Occurrence of invasive mammals and native carnivores in northern Patagonia

By
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The study of biological invasions is important to management and conservation. I assessed the occurrence of invasive mammals and native mesocarnivores in northern Patagonia. Invasive species had varying responses to anthropogenic disturbance, and were differentially influenced by environmental and anthropogenic factors. Invasive species were also a substantial part of native mesocarnivores diets and appeared to influence their temporal activity, but not occupancy. Overall, I observed high spatial and temporal overlap between native carnivores and coexistence seemed facilitated by diet. Humans had both a positive and negative influence in this community, being responsible for the introduction of invasive species and possibly further facilitating their expansion, while also limiting other invasive species and potentially benefiting native species directly and indirectly. Undoubtedly, biological invasions, anthropogenic disturbance, and native communities can present complex interactions which will require further study to provide effective tools for protected areas.
DEDICATION

I dedicate this thesis to my loved ones. To my friends, for their support and companionship in all these years. To my family, for their unconditional support in all my interests and projects, since childhood until today, always reassuring me when in doubt and helping me when I needed it. To Diego, for his infinite patience and support, giving me strength and inspiration in every step of the way, helping me to keep going and achieving my best. I could not have done this without all of you.

Dedico esta tesis a todos mis seres queridos. A mis amigas, por su apoyo y compañía en todos estos años. A mi familia, por su incondicional apoyo en todos mis intereses y proyectos, desde la infancia hasta el día de hoy, siempre dándome confianza cuando tenía dudas y ayudándome cuando lo necesite. A Diego, por su infinita paciencia y apoyo, dándome fuerza e inspiración a cada paso, ayudándome a seguir adelante y logrando lo mejor de mí. No podría haber hecho esto sin todos ustedes.
ACKNOWLEDGEMENTS

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Chapter I

Introduction

Much of the Earth's surface has been transformed by human activities, and even where the primary components of habitats have been retained they have often been degraded through direct exploitation and the introduction of invasive species (Gaston et al. 2008). Biological invasions are a consequence of anthropogenic disturbance and the cause of recent extinctions and species endangerment (Vitousek et al. 1997; Brown and Lomolino 1998), and in many cases, species introductions have resulted in the creation of novel ecosystems (Davies 2009).

A key strategy for protecting biodiversity from such pressures has been the establishment and maintenance of protected areas (Gaston et al. 2008) which are generally considered keystones of biodiversity conservation (Noss 1996; Bruner et al. 2001). Nevertheless, human intrusions and threats to protected areas are common (Liu et al. 2001) and the interface between human settlements and protected areas is the starting point of invasions into protected areas (Pauchard and Villarroel 2002), which often result in management concerns (Davies 2009).

The ways in which invasive species can impact natives are as intricate as the ways that any species can interact with any others in complex and diverse communities (Simberloff and Rejmánek 2011). The ability of natives to evolve in response to invaders may lessen the negative impacts of some invaders or even allow natives to benefit from
them (Novaro et al. 2000). In contrast, the inability of natives to adapt to antagonistic invaders can lead to extirpation or massive declines in native species (Simberloff and Rejmánek 2011).

To effectively plan and manage biodiversity within protected areas it is crucial to identify the environmental conditions within which invasive species are present (Karatayev et al. 2009), and how native communities adapt to invasive species once established (e.g., Novaro et al. 2000). Within the National Parks System of Argentina, the level of occurrence of invasive mammal species is high, almost 80% of the areas host ≥ 1 species, and in Nahuel Huapi National Park (Fig. 1), the most abundant invasive mammals species are European hares (*Lepus europaeus*) and wild boars (*Sus scrofa*) (Merino et al. 2009). Furthermore, a major component of biological invasions is anthropogenic disturbance (Nuñez and Pauchard 2010), which can also affect native communities’ abundance and distribution (Vanthomme et al. 2013). My thesis objectives are to study factors influencing occurrence of invasive mammals, and to examine coexistence between native carnivore in the presence of invasive prey and anthropic disturbances in Nahuel Huapi National Park, northern Argentinian Patagonia.
Figure 1.1  Location of study area: Nahuel Huapi National Park, Argentina. Black line represents limit between Argentina and Chile. Gray line represents park boundaries.
References


CHAPTER II
ANTHROPOGENIC AND ENVIRONMENTAL EFFECTS ON INVASIVE MAMMAL DISTRIBUTION IN NORTHERN PATAGONIA, ARGENTINA

Introduction

Few ecosystems are free of introduced invasive species, and an increasing proportion of habitats are becoming dominated by them (Pyšek and Richardson 2010). A major component of biological invasions is anthropogenic disturbance (Nuñez and Pauchard 2010), which acts largely as a facilitating agent at local and global scales (Meyerson and Mooney 2007). The benefit of disturbance on invasive species can result from the avoidance or reduction in the intensity of biotic resistance, manifested through decreased interspecific competition or predation in the invaded community (Elton 1958; Hobbs and Huenneke 1992). As a result, human actions such as poaching, tourism, or land-use change can facilitate invasions, and in turn cause substantial environmental damage (Podgorski et al. 2013; Kang et al. 2007).

The Patagonian region of South America has suffered several introductions of invasive mammal species (Long 2003; Merino et al. 2009). Particularly, introduced herbivores have been found to disturb the establishment and growth of native vegetation (e.g. Vazquez 2002; Veblen et al. 1992), and can decrease native herbivores’ access to resources (e.g., Galende and Grigera 1998). The European hare (Lepus europaeus) and wild boar (Sus scrofa) are invasive species introduced to Argentina during the early
1900s (Novillo and Ojeda 2007). Hares and boars can cause substantial environmental damage and are the two most widespread invasive species in the National Parks System of Argentina (Merino et al. 2009), and among the 100 worst invasive species in the world (Lowe 2000). I compared the relative importance of anthropogenic disturbances and environmental factors on the distribution of European hares and wild boars in Nahuel Huapi National Park, Argentina. Additionally, I looked for support for the disturbance hypothesis (Elton 1958) which states that human alterations of the environment facilitate invasive species. As a result, I predicted human disturbance would be a positive driver of hare and boar distribution, causing occupancy to be greater closer to areas of human development, such as roads or settlements.

Methods

Study area

The study area was in the southern portion of Nahuel Huapi National Park, Argentina (Figure 1). There are three primary ecological regions in the park based on annual precipitation and elevation: Altoandino, Andino-Patagonico, and Patagonic steppe (Veblen et al. 1992). I deployed cameras in the Andino-Patagonico region, which comprises transitional forests and shrublands from 700 to 1700 m elevation with annual precipitation varying from 600 to 1200 mm. Dominant trees include ñire Nothofagus antarctica, coihue N. dombeyi, and lenga N. pumilio (IUCN 1982; Veblen et al. 1992). All places surveyed corresponded with public areas in the national park used for touristic activities.
Data collection

I established 80 camera stations about 1 km apart along hiking trails from 700 to 1600 m elevation during February to May 2012 and January to April 2013, representing about 60% of available hiking trails in the southern section of the park (Figure 1). Within the constraints of trails, stations were located to spatially represent the range of conditions that occur within the Andino-Patagónico region and encompassed 90% of the elevational gradient (Figure 1). I mounted infrared cameras (Bushnell 8MP Trophy Cam Night Vision Trail Camera, Bushnell, Kansas, USA) to trees 30–130 cm above ground and oriented cameras to detect animals traversing trails. I programmed cameras to take three photographs each time the camera was activated, with 10-second intervals between each event. Cameras were operated at each station for 21 days.

I recorded the location of each station with a GPS device (Garmin eTrex, Garmin International, Inc., Olathe, Kansas, USA) and measured three environmental (land cover, horizontal cover, and percentage of herbaceous vegetation) and three anthropogenic (distance to nearest human settlement, distance to nearest road, and average daily number of people) variables. I assigned each camera station to one of three coarse scale land covers (*N. dombeyi*, *N. antarctica* or *N. pumilio*) using as reference a vegetation map of the park (Res.:500 m; Mermoz and Martin 1987). I estimated horizontal cover using the cover cylinder method, modified from Ordiz et al. (2009). At each point, I placed a white fabric and steel spring wire cylinder (50 cm high by 30 cm diameter) and measured the minimum sighting distance (D; the minimum distance at which the cylinder can no longer be seen) in the four cardinal directions. I took measurements at a height of 40 cm to mimic eye level of a medium-sized mammal. I then calculated the mean cover value for
each point by averaging the four values. I measured herbaceous vegetation (i.e. percentage of herbs and grasses) in each cardinal direction 5 meters from the camera and directly under it. I placed a wooden square (30 x 30 cm) divided with wire into 9 10 x 10-cm squares and counted the number of smaller squares with >50% cover. I converted the number of smaller squares with >50% cover to a percentage and averaged percentages from the 5 locations. I measured distance to nearest human settlement and road using satellite images (Google Earth, Google Inc., Mountain View, California, USA) and calculated the mean daily number of people from camera detections at each site.

**Data analysis**

I identified mammals in images to species. For each site, I created an encounter history using three 7-day survey periods, for a total of 21 days. I used likelihood-based occupancy modeling (MacKenzie et al. 2002) using program PRESENCE (MacKenzie et al. 2006) to estimate site occurrence (probability that the species occurred at a site) and detectability (probability that the species was detected if present) from detection-non-detection data. I included the six variables collected as covariates in the occupancy models for hares, and all covariates except herbaceous vegetation for boars. I tested for correlation between variables \((r > 0.7;\) Dormann et al. 2013) and evaluated if season (i.e., 2012, 2013) had an effect in detectability or occupancy. Although possible, I consider unlikely that the same animals might be detected in more than one camera causing spatial autocorrelation, especially given the distance between cameras (1 km) and the short sampling period (21 days). In Europe, mean distance traveled by hares in annual home ranges usually varies between 170 and 330 m (Ferreti et al. 2010; Ruhe and Hoffman 2004), and core area for wild boars ranges between 50 and 90 ha (Massei et al 1997).
measured model fit by estimating the overdispersion parameter (c-hat; \( n = 1000 \) bootstrap samples) of the full model for each species (MacKenzie and Baley 2004). Values > 1 suggest there is overdispersion in the observed data and therefore the associated Akaike Information Criterion (AIC) value should be adjusted to perform comparisons between models. Values < 1 suggest underdispersion but do not represent a problem for interpreting simpler models with AIC (MacKenzie and Baley 2004). To compare the relative influence of anthropogenic and environmental factors on hare and boar occupancy, I compared the full environmental and full anthropogenic models. I ranked these models for parsimony using AIC with adjustment for small sample sizes (AICc; Burnham and Anderson 2002) for each species, and considered models equally supported if \( \Delta AICc < 2 \) of the best supported model. I then combined covariates from both sets (i.e., environmental and anthropogenic) to develop models of hare and boar occupancy and evaluate if they offered support for the disturbance hypothesis. I used sequential model fitting to reduce the total number of models used (Dinsmore et al. 2002). For each species, starting with the two previous models (i.e., anthropogenic and environmental), I identified the most important variables in each set (\( P < 0.15 \)). I then ran all possible combinations of all covariates always including those previously identified as important. I ran models without interaction terms and included a null model. Model averaging is considered superior to the best-model strategy (Burnham 2004), therefore, for each covariate contained in competing models (\( \Delta AICc < 2 \)), I estimated averaged parameter coefficients, unconditional standard errors, and 85% confidence intervals (CIs; Arnold 2010). Using 85% CIs with AICc model ranking is used increasingly as results are
congruent with model selection and parameter evaluation criteria (e.g. Marini et al. 2013, Steen et al. 2014).

**Results**

I obtained 480 independent detections of hares and 134 of boars, in 1680 camera days. No variables were correlated and season (i.e., year) had no effect on detectability or occupancy for either species. I placed 13 cameras in *N. pumilio* land cover, 33 in *N. antartica* and 34 in *N. dombeyi*. Mean (± standard deviation) for horizontal cover was 6.06 m ± 3.02 m, and for herbaceous vegetation was 29.3% (± 20.1 %). Average distance to the nearest settlement was 1.92 km (± 1.50 km), and to nearest road was 1.48 km (± 1.49 km). Mean number of people per day per site was 11.5 (± 26.3; range = 0–127).

The naïve occupancy estimate (i.e., uncorrected for detection probability) of hares was 0.5. Detection probability for hares being was high (78% in a 7-day survey) and equal among sampling periods, with an overall estimated hare occupancy of 0.52. The global model for hare occupancy had a c-hat estimate of 1.17, which suggests good fit and allowed me to compare simpler models with AICc. The environmental model outperformed the anthropogenic model (ΔAICc = 7.9; Table 1), suggesting that overall environmental variables better explained hare occupancy than anthropogenic variables.

Horizontal cover and distance to nearest settlement were identified as important covariates, and were therefore included in all final models for hare occupancy, represented by 3 competing models (Table 2). Using model-averaged parameter estimates (Table 3), I found that hare occupancy was greater near human settlements (average 0.85 when distance <0.5 km, 0.20 when >5 km) and with less dense cover, represented by increasing D (average occupancy 0.48 when D <10 m; 0.87 when D> 10 m). Occupancy
was lower in the *N. dombeyi* (0.31) land cover than in *N. pumilio* (0.85) and *N. antartica* (0.63) land covers. Herbaceous vegetation and number of people using trails did not influence hare occupancy.

The naïve occupancy estimate for boars was 0.35. Boar detectability was lower than for hares and variable among sampling occasions (20 %, 25 % and 50 %, respectively), with an overall estimated occupancy of 0.53. The global model for boar occupancy had a c-hat estimate of 0.96, suggesting good fit. The full anthropogenic and environmental models were equally supported, and both were outperformed by the global model (Table 1), suggesting that boar occupancy is better explained by a combination of both sets of covariates.

Land cover and distance to nearest settlement were identified as important covariates and were included in all final models for wild boar occupancy, represented by 4 competing models (Table 2). Boar occupancy was greater in *N. dombeyi* (0.53) and *N. antartica* (0.53) land covers than in *N. pumilio* (0.00). As no boars were detected in *N. pumilio* land cover, parameter estimates for the 3 land covers (Table 3) are most likely inaccurate. To assess how this may impact other parameter estimates, I designated sites where the models predict total absence (i.e., all *N. pumilio* sites) as non-habitat, and modeled occupancy on the remaining sites. Complete omission of land cover as a covariate offers no information about the influence of this strong and therefore relevant factor, so excluding it would be inappropriate for ecological interpretation (Heinze and Shemper 2002). As parameter estimates for other covariates were similar after removing *N. pumilio* sites (within 10% and same direction), I included land cover parameter estimates (Table 3), acknowledging that they are likely not precise but nevertheless
informative. In addition to land cover, boars were also affected by distance to settlements, occupancy was greater as distance increased (average 0.30 when <0.5 km, 0.75 when >5 km) (Table 3). Distance to roads had a lesser but significant negative influence (average 0.6 when <0.5 km, 0.4 when >5 km) and horizontal cover and people per day did not influence occupancy (Table 3).

**Discussion**

Hare occupancy was more influenced by environmental factors than anthropogenic disturbance; however, hare occupancy was greater closer to human settlements offering support for the disturbance hypothesis. Lanstcher et al. (2013) also found that hares favored disturbed areas in Patagonia, which is likely related to reduced predation risk, as areas with greater human presence can have a negative effect on mammalian predator occurrence (Hebblewhite et al. 2005). Cardarelli et al. (2010) found that hares selected areas with denser cover that could likely protect them from predation, which contradicts with my findings of greater hare occupancy in areas with more open vegetation, also found by Lanstcher et al. (2013). Greater cover may be less influential at reducing predation risk in developed areas that already deter predators, and open areas could also provide better visibility. Percentage of herbaceous vegetation, although being hares’ primary food source (Galende and Grigera 1998), did not influence occupancy, which is possibly explained by hares’ flexible diet. Hares inhabiting Patagonian grasslands have been found to select true grasses (Poaceae) when available, but can switch to graminoids, forbs, and shrubs when true grasses are less available in more degraded areas (Somlo et al. 1994).
Boar distribution was similarly influenced by anthropogenic disturbance and environmental factors, and offered mixed support for the disturbance hypothesis; occupancy was lower closer to human settlements and greater closer to roads. Red river hogs (*Potamochoerus porcus*) in Gabon, Africa, were also positively influenced by road presence, possibly a result of increased forage; however, they were not influenced by human settlements and appeared to select areas with lower hunting risk (Vanthomme et al. 2013). Alternatively, disturbed areas were potentially advantageous to wild boars in southern Brazil (Desbiez et al. 2009). Although wild boars were intentionally introduced to Patagonia by humans (Novillo and Ojeda 2007), and human activity possibly deters predators (Hebblewhite et al. 2005), unlike European hares, wild boars in Nahuel Huapi National Park are legally (Asociación Parques Nacionales 2011) and illegally hunted (Nahuel Huapi National Park staff, pers. comm.), which might explain their avoidance of human settlements. Hunting risk influences wild boar activity patterns (Ohashi et al. 2013) and space use (Tolon et al. 2009), causing temporal and spatial avoidance of human activity. In this study, boar detectability was low and variable (i.e., although present they were difficult to detect) which could be a consequence of vigilant behavior in the presence of predation risk (i.e., hunting). In addition, the observed nocturnal activity of wild boars in this area (Gantchoff et al. 2013) is similar to the behavior of this species when hunted (Caley et al. 1997). I also found boars occurred only in humid land covers (*N. dombeyi* and *N. antartica*) with no detections in the drier cover (*N. pumilio*), which is in agreement with other studies of this species in Patagonia (e.g., Pescador et al. 2009; Schiaffini and Vila 2012). Greater occupancy in humid forests is likely related to
increased food resources (Pescador et al. 2009), such as plant material, which is a substantial portion of boars’ diet (Ballari et al. 2010).

Hares and boars had diverse responses to human disturbance, indicating a more complex relationship than I originally predicted. These results suggest that species distributions can be differentially influenced by environmental and anthropogenic factors, and each species’ response can vary according to life history traits (Markovchick-Nicholls et al. 2008) and role in human society (e.g., food source). As increased human disturbance leads to increasing habitat fragmentation and degradation (Tabarelli et al. 2010), identifying how humans directly and indirectly influence the distribution and abundance of species will become increasingly important for managers and conservationists (Fletcher and Hutto 2007) who need to distribute limited resources optimally for effective management.
Table 2.1  Global anthropogenic and environmental occupancy models for European hare (a) and wild boar (b), Nahuel Huapi National Park, Argentina, February–May 2012 and January–May 2013. $K =$ number of parameters, $\Delta AICc =$ difference in Akaike Information Criterion score corrected for small sample between best supported model and competing models, $LL = -2 \log$ likelihood, $w =$ Akaike weight.

<table>
<thead>
<tr>
<th>Model(^a)</th>
<th>$K$</th>
<th>$\Delta AICc$</th>
<th>$LL$</th>
<th>$w$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Environmental</td>
<td>6</td>
<td>0.00</td>
<td>204.72</td>
<td>0.52</td>
</tr>
<tr>
<td>Global</td>
<td>9</td>
<td>0.26</td>
<td>198.98</td>
<td>0.46</td>
</tr>
<tr>
<td>Anthropogenic</td>
<td>5</td>
<td>7.91</td>
<td>214.69</td>
<td>0.05</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>9.32</td>
<td>222.04</td>
<td>0.01</td>
</tr>
<tr>
<td>(b) Global</td>
<td>10</td>
<td>0</td>
<td>168.64</td>
<td>0.75</td>
</tr>
<tr>
<td>Anthropogenic</td>
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<td>3.51</td>
<td>178.15</td>
<td>0.13</td>
</tr>
<tr>
<td>Environmental</td>
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<td>3.09</td>
<td>178.54</td>
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</tr>
<tr>
<td>Null</td>
<td>4</td>
<td>10.60</td>
<td>189.04</td>
<td>0.01</td>
</tr>
</tbody>
</table>

\(^a\)Models include: anthropogenic (distance [km] to nearest human settlement, distance [km] to nearest road, and average daily number of people), environmental (land cover [N. pumilio, N. antartica and N. dombeyi], horizontal cover [average maximum visibility in meters of a 30 x 50 cm white cylinder], and, for hares only, herbaceous [average percentage herbaceous vegetation cover]), Null (no covariates), and Full (anthropogenic and environmental covariates).
### Table 2.2

Modeling results describing occupancy for European hare (a) and wild boar (b), Nahuel Huapi National Park, Argentina, February–May 2012 and January–May 2013. K = number of parameters, ΔAICc = difference in Akaike Information Criterion score corrected for small sample between best supported model and competing models, LL = log likelihood, w = Akaike weight. Only models with ΔAICc < 2 are shown.

<table>
<thead>
<tr>
<th>Modela</th>
<th>K</th>
<th>ΔAICc</th>
<th>LL</th>
<th>w</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td>(a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Land cover + Settlements + HC</td>
<td>6</td>
<td>0.00</td>
<td>200.46</td>
<td>0.42</td>
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<tr>
<td>Land cover + Settlements + HC + Herbaceous</td>
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<td>1.82</td>
<td>199.87</td>
<td>0.21</td>
</tr>
<tr>
<td>Land cover + Settlements + HC + People</td>
<td>7</td>
<td>1.87</td>
<td>199.92</td>
<td>0.20</td>
</tr>
<tr>
<td>(b)</td>
<td></td>
<td>(b)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Land cover + Settlements + Roads</td>
<td>8</td>
<td>0.00</td>
<td>172.03</td>
<td>0.21</td>
</tr>
<tr>
<td>Land cover + Settlements + Roads + People</td>
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<td>0.73</td>
<td>169.84</td>
<td>0.22</td>
</tr>
<tr>
<td>Land cover + Settlements + Roads + HC</td>
<td>9</td>
<td>1.65</td>
<td>170.94</td>
<td>0.13</td>
</tr>
<tr>
<td>Land cover + Settlements + Roads + People + HC</td>
<td>10</td>
<td>1.97</td>
<td>168.64</td>
<td>0.14</td>
</tr>
</tbody>
</table>

*aCovariates include land cover (*N. pumilio*, *N. antartica* and *N. dombeyi*), settlements (distance [km] to nearest human settlement), roads (distance [km] to nearest road), people (average daily number), HC (horizontal cover; average maximum visibility [m] of a 30 x 50 cm white cylinder), and herbaceous (average percentage herbaceous vegetation cover).
Table 2.3  Linear covariates for modeling European hare (a) and wild boar (b) occupancy, averaged from competing models (ΔAICc [difference in Akaike Information Criterion score corrected for small sample between best supported model and competing models] < 2), Nahuel Huapi National Park, Argentina, February–May 2012 and January–May 2013. SD = standard deviation. CI = confidence interval.

<table>
<thead>
<tr>
<th>Covariate</th>
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<th>Upper</th>
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</table>

*aModel-averaged parameter estimates. Covariates include: land cover (N. antartica and N. dombeyi in relation to N. pumilio) settlements (distance [km] to nearest human settlement), roads (distance [km] to nearest road), people (average number per day), horizontal cover (average maximum visibility [m] of a 30 x 50 cm white cylinder), and herbaceous (average percentage of herbaceous vegetation cover).
Figure 2.1 Location of Nahuel Huapi National Park, Argentina (solid black square; inset), and study area (southern portion of the national park). Camera traps were located about 1 km apart along trails shown during February–May 2012 and January–May 2013.
References


CHAPTER III
PATTERNS OF COEXISTENCE BETWEEN TWO MESOCARNIVORES IN NORTHERN PATAGONIA

Introduction

Coexisting species usually have similar characteristics resulting from adaptations to the same environment (Grant 1972), while simultaneously diverging in certain traits to reduce competition (Brown and Wilson 1956; Hutchinson 1959). Although the role of inter-specific competition in structuring communities has been debated (Losos 2000; Hubbell 2001), evidence for its importance is increasing (e.g., Davies et al. 2007; Dayan and Simberloff 2005). The competitive exclusion principle (Gause 1934; Hardin 1960) states that two species cannot coexist if they overlap completely in resource requirements, consequently, natural selection for divergent resource use will reduce competition by means of niche partitioning (Davies et al. 2007). If neither competing species is excluded from the community, they may coevolve to achieve morphological segregation (Dayan and Simberloff 2005; Di Bitetti et al. 2010). But species can also coexist by means of behavioral mechanisms, particularly spatial or temporal differences in activity (Schoener 1974a; Kronfeld-Schor and Dayan 2003) or dietary segregation (Walker et al. 2007).

Carnivores face many ecological constraints while seeking to maximize fitness, including prey abundance, spatial distribution and size of prey, hunting cover, presence
of offspring, and competition (Berg 2003). Apart from direct competition for prey, coexistence of multiple carnivore species can also be influenced by intra-guild competition and partitioning of resources. For example, Patagonian grey fox *Pseudalopex grisaseus* and culpeo fox *P. culpaeus* are morphologically similar where allopatric but increase body size segregation when sympatric, presumably to facilitate coexistence (Fuentes and Jaksic 1979; Zapata et al. 2005; 2008). Morphologically similar sympatric species had the most contrasting activity patterns in a tropical felid assemblage (Di Bitetti et al. 2010) and temporal segregation facilitated coexistence between two South American fox species (Di Bitetti et al. 2009). Moreover, habitat segregation between large carnivores in multiple-use European landscapes appears to facilitate coexistence (May et al. 2008).

Patagonian carnivore guilds are poorly understood. Most carnivore studies in Patagonia have emphasized feeding ecology (e.g. Franklin et al. 1999; Delibes and Travani 2003; Pereira et al. 2012); fewer studies have addressed interactions between species (Novaro et al. 2000; Zapata et al. 2007; Palacios et al. 2012). I studied coexistence patterns between Geoffroy’s cat (*Leopardus geoffroyi*) and culpeo fox (*Pseudalopex culpaeus*) in Nahuel Huapi National Park, Argentina. Other similar sized carnivores in this area (i.e., grey fox *P. griseus*, huïña cat *L. guigna*, Pampas cat *L. colocolo*; Ubeda et al 1994), are rare (S. Seijas Nahuel Huapi National Park staff pers. comm.). Geoffroy’s cat average body mass is 4–5 kg (Lucherini et al. 2006) and culpeo foxes weigh 4–9 kg (Novaro 1997). When present, an important part of Patagonian carnivores’ diet is European hare (*Lepus europaeus*; Novaro et al. 2000; Palacios et al. 2012), which is abundant in the park (Merino et al. 2009). In addition, culpeo foxes are
the most carnivorous of South American foxes (Novaro 1997); therefore overlap between these species is likely.

I hypothesized coexistence of Geoffroy’s cats and culpeo foxes would be facilitated by niche segregation, considering species’ similar body size and potential diet. I assessed 4 factors that could influence coexistence categorized as spatial (land cover, anthropogenic disturbance, invasive prey distribution) and temporal (activity patterns of carnivores and invasive prey), predicting segregation in one or more of these factors as a mechanism for coexistence. I also hypothesize that carnivore occupancy will be influenced by tolerance to human disturbance. As with most felids, I expect Geoffroy’s cats to have lower occupancy closer to human disturbance; conversely, I expected culpeo foxes to have greater occupancy closer to human activities given their ecological plasticity (Sillero-Zubiri et al. 2004).

Methods

Study area and sampling

The study was conducted in southern Nahuel Huapi National Park, Argentina (Figure 1). There are three primary ecological regions in the park based on precipitation and elevation: Altoandino, Andino-Patagonico and Patagonic steppe (Veblen et al. 1992). I deployed cameras only in the Andino-Patagonico region, which comprises transitional forests and shrublands from 700 to 1700 m elevation with annual precipitation varying from 600 to 1200 mm. Dominant trees include ñire Nothofagus antarctica, cohiue N. dombeyi, and lenga N. pumilio (IUCN 1982; Veblen et al. 1992). All places surveyed corresponded with areas of the park open to the public.
I established 80 camera stations about 1 km apart along hiking trails from 700 to 1600 m elevation, covering about 60% of available trails in the southern section of the park. Within the constraints of trails, stations were located to spatially represent the range of conditions within the Andino-Patagónico region, encompassing 90% of the elevational gradient (Figure 1). I mounted cameras to trees 30–130 cm above ground and oriented cameras to detect animals traversing trails. I used 30 passive infrared-triggered cameras (Bushnell 8MP Trophy Cam Night Vision Trail Camera, Bushnell, Kansas, USA). I programmed cameras to take three photographs each time the camera was activated, with 10-second intervals between events. At each station, cameras were operative for 21 days. Cameras were deployed from February to May 2012 and January to April 2013.

For each station, I recorded location with a GPS device (Garmin eTrex, Garmin International, Inc., Olathe, Kansas, USA) and measured two environmental (land cover, horizontal cover) and three anthropic (distance to nearest human settlement, distance to nearest road, and average daily number of people) variables. I assigned each camera station to one of three land cover types (N. dombeyi, N. antarctica or N. pumilio) using a vegetation map of the park (500 m resolution; Mermoz and Martin, 1987). I estimated horizontal cover using a cover cylinder (Ordiz et al. 2009). At each station, I placed a white fabric and steel spring wire cylinder (50 cm high by 30 cm diameter) and measured the minimum distance at which the cylinder can no longer be seen ($D$) in the four cardinal directions. I took measurements 40 cm above ground to mimic eye level of a medium-sized mammal. I calculated the mean cover value for each point by averaging the four values. I measured distance to nearest human settlement and road using satellite images (Google Earth, Google Inc., Mountain View, California, USA) and calculated the mean
daily number of people from camera detections at each site. Finally, I performed a single-
species occupancy model for hares, using environmental and anthropic covariates, to
obtain hare (i.e., prey) occupancy probability for each site

**Spatial analysis**

Occupancy modeling addresses several criticisms regarding interspecific
competition studies (Steen et al. 2014). These models allow estimation of detection
probability and species occupancy (MacKenzie et al. 2002; 2006) and to evaluate
whether species co-occupancy happens more or less often than expected by chance
(MacKenzie et al. 2004). Explanatory variables, such as land cover or anthropic
disturbance can be incorporated into the models as covariates to estimate their influence
on co-occupancy patterns. By ranking models, it is possible to determine whether there is
evidence for nonrandom co-occupancy.

For each site, I identified mammals in images to species and created an encounter
history using three 7-day survey periods, for a total of 21 days. I used program
PRESENCE (MacKenzie et al. 2006) to perform a two-species co-occupancy model,
estimating each species occupancy (i.e., probability that the species occurred at a site),
detectability (i.e., probability of a species being detected if present), and the Species
Interaction Factor (SIF; parameterized as φ, explained below). If the most supported
model(s) suggested occupancy probabilities of Geoffroy’s cat and culpeo fox were
independent, I interpreted this pattern most likely due to random processes; however, if
top models explaining occupancy revealed a negative relationship between occupancy
probabilities, I considered this as evidence supporting spatial segregation (Steen et al.
2014). The scale of the study and distance between cameras was large enough to
minimize spatial autocorrelation and pseudoreplication (May et al. 2008). Average
distance movements for Geoffroy’s cats in Argentinian grasslands, using between 3-24
months of tracking data, was 800–1000m (Manfredi et al. 2011) and mean distance
traveled in Spring-Summer in Lihue Calel National Park, Argentina, was 500–900m
(Pereira et al. 2012). Average summer home ranges of culpeo foxes in Chile were 2.2km²
(Salvatori et al. 1999). Thus, it is unlikely that the same animals were detected in more
than one camera causing spatial autocorrelation, especially given the distance between
cameras (1 km) and short sampling period (21 days).

I included the six variables collected as covariates and compared their influence in
coop-occupancy. I performed 12 models, six univariate (i.e., main effect) models assuming
coop-occupancy as independent (SIF = 1) and six assuming an interaction (SIF not fixed). I
also performed two null models (SIF = 1 and SIF not fixed) and tested if season (i.e.,
year) influenced detectability or occupancy. I calculated average parameters values with
85% confidence intervals (CIs), so that results are congruent with model selection and
parameter evaluation criteria (Arnold 2010). I ranked models using Akaike Information
Criterion adjusted for small samples (AICc), considering models equally supported if
ΔAICc was < 2 of the best supported model, and compared models using Akaike weights
(w). I did not correct AICc values for possible overdispersion since no test of model fit
exists for multispecies occupancy models. Then, using the same set of covariates, I
performed single-species occupancy models for Geoffroy’s cats and culpeo foxes
individually, consisting of 5 univariate models and the null model for each species. I
measured model fit by estimating the overdispersion parameter (c-hat; n = 1000 bootstrap
samples) of the global model (i.e., all covariates) for each species (MacKenzie and Baley
Values > 1 suggest there is overdispersion in the observed data and therefore the associated Akaike Information Criterion (AIC) value should be adjusted to perform comparisons between models. Values less than 1 suggest underdispersion but do not represent a problem for interpreting simpler models with AIC (MacKenzie and Baley 2004).

Temporal analysis

I used the package Overlap (Ridout and Linkie 2009; Linkie and Ridout 2011) in program R (R Development Core Team 2013) to estimate the extent of overlap between activity patterns of Geoffroy’s cat and culpeo fox. In addition, I analyzed each carnivore in relation to hare activity. For each species, I categorized data at hourly intervals using time of day of independent detections (i.e., detections separated by > 1 hr; Di Bitetti et al. 2010). Package Overlap estimates species diel activity as a probability density function, and for a pair of species, calculates the degree of overlap between the two estimated densities. I used the overlap coefficient (Δ; Ridout and Linkie 2009) to estimate similarity in activity, which represents the area under the curve formed by taking the minimum of the two density functions at each time point. The overlap coefficient (Δ) can range from 0 (no overlap in activity) to 1 (complete overlap), and 95% confidence intervals were obtained from 500 bootstrap samples. I used Δ₁, suggested for small sample sizes (Ridout and Linkie 2009).

Results

I obtained 51 independent detections of Geoffroy’s cats and 481 of culpeo foxes in 1680 camera days, no other medium-sized carnivores were detected. I placed 13
cameras in *N. pumilio* land cover, 33 in *N. antartica* and 34 in *N. dombeyi*. Average distance to the nearest human settlement was 1.92 ± 1.50 km, and to nearest road was 1.48 ± 1.49 km. Mean daily number of people per site was 11.5 ± 26.3 (range = 0–127). I obtained 485 independent detections of hares; estimated hare occupancy probability was 0.52 ± 0.25. Year had no effect on occupancy or detection probability for either species.

**Occupancy**

Competing models for two-species co-occupancy models (ΔAICc < 2) included the null model with no interaction, distance to roads with and without an interaction between species, and distance to settlements and hares without interaction (Table 3.1). No other covariate influenced co-occupancy. Models assuming no interaction between species accounted for 69% of the AICc weight (w), and models assuming interaction accounted for 31%.

Single –species naïve occupancy estimate for Geoffroy’s cat was 0.25, detection probability was low and constant across periods (28% in a 7-day survey), and estimated occupancy was 0.40. Single species global model for Geoffroy’s cats showed no overdispersion (c-hat = 0.85) and distance to nearest roads was top model explaining occupancy, with no competing (ΔAICc < 2) models. Estimated coefficient for distance to nearest road on Geoffroy’s cat occupancy (± 85% CI) was -0.45 (-0.95 – -0.04). Culpeo fox naïve occupancy was 0.67, detectability was constant and greater (57% in a 7-day survey), and estimated occupancy was 0.75. Single species global model for culpeo fox also revealed no overdispersion (c-hat = 0.80), and none of the covariates was better than the null model explaining occupancy patterns. Culpeo fox occupancy probability within 1 km of anthropogenic disturbance was high, (< 1 km from roads = 0.65 – 0.99; < 1 km
settlements = 0.70 – 0.78) and for Geoffroy’s cats was moderate to low (< 1 km roads = 0.35 – 0.65; < 1 km settlements 0.30 – 0.45). Most sites surveyed with both Geoffroy’s cat and culpeo fox present (11 of 13) were < 1 km from the nearest road.

**Temporal activity**

Activity patterns of Geoffroy’s cat and culpeo fox were similar and coefficient overlap (± 95 CI) was high, (Δ1 = 0.89; 0.68–0.91). Both species were mostly nocturnal with an activity peak between 22 and 00hs (Figure 3). Geoffroy’s cats also had a minor activity peak after dawn (Figure 3). Overlap coefficients were also high between hares and Geoffroy’s cats (Δ1 = 0.89; 0.65–0.90) and hares and culpeo foxes (Δ1 = 0.79; 0.60–0.85; Figure 3). Timing of greatest increases in activity for both carnivore species coincided with hares’ greatest activity increase.

**Diet analysis**

Since I found no strong interactions between Geoffroy’s cat and culpeo fox in relation to spatial and temporal aspects of coexistence, I conducted a literature review of both species’ diet. Publications were located on Scopus and Web of Science using the search terms “*Leopardus geoffroyi* and diet” and “*Pseudalopex culpaeus* and diet”. Studies described diet using various metrics, but percentage frequency (% of identified prey items) was the most commonly reported descriptor, and was therefore chosen for comparison. I found 8 diet studies for Geoffroy’s cat and 10 for culpeo foxes suitable for meta-analysis (Table 3.2). Papers comparing more than one site were treated as different studies, and papers reporting seasonal diet changes in the same area were averaged.
I extracted percentage data for each study and species for 7 categories: small mammals (rodents and small marsupials; < 0.5 kg), medium mammals (≥ 0.5 and < 5 kg; e.g., hares *Lepus europaeus*, pichi armadillo *Zaedyus pichi*), large mammals (≥ 5 kg; e.g., guanaco *Lama guanicoe*, sheep *Ovis aries*, carrion), birds, reptiles and amphibians, arthropods, and plant material. I calculated the weighted mean percentage for each category, using as a weighting factor the number of prey items in a particular study / total number of prey items examined in all studies. I calculated standard 95% confidence intervals for each category by species. I used discriminant function analysis to assess whether the proportions of items consumed in each category across studies could be categorically assigned to Geoffroy’s cats or culpeo foxes, fitting prey categories as a single group of independent variables and species as a fixed factor. Statistical analyses were performed using SPSS v. 19 (IBM, Chicago, IL, USA).

Geoffroy’s cats and culpeo foxes consumed primarily small and medium mammals, including invasive lagomorphs (European hares and rabbits *Oryctolagus cuniculus*; Figure 4a). However, Geoffroy’s cats consumed more birds, reptiles and amphibians, and culpeo foxes consumed more large mammals (including carrion) and plant material. There was strong differentiation between Geoffroy’s cat and culpeo fox diet, with 99% of variation retained in one canonical function (Eigenvalue = 1.76, canonical correlation = 0.79). Negative values of the canonical function were associated with Geoffroy’s cats’ diet and positive values with culpeo foxes ‘diet (Figure 4b).

**Discussion**

When examining species coexistence, it is often difficult to determine whether observed patterns result from interspecific interactions or from alternate processes (Steen 32
et al. 2014). My results suggest that, spatially, Geoffroy’s cats and culpeo foxes coexistence is not influenced by land cover, anthropogenic disturbance, or invasive prey occupancy. Overall, culpeo foxes occupied a bigger proportion of the study area than Geoffroy’s cats, and their occupancy probability had little variation in relation to measured covariates, which could be a result of culpeo fox ecological plasticity (Sillero-Zubiri et al. 2004) or may point to a need to find more fine-scale relevant covariates. Anthropogenic disturbance, in the form of roads, appeared to have a positive influence in Geoffroy’s cats occupancy, which may be related to their use as corridors, as suggested for some carnivores (Beier 1995). Roads and settlements can also act as an area of potentially greater food abundance. For example, Geoffroy’s cats occasionally predate domestic species such as chickens (Gallus gallus domesticus) and have been observed scavenging close to settlements (L. Fonzo Nahuel Huapi National Park staff pers. comm.). Also, greater rodent abundance can occur in areas near roads (Rytwinski and Fahrig 2007). As expected, culpeo foxes had greater occupancy closer to human activities (i.e., roads and settlements) than Geoffroy’s cats. The same pattern of differential occupancy was found between gray foxes (Urocyon cinereoargenteus) and bobcats (Lynx rufus) in a protected area (Riley 2006), and between coyotes (Canis latrans) and bobcats in a fragmented-landscape (Riley et al. 2003).

I found no evidence for temporal segregation between Geoffroy’s cats and culpeo foxes, in contrast with findings of other similar sized sympatric carnivores (e.g., Di Bitetti et al. 2009; Lucherini and Repucci 2009; Gerber et al. 2012). Activity of both species was mostly nocturnal with main activity increasing from dusk to midnight. This activity peak corresponded with European hares’ greatest activity increase. Both
carnivores could be adjusting their activity to maximize encounters with an important prey; I documented 2 occasions of culpeo foxes carrying predated hares at night. Predators that hunt when the probability of prey capture is greatest should have greater prey capture success, and at lower cost, than individuals that forage at random (Schoener 1974b; Belovsky et al. 1989).

Geoffroy’s cat were typically inactive during the day, in contrast with other studies which documented activity more evenly distributed throughout the day (Manfredi et al. 2011; Cuellar et al. 2006). Geoffroy’s cats alter their activity based on prey availability (Pereira 2010), suggesting that primary prey in this study (e.g., rodents and hares) were most vulnerable to predation at night. Culpeo fox activity was primarily nocturnal, in agreement with other studies (e.g., Olarte et al. 2009; Lucherini and Repucci 2009). As with Geoffroy’s cats, culpeo foxes are less nocturnal when small mammal density is low (Salvatori et al. 1999). The assumption that culpeo foxes are more nocturnal when influenced by human disturbance, such as hunting, appears to have little support; culpeo foxes’ activity is better explained by the activity of its prey (e.g., nocturnal rodents; Monteverde and Piudo 2011).

Though relying on vertebrate prey, Geoffroy’s cats and culpeo foxes have diverse diets, as expected for smaller carnivores compared to larger carnivore species (Gittleman 1986). Nonetheless, proportional diet between species varied among some food categories, supporting dietary niche segregation. Although body size of these two carnivores is similar, the slightly larger culpeo fox consumed larger prey than Geoffroy’s cat, consistent with Gittleman (1986), which states that prey size increases with body size. Studies of thropic segregation between sympatric culpeo fox and grey fox
*Pseudalopex griseus* reported results similar to this study (Jiménez et al. 1996; Zapata et al. 2008), with both species having similar diet diversity but the smaller grey fox consuming more rodents and culpeo fox consuming more lagomorphs. From an energetic perspective, carnivores weighing less than 21.5 kg should feed mostly on prey ≤ 45% of their body mass (Carbone et al. 2013). My findings support this prediction, as the main prey for culpeo foxes were small- and medium-sized mammals, representing 5–50% of its’ body mass. For Geoffroy’s cats, main prey items were small mammals, representing < 12% of its body mass.

Coexistence in some carnivore guilds appears facilitated more by spatial or dietary segregation than temporal activity patterns (Fedriani et al. 1999; De Almedia et al. 2004). I found considerable spatial and temporal overlap between Geoffroy’s cats and culpeo foxes, with no evidence of partitioning in activity patterns, land cover occupancy, occupancy in relation to invasive prey or anthropogenic disturbances. However, I found evidence supporting dietary segregation; coexistence between these two mesocarnivores in Nahuel Huapi National Park would appear to be facilitated by partitioning of dietary resources.
Table 3.1 Co-occupancy model results between Geoffroy’s cat and culpeo fox in Nahuel Huapi National Park, Argentina, February to May 2012 and January to April 2013. Species Interaction Factor (SIF) = 1 means occupancy of both species is fixed as independent (i.e., no interaction between species). \( \Delta AIC_c \) = difference in Akaike Information Criterion score corrected for small sample between best supported model and competing models, \( w = \) Akaike weight, \( K = \) number of parameters, \( LL = -2 \) log likelihood.

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<th>( K )</th>
<th>( LL )</th>
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<td>456.58</td>
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<td>People SIF≠1</td>
<td>4.77</td>
<td>0.02</td>
<td>9</td>
<td>456.67</td>
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</table>

\( a \) Variables include land cover (\( N. \) pumilio, \( N. \) antartica and \( N. \) dombeyi), settlements (distance [km] to nearest human settlement), roads (distance [km] to nearest road), people (average daily number), and horizontal cover (average maximum visibility [m] of a 30 x 50 cm white cylinder).
Table 3.2 Literature used for (a) Geoffroy’s cat (*Leopardus geoffroyi*) and (b) culpeo fox (*Pseudalopex culpaeus*) dietary meta-analysis.

<table>
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<td>Johnson &amp; Frankling 1991</td>
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<td>Novaro et al 2000</td>
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Figure 3.1  Location of Nahuel Huapi National Park, Argentina (solid black square; inset), and detail of study area (south section of the national park; left panel). February–May 2012 and January-May 2013. Camera traps were located about 1 km apart along trails shown.
Figure 3.2  Activity density pattern by time of day for Geoffroy’s cat (solid black line), culpeo fox (solid gray line), and European hare (dashed line) in Nahuel Huapi National Park, Argentina, February to May 2012 and January to April 2013.
Figure 3.3  Meta-analysis of Geoffroy’s cat (black, left) and culpeo fox (white, right) diet. (a) Weighted mean percentage (and 95% confidence intervals) for each food category. (b) Discriminant function analysis between Geoffroy’s cat (black circles) and culpeo fox (white circles) diet. Correlation between food categories and discriminant function are shown. Mammal categories include small (< 0.5 kg), medium (≥ 0.5 kg and < 5 kg) and large (≥ 5 kg) species.
References


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CHAPTER IV
SUMMARY AND CONCLUSIONS

Many introduced species fail to establish populations or remain restricted to the immediate vicinity of the new sites of occurrence, while others establish populations and invade new habitats, occasionally spreading well beyond the initial point of introduction (Simberloff and Rejmánek 2011). South America accounts for 37 mammal species introductions, from which 25 are successfully established (Long 2003), and most (76%) occur in the southern cone of Argentina and Chile. Protected areas are generally expected to be less susceptible to species invasions, but in the National Parks System of Argentina, the level of occurrence of invasive mammal species is high, almost 80% of the parks host ≥1 species (Merino et al. 2009). In Nahuel Huapi National Park, the most abundant invasive mammals are European hares (Lepus europaeus) and wild boars (Sus scrofa) (Merino et al. 2009), introduced to Patagonia in the 1900s (Novillo and Ojeda 2008).

Hares and wild boars in Nahuel Huapi National Park overall responded differentially to anthropogenic disturbances and environmental factors. Although both species were intentionally introduced to Patagonia (Novillo and Ojeda 2008), at present evidence suggests opposite responses to human settlements; hare occupancy was greater while boar occupancy was lower closer to settlements. In addition, wild boars appeared to be positively influenced by roads. This suggest that generalizations on invasive species
might not always be appropriate; factors like intrinsic traits and how they interact with humans (e.g., hunting) should not be overlooked. Since humans can also be considered an invasive species, one could consider human facilitation of invasives as a special case of invasional meltdown, as suggested by Simberloff and Holle (1999).

To further understand the impact of invasive species, it is vital to study how native communities adapt to them once established; however, this is inherently difficult, since the ways in which invasive species can influence natives can be complex (Simberloff and Rejmánek 2011). In Argentina, invasive mammal species can compete with or displace native herbivores (Galende and Grigera 1998) and become novel prey for native carnivores, even leading to the ecological extinction of native prey (Novaro et al. 2000). In particular, in Patagonic areas where European hares occur, they have become an important part of native carnivores’ diet (Palacios et al. 2012) and this change in prey availability should in turn influence how these carnivores coexist.

While assessing the potential influence of hares and anthropogenic disturbance on native species, I found high spatial and temporal overlap between Geoffroy’s cats \textit{(Leopardus geoffroyi)} and culpeo foxes \textit{(Pseudalopex culpaeus)}. I observed European hare distribution did not influence these carnivores’ occupancy patterns; however, both carnivores appeared to adjust their activity to maximize encounters with this invasive prey. These results support the diet meta-analysis, which demonstrated that a considerable part of Geoffroy’s cat and culpeo fox diet includes medium sized mammals. The dominant medium-sized prey in Nahuel Huapi National Park was European hare, as evidenced by my camera surveys. A possible explanation for hare distribution not influencing carnivore occupancy may be that hare abundance was not low enough to
become a spatially limiting resource. In addition, I found no evidence for anthropogenic disturbance influencing Geoffroy’s cat and culpeo fox spatial coexistence; however, Geoffroy’s cat occupancy was greater closer to roads, most likely due to increased food sources.

Humans appeared to act as both a positive and negative influence in this community, being responsible for the introduction of invasive species and further facilitating their expansion, while at the same time limiting the distribution of some invasive species. In addition, humans are a potential benefit to native species, for example, by introducing novel prey sources. I recommend that future studies survey more areas and conduct local carnivore diet studies in addition to abundance or occupancy surveys for important prey. I also recommend including human population density, type of road, and measure hunting intensity to better comprehend the impact of anthropogenic activity. This will provide knowledge needed to further understand species interactions within this community and what influences species’ distributions. Undoubtedly, biological invasions, anthropogenic disturbance, and native communities can have complex interactions. Understanding their ecology can help provide effective tools for management and conservation in protected areas.
References


