, 1997).

One of the predictions of optimal foraging models is that when food is scarce in the environment, the animal will have greater foraging efforts in the patch, and hence the time allocated to vigilance has to be shorter (Brown, 1992; Brown, 1999; Olsson *et al.*, 2002). The model also predicts that the animal is going to consume more food from patches of higher initial densities compared to the patches of lower initial density (Valone and Brown, 1989).

In order to tests some predictions of optimal foraging theory we used maras (*Dolichotis patagonum*) as a biological model. The maras is a big sized endemic rodent inhabiting central and southern Argentina. Previous studies in Peninsula Valdes in the argentinian Patagonia, have shown that feeding behavior takes 46% of mara's time (Taber, 1987). Regarding their temporal activity, it has been categorized as a diurnal animal (Mares and Ojeda, 1982), with peaks of activity in the morning and in the evening, avoiding periods of higher temperature, except during winter, when maras have a unimodal pattern (Kufner, 1995).

Here, we first describe the daily activity pattern of maras. Second, we hypothesized that individual vigilance depends on group size. As a prediction we propose that individual vigilance will decrease with the presence of co-specifics. Third, food intake is positively correlated with the initial density of food in the patch. Finally, the quality of the patch is positively correlated with the vigilance time. It is expected that an increase in the quality of the patch will increase the vigilance time.

MATERIALS AND METHODS

BIOLOGICAL MODEL AND STUDY AREA

The mara is an endemic rodent from Argentina. It is a monogamous mammal and exhibits communal breeding (Taber and Macdonald, 1992a). It uses open habitats, and many authors have hypostatized that predator detection in this species is visual (Baldi, 2007; Kufner and Chambouleyron, 1991; Taber and Macdonald, 1992b).

The study was carried out at the National Park Sierra de las Quijadas (32°47' S, 67°10' O), located 116 km from the city of San Luis, Argentina (Research authorization DRC 262). In the park the average annual rainfall is 350 mm, the habitat is an ecotone between the Monte (xerophytic, resinous and thorny shurbs) and the Chaco (hardwood forests; Cabrera, 1976). The maximum monthly mean temperature is 31 °C and corresponds to the month of January and the minimum is 3.1 °C for the month of July (APN, 2017). The average maximum temperature during the experiment was 25.6 °C (SE: 0. 95) and the minimum of 9.3 °C (SE: 0.82), data taken from the weather station of the park. The biomass availability at the Park is 434± 180 kg ha-1 of creosote bush, 22.1 ± 20 kg ha-1 of cacti and 9.47 ± 6.6 kg ha-1 of dry mass for grasses. The diet of maras in the Park is composed of 70% grasses (Sombra and Mangione, 2005).

EXPERIMENTAL DESING

The study was conducted during the months of September-October 2013. Four grids of 25 wooden boxes each, was set in the field separated by more than 300 m one from each other. Each box contained alfalfa pellets (Vasquetto®) mixed with sieved soil. To habituate the animals with eating from the boxes, we conducted 5 sessions of 48 h with 100 g of alfalfa pellets per box. We considered the beginning of the trial when the animals started eating from the boxes regularly (at least one visit every 48 h). We prepared three food densities by adding 100g, 70 g and 40 g to 5 kg of sieved soil inside a wooden box. Five consecutive sessions of 48 hours each were carried out at every food density: 100 g, 70 g and 40 g, in this order. Food consumption was calculated as the difference between initial amount of food in the wooden box and food leftovers at the end of each 48 hours period.

One camera trap (MOULTRIE MHF-DWG-5.0) was set on in each grid in front of one of the most used wooden boxes. When an animal moved in front of the camera trap, the camera took three consecutive pictures and after a one-minute delay it is ready to take three new pictures. The four camera traps took 1,071 photographs of the maras, which were used to assess the pattern of their temporal activity and behavior.

We created a histogram quantifying the number of photographs in which maras appeared, in relation to the time of day at which they were taken. Four behavioral categories were established from pictures: walking (w), eating (e), vigilance (v) and other (o). The maras were considered to be eating when they had their heads inside the wooden box, and being vigilant when they were (sitting or standing) with their heads up (Figure 1). Any activity between these two, that was not clearly one of the categories mentioned above, was considered as other, so as not to overestimate any of the behaviors (Figure 1).

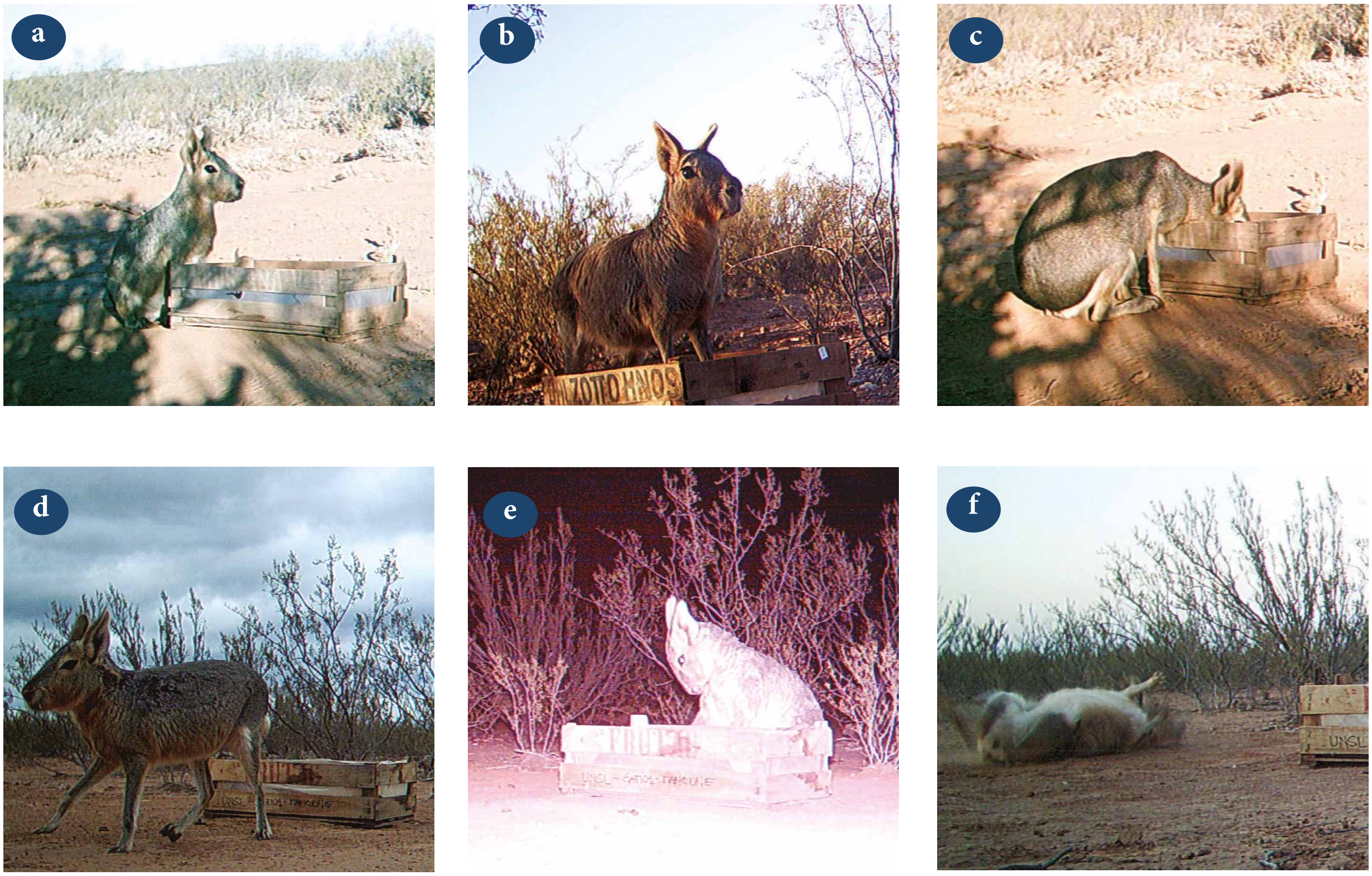

Figure 1. Different behaviors captured (a and b) vigilant, (c) eating, (d) walking, (e and f) other. Photos: Ailin Gatica.

DATA ANALYSIS

We analyzed by using Chi-square (χ^2): a.- the frequency of behaviors (e, v, w, o) during day and night, b.- these behaviors in relation to whether maras had their partner close each other or not, in this case all the activities were considered for each mara individually and summed up together, and c.- the frequency of behaviors (e, v and o + w) displayed between the three densities of food.

The Kruskal Wallis test (*H*) was used to assess if different densities affected the number of pictures, and it was also used to evaluate the effect of the densities of food on consumption.

Finally, the Spearman correlation (ρ) was used to evaluate the relationship between food consumption and the number of pictures at each food density. The same test was used to assess the relationship between consumption and the number of minutes recorded by the cameras at different food densities. This latter dataset was a log-transformed and a Student's t-test (*t*) for comparison of two slopes were performed. Significance level was set at 0.05.

RESULTS

During the trial 1,096 photographs of animals were taken: 1,071 of *D. patagonum*, 10 of *Bos taurus*, 5 of *Equus africanus asinus*, 3 of *Equus ferus caballus*, 3 of *Pecari tajacu*, 2 of *Tolypeutes matacus* and 2 of *Puma concolor*. Therefore, the maras were the largest contributor to food intake. Maras appeared alone in 960 out of 1,071 photographs, 106 pictures showed two maras. Only five photographs showed three maras, all taken at a single event, so they were removed from the analysis.

Maras were most active during early morning and late in the evening. While 62.7% of activity was registered during daylight hours, 37.2% of the photographs were obtained in hours of darkness (Figure 2). Although there was less nocturnal than diurnal activity, both night and day have the same ratio of 3/2 between eating/vigilant photographs. No significant differences were observed between the frequencies of night and day activities (χ^2=7.30, p = 0.06, df = 3). Although close to significance, this seeming difference is given by the activity of 'walking' since at night the visits were shorter, therefore the frequency of entries and exists was higher than during the day (Figure 2).

A significant difference in mara´s behaviors was observed between maras grouped in pairs or solitary (χ^2=39.37, $p < 0.0001$, $df = 3$). Vigilance constituted the main contribution to this difference. When maras were in pairs greater vigilance was observed, compared to solitary maras (Tables 1 and 2). It was observed that the most common behavior in the pair was that while one of the animals was eating the other was vigilant (Tables 1 and 2).

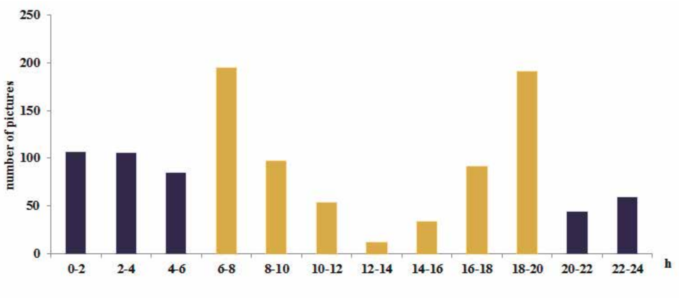

Figure 2. Daily activity pattern of *D. patagonum*.

A positive correlation between the number of pictures taken and food consumption ($p < 0.0001$, ρ=

Table 1. Percentages of behaviors in the pictures. Solitary: activities observed in photographs with only one mara present. Paired: sum of individual behaviors when there were two maras in the picture.

	Behavior			
	Eating	Vigilant	Walks	Others
Paired	30.84%	44.86%	22.43%	1.87%
Solitary	45.62%	29.69%	15.21%	9.48%

Table 2. Number of pictures with different combinations of behavior in the couple.

	Behavior			
	Eating	Vigilant	Walks	Others
Vigilant	42.03%	7.97%	28.99%	2.90%
Eating	2.17%	-	-	-
Walks	10.14%	-	5.07%	-
Others	0.73%	-	-	-

0.86, N=60) was observed. Eating, vigilance and other behaviors were compared among food densities for pictures with only one mara. We did not detect significant differences between the three behaviors (χ^2=0. 74, *p* = 0.94, *df* = 4) at different food densities.

There was a decrease in the number of pictures when food density was reduced (Figure 3a). The consumption (*H*=14.45, *p* = 0.0007, *df* = 2) and the number of pictures (*H*= 16.84, *p* = 0.0002, *df* =2) varied between food densities. Significant differences were observed between 100 g and the other two food densities, but no significant differences were observed between 70 g and 40 g.

There was a positive correlation, between food intake and time spent by maras in the box, for each densities of food offered: 100 g (*ρ*= 0.87, *p* = 0.00014, N=20), 70 g (*ρ* = 0.82; *p* = 0.00033, N=20), 40 g (*ρ*= 0.74, *p* = 0.00124, N=20; Figure 3b). We also found differences between some of the slopes of the regressions between food intake and time for each density. Slope for 100g density differ from 40 g food density (*t*=4.05, *p*=0.00025, *p*=0.00025 Bonferroni-adjusted) but not from 70 g (*t*=0.99, *p*=0.327, *p*=0.981 Bonferroni-adjusted). However, the slope of 70 g differs from 40 g (*t*=2.79, *p*=0.0082, *p*=0.024 Bonferroni-adjusted; Figure 3b).

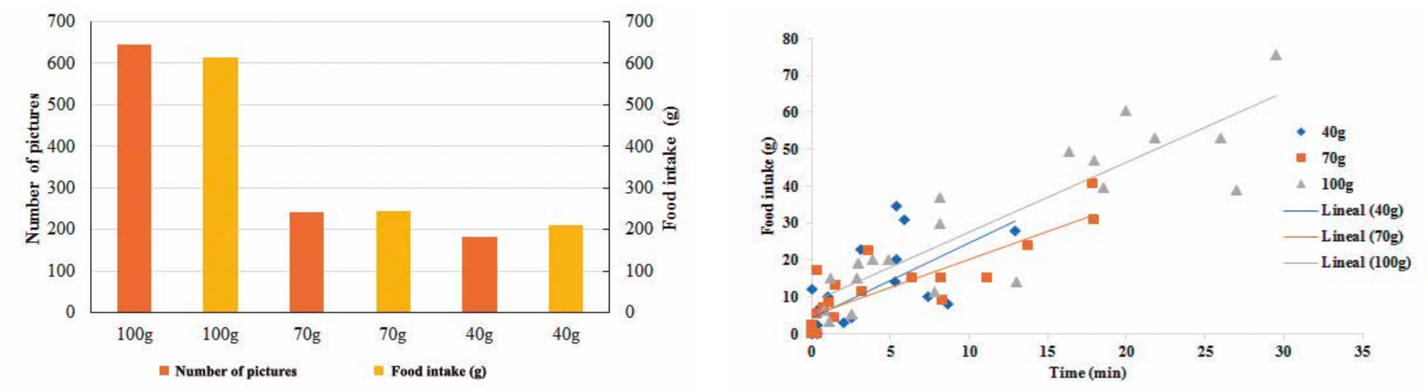

Figure 3. (a) Total sum of food consumption in grams and total number of photographs for each densities of food, (b) relationship between food consumption and number of minutes per session in the three densitiess of food: 40 g (y=2.044x + 4.296), 70 g (y= 1.581x +4.902) and 100 g (y= 1.897x + 8.463).

DISCUSSION AND CONCLUSIONS

Dolichotis patagonum presents a bimodal pattern of daily activity during the period that the study was conducted. Contrary to our expectations, maras show 37.2% of nocturnal activity. Maras also showed an increase in vigilance when they were with their partner compared to when they were alone. There was no variation in vigilance when exposed to changes in food density and food intake only changed between 100 g and the other two food densities.

Maras shown peaks of activity during the early morning and late afternoon, probably to avoid high temperatures. The same pattern was described by Kufner (1995) for maras in spring and summer in Nacuñan, Mendoza, Argentina. Eventhough maras has been described as diurnal animals (Kufner, 1995; Mares and Ojeda, 1982), in this study we detected they have also night time activity and forraging was the main activity in both periods. Therefore we propose that maras are cathemeral animals rather than a strictly diurnals. Cathemeralism is a behavioral strategy used my some animals to avoid high temperatures (Bennie *et al.*, 2014) and reduce water losses, which in desert environments, with low humidity and high temperatures, are particularly important (Cain III *et al.*, 2006; Christian, 1978; Cortés *et al.*, 2000). The camera trap methodology has allowed, on previous occasions, to detect nocturnal activity in animals considered strictly diurnal, as is the case of the presumably diurnal primate Rhinopithecus brelichi (Tan *et al.*, 2013).

Taber and Macdonald (1992b), observed that vigilance varies between 20% and 30% in breeding periods when the couple was away from the burrow. We observed that when maras were alone, they spend 30% of the time being vigilant, but when they were with their couple, this percentage raised to 45%; thus, the probability of detecting predators should increase when it is close to its couple.

In this study the most frequent behavior observed in paired maras was: one feeding itself and the other vigilant. Taber and Mcdonald (1992b) on the contrary showed that for maras in Patagonia, both were feeding or both were vigilant. It has been suggested that vigilance increased with predatrion risk (Brown, 1999). We propose this could explain the difference between both habitats. There are striking differences between the diet of *Puma concolor* (puma) in the Park and in Chubut, Patagonia. While in Sierra de las Quijadas de puma´s diet is composed of mainly maras (44%), in Chubut, Patagonia, maras only represent 2.2 to 3.9%, and guanacos are the most abundant item (Donadio *et al.*, 2010; Fernández and Baldi, 2014).

Regarding feeding time, solitary animals spent 45% of their time feeding (Table 1) in agreement to what was observed by Taber (1987). Food offered in wooden boxes (alfalfa pellets), is a higher quality food item (16% protein, Vasquetto®), compared to food available in the wild (7% protein, Sombra and Mangione, 2005). Evethough food in the box did not seem to change substantially maras´s feeding time.

It is expected that animals will consume less from the food patches of lower quality, redirecting its efforts to better quality patches (Abu Baker and Brown, 2009; Hochman and Kolter, 2006). In our experiment, animals did not have different offers simultanously because we were looking to observe the animal perception of patch quality change over time. We observed that when we reduced the quality of the patch from 100 g to 70 g, animals did not visit the patch as often. While maras noticed the difference between 100 g to 70 g, they did not notice the differences from 70 g to 40 g, as indicated by food consumption or number of visits to the patch. It is important to point out that the animals spent 20 days feeding from patch of 100 g (the priming period and the test), but only 10 days consuming 70 g. It may be that the longer exposure time allowed them a better assessment of the change in patch quality. Probably, the knowledge about the patch was not sufficient to evaluate the difference from 70 g to 40 g. It has been observed that giving prior information to an animal facilitates its selectivity when exploiting a patch (Kohlmann and Risenhoover, 1998; Vásquez *et al.*, 2006). Thus, maras might fed in a density-dependent manner between 100 g and 70 g, in other words food intake diminish whith food density. However at 40 g patches maras were feeding at the same rate that at 70 g patches overexploiting 40 g patches. Although maras consumed faster in 40 g they did so without compromising other activities, the relationship of eating over total activity remained the same for all three food densities.

The lack of relationship between food density and vigilance has been observed in some studies. It has been hypothesized that this may be due to the fact that there are no time constraints, or the animal can be vigilant while manipulating the food (Beauchamp, 2009). Maras decreased the frequency of visits when they realize there is a decreased in patch quality, however no variation in vigilance was observed.

Furthermore, maras kept the same level of vigilance in the three different food densities, which may be due to the lack of temporal constraints, since bite size allows the animal to be vigilant while chewing. One way to assess this behavior in the future would be to reduce the bite size and evaluate if the vigilance changes in relation to food density. Regarding the variation of food intake, we hypothesized that in these species, previous information of the patches is critical to assess patch quality.

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