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Evaluation of neophobia and its potential impact upon predator control techniques: A study on two sympatric foxes in southern Patagonia

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ABSTRACT

An alternative approach to increase the efficiency of predator control and selectivity is to consider the natural behavioural repertoire of the target species and how such behaviours may increase their vulnerability. Neophobia, or the hesitancy to approach a novel food item, object, or place, is an important factor influencing the investigative behaviour of animals, and its incorporation to predator control techniques may help to reduce losses of livestock to predators. In this study, we simultaneously evaluated the existence and intensity of neophobic responses in two sympatric fox species, the Culpeo (*Pseudalopex culpaeus*) and the Grey (*P. griseus*) foxes in southern Patagonia, Argentina. For this purpose, we used bait stations to compare fox behavioural responses in the absence (pre-treatment), presence (treatment) and removal (post-treatment) of a novel stimulus, which consisted of an orange PVC-traffic cone. Both fox species showed a neophobic response: bait-station visitation rates decreased ($P = 0.005$ and $P = 0.048$, for Culpeo and Grey foxes, respectively) in the presence of the novel object. The intensity of the response differed between species being higher for Culpeo foxes (approximately 80% of reduction in visitation rate during treatment for Culpeo foxes vs. 10% for Grey foxes). However, the bait-station visitation pattern after novel object removal indicated that animals probably increased exploration of the station. The high level of neophobia achieved by the Culpeo fox, together with an increase in post-treatment site exploration, suggests that behavioural manipulations (reduction of neophobia and its consequent increase in risk taking) could improve selective and efficient fox control in rural areas where livestock production is a major economic activity.

1. Introduction

Behavioural responses of animals to novelty are a function of the discrepancy between past experience and present sensation (Corey, 1978). These responses may occur when animals are confronted with new stimuli such as a novel food item, object, or place (Greenberg, 1990a, 1990b; Harris and Knowlton, 2001). Animals can be attracted to (neophilic), deterred by (neophobic), or indifferent to novelty (Montgomery, 1955). Neophobia, the fear of novelty (Greenberg, 1983), is an indicator of an animal's internal state of risk perception as well as its propensity to take the risk (Mettler and Shivik, 2007; Wilson et al., 1994); it is typified by hesitation, avoidance, and caution (Harris and Knowlton, 2001). Behavioural responses fall along a bold-shy continuum (Wilson et al., 1994). Bold animals, those with greater propensity to take risks or to investigate potentially dangerous novel stimuli, are readily eliminated from wild populations undergoing predator control (Brand and Nel, 1997; Windberg and Knowlton, 1990). Consequently, reduction of neophobia should counterbalance such artificial selection favouring shy behaviour in carnivore populations undergoing predator control (Travaini et al., 2001). For management purposes, this behavioural manipulation could be used to increase the selectivity and efficiency of predator control efforts, by increasing the target species propensity to take risks (Wilson et al., 1994), while for conservation purposes, it could aid in maintaining populations of carnivores in coexistence with people (Musiani et al., 2003).

Bait placement or capture-based control methods are dependent on the behavioural responses of target individuals towards the specific novel stimuli placed to attract them (Travaini et al., 1996). Wariness of many carnivores (caution towards a situation because of its association with the threat of capture, Séquin et al., 2003) reduces vulnerability to capture because resident

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individuals detect and recognize trapping devices as novel foreign elements within their landscape (Harris and Knowlton, 2001; Lehner et al., 1976; Windberg, 1996). However, Heffernan et al. (2007) suggested that neophobic response could be attenuated by placing large novel objects over the bait or trapping device sets, and removing such objects after a few days. This may increase the exploratory behaviour and consequently increase bait consumption or efficiency in capture success (Brand et al., 1995; Harris and Knowlton, 2001). Additionally, intra- as well as inter-specific differences in these responses to novelty may increase selectivity and efficiency to control targeted individuals, local populations or species. Neophobia manipulation may be a promising behavioural tool in selective predator control, if for instance, its initial attenuation allows an increase in investigative behaviour and bait consumption or in capture probabilities (Harris and Knowlton, 2001; Heffernan et al., 2007).

Conflicts with large carnivores attacking livestock originated several thousand years ago, when humans first domesticated animals (Kruuk, 2002). Predator control in Patagonia started over a century ago, along with European settlement (Travaini et al., 2000), and nowadays wildlife managers are tasked with protecting privately owned livestock from publicly owned predators. Control was formerly oriented towards the elimination of cougars (*Puma concolor*) and Culpeo foxes (*Pseudalopex culpaeus*) (García Brea et al., 2010), but because of the highly non-specific and inefficient methods used, most efforts heavily impacted non-target species, a problem of increasing concern throughout the world (Breitenmoser et al., 2005). Fortunately, conservation issues have emerged evidencing a need to develop and improve selective and efficient methods to control problem predators, also in South America (Rodriguez et al., 2007). New initiatives concentrate on "target individuals" (Blejwas et al., 2002; Jaeger, 2004; Williams et al., 2003). However, this methodology has not been responsibly implemented in Patagonia. In the meantime, any effort aimed to increase efficiency and selectivity of prevailing control methods is welcome. McIlroy and Saunders (1998) proposed that bait-delivered agents (contraceptive, abortive, poison, etc.) are likely to be, in short- and long-terms, the most effective methods for predator control. Baiting has been tested in Santa Cruz Province (Travaini et al., 2001), and was utilized previously by Patagonian sheep ranchers (Travaini et al., 2000).

When designing control methods that include the use of different bait flavours and baiting procedures, attractants, or capture devices, it is important to assess the responses of target wild species to these novel stimuli. This is because the efficiency and potential selectivity of control methods most likely depend, in part, on intra- and inter-specific differences in responses to novelty. Towards this end it is necessary to evaluate a priori its existence and to quantify the strength of neophobic responses and possible inter-specific differences.

Two wild, closely related fox species (Wayne et al., 1989) occur throughout southern Patagonia (Redford and Eisenberg, 1992): the Culpeo fox (Novaro, 1997) and the Grey fox (*Pseudalopex griseus*) (Duran et al., 1985). Both species live mostly in sympatry in Santa Cruz province (Johnson et al., 1996; Travaini et al., 2003). The Culpeo weighs about 9 kg (Zapata et al., 2008a) and is considered to be, along with the cougar, as one of the main causes for failure of sheep ranches (García Brea et al., 2010; Travaini et al., 2000). In contrast, the Grey fox weighs about 3 kg (Fuentes and Jaksic, 1979; Novaro et al., 2004) and is not widely considered as a pest (Travaini et al., 2000). Roughly, Grey fox abundance is at least threefold that of Culpeo foxes (Travaini et al., 2010), both species use habitat similarly, and consume similar prey types but at different proportions (Zapata et al., 2005).

We performed a field experiment to evaluate and quantify neophobia in both sympatric Patagonian foxes. Our aims were to document the existence of neophobia in both species; to quantify its prevalence; and to determine whether neophobia could be utilized to increase investigative and consumptive behaviours.

2. Materials and methods

2.1. Study area

Field research was conducted between 12 and 28 April 2009 at a protected area ("Monumento Natural Bosques Petrificados"; 47°39.887′S; 67°59.729′W; Fig. 1). This area is composed of three sub-areas: the original protected area which covers 100 km^2, and two adjacent abandoned ranches that were incorporated into the protected area and cover ~200 km^2: Cerro Horqueta (47°41.086′S; 68°07.564′W) and El Cuadro (47°34.864′S; 67°58.118′W). This area belongs to the Departamento Deseado, Santa Cruz Province, Patagonia, in southern Argentina. Most of the landscape is covered by tussock grasses and low, dome-shaped, spindly shrubs (Soriano, 1983), with cover ranging from less than 10% in the most arid areas to >60% (Ares et al., 1990; Bertiller and Bisigato, 1998).

We conducted all surveys during fall, a period of relatively calm and dry weather, so the destruction of bait stations by wind was rare.

2.2. Neophobia test

To assess response to novelty and to compare differences between Culpeo and Grey foxes, we used an experimental design based on scent-station methodology (Linhart and Knowlton, 1975) and meat baits (Travaini et al., 2001), which were considered as "bait-stations" (Allen et al., 1989). Scent stations have emerged as a useful, cost-effective tool in the research and management of carnivores (Johnson and Pelton, 1981; Lindzey et al., 1977; Roughton and Sweeny, 1982). Bait-stations are increasingly being used in an attempt to control unwanted predators (Henderson et al., 1999; Jackson et al., 2007; Saunders et al., 1999), as well as for monitoring (Clark et al., 2005; Travaini et al., 2010), sanitary control (Boulanger et al., 2006), research and conservation (Armstrong et al., 2006). Their use is also increasing both in wild (Heffernan et al., 2007) and captive (Windberg, 1996) behavioural studies.

To assess responses to novelty in fox species we followed general protocols used in previous studies with birds and mammals (e.g. Webster and Lefebvre, 2001). We evaluated initial and successive responses of free-ranging foxes (i.e. visitation and bait consumption rates; bait station use) when a novel object was present or absent. Initial behavioural responses also were compared with successive trials with and without the novel object.

To evaluate fox visitation pattern and behaviour, we established nine or 10 transects (depending on secondary road availability and condition), each consisting of six bait stations, in El Cuadro and Cerro Horqueta, both located in the protected area (Fig. 1A). A bait-station consisted of a 1-m-diameter circle of smoothed earth with the bait placed at the centre (Travaini et al., 2001). Stations were spaced 0.5 km apart and transects were at least 1 km apart. Each transect was regarded as an independent sampling unit, and we assumed that individual foxes might visit more than one station within a transect, but would rarely encounter more than one transect per night (Travaini et al., 2010). This methodology assumes that individual foxes could make multiple visits during a single night, or more than one individual from the same or different species, could visit one single bait station, and that such behaviour could not be determined by the researcher (Harris and Knowlton, 2001; Heffernan et al., 2007). The hand-prepared meat bait (Travaini et al., 2001) weighed about 30 g and was made of minced beef (80.6%), hydrogenous oil (9.7%), corn starch (8.1%) and an attractant scent

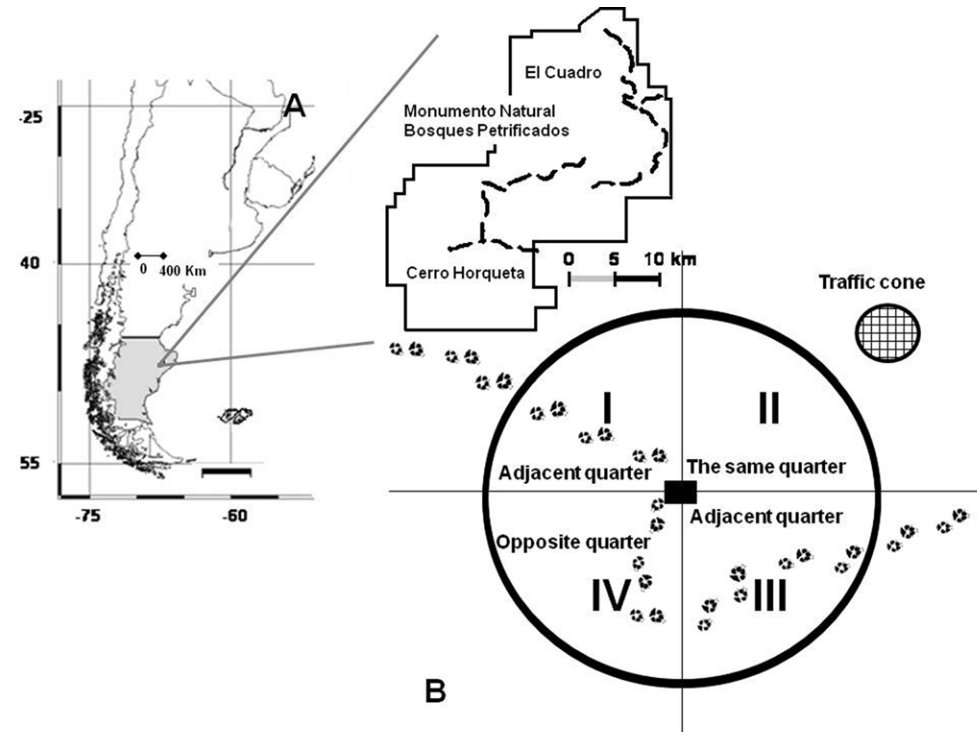

Fig. 1. (A) Study area at Santa Cruz Province (southern argentine Patagonia). Polygon delineates the limits of the whole protected area; while lines represent bait station lines. (B) Schematic example of a fox visit to a bait station. There are fox tracks on three (I, IV and III) out of the four quarters, in the opposite, and the adjacent to the novel object. This single path, with no forward and backward tracks, was considered as a "moderate walk" through the bait station.

(1.6%), which consisted of a commercial trap lure called Cat Passion (O'Gorman Enterprises Inc., Broadus, MT, USA). Cat Passion proved to be efficiently attractive for both fox species (Travaini et al., 2001). Our field protocol for bait stations was quite similar to those used by other authors to evaluate the behavioural responses of wild coyotes (*Canis latrans*) to novel stimuli (Harris and Knowlton, 2001; Heffernan et al., 2007).

Each test required 6 days to complete and was organized into three experimental phases. On the first day, we established the stations on alternate sides of secondary, unpaved roads. In order to establish a baseline visitation rate, on the following two mornings (pre-treatment phase), we checked the stations, identified and erased tracks of visitors to stations, and added more earth and baits when necessary. On the third day, after checking the stations, we installed a large, 75-cm-tall by 25-cm-diameter orange PVC-traffic cone (the novel object) outside the station and 10 cm from the edge. On the next morning (day 4) we checked the stations and moved the plastic cone to the diagonally opposite quarter of the bait-station circle (Fig. 1B). On day 5, we checked the stations and removed the cone. Finally, we checked stations for an additional day (day 6) after removing the cones. Thus, following an initial day to place stations, we had two pre-treatment days, with bait-station activation, followed by two treatment days with a traffic cone as the novel object in stations, and a single post-treatment day, without cone. We recorded baits as consumed if they could not be found on or in the proximity of the station because preliminary observations showed that baits are mostly consumed at or adjacent to the station. Despite their similarity in shape, Grey and Culpeo foxes' tracks were easily identified because when left on soft surfaces because Culpeo tracks are longer and wider than those of Grey fox tracks (Travaini et al., 2001). Nevertheless, if fox tracks could not be clearly identified, they were recorded as unidentified fox species and excluded from analyses. Stations that were destroyed by wind were not considered as operative, and were excluded from the analyses. After each survey we collected and destroyed all uneaten baits.

2.3. Behavioural variables

Each time a fox track was identified at a bait-station, we took note of the fox species and if the bait was consumed or not. Then we estimated:

(i) Visitation rate, which was calculated for each transect as the total number of visited stations divided by the total number of operative stations; and bait consumption rate, which was calculated for each transect as the total number of stations where bait was consumed divided by the total number of operative stations. Statistical comparisons for each fox species were based on data collected during the final pre-treatment day and the first treatment day on one hand, and between the final pre-treatment day and the post-treatment day, on the other, because during these days behavioural responses were strong in each experimental phase (i.e. the contrast between familiar and novel condition).
(ii) Bait-station visitation pattern, which was assessed by counting the number of individual footprints within the bait-station, and by estimating the proportion of the bait-station used by each individual fox. For the latter variable, the 1 m circle of each bait-station was divided in four equal parts (quarters), and the number of quarters covered by tracks was recorded (Fig. 1B).

We installed two infrared automatic video cameras (Apollo Scouting Camera, BuckEye Cam^{TM}, http://www.buckeyecam.com, Athens, OH, USA) at two randomly selected bait-stations located in El Cuadro (Fig. 1A), and later moved them to two other bait-stations located in Cerro Horqueta (Fig. 1A). Cameras were operative for each complete 6-day test period (5 nights), and were set to record any moving animal at the bait-station for up to 60 s. Then recording stopped for 5 s while data were stored onto the SD memory card, and then started again for another 60 s, and this sequence continued until recording ceased. However, cameras did not performed as expected and only provided a few informative recordings, the content of which will be presented for illustrative purposes only.

2.4. Statistical analyses

To test the effect of a novel object on differences in the visitation rate and number of tracks between experimental phases we performed Generalized Linear Mixed Models (thereafter GLMM) (Crawley, 2007; Pinheiro and Bates, 2000). We used GLMMs as they allow both fixed and random effects to be defined (Pinheiro and Bates, 2000). Random effects allow the analysis to account for repeated measures or related data; transect identity was fitted as a random effect in all models. Models for Culpeo and Grey foxes were run separately. We assessed the fit of models by visually inspecting plots of standardized deviance residuals for each model. Significance of fixed effect was tested with a likelihood ratio test (thereafter LRT), which was $-2 \times$ difference in likelihood between hierarchical models tested as a chi-squared distribution with the difference in the number of variance components between the models as the associated degrees of freedom (Pinheiro and Bates, 2000). All models were carried out using R software, Version 2.7.2 (R Development Core Team, 2008).

We performed a GLMM with binomial error structure and log link function (Pinheiro and Bates, 2000; Crawley, 2007). In this analysis we compared visitation rates (response variable) during pre-treatment (i.e. without cone) and treatment (i.e. with cone) conditions. The relationship between visitation rate and experimental phase was modelled with experimental phase (two categories: pre-treatment and treatment) as fixed effect. To analyze visitation rates after removal of novel objects we employed another GLMM with the same error structure and link function. In this case we compared visitation rates during pre-treatment and post-treatment conditions. The relationship between the visitation rates and experimental phase was modelled with experimental phase as a fixed effect. To test the effect of a novel object on the number of tracks registered in each station, we performed a GLMM with Poisson error structure and identity link function (Pinheiro and Bates, 2000). This analysis compared the number of tracks registered during pre-treatment and treatment phases. For Culpeo foxes, data from the treatment condition were insufficient to fit any model. The relationship between the number of Grey fox tracks and experimental phase was modelled with experimental condition as fixed effect (Crawley, 2007).

To evaluate possible differences in bait-stations' visitation pattern performed by fox species at different conditions [i.e. familiar (pre-treatment, post-treatment) and novel (treatment)], and the effect of changing the novel object to an opposite position at the station, we used Kolmogorov–Smirnov tests. For the first comparisons we considered four categories of space use (1, 2, 3 and 4 bait-station quarters showing tracks), and for the second, we considered three categories of the locations of fox tracks according to the position of the novel (i.e. at the quarter closest to the cone, at adjacent quarters, and at the opposite quarter).

3. Results

3.1. General results

Culpeo foxes visited 10 (52.6%) of the 19 transects and 42 (7.4%) of the 570 bait-stations available during the experiment. They consumed the bait in 41 of the 42 visited bait stations. In contrast, Grey foxes visited 100% of the 19 transects and 394 (69.1%) of the total available bait-stations. Grey foxes consumed the bait in 100% of the visited bait-stations (Appendix 1). We were unable to identify the visiting fox species on 48 (8.4%) occasions.

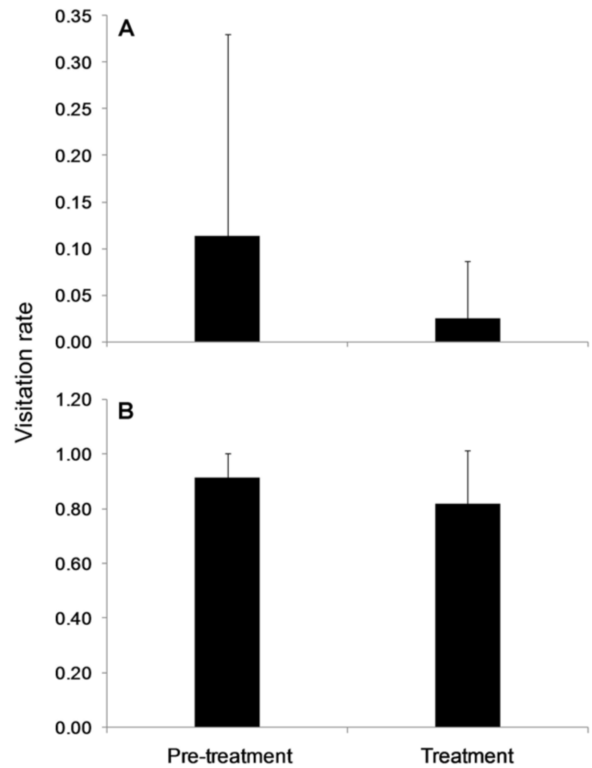

Fig. 2. Bar plot (mean ± SD) of visitation rates (number of visited bait stations/number of operable bait-stations) in two experimental conditions: before a plastic cone was placed near the bait-station (pre-treatment) and in the presence of the plastic cone (treatment) for (A) Culpeo and (B) Grey foxes.

Bait-stations were visited by both species only on six occasions during the same night (three during the pre-treatment phase, two during the treatment phase, and one during the post-treatment phase). We excluded these cases from analyses, because we did not know which species consumed the bait. We also recorded the presence of other species such as cougars (*Puma concolor*), skunks (*Conepatus humboldtii*), European hares (*Lepus europaeus*) and guanacos (*Lama guanicoe*), however, none ingested baits. Finally, two bait stations were rendered inoperable and six others were seriously damaged by wind.

3.2. Responses to novelty evaluation

3.2.1. Bait-station visitation rate

Visitation rates decreased from pre-treatment to treatment phases both in Culpeo [mean ± SD = 0.114 ± 0.215 (pre-treatment) vs. 0.025 ± 0.061 (treatment), respectively] and Grey foxes [mean ± SD: 0.914 ± 0.089 (pre-treatment) vs. 0.817 ± 0.197 (treatment), respectively]. The presence of the novel object significantly reduced visitations to bait-stations (GLMM; LRT: $\chi^2 = 7.69$, $P = 0.005$ and LRT: $\chi^2 = 3.89$, $P = 0.048$, for Culpeo and Grey foxes, respectively) (Fig. 2). For Culpeo foxes, the coefficient from the visitation rate model was 1.72 times higher during pre-treatment compared to treatment phase, i.e. when the novel object was present. This species reduced ≈80% of its visitation rate from pre-treatment to treatment experimental phases. For Grey foxes, we observed the same pattern of response, but the novel object effect was weaker, with a coefficient of 0.94, which corresponds to only about a 10% reduction between the phases.

Bait consumption also decreased significantly from pre-treatment to treatment phases, foxes that visited stations during the treatment, ate the bait in 99 and 100% of cases (Culpeo and Grey fox, respectively).

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Table 1
Coefficients (±SE) from Generalized Linear Mixed Model on the number of tracks registered in each visited bait station (N = 129) by Grey foxes before and after a traffic cone was placed on stations.[a] The condition "with cone" was used as reference category.

Model	Fixed effects	Categories	Coefficient ± SE	P
Treatment + transect	Intercept		2.96 ± 0.07	<0.0001
	Treatment	With cone		
		Without cone	−0.43 ± 0.04	<0.0001
Transect	Intercept		2.79 ± 0.07	<0.0001
LRT[b]			$\chi^2 = 78.14$	<0.0001

[a] This relationship was modelled with transect identity as a random effect and treatment condition as fixed effect.
[b] Likelihood ratio test: −2 × difference in likelihood between hierarchical models tested as a chi-squared distribution (Pinheiro and Bates, 2000).

After novel object removal, visitation rates recovered (mean ± SD = 0.088 ± 0.170 and 0.816 ± 0.277 for Culpeo and Grey fox, respectively) and no significant differences for either fox species were detected between pre- and post-treatment visitation rates (GLMM; LRT: $\chi^2 = 0.64$, $P = 0.420$ and LRT: $\chi^2 = 1.84$, $P = 0.174$, for Culpeo and Grey foxes, respectively).

3.2.2. Bait station visitation pattern

During the treatment phase, the data obtained from bait-station visitation patterns for Culpeo fox were insufficient to fit any model. However, the presence of the novel object resulted in fewer tracks left at bait-stations by Grey foxes (mean ± SD = 21.73 ± 10.30 and 13.93 ± 8.87 for pre-treatment and treatment respectively). The parameter estimate was 0.43 times lower in the presence of the novel object compared with the pre-treatment (GLMM; LRT: $\chi^2 = 78.14$, $P < 0.001$, Table 1). Conversely, the analysis of tracks left by individuals showed that, after novel object removal, animals increased exploration of the station. This was particularly evident for the Culpeo fox. For this species, bait-station use during pre-treatment (based on tracks' density) showed no clear spatial pattern (Kolmogorov–Smirnov test; $d_{max} = 3.0$, $P > 0.05$), i.e. animals' tracks indicated both a moderate (2/4 of the surface) as well as a more intensive (3/4 and 4/4 of the surface) tracking within the stations (Fig. 3A). Unfortunately, this could not be statistically tested during the treatment phase, because of the small number of visits. In contrast, during post-treatment visits, the number of Culpeo fox tracks increased and were found over the entire bait-station surface area (Kolmogorov–Smirnov test; $d_{max} = 4.5$, $P < 0.05$) (Fig. 3A). Grey foxes also changed their visitation pattern when a novel object was present (Fig. 3B). During pre-treatment their tracks were most often found over 3/4 and 4/4 of the total bait-station' surface (Kolmogorov–Smirnov test; $d_{max} = 19.0$, $P < 0.001$) (Fig. 3B). However, during treatment trials, surface used decreased on average to 1/4 [Kolmogorov–Smirnov test; $d_{max} = 27.0$, $P < 0.001$ (Fig. 3B)]. Conversely, during the post-treatment, bait-station use increased and animals resumed walking across the entire station surface [Kolmogorov–Smirnov test; $d_{max} = 37.0$, $P < 0.001$ (Fig. 3B)].

Additional evidence about fox visitation patterns, when the novel object was present, was obtained by analyzing the specific quarter of the sample circle (bait-station) visited during the experimental treatment phase. During the first treatment day, Culpeo foxes visited only three bait stations, during the second day when the plastic cone was moved to the diagonally opposite quarter of the bait-station circle they did not show a clear tendency to use a specific quarter (Kolmogorov–Smirnov test; $d_{max} = 3.0$, $P > 0.05$). Conversely, Grey foxes consistently visited the opposite quarter (Fig. 1B) to that of the traffic cone [Kolmogorov–Smirnov test, day 1: $d_{max} = 26.0$ and day 2: $d_{max} = 42.0$, both $P < 0.001$ (Fig. 4)].

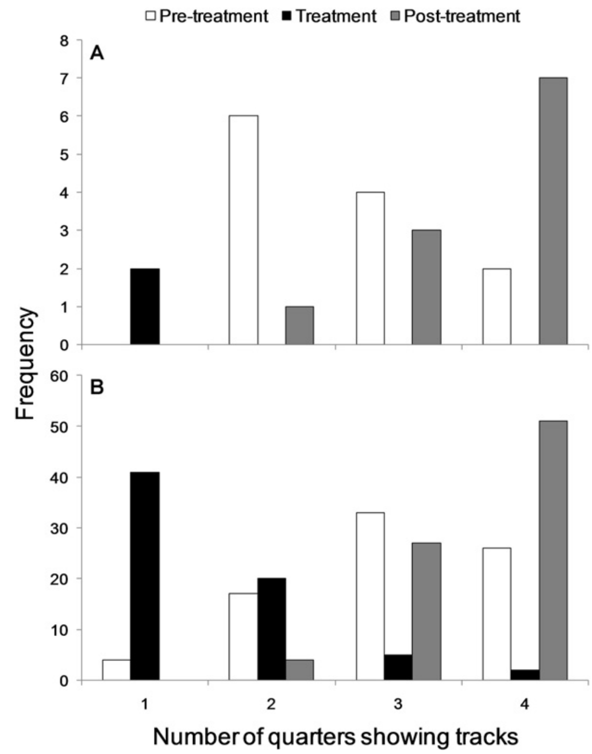

Fig. 3. Bait-station's visitation pattern by (A) Culpeo and (B) Grey foxes. Numbers (1–4) on the x-axis represent quarters of the circular 1 m-station showing tracks.

4. Discussion

Wildlife management efforts might take advantage of quantifying neophobia/neophilia levels of target species in order, for instance, to develop adequate selective control protocols. One experimental approach to detect the strength of responses to novelty is to place a novel stimulus next to a familiar food type and measure changes in site visitation rate, latency to feed, and food consumption (Greenberg, 1990b). In this study, we found that bait-stations and plastic cones proved to be an appropriate way to evaluate and quantify responses to novelty in Culpeo and Grey foxes.

Two main findings can be drawn from our experimental study. First, for foxes, visitation and bait consumption rates were significantly affected by the nearby presence of the novel object,

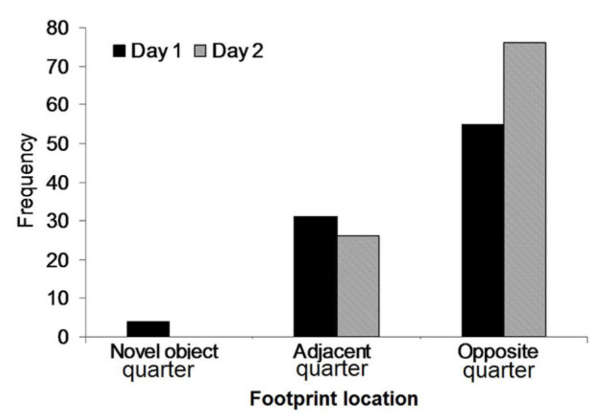

Fig. 4. Frequency of visits of Grey foxes to the four different quarters of bait-stations during the treatment phase. The 1 m circle of each bait-station was divided in four equal parts (quarters) according to the position of the cone: novel object (the same quarter), adjacent and opposite to the cone.

suggesting a neophobic response. Second, after novel object removal both species recovered quickly their pre-treatment visitation rates. Tracks left over the entire surface of the bait-station suggest intensive exploratory behaviour, which was particularly evident for the Culpeo fox. Foxes were most likely cautious about traffic cones because they represented a novel element in a familiar environment, i.e. true neophobia, and not because of wariness of, or their association with humans (Séquin et al., 2003), as difference between pre-treatment and treatment phases could not be attributable to any experimental difference in human presence and their associated scent. However, for those individuals which visited the stations during treatment trials, bait consumption was apparently not affected by the presence of the novel object; those less neophobic animals that visited the stations during the treatment also consumed the baits. Nevertheless, fox behaviour documented through video-recording showed that, during the treatment phase, a particular bait-station could be visited several times a night by a single fox species, and probably by a single individual, within a few minutes or hours (contrasting with the almost single approach needed to take the bait in pre-treatment video-recorded bait-stations). After these multiple visits the bait was consumed, and despite the difficulties imposed by the novel object, we registered the consumption of the bait in that station the next morning. The presence of the cone also produced body postural changes and vigilance behaviours resembling the ones observed in other avoidance responses to novel objects (Harris and Knowlton, 2001) or stress situations (McLeod, 1996) in canids.

For a more complete interpretation of our results, two points should be considered. Earlier studies of neophobic responses were mostly evaluated in highly controlled experimental conditions where captive trial animals had only one opportunity to confront the task in the presence of the novel object before the experiment was completed (Windberg, 1996). In our field trials the decision of foxes to consume or not to consume the bait after the first visit, would likely have resulted in less bait consumption during the treatment phase. The use of appropriate video equipment should be considered in future experiments. Additionally, similar studies with wild coyotes and black-backed jackals (*Canis mesomelas*) were performed in areas normally subjected to predator control or scientific trapping with variable intensity (Brand and Nel, 1997; Brand et al., 1995; Heffernan et al., 2007), with the consequent reduction in the proportion of bold animals in the population. Throughout our study area no trapping or any other fox control efforts had been undertaken during the last 50 years, so there was likely a higher proportion of bold animals present compared with neighbouring sheep ranches with active predator control, which would have had a higher proportion of shy individuals. To test this point, similar experiments should be undertaken outside the protected area.

It was claimed that interspecific differences in responses to novelty in birds (Greenberg, 2003) and mammals (Sunnucks, 1998) underlie ecological specialization (Wilson et al., 1994), in terms of ecological attributes such as habitat preference (Mettke-Hofmann et al., 2002) or trophic-niche amplitude (Biondi et al., 2010; Greenberg, 1989). Relatively specialized species are expected to show higher levels of neophobia than cogeneric generalists (Echeverría et al., 2006; Greenberg, 1990a; Greenberg and Mettke-Hofmann, 2001; Martin and Fitzgerald, 2005). Previous studies in Patagonia habitats suggest that the Grey fox is a more opportunistic predator than the Culpeo fox (Jimenez et al., 1996; Johnson and Franklin, 1994; Zapata et al., 2008b). Accordingly, the Culpeo fox showed a stronger neophobic response towards novel objects than did the Grey fox. This is shown by the greater coefficient yielded by the GLMM for visitation rate, together with a strong decrease in their visitation rate during the treatment compared to the pre-treatment.

Fig. 5. (A) A Grey fox visiting a pretreatment control bait-station (without novel object). The individual is eating inside the station circle. (B) A Culpeo fox visiting a bait station with the novel object.

The strongest influence effect of novel objects was seen from the behaviour of the animals at bait stations, as measured by the number of tracks left and the fraction of station's surface area used by the animals. During the pre-treatment phase, the higher number of tracks occupying a considerable surface area of the stations indicates that the animals not only consumed the baits but also explored the bait station. This observation was supported by the behaviour of those animals that were video-recorded during pre-treatment; after bait consumption, which took only a few seconds, individuals explored the area by changing their walking direction, sniffing the soil and the air, as well as repeatedly visiting the station (Fig. 5A). Conversely, in the presence of the novel object, animals exhibited a neophobic behaviour: they avoided those areas near the cone by entering the station and taking the baits from a position opposite to that of the cone. Additionally, the number of tracks decreased markedly compared to the pre-treatment, suggesting less tendency to explore the site. It was also clear from videos that the station and the surrounding area were only visited briefly, and during the treatment phase, baits were transported and consumed near the edge of the station (Fig. 5B). This type of behaviour is a typical response of vertebrates, particularly mammals and birds, towards novel foods or objects; that is to display signs of fear, e.g. fur/feather erection, body postural changes, "jumping jacks", where approaches are punctuated by backward movements, and accentuated vigilance behaviours (Christensen et al., 2005; Halliday, 1996). We observed several of these displays, together with body postural changes, "jumping jacks" and visual awareness of the cone.

After novel object removal, both species recovered investigative behaviour quickly, but did not exceed their pre-treatment visitation rates. The lack of stronger differences in the visitation rates to bait station between the pre- and post-treatment for Grey foxes could be attributable to a high initial visitation rate during pre-treatment, with a reduced margin to improve it after cone removal. This might be related to the high abundance of this fox species in the protected area, together with a large proportion of non-neophobic individuals, as there was no artificial selection against bold behaviour (Mettler and Shivik, 2007). Nevertheless, a significant increase was observed in the number of tracks in the post-treatment phase compared to the pre: overall, individuals tended to walk on the entire bait station during the post-treatment, indicative of an increased exploration of the site. Heffernan et al. (2007) also found a significant increase in investigative behaviour after removing a novel object (a traffic cone similar to that used in the present study) in both, captive and wild coyotes.

From a practical point of view, our manipulation of behaviour, based on bait-station methodology (Travaini et al., 2010), has a potential to improve selective and efficient control methods for Culpeo foxes. Alternative protocols should be evaluated in the field to increase efficiency, as well as selectivity throughout those areas where Culpeo foxes live in sympatry with non target species, such as the Grey fox. For example, because of the increased likelihood of investigating sites after placement and removal of a novel stimulus, a short treatment period using plastic cones or other novel objects, should be considered as an effective mechanism to increase the success of capture devices (Heffernan et al., 2007), especially in those areas where control of Culpeo foxes has been undertaken for long periods (Novaro, 1995), and where shy animals have been artificially and involuntary selected. Further research needs to be undertaken in these areas to compare the investigative behaviour of the same species under different predator-control histories, and to more clearly assess the potential of our protocol for selective control purposes. Research in these areas should reveal if remaining foxes that are most neophobic, as a result of first removing those animals easiest to catch (Brand et al., 1995) or those harder to trap because they have previously been exposed to culling (Sacks et al., 1999). Both possibilities should be considered when attempting to increase visitation and consumption rates by resident shy foxes.

The proper manipulation of novel items should increase the investigative behaviour of shy foxes, and so their chances of being selectively extirpated from the area. This alternative method should greatly improve the conservation of non-target species, almost devastated by the traditional and highly unspecific use of poison by local ranchers (García Brea et al., 2010; Olrog, 1979). Plastic cones performed very well for our purposes; they are relatively cheap, easily transportable and could serve as advertising to anyone in the area that a control campaign is being undertaken. This is very important for sheep ranchers in southern Patagonia, so as to prevent the accidental poisoning or injury of the large number of guard dogs used by residents to protect livestock.

A brief economic analysis shows the potential of this methodology. Based on a cost of $0.15 US per bait (Travaini et al., 2001) and an approximate cost of $15 US per plastic cone, a rancher could make a total investment of $94.5 US to activate a complete transect during a 5-day period. Based on our knowledge of Santa Cruz province, most ranches have an adequate number of secondary roads to install up to 10 transects. These conditions require an initial investment of $900 US for plastic cones and an additional $45 US for baits. Considering the value of a lamb is about $105 US, ranchers would recover their total initial investment in plastic cones with only nine lambs saved from predation. We did not consider in these calculations fuel, traps and poison costs because these are already expenses incurred by ranchers.

5. Conclusion

Neophobia and neophilia (or exploration), both are important components of the behavioural repertoire of wild animals. Addressing the factors governing these behaviours and their incorporation into predator-control techniques may be helpful to wildlife managers.

For both fox species, we found that visitation and bait consumption rates were significantly affected by the presence of a novel object. However, bait station visitation patterns after novel object removal indicates that animals increased their exploration of the station, which was particularly evident for the Culpeo fox, the target species in our study area.

For applied purposes, such a manipulation of responses to novelty could be used to increase predator control selectivity and efficiency by increasing Culpeo fox propensity to take risks. Because of an increased likelihood of foxes investigating sites after placement and removal of a novel stimulus, a short treatment period using plastic cones or other novel objects, could be a practical and cheap method to increase the success of capture devices. Placement and removal of novel visual stimuli might also be a method for targeting the capture of foxes that include phenotypically shy or wary foxes i.e. resulting from artificial selection against those animals with a greater propensity to take risk or to investigate potentially dangerous novel stimuli, in populations under predator control.

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Appendix 1.

Number of bait-stations visited and baits consumed by Culpeo and Grey foxes in the two study areas during our field experiment. PrT, Pre-treatment phase: initial conditions without novel object (traffic cone) at bait-stations; Trt, Treatment phase: a traffic cone was placed at bait-stations, and PsT, Post-treatment phase: the traffic cone was removed. Number of visits and baits consumption during the first and second day of both PrT and Trt are separated by a dash.

Locality	El Cuadro ($N=10$)						Cerro Horqueta ($N=9$)					
Fox species	Culpeo fox			Grey fox			Culpeo fox			Grey fox		
Experimental phase	PrT	Trt	PsT	PrT	Trt	PsT	PrT	Trt	PsT	PrT	Trt	PsT
Visits	5–9	2–8	9	38–36	36–46	48	0–4	1–2	2	30–48	33–35	44
Baits consumed	5–9	2–8	8	38–36	36–46	48	0–4	1–2	2	30–48	33–35	44

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