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Breeding success of the endemic mara *Dolichotis patagonum* in relation to habitat selection: Conservation implications

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Abstract

Although maras (*Dolichotis patagonum*) are among the most representative mammals of South America, knowledge on the ecological processes affecting their conservation is scarce. In particular, the study of habitat requirements and its relationship with breeding success is necessary to identify possible threats and develop conservation action for this endemic mammal. I investigated habitat selection patterns by maras and their relationship with breeding success in Península Valdés, Argentine Patagonia. Maras bred from mid-August to late December, and they tended to build the breeding warrens in open, grass-dominated habitats more than expected while avoided closed habitats dominated by taller shrubs. Mean number of breeding adults per warren was 4.26, while mean number of pups born per warren was 4.46. Overall, 30 (45%) of 67 pups survived until the 6th week of life, but pups born in warrens located in open habitats survived significantly better than pups born in warrens located in closed habitats (50% vs. 30% of the pups born). As grass-dominated areas uphold the highest densities of domestic sheep and habitat modification due to overgrazing is a widespread process across arid Patagonia, effects on the availability of suitable breeding sites for maras are likely to occur and require further investigation.

Keywords: Arid Patagonia; Península Valdés; Cavidae; Breeding cycle; Pup survival

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1. Introduction

Maras (*Dolichotis patagonum*) are large (8–12 kg) cavid rodents endemic of Argentina, distributed throughout a range of arid lands from 28°S in the north, towards the south along the western Monte, and to the east across the Patagonian steppe until 50°S (Redford and Eisenberg, 1992). Although maras are among the most representative mammals of South America, research on this species has been scarce and discontinued. In Patagonia, pioneering work conducted by Taber (1987), Taber and MacDonald (1992a, b) has shown that maras are monogamous and breed communally, an unusual combination among mammals. In Península Valdés, Argentine Patagonia, clusters of breeding warrens were associated with relatively large clearings, usually surrounding shepherds' outstations (Taber and MacDonald, 1992b). Although isolated warrens occurred also in shrubby areas, they were frequently located in small clearings in the bush (Taber and MacDonald, 1992b).

Mara preference for open habitats at the time of breeding has been hypothesized to be a response to predation risk (Taber and MacDonald, 1992a). Functional responses are the basis of antipredatory strategies in several species, but particularly in ungulates living in open habitats (Kie, 1999). Although the mara is a rodent, its antipredatory behaviour is similar to the ungulates as it is based on early detection and escape from predators, including stotting behaviour (Dubost and Genest, 1974; Taber and MacDonald, 1992a). However, little is known about the relationship between habitat preferences and breeding success.

The identification of critical ecological variables for maras is a priority to understand their conservation needs. Although mara conservation status has been assessed as of "lower threat" 10 years ago (IUCN, 1996), human-induced habitat degradation and poaching are believed to be major processes affecting mara populations (Cabrera, 1953; Ojeda and Mares, 1982; Ojeda and Díaz, 1997). Both processes are widespread across the arid Patagonia due to overgrazing by sheep, its associated human activities and poor control of poaching by the regional Governments (Ojeda and Mares, 1982; Baldi et al., 2001). Therefore, it is urgent to provide updated information on the ecological processes relevant for mara conservation, and to identify threats for their populations. A first step in this direction is to assess how variation in habitat attributes is related to variation in survival and breeding success.

The objectives of this work were to describe habitat preferences by the mara at the time of breeding, to estimate pup production and survival, and to explore the relationship between habitat selection patterns and breeding success. If habitat selection patterns are a response to predation risk, then I expect that (1) maras build their breeding warrens in open, grass dominated sites more than expected; and (2) pup survival is higher at warrens located in open than in closed habitats.

2. Materials and methods

2.1. Study area

The study area was located in the semi-arid steppe of Península Valdés, Argentina (Fig. 1). Average annual rainfall is 230 mm with high inter-annual variation (CV 40%) (Barros and Rivero, 1982). Mean annual temperature is 12.9 °C (6 °C during July and 21 °C during January). The landscape is a plateau of gravel (plio-pleistocene age) and sand

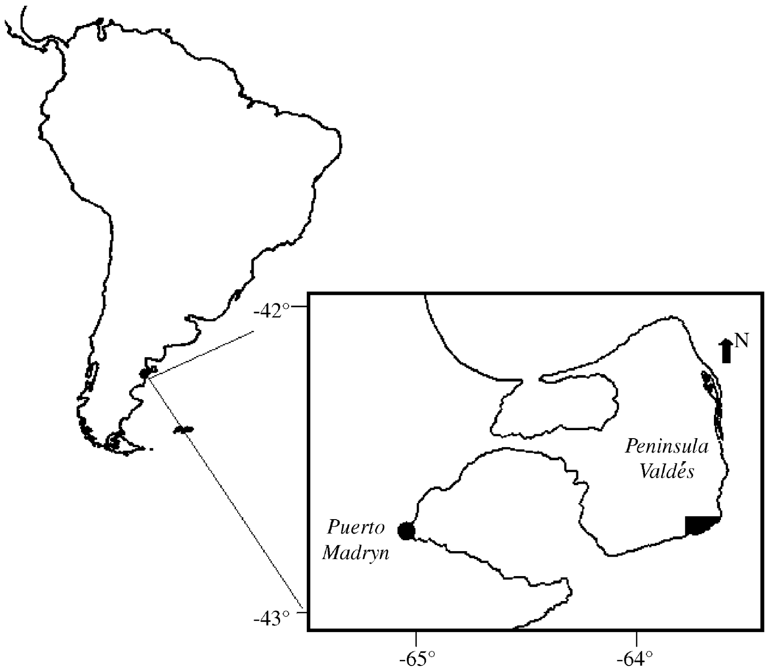

Fig. 1. Location of the study site (shaded area) in Península Valdés, Argentine Patagonia.

deposits (Haller et al., 2000), where wind is the dominant transport and depositional agent (del Valle et al., 2000).

The vegetation is characteristic of the southern Monte Phytogeographic Province, but sharing plant species with the northern Patagonian Province (León et al., 1998). The Monte Phytogeographic Province is characterized by an tall shrubland covering 40–60% of the soil surface. Whereas, foliage cover in the Patagonian Province varies from 35% to 65%, but may increase substantially in rainy periods when annual plants contribute a high proportion of the total cover (Beeskow et al., 1995). The most common shrub species in the study site are *Chuquiraga avellanedae* and *Hyalix argentea*, while the most abundant grasses are *Sipa tenuis* and *Sporobolus rigens*.

The study site was a 3800 ha private ranch where extensive sheep ranching for wool production is the main economic activity. Sheep density for the area was up to 70 animals km^{-2}, the highest estimate for eastern Patagonia (Baldi et al., 2001). Buildings are restricted to one location within the ranch, where one permanent resident lives all-year round. Also, there are two outstations comprising corrals to keep sheep temporarily after gathering for shearing or lamb marking. The ranch is divided within four paddocks by 1 m-high fences. Water for the sheep is ensured by three wind-driven pumps to artificial water-points in different locations within the ranch.

2.2. Mara surveys

Three people surveyed the ranch intensively on foot and by vehicle to search for mara burrows throughout the breeding season, from early August to late December 2000. Mara burrows were considered to be active whenever there were signs of soil recently removed at the entrance and fresh footprints or faeces close by. Geographic location for each active burrow was recorded using a Garmin 12XL portable GPS system. Also, the habitat within 50 m surrounding each burrow was classified after visual assessment of the relative proportion of different vegetation layers (Reynolds et al., 1997) such as herbs, dwarf-shrubs (woody plants < 30 cm height) and shrubs (woody plants > 30 cm height). Habitat categories were based on vegetation structure (see Table 1 for the description of habitat types) and were the same categories used during the subsequent image analysis. I named warrens either to the associations of more than one burrow separated by less than 50 m from each other, or to isolated burrows (sensu Taber, 1987).

I kept detailed records about the breeding history of 15 selected warrens intensively followed throughout the season. These warrens were selected according to their accessibility and because they were all detected early in their activity. Each warren was visited on average 16 times per week (range 5–35 times) approaching by vehicle or on foot. During every visit, I recorded the number of adults in the vicinity ($\leqslant$100 m) of each warren and defined them as breeding individuals assuming that they were all involved in reproduction. Mean number of adults per warren was calculated weekly. Total number of adults per warren was assessed after counting adults at each warren during the peak of the breeding season. At each visit, I took sufficient time (15–90 min) to record the number of pups as they came out of the burrows to meet the arriving adults and lactate. I assessed pup age by categorizing pup size relative to adult size according to Taber and MacDonald

Table 1
Description and classification of habitat types in the study area, and number of active mara warrens per habitat. Habitat structure (closed and open) was defined according to the presence/absence of tall shrubs (> 30 cm height) assumed to be obstructive to maras' sight

Habitat type	Description	Area (ha)	% Landscape	Habitat Structure	Number of warrens
Herbaceous steppe (HS)	Grass steppe of *Stipa tenuis* and *Sporobolus rigens*. Includes denudated patches of sand deposits.	943	24.8	Open habitat	13
Herbaceous and dwarf-shrub steppe (HDS)	Mosaic of grass (*S. tenuis* and *S. rigens*) and dwarf-shrub steppe of *Hyalix argentea* ($\leqslant$30 cm height).	536	14.1	Open habitat	6
Shrub and grass mosaic (SGM)	Shrub patches dominated by *Chuquiraga avellanedae* (30–80 cm height) interspersed with grass clearings of *S. tenuis*.	777	20.5	Closed habitat	5
Shrub and grass steppe (SGS)	Continuous shrub and grass steppe dominated by *Ch. avellanedae* and *S. tenuis*.	1379	36.3	Closed habitat	7
Shrub steppe (SS)	Dominated by *Schinus johnstonii, Suaeda divaricata* and *Ch. avellanedae* ($\leqslant$200 cm height)	164	4.3	Closed habitat	2

(1992a). Pups categorized as class 1 (tiny and uncoordinated, smaller than 1/4 adult size) were assumed to be less than 1-week old, class 2 pups (1/4 adult size in profile) were 2–3-weeks old, class 3 were about 1/2 adult size and 4–5-week old, while class 4 (3/4 adult size) pups, well coordinated and ran easily, were at least 6-week old (Taber and MacDonald, 1992a). I estimated the total number of pups born per warren as the number of class-1 pups seen outside the warrens throughout the season, as I did not inspect the burrows inside. Pup survival at each warren was estimated as the number of class-4 pups divided by the number of class-1 pups recorded throughout the season. At each warren, surviving pups per adult was estimated as the number of class-4 pups divided the total number of breeding adults.

2.3. Remotely sensed data

The study was supported by Landsat 5TM data of October 15, 2000 (path-row: 227-90). This was the only cloud-free, high quality image recorded during the fieldwork period. Landsat 5 TM imagery has consistently exhibited very high standards of radiometric and geometric quality (Barker and Seiferth, 1996; Helder et al., 1998). Ground truth-points randomly distributed in the area were employed to rectify the remotely sensed data and to pinpoint training sites for the classification image. Supplementary data were incorporated to improve the accuracy of the Landsat image classification: 1. Vegetation map (Bertiller et al., 1980). 2. Soil map (Rostagno, 1981) and 3. Digital Terrain Model (DTM) extracted and clipped from Stereo Panchromatic scene with grid size of 10 m (del Valle et al., 2000). Classification procedures applied on the Landsat scene included both unsupervised supervised classification, and spectral mixture analysis.

2.4. Statistical analysis

I used a goodness-of-fit test to assess whether the observed distribution of warrens across habitats was different from expected if there were no preferences by maras. Expected frequencies were obtained based on the null hypothesis that the number of warrens in each habitat type was related to the proportion of each habitat type available in relation to the total area. Statistical significance of the variables *number of burrows per warren*, *adults per warren*, *pups born per warren*, *pups born per adult*, *surviving pups per warren* and *surviving pups per adult* between open and closed habitats was analysed by randomization tests. For every case, I calculated the mean value of each variable for each habitat structure (open and closed). To test if the differences between mean values by habitat structure were significant compared to those expected at random, values were taken from pooled data and assigned to each group (open and closed habitat, $n = 8$ and 7 warrens, respectively) at random. After obtaining a simulated mean per habitat, I calculated the difference between simulated means. The simulation was run 1000 times in each case. Difference between observed means was accepted as biologically significant ($p<0.05$) if $\leqslant$than 5% of the differences between simulated means obtained after randomization were higher than the observed difference between means of open and closed habitats (Manly, 1997). For example, there were on average 1.7 more adults breeding at warrens located in open habitats than in warrens located in closed habitats. To test if this difference was significant or due to random effects, I pooled all the data on adults per warren and assigned values at random to both groups (open and closed habitats). When both groups were complete, I calculated the new "simulated" means and the difference between them. The process was iterated 1000 times. Then, if the number of simulated differences higher than 1.7 was below 50 (5% of 1000 times), the difference between adults per warren located in closed and open habitats was accepted as biologically significant.

3. Results

3.1. Breeding cycle and social context

The birth season spanned across 20 weeks from mid-winter to early summer. The first pups were born by mid-August while the last was recorded during the fourth week of December (Fig. 2). Around two-thirds (67%) of 67 pups in 15 warrens were born within six weeks, from September 22nd until October 26th, and the peak occurred during the third week in October (Fig. 2). Across the same warrens, the average number of adults per week observed nearby ($\leqslant$100 m) was associated with the distribution of births (Fig. 2; $R = 0.64$). The number of adults near the breeding warrens increased steadily from 10 early in the season, when there were five pups born, to 45 at peak season when most of the pups were born (Fig. 2), and showed a subsequent decrease as the season progressed. Overall, 64 adults were estimated to have been involved in reproduction across the 15 followed warrens.

Mean number of adults per warren was 4.26 (*range* 2–10, $n = 15$ warrens), while mean number of pups born per warren was 4.46 (*range* 0–15, $n = 15$ warrens). Thus, on average an adult pair produced two pups (*ratio pups born/adults* = 1.05; *range* 0–2.0). I did not record any pup at two out of 15 warrens that were active, although both warrens had an adult pair associated.

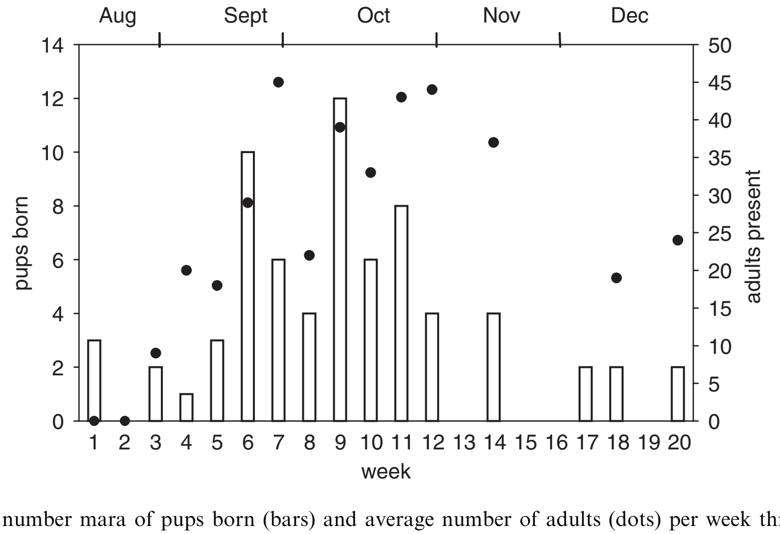

Fig. 2. Total number mara of pups born (bars) and average number of adults (dots) per week throughout the breeding season in Península Valdés, Argentine Patagonia.

Overall pup survival was 45% (30 survivors by December 28th out of 67 pups born until six weeks earlier, *range*: 0–67%, $n = 15$ warrens). Thus, on average an adult pair produced one surviving pup (*ratio surviving pups/adults* = 0.48, *range*: 0–1.0, $n = 15$ warrens).

A pair composed by a male and a female in close association was the predominant social category observed among adult maras (62.5% of 507 observations throughout the season). Less frequently, adult maras were observed alone (21.5% of the times), while associations of three (10%) or more individuals (6%) were less common.

Breeding warrens were composed for up to three burrows in close proximity, although most (70%) of 33 active warrens had a single burrow. Active warrens occurred isolated, separated by more than 500 m from any other warren, or clustered in settlements (sensu Taber and MacDonald, 1992a) of up to 6 warrens separated by less than 500 m of each other. Across the area, 11 warrens were isolated while 22 (66%) out of 33 warrens were clustered in settlements. Eight out of nine settlements had two warrens, while the remaining settlement was a cluster of six warrens near the ranch buildings.

3.2. Habitat types and breeding-site selection

I defined 5 different habitat types based on vegetation structure (Table 1, Fig. 3). Two habitat types (HS and HDS) were open habitats dominated by herbaceous or dwarf-shrub layers ($\leqslant$30 cm height) comprising 39% of the area and containing 58% of 33 active mara warrens (Table 1). I defined as closed habitats those potentially obstructive to mara's sight ($>$30 cm height) when either shrubs (SGS and SS) or a mosaic of shrubs and grass (GSM)

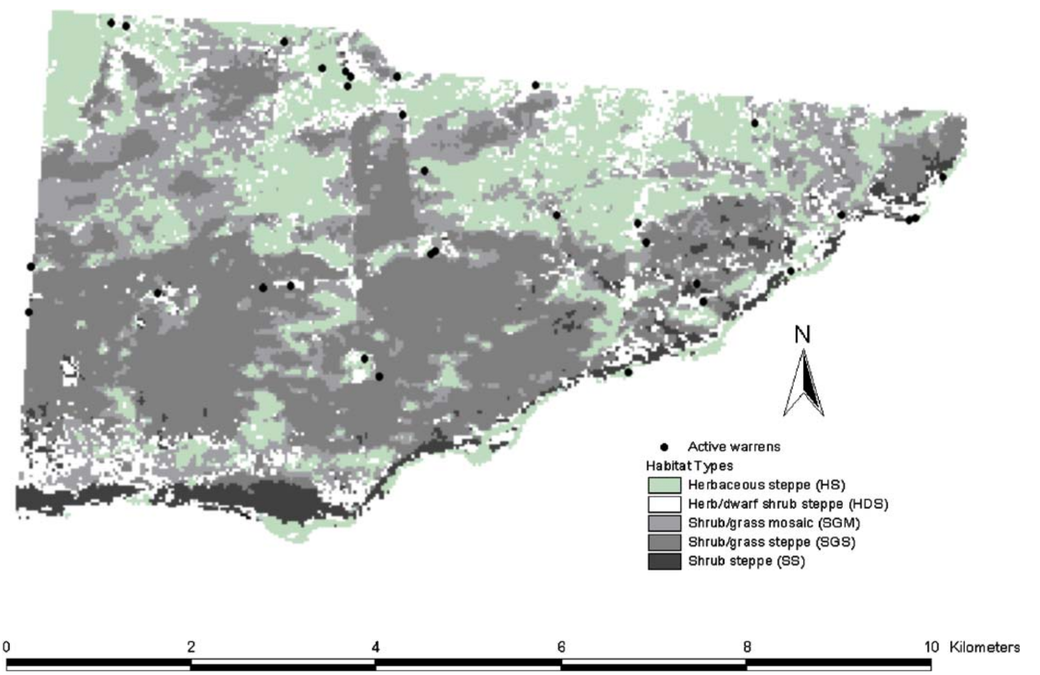

Fig. 3. Habitat types and location of mara warrens in Península Valdés, Argentine Patagonia.

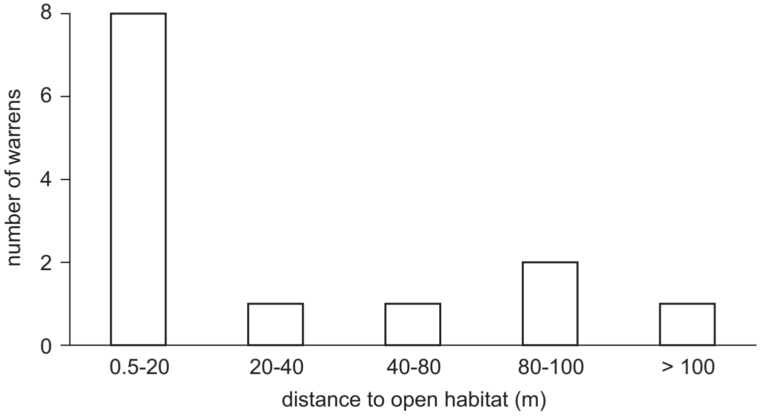

Fig. 4. Distance to open habitat from warrens located in closed habitats ($n = 14$).

Table 2
Warren composition, pup production and survival in open ($n = 8$) and closed ($n = 7$) habitats for 15 warrens intensively followed during the breeding season

	Open habitat, mean (range)	Closed habitat, mean (range)	Difference	*p*-value
Burrows per warren	1.5 (1.0–3.0)	1.1 (1.0–2.0)	0.4	0.05
Adults per warren	5.0 (2.0–10.0)	3.3 (2.0–5.0)	1.7	0.09
Pups born per warren	5.6 (2.0–15.0)	3.1 (0.0–8.0)	2.5	0.11
Pups born per adult	1.2 (0.4–2.0)	0.8 (0.0–1.6)	0.4	0.08
Surviving pups per warren	0.5 (0.3–0.7)	0.3 (0.0–0.5)	0.2	0.02
Surviving pups per adult	0.6 (0.1–1.0)	0.3 (0.0–0.8)	0.3	0.03

were predominant (Table 1). Closed habitats comprised 61% of the area and contained 42% of the active warrens (Table 1). Maras tended to build the breeding sites in open habitats significantly more than expected while avoided closed habitats where taller shrubs were common ($G = 4.5$, $p = 0.03$, df $= 1$). In addition, most (62%) of the warrens located in closed habitats were within 20 m distance from open habitats (Fig. 4). Warrens located in open habitats had on average more burrows than those in closed habitats, which typically consisted in one isolated burrow (Table 2).

3.3. Pup production in relation to breeding site

Mean pup survival per warren was significantly higher in open than in closed habitats (Table 2). This resulted in a higher proportion of surviving pups per adult breeding at warrens located in open habitats. Between habitats, there were no significant differences in the mean number of pups born per warren, mean number of breeding adults per warren and pups born per adult, although all variables tended to be higher for open habitats (Table 2). All warrens located in open habitats produced pups. Whereas, I did not record any class-1 pup at two out of seven warrens located in closed habitats. Also, the only warren where pup mortality was 100% (3 of 3 pups born) was located in closed habitat. Both the maximum number of breeding adults and the maximum number of pups born at a single warren were recorded for open habitats, doubling the maximum recorded for closed habitats (Table 2).

4. Discussion and conclusions

In Península Valdés, maras selected for open habitats to set their breeding warrens, while tended to avoid habitat types dominated by tall shrubs. Also, adult maras produced significantly more surviving pups when breeding in open habitats. Whether this is entirely due to the differences in pup mortality rate between habitats, or it is influenced by differences in natality rates (see Table 2) is still unclear, but mara selection for open habitats was associated with a higher reproductive success at the end of the breeding season.

Mara preference for open habitats has been already described across its range. In the Monte of Mendoza, western Argentina (lat: -33°, long: -68°) Kufner and Chambouleyron (1991) found that the abundance of mara faeces, as an indicator of habitat usage, was higher in denudated areas than in shrub-dominated habitats. Similar results were reported for La Pampa province (lat: -39°, long: -63°) by Rodríguez (2003). In Península Valdés, Daciuk (1974) reported that maras prefer low-shrub or sandy habitats. Taber (1987) and Taber and MacDonald (1992a) found that most warrens were located either in clearings surrounding shepherd's outstations, sand dunes or clearings in the bush. My results showed that active warrens were located in open habitats, and they occurred more than expected according to the proportion of open habitat available.

Vigilance against predators has been hypothesized to account for mara preference for open habitats at the time of breeding (Taber and MacDonald, 1992b). As adult pairs do not enter to the burrows but remain vigilant while attending the pups, vigilance can be improved in open places where vegetation structure allows for an early visual contact between maras and a potential predator (Taber, 1987; Taber and MacDonald, 1992a). Grison (*Galictis cuja*), Patagonian grey fox (*Dusicyon griseus*) and the red-backed hawk (*Buteo polysoma*) have been reported as predators of the mara in Patagonia (Taber, 1987). Unsuccessful attacks on maras by red-backed hawks were observed during my study, as well as grisons and grey fox in the vicinity of active warrens. Although the design of this study does not allow to assess the effect of predation on pup mortality, my results are consistent with the hypothesis of antipredatory strategies. Pup mortality varied between 30% and 100% across different warrens, similar to the only estimate available for Península Valdés (mortality 20–100%, Taber, 1987), but mortality was lower at warrens located in open habitats.

Although mara populations have been reported to be dwindling (Campos et al., 2001), there is a lack of information on the processes driving the decline. It is possible that habitat modification by overgrazing resulted in the loss of preferred sites by maras at the time of breeding. In northeastern Patagonia, overgrazing by sheep resulted in the reduction of total plant cover and changes in vegetation composition. At a high grazing pressure, large vegetation patches dominated by palatable grasses and forbs are replaced by smaller patches dominated by woody plants (Bisigato and Bertiller, 1997; Bertiller et al., 2002). In Punta Ninfas, an area similar to my study site where *C. avellanedae* is dominant in the shrubby layer, Beeskow et al. (1995) found that the main vegetation change associated with a gradient of utilization was the transformation of a grass steppe into a shrub steppe. High sheep densities of up to 70 animals km^{-2} have been reported for my study site while other native species such as guanacos, *Lama guanicoe*, have been extirpated as a result of interspecific competition for forage (Baldi et al., 2001). Interactions with introduced species can also involve disease transmission. Ongoing research is showing that maras are exposed to infectious disease like Jonhe'disease and toxoplasmosis due to the spreading of invasive alien species such as the European hare, *Lepus europaeus*, and the domestic sheep (Marull et al., 2004).

It is true that maras also occupy denudated areas surrounding ranch buildings, outstations or artificial waterpoints, and therefore could benefit from human activities by obtaining additional habitat (Taber, 1987; Kufner and Chambouleyron, 1991). However, patches of bare soil around those specific sites are kept clean of vegetation by human activity and livestock trampling, while overgrazing throughout the rest of the area do not result necessarily in open habitat but rather in an increase of woody-plant cover. In addition, maras in the vicinity of human dwellings are exposed to poaching and harassment by dogs. In Patagonia, although not reported by ranchers as a conflictive species, maras are poached for consumption as food (Taber, 1987). Adult maras are killed with guns or wire snares and pups are caught in nets when coming outside the dens (Marull, personal communication).

The effects of land-use practices on habitat structure, and the interactions with introduced species and humans are likely to affect maras' habitat selection patterns and subsequent breeding success and survival. Therefore, it is crucial to develop studies to identify the factors affecting the local population dynamics across the range of the mara, in order to implement conservation-oriented management and prevent the demise of this endemic mammal.

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