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Macro- and micro-habitat selection of small rodents and their predation risk perception under a novel invasive predator at the southern end of the Americas

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Abstract

Invasive predators are responsible for the extinction of numerous island species worldwide. The naïve prey hypothesis suggests that the lack of co-evolutionary history between native prey and introduced predators results in the absence of behavioral responses to avoid predation. The lack of terrestrial mammal predators is a core feature of islands at the southern end of the Americas. Recently, however, the American mink (*Neovison vison*) established as a novel terrestrial predator, where rodents became a main portion of its diet. Here, we investigated on Navarino Island, Chile, macro- and micro-habitat selection of small rodents using Sherman traps. Additionally, we experimentally tested behavioral responses of small rodents to indirect cues of native raptorial predation risk (vegetation cover) and direct cues of novel mink predation risk (gland odor) using Sherman traps and foraging trays (giving-up density (GUD)). At the macro-habitat level, we detected native rodents of the species *Abrothrix xanthorhinus* and *Oligoryzomys longicaudatus* and the exotic *Mus musculus*. In general, rodents preferred scrubland habitats. At the micro-habitat level, we only captured individuals of *A. xanthorhinus*. They preferred covered habitats with tall vegetation. GUD increased in opened areas (riskier for raptorial predation) regardless of the presence or not of mink odor. These results suggest that *A. xanthorhinus* can perceive predation risk by raptors, but not by mink, results that accord with the hypothesis that co-evolutionary history is important for rodents to develop antipredator behavior. Given that these rodents represent an important proportion of mink diet, the low abundances together with the apparent lack of antipredator response raise conservation concerns for the small rodent populations inhabiting the southernmost island ecosystems of the Americas.

Keywords American mink · Cape Horn · Giving-up densities · Habitat use · Invasive species

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Introduction

The introduction of invasive predators has caused the extinction of numerous island species worldwide (Doherty et al. 2016). At least part of these extinctions might have resulted from the lack of co-evolutionary history between prey and novel predators (Strauss et al. 2006). The "naïve prey" hypothesis proposes that the mismatch of evolutionary history between native prey and introduced predators results in high rates of predation because prey lack behavioral responses to avoid predation (Cox and Lima 2006; Sih et al. 2010).

Rodents are prey of many vertebrate predators in terrestrial ecosystems, and the evidence suggests that rodents can recognize predation risk cues and alter their foraging behavior in response. Rodents respond to indirect cues of predation risk, for example preferring to forage under vegetation cover where avian predation risk is lower (Kotler et al. 1991; Orrock 2004),

avoiding forest edge where predation risk is higher (Morris and Davidson 2000), or reducing foraging activity as a response to high temperatures that increase snake activity (Falcy and Danielson 2013). In addition, rodents can respond to direct cues of predation risk, such as the odor of terrestrial predators, altering their behavior to avoid predation (Jędrzejewski et al. 1993; Kats and Dill 1998; Apfelbach et al. 2005; Staples 2010). The ability to respond to predator cues, however, may depend on the co-evolutionary history of prey species with their predators (Apfelbach et al. 2005; Blumstein 2006; Sih et al. 2010). For instance, odors from a sympatric predator are more effective in triggering rodent antipredator behavior than the odor of novel predators (Apfelbach et al. 2005) and a lack of response has been recorded in rodent populations of islands where native mammal predators have been absent (Orrock 2010). While some species adapt to novel predatory pressures (Langkilde et al. 2017), others fail to develop antipredator behaviors, and in these occasions, the high predation rate may result in local extinctions (Clavero and García-Berthou 2005; Strauss et al. 2006; Carthey and Banks 2012).

At the southernmost extreme of the Americas, in southern Chile, the Cape Horn Biosphere Reserve (CHBR) is located. It protects the Magellanic Sub-Antarctic forest ecoregion (Rozzi and Jiménez 2014). The area encompasses large archipelagoes where only a few species of native small rodents occur. Within the CHBR, Navarino Island is one large island that was free of terrestrial mammalian predators (Rozzi and Jiménez 2014). On this island, only two native rodents are present, *Abrothrix xanthorhinus* and *Oligoryzomys longicaudatus*, and only three raptor species are relatively common, *Milvago chimango*, *Caracara plancus*, and *Glaucidium nana* (Ippi et al. 2009), providing a potential constant diurnal and nocturnal predatory pressure to the populations of small rodents. At the end of the 1990s, however, the American mink (*Neovison vison*; hereafter, mink), a semi-aquatic mammalian predator, established on Navarino Island (Rozzi and Sherriffs 2003).

The mink was introduced into Tierra del Fuego Island, Argentina, as a result of accidental and deliberate releases from fur farms (Jaksic et al. 2002). It was first recorded on Navarino Island, on the other side of the Beagle Channel, in 2001, and since then, mink have colonized an increasing number of islands across the CHBR (Rozzi and Sherriffs 2003; Anderson et al. 2006; Crego et al. 2015). On Navarino Island, small mammals became a significant portion of mink's diet (Schüttler et al. 2008; Ibarra et al. 2009; Crego et al. 2016). In addition to having little information about the ecology of small rodents on the area and the ecological role they may play in the native ecosystems, one recent study showed relative abundances of native small rodent species up to ten times lower than relative abundances in the beginning of 2000s (Crego et al. 2014), rising conservation concerns.

To predict if native species extinctions are likely or not to occur in the near future, more research is needed to clearly understand how native species respond to invasions (Sax and Gaines 2008). Besides the number of invasive species in the Cape Horn region, most studies conducted were merely descriptive, with a lack of experimental research to elucidate ecological mechanisms (Quiroz et al. 2009; Valenzuela et al. 2014). In this study, we aimed to better understand the ecology of native small rodents and to test the naïve prey hypothesis that could explain the small rodent's population decline, given the high predation pressure that the mink is imposing. Specifically, we evaluated (1) macro- and (2) micro-habitat selection of small rodents and (3) whether small rodents could recognize indirect cues of predation risk from native predators (exposed or sheltered habitats) and direct cues of the novel mink predator (mink odor). Because the mink represents a novel terrestrial predator on Navarino Island, we predicted that small rodents will not respond to mink odor as a direct cue of predation risk. Conversely, given the co-evolutionary history between rodents and raptors, we predicted that small rodents will prefer to forage in covered habitat, using vegetation cover as an indirect cue of raptorial predation risk.

Materials and methods

Study area and system

Navarino Island (68° W, 55° S, ca. 2,500 km²) is located at the southern extreme of South America within the CHBR (Fig. 1). The island is largely covered by evergreen forests dominated by *Nothofagus betuloides* and *Drimys winteri*, deciduous forests dominated by *Nothofagus pumilio* and *Nothofagus antarctica*, and extensive areas of mixed evergreen and deciduous forests co-dominated by the former species. Forest cover along the north side of the island can be divided into primary forests, i.e., forest with no human intervention, and secondary forests, i.e., patches of forest recovering from forest logging and clearing (Rozzi and Jiménez 2014). Forests are embedded in the Magellanic moorland complex, composed by a matrix of peatlands and meadows (Rozzi et al. 2006). Another important habitat is the scrublands, dominated by *Chiliotrichum diffusum*, *Gaultheria mucronata*, *Baccharis* spp., and *Berberis buxifolia* (Rozzi and Jiménez 2014). The climate is oceanic and cold, with a mean annual temperature of 6 ± 5 °C and uniform precipitation all year long, with an annual average of 467.3 mm (Rozzi and Jiménez 2014).

The two small rodent species that inhabit Navarino Island, *A. xanthorhinus* and *O. longicaudatus*, are also the most common species across the CHBR (Anderson et al. 2006). Native predators include both nocturnal and diurnal raptors. In addition to the common raptors *Milvago chimango*, *Caracara plancus*, and *Glaucidium nana*, records include the following:
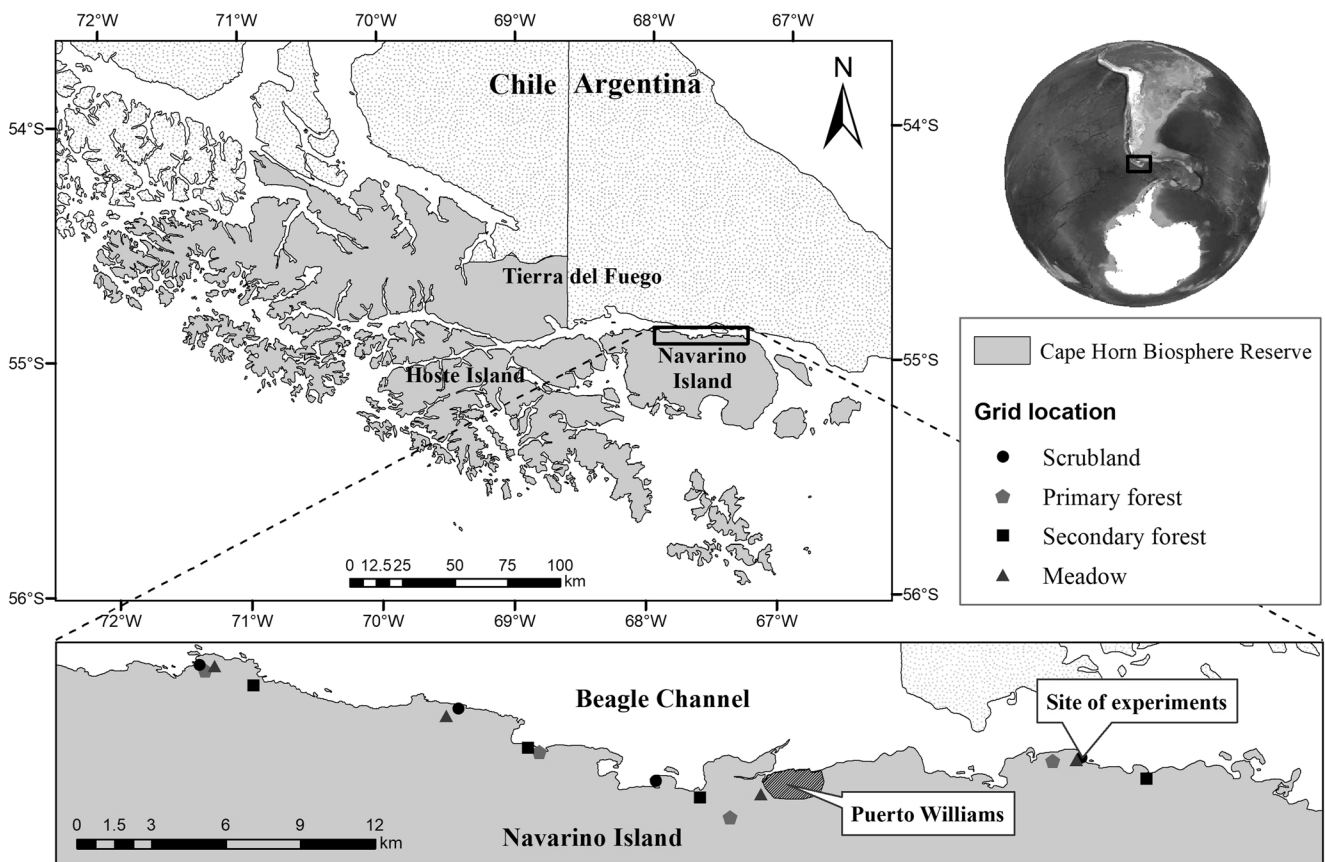
Fig. 1 The study area was located on Navarino Island, Chile. Sixteen grids were placed along the northern slope of the island, in four main macro-habitat types, during austral summer (Feb.–Mar.) 2014 and 2015 and austral spring (Oct.–Nov.) 2014 and eight grids during austral winter (Jun.–Jul.) 2014. Additionally, micro-habitat selection and experiments to assess rodent predation risk were conducted on the site marked as "Site of experiments" during September 2014

Asio flammeus, *Bubo magellanicus*, *Strix rufipes*, *Tyto alba*, *Accipiter bicolor*, *Buteo ventralis*, *Geranoaetus melanoleucus*, *Falco peregrinus*, *Falco femoralis*, *Falco sparverius*, and *Phalcoboenus albogularis* (Rozzi et al. 2006). Only on Tierra del Fuego and Hoste Island within the CHBR, a terrestrial native mammalian predator, the Culpeo fox (*Lycalopex culpaeus*), has been recorded (Sielfeld 1977; Anderson et al. 2006). Hence, most islands of the CHBR, including Navarino Island, were free of terrestrial predators. There is no information about the historical distribution of rodents in this area to know for how long these two native species have been isolated from foxes. However, the period of isolation may date back to the last glaciation, approximately 10,000 years ago, when the Beagle Channel started to form (Rabassa et al. 2000).

Macro-habitat selection

We estimated the abundance of small rodents using 16 grids of 25 Sherman traps in a 5×5 grid configuration (10-m spacing) during austral summer (Feb.–Mar.) 2014 and 2015 and austral spring (Oct.–Nov.) 2014 and using 8 grids during austral

winter (Jun.–Jul.) 2014. We identified four areas in which we had access along the northern slope of Navarino Island and placed four grids per habitat type: scrublands, primary forest (unperturbed forest), secondary forest (perturbed forest), and meadows (Fig. 1). Traps were baited with rolled oats and were active for 5 days and five nights. We placed a ball of lichens inside the traps as nesting/insulating material. We checked traps early in the morning right after sunrise. All rodents were ear-tagged and released.

Micro-habitat selection

Between the 10 and 15 of September 2014, we live-trapped small rodents using 105 Sherman traps in a 7×15 grid configuration (10-m spacing). The grid was placed in a large patch of scrubland where we previously documented (summer and winter) a high abundance of rodents to obtain enough captures to estimate micro-habitat selection. Traps were baited with rolled oats and were active for 5 days and five nights. We placed a ball of lichens inside the traps as nesting/insulating material. We checked traps twice a day: early in the mornings, right after sunrise, and late in the afternoons approximately

2 hours before sunset. All rodents were ear-tagged and released.

At each trap location on the last day of trap checking, we measured vegetation using a square frame of 1 m² centered at each trap. We estimated vegetation cover of shrubs (*Berberis* ssp., *Gaultheria mucronata*, and *C. diffusum*), grasses, and litter to the nearest 5%. We also recorded the closest lineal distance from each trap entrance to the border of a nearest shrub of > 50 cm of crown diameter. Finally, we measured vegetation height at the center and each corner of the frame and estimated the average vegetation height.

Experimentally testing rodent response to mink odor

To assess whether small rodents perceive mink odor as a cue of predation risk, we conducted two different experiments. The first experiment was conducted 3 days after we finished the micro-habitat selection trapping. We set 20 stations, 30 m apart to avoid the odor in one station affecting a near station. Each station consisted of four Sherman traps, two placed under vegetation cover (shrubs) and two in open habitat, 1 m from the closest shrub. We randomly applied mink gland odor (commercial mink gland extract) to all traps in 10 of the 20 stations and tap water to the traps of the other 10 stations as control. Odor or tap water were applied to a cotton ball, which were placed inside a plastic tube and fixed to the ground at 2–3 cm from the trap door, ensuring that the cotton was exposed to the outside of the tube. The design consisted then in four categories: open mink odor, covered mink odor, open control, and covered control. Traps were active during five nights and baited with rolled oats. We placed a ball of lichens inside the traps as nesting/insulating material. Traps were checked every morning, and if successful, they were replaced with a new, clean trap, and new insulation material to avoid rodent odor affecting the treatment. Rodents were ear-tagged and released. The design attempted to assess predation risk from raptors by assessing the proportions of captures in traps under the vegetation cover and in the open and, likewise, to assess predation risk from mink with the odor/no odor trap sets.

The second experiment was based on the optimal foraging theory (MacArthur and Pianka 1966), which evaluates the perception of predation risk on food trade-off. If an animal perceives predation risk, it should be a point in time when the animal will leave a source of food when the cost of predation becomes higher than the benefits obtained from harvesting the food resource (Brown 1988; Altendorf et al. 2001). This method has been widely used to study foraging behavior in granivorous rodents (Brown 1988; Orrock 2004; Mahlaba et al. 2017). We also investigated predation risk perception by small rodents via quantifying giving-up densities (GUDs) and comparing among treatments: open mink odor, covered mink odor, open control, and covered control. Following the previous design, we used the 20 stations with the same

configuration to avoid odor from the previous experiment affecting the second. We used trays that consisted of 11 × 11 × 9 cm plastic boxes, with two opposite, circular entrances of 2.5 cm in diameter on the sides, an entrance small enough to allow small rodents to enter but to exclude birds (Fig. 2). At each station, one tray was set under vegetation cover and the other in open habitat, 1 m from the closest shrub (a total of 40 trays in 20 stations). Similarly, at 10 stations, we added mink odor at each entrance of each tray and tap water to the trays of the other 10 stations, as explained before. Each tray was filled with 600 cm³ of fine soil and 20 g of dried wheat seeds. After three nights, remaining seeds were sieved from the soil and collected. Trays were reset with 20 g of dried seeds. This process was sequentially repeated three times. Ants or termites are absent on Navarino Island, and we made sure that no insects that could have removed seeds were present in the tray at the time of collecting the remaining seeds. At the laboratory, we dried seeds in the stove for 5 h at 60 °C and weighed them to the nearest 0.1 g. Wheat seeds were also dried in the same manner before setting them in the trays. After we weighed the remaining seeds, we calculated GUD as the proportion of seeds that remained from the original 20 g. For the analysis, we only used trays in which rodent activity was evident. Five days before beginning the odor treatment, we set the trays in place and let rodents feed at leisure with no treatment to become accustomed.

Statistical analysis

We estimated the relative abundance of rodents per season and per macro-habitat as the minimal number known alive (MNKA), because of the low abundances documented (Krebs 1966). Given the low abundance of rodents recorded, we summed the MNKA per macro-habitat across all seasons to test for macro-habitat selection using the Manly's selection index (proportion of use/proportion available; Manly et al. 2002). This index indicates the level of preference, given the availability under the assumption of independence among individuals and that all individuals are selecting the habitat in the same way. We used 25% available for each macro-habitat type, given that we had the same number of traps per each of the four habitat types. For the index, numbers > 1 indicate that the habitat type is selected and numbers < 1 indicate that it is avoided (Manly et al. 2002). We estimated selection at the population level using the design I selection function (see Manly et al., 2002) in the adehabitatHS package within R programing language (R Development Core Team 2016).

To analyze micro-habitat selection, we used a principal component analysis (PCA). We organized the data as a matrix of traps (rows) versus vegetation and captures (columns). We run the PCA using the vegetation information as active variables (SH: shrub cover; GS: grass cover; L: litter cover; VH: vegetation height; DS: distance of trap from the nearest shrub)

Fig. 2 Feeding trays used to assess giving-up density on *Abrothrix xanthorhinus* during September 2014 on Navarino Island, Chile. The picture on the left shows an example of a tray set under shrub cover, and the picture on the right shows a tray set on an open habitat. Odor from mink gland and water as control were placed at the two opposite entrances of each tray

and traps with captures and traps with no captures as illustrative. Second, we used the Wilcoxon rank-sum test to assess whether vegetation measures were significantly different between traps with captures and traps with no captures.

For the first experiment, we estimated the mean number of captures per night per treatment, omitting recaptured animals to maintain independence. We tested for significant differences of mean captures per night between mink odor versus control using the Wilcoxon rank-sum test, omitting the traps placed on open habitat, given that all captures happened in traps placed under vegetation cover. For the second experiment, we tested for significant differences in GUD among the four treatments (fixed effect) using a mixed model ANOVA. To account for autocorrelation, we specified time (repeated measures on the same feeding tray) and site (feeding tray) as random effects. We checked for model assumptions, normality of residuals, and homogeneity of variances, using visual inspection of residuals. We performed a Tukey's post hoc test for treatment comparisons. We used R programing language for statistical analysis (R Development Core Team 2016). Specifically, we fit the mixed model ANOVA and performed Tukey's test using packages nlme (Pinheiro et al. 2017) and multicom (Hothorn et al. 2008), respectively.

Data availability The datasets analyzed during the current study are available in the Mendeley repository (doi: https://doi.org/10.17632/mz2tsmhhzm.1).

Results

Macro-habitat selection

During summer 2014, in total, we live-captured 20 individuals of *A. xanthorhinus*, 1 of *O. longicaudatus*, and 4 of *Mus musculus*; during winter 2014, 7 individuals of *A. xanthorhinus* and 4 of *M. musculus*; during spring 2014, 4 individuals of *A. xanthorhinus*, 1 individual of *O. longicaudatus*, and 1 of *M. musculus*; and during summer 2015, 6 individuals of *A. xanthorhinus*, 4 of *O. longicaudatus*, and 7 of *M. musculus*. Mean MNKA per macro-habitat type

and per species are shown in Table 1. For *O. longicaudatus*, abundance was too low (six individuals in total) to calculate Manly's selection index. Summing up the MNKA per season for the entire year, we found that *A. xanthorhinus* selected scrublands and avoided primary forest, secondary forest, and meadows (Table 1). *M. musculus* selected scrublands, used meadows as expected, and was not detected on primary or secondary forests (Table 1).

Micro-habitat selection

For micro-habitat analysis, we totalized 39 captures throughout the 5 days and five nights of trapping. These captures corresponded to nine different adult individuals of *A. xanthorhinus*. Regarding temporal patterns of activity, 70% of the captures occurred during the night trapping period, whereas the other 30% occurred during the day period, suggesting that *A. xanthorhinus* exhibited both nocturnal and diurnal activities. Regarding spatial patterns of activity, the first two axes of the PCA explained 87.6% of the variation (PC1 = 57.7%, PC2 = 29.9%). The PCA analysis shows that capture of individuals was linked to higher shrub cover and taller vegetation (Fig. 3). Similarly, when comparing traps with captures versus traps with no captures, capture of individuals was related to higher shrub cover and lower grass cover, higher vegetation, and traps closer to shrubs (Table 2). Litter cover did not show significant differences (Table 2).

Rodent response to mink odor

During the first experiment, we live-trapped 10 adult individuals of *A. xanthorhinus*, 7 off them were previously trapped during the micro-habitat selection trapping and 3 were new individuals. Captures occurred only on covered traps, and there was no significant difference in the number of captures between mink odor and the control treatments ($W = 49.5$, p value = 1; Fig. 4a).

For the second experiment, we examined 120 observations taken from 40 trays for a total period of 9 days (three surveys). We detected foraging activity in 62.5% of the observations

Table 1 Abundance of three rodent species (*Abrothrix xanthorhinus*, *Oligoryzomys longicaudatus*, *Mus musculus*) measured as the mean minimal number known alive (± 1 SD) during austral summer (Feb.–Mar.) 2014 and 2015, austral winter (Jun.–Jul.) 2014, and austral spring (Oct.–Nov.) 2014, and Manly's selection index (± 1 SD) calculated for the four seasons combined for four different macro-habitats on Navarino Island, Chile

Habitat	Summer 2014 (2000 trap nights)			Winter 2014 (1000 trap nights)			Spring 2014 (2000 trap nights)
	A. xanthorhinus	*O. longicaudatus*	*M. musculus*	*A. xanthorhinus*	*O. longicaudatus*	*M. musculus*	*A. xanthorhinus*
Scrubland	4.00 (6.73)	0.25 (0.50)	1.00 (2.00)	2.50 (2.12)	0.00 (0.00)	1 .50 (2.12)	1.00 (2.00)
Primary forest	0.50 (0.57)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Secondary forest	0.25 (0.50)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Meadow	0.25 (0.50)	0.00 (0.00)	0.00 (0.00)	1.00 (1.41)	0.00 (0.00)	0.50 (0.70)	0.00 (0.00)

Habitat	Spring 2014 (2000 trap nights)		Summer 2015 (2000 trap nights)			Manly's selection index for all seasons combined		
	O. longicaudatus	*M. musculus*	*A. xanthorhinus*	*O. longicaudatus*	*M. musculus*	*A. xanthorhinus*	*O. longicaudatus*	*M. musculus*
Scrubland	0.00 (0.00)	0.25 (0.50)	1.00 (1.41)	0.50 (1.00)	1.25 (2.25)	3.19 (0.27)	–	3.25 (0.39)
Primary forest	0.25 (0.50)	0.00 (0.00)	0.25 (0.50)	0.00 (0.00)	0.00 (0.00)	0.32 (0.18)	–	0.00 (0.00)
Secondary forest	0.00 (0.00)	0.00 (0.00)	0.25 (0.50)	0.25 (0.50)	0.00 (0.00)	0.22 (0.15)	–	0.00 (0.00)
Meadow	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.25 (0.50)	0.50 (1.00)	0.32 (0.18)	–	0.75 (0.39)

For the index, numbers > 1 indicate that the habitat type is selected and numbers < 1 indicate that it is avoided. For summers and springs, there were four grids per habitat type, whereas for winter, there were two grids per habitat

which occurred across 28 different trays. The amount of seeds left on the feeding trays by rodents (GUD) was affected by treatments ($F_{3,32} = 36.73$, $p < 0.0001$). Tukey's post hoc tests showed that GUD was significantly lower for covered trays compared to open trays regardless of trays having mink odor or water as control (covered control vs. open control: $Z = 5.3$, $p < 0.0001$; covered control vs. open mink: $Z = 4.7$, $p < 0.0001$; covered mink vs. open control: $Z = 6.3$, $p < 0.0001$; covered mink vs. open mink: $Z = 8.9$, $p < 0.0001$; Fig. 4b); however, there were no significant differences between mink odor and the control in covered or open trays (covered control vs. covered mink: $Z = -2.1$, $p = 0.14$; open control vs. open mink: $Z = 0.4$, $p = 0.97$; Fig. 4b).

Discussion

In this study, we documented the presence of two native rodent species (*A. xanthorhinus* and *O. longicaudatus*) on Navarino Island in low abundances, and for the first time, we consistently recorded the introduced *M. musculus* outside the urban area in natural habitats. The low density of the native species is in accordance with recent studies on Navarino Island (Schüttler et al. 2008; Crego et al. 2014). Moreover, the results of the experiments add evidence to the naïve

hypothesis, suggesting that *A. xanthorhinus* cannot perceive mink as a predator threat.

In general, rodents of all three species were more abundant on the scrubland habitat. The low abundance of *O. longicaudatus* impeded us from assessing habitat preferences. *A. xanthorhinus* was the dominant species in the small rodent community of Navarino Island, similar to that described for Tierra del Fuego (Lozada et al. 1996), preferring scrublands and avoiding forests and meadows. The preference of this species for scrublands is similar to other regions in northern Patagonia (Lozada et al. 1996). Individuals of the exotic *M. musculus* also preferred scrublands. However, 67% of all captures of *A. xanthorhinus* occurred in one of the 16 grids and all individuals of *M. musculus* were captured in two grids located close to the town of Puerto Williams. For this reason, results of macro-habitat selection in this study should be taken with caution.

For the analysis of micro-habitat selection and the experiments, we only captured individuals of *A. xanthorhinus*. They were captured during day and night periods, suggesting that they were active throughout the daily cycle, similar to other populations of *A. xanthorhinus* in southern Patagonia (Tapia 1995). Individuals preferred high cover of shrubs and tall vegetation, avoiding open areas. These results are in line with studies in northern Patagonia, where *A. xanthorhinus* prefers habitats with abundant vegetation cover (Lozada et al. 1996, 2000). The use of high covered areas by *A. xanthorhinus* for
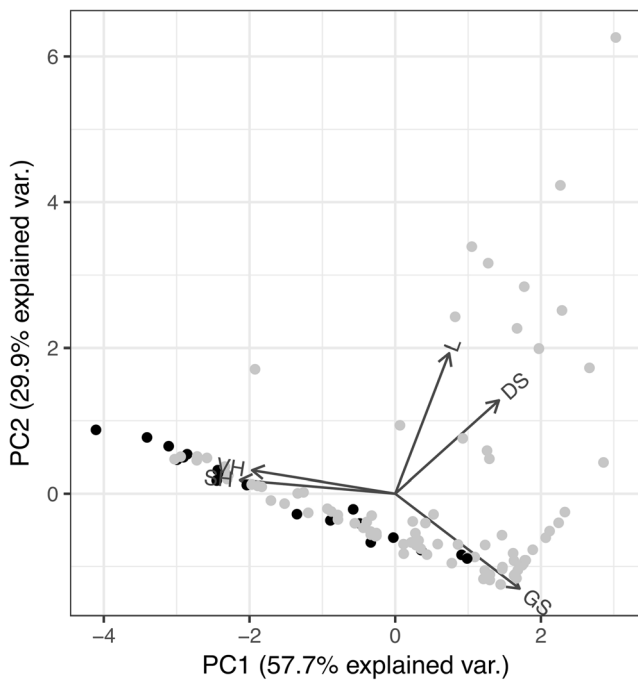
Fig. 3 Principal component analysis based on microhabitat variables associated to the capture of *Abrothrix xanthorhinus* during September 2014 on Navarino Island, Chile. Gray dots indicate traps with no captures, and black dots indicate traps with captures during the 5-day and five-night sampling period. SH shrub cover, GS grass cover, L litter cover, VH vegetation height, DS distance of trap to nearest shrub

Fig. 4 a Mean number of captures of *Abrothrix xanthorhinus* ($\pm$ 1 SE) per treatment. **b** Mean giving-up density (GUD) measured as the proportion of seeds left ($\pm$ 1 SE) in foraging trays by *A. xanthorhinus* per treatment during September 2014 on Navarino Island, Chile. Different letters indicate significant differences after Tukey's test ($p < 0.0001$). The four treatments correspond to covered control, with traps or trays set in sheltered (shrub cover) habitat and with water as control; covered mink, with traps or trays set in sheltered (shrub cover) habitat and with mink odor; open control, with traps or trays set in exposed habitats (1 m from the nearest shrub) and with water as control; and open mink, with traps or trays set in exposed habitats (1 m from the nearest shrub) and with mink odor. For each treatment category in **a**, $n = 10$. For the GUD: covered control, $n = 19$; covered mink, $n = 20$; open control, $n = 17$; and open mink, $n = 19$
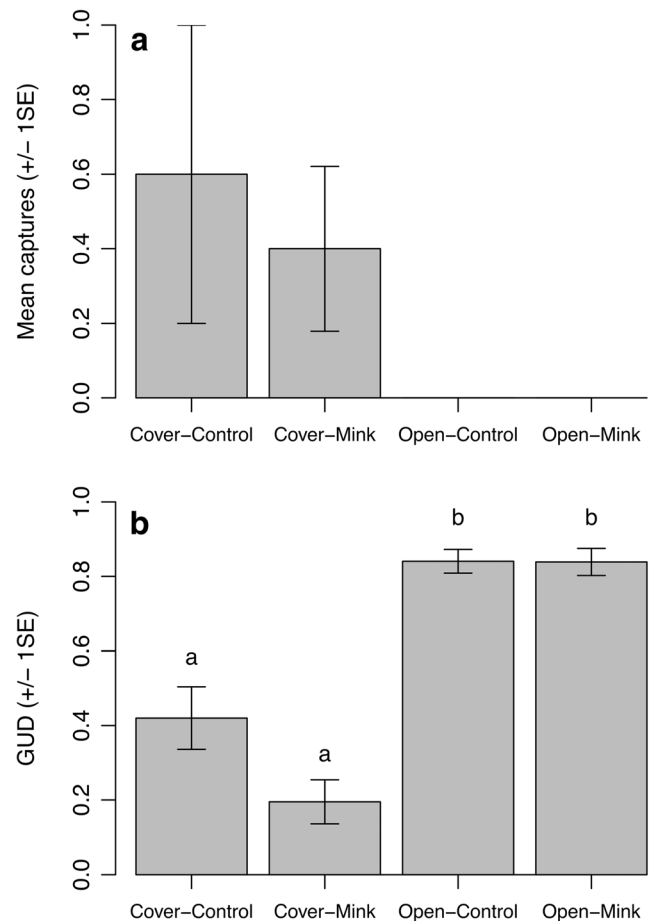
daily activity was further supported by both of our experiments. Rodents were only trapped on covered traps, and GUD was close to 100% in open areas, showing they barely forage in the absence of vegetation cover. The use of vegetation as an indirect cue of low predation risk by individuals of *A. xanthorhinus* is in accordance with the co-evolution of rodents with raptorial predators (Kotler et al. 1991; Orrock 2004). This is also in accordance with previous research that shows that indirect cues are effective indicators of predation risk for small rodents (Orrock 2004).

In contrast to results based on vegetation cover, *A. xanthorhinus* did not show changes in foraging behavior when exposed to the mink odor. These results are in accordance with research that shows similar lack of rodent responses to novel terrestrial predators (Orrock 2010), supporting the thesis that short periods of time do not allow prey to develop antipredatory behavior (Blumstein 2006;

Orrock 2010; Kovacs et al. 2012). Identification of new predators require experience (Griffin et al. 2001), and the time needed to adapt to a novel predator may be in the order of

Table 2 Vegetation and distance to shrub (means $\pm$ 1 SE) relationships between trap sites with and without captures of *Abrothrix xanthorhinus* on Navarino Island, Chile

	Traps with captures ($n = 18$)	Trap with no captures ($n = 87$)	p value
Shrub (%)	60.83 $\pm$ 6.63	28.79 $\pm$ 2.96	0.00009
Grass (%)	39.16 $\pm$ 6.63	63.73 $\pm$ 3.11	0.00248
Litter (%)	0.00 $\pm$ 0.00	5.00 $\pm$ 1.32	0.06000
Vegetation height (cm)	39.32 $\pm$ 7.45	15.75 $\pm$ 25.01	0.00014
Distance to shrub (cm)	19.38 $\pm$ 5.73	157.14 $\pm$ 1.62	0.00056

The p values indicate whether differences are significant ($p < 0.05$, Wilcoxon rank-sum tests)

thousands of years, as shown in individuals of a native Australian marsupial that can recognize dogs (*Canis lupus familiaris*) as predators that are close relative to the dingoes (*Canis lupus dingo*) introduced 4000 years ago, but do not respond to cats (*Felis catus*) that were more recently introduced (Carthey and Banks 2012). Additionally, prey naïveté toward a novel predator may be reduced if the prey co-existed with ecological analogue predators (Blumstein 2006; Cox and Lima 2006). On Navarino Island, however, small rodents have been probably isolated from other terrestrial predators (e.g., foxes) for several thousands of years, since the formation of the Beagle Channel (Rabassa et al. 2000). Additionally, small rodents have co-existed with the invasive mink for just near 20 years, probably not enough time of co-existence for rodents to develop antipredator behavior. However, evidence shows rapid adaptations in species of lizards, fish, and amphibians to novel predators (Langkilde et al. 2017). The lack of response to mink odor could be explained by rodents being unable to recognize mink gland odor when they can recognize other mink cues as predation risk. For instance, fur-derived odors have been shown to be a more effective cue of predation risk for mammalian prey than predator's fecal, urine, or gland odors (Apfelbach et al. 2005). Further research will be needed to elucidate this different alternative explanation to the lack of response to mink gland odor and to assess whether rodents respond to odor of Culpeo foxes.

The lack of antipredator response to the mink together with the fact that small rodents are an important prey item for the mink population (Schüttler et al. 2008; Ibarra et al. 2009; Crego et al. 2016) may explain the decrease in rodent abundances in the area as compared to the early 2000s, when the mink was just establishing on Navarino Island (Crego et al. 2014). Schüttler et al. (2008) suggested that mink predation was not a threat to native rodents. However, more recent studies found that mink are still preying heavily on small rodents in spite of their current low abundances (Crego et al. 2016). Declines in other rodent species, such as several species of voles, have been documented in Europe as a consequence of mink predatory pressure (Macdonald et al. 2002; Bonesi and Palazon 2007). However, in addition to top-down forces, rodent populations are controlled by bottom-up forces (Meserve et al. 2003) and periods of high productivity can trigger small mammal population outbreaks (Jiménez et al. 1992). With small rodents suffering high rates of mink predation, if they are naïve to mink presence, as suggested by our results, the fitness cost suffered in the long term can potentially bring the species to local extinction despite the productivity of the ecosystem (Clavero and García-Berthou 2005; Strauss et al. 2006; Carthey and Banks 2012).

This study provides the first data on habitat selection of native rodent species in the CHBR. Despite the small abundances documented that limit the scope of this study, results are in line with the thesis that co-evolutionary history is important for rodents to develop antipredator behavior. Such potential lack of antipredator behavior toward an invasive novel predator rises concerns for the conservation of the native small rodent populations and the potential loss of their ecological functions in the southernmost island ecosystems of the Americas. More research is urgent to monitor rodent populations in the long term, further testing of rodent antipredator responses to mink, and to better understand mink effects on small rodent populations and the indirect effect on the ecosystems of the southernmost islands of the Americas.

Compliance with ethical standards

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All animal capture and handling procedures followed guidelines set by the American Society of Mammalogists (Sikes and Gannon 2011). Permits to capture rodents were given by the Livestock and Agricultural Bureau, Chile (Servicio Agrícola y Ganadero, Resolution Nos. 6518/2013 and 8547/2014).

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