FACULTAD DE CIENCIAS – UNIVERSIDAD DE CHILE

# *Lycalopex culpaeus* in agricultural landscapes of central Chile: effects of neighboring natural area and prey availability on the abundance and activity of a native fox

## Tesis

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**Por**

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# FACULTAD DE CIENCIAS

# UNIVERSIDAD DE CHILE

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**Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Magíster presentada por la candidata.**

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**Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Magíster en Ciencias Biológicas, en el examen de Defensa Privada de Tesis rendido el día …………………………….**

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**RESUMEN**

Los carnívoros son uno de los grupos de vertebrados más amenazados por la pérdida de hábitat. Dado que los carnívoros desempeñan importantes funciones ecosistémicas (e.g., control poblacional de presas y plagas) es prioritario entender cómo responden a los cambios del paisaje. Chile central se caracteriza por paisajes complejos con tierras productivas intensivas y remanentes de bosques esclerófilos. Bajo este contexto, monitoreamos la actividad diaria del zorro nativo *Lycalopex culpaeus* y sus potenciales presas utilizando trampas cámara en plantaciones de cerezo y manzano, con diferentes porcentajes de área natural a su alrededor. Analizamos los patrones de actividad diaria tanto para el zorro como para sus posibles presas. Para evaluar el efecto del paisaje y potenciales presas en la abundancia del zorro, generamos modelos lineales utilizando la vegetación nativa que rodea los huertos y la abundancia de posibles presas como variables predictoras. Los patrones de actividad diaria del zorro mostraron una actividad mayormente diurna en los huertos de agricultura intensiva y mayor solape de actividad diaria con la liebre exótica *Lepus europaeus*. La cobertura de vegetación nativa y la posible presa *Lepus europaeus* tienen una relación positiva con la abundancia de *Lycalopex culpaeus*. Este estudio entrega una importante visión de las poblaciones de carnívoros nativos dentro de los agroecosistemas de Chile central.

## ABSTRACT

Carnivores are one of the most threatened groups by habitat loss. Given the important ecosystem functions that carnivores perform (e.g. prey and pest populations control) it is important to understand how they respond to landscape change. Central Chile is characterized by complex landscapes with intensive productive lands and remnants of sclerophyllous forests. Under this context, we monitored the daily activity of *Lycalopex culpaeus* and its potential prey using camera traps in cherry and apple plantations of Central Chile surrounded by different amounts of natural area. We recorded the daily activity pattern and analyzed both the carnivore and potential prey activity. To assess the effect of the potential prey and the landscape in the fox abundance, we performed linear models using the natural area surrounding the orchards and the possible prey records. Daily activity patterns of foxes showed mostly diurnal activity in intensive agricultural orchards and greater overlap of daily activity with the exotic hare *Lepus europaeus*. Native vegetation cover and potential prey *Lepus europaeus* have a positive relationship with *Lycalopex culpaeus* abundance. This study provides important insight into native carnivore populations within the agroecosystems of central Chile.

# INTRODUCTION

Agricultural activity is one of the main causes of land use change, due to the exponential growth of the human population and their resource demand (Boserup, 1975; Schneider et al., 2011). This scenario limits resource availability, affecting animal behavior and their distribution in different ways (Bentley et al., 2000; Schneider, 2001; Wiegand et al., 2005). Despite the important and positive effects in regulating pests and invasive species in agroecosystems that native carnivores perform (Roemer et al., 2009; Williams et al., 2018), their populations are highly threatened by habitat loss, resource depletion, attacks by feral dogs, direct persecution by the livestock ranchers, and mortality due to diseases transmitted by exotic species (Acosta-Jamett et al., 2011; Galvez et al., 2021; Moreira-Arce et al., 2015; Silva-Rodriguez & Sieving, 2011; Silva-Rodriguez et al., 2009; Thorn et al., 2012; Treves & Karanth, 2003; Vanak et al., 2009).

Notwithstanding, in many cases, carnivores have been able to adapt to environmental modifications by maintaining their populations, obtaining food resources from agroecosystems (Curveira-Santos et al., 2017; Verdade et al., 2011), but also undergoing changes in their activity and prey selection patterns (Crooks, 2002; Newbold et al., 2020; Salek et al., 2015). The study of activity patterns is an important approach for ecology, as it gives an insight into animal behavior and physiological response to external stress factors, such as human activity and exotic fauna (Ouboter et al., 2021; Zapata-Ríos & Branch, 2016).

Moreover, the animal circadian clock is the result of millions of years of evolution, and so any change in it means an important energy cost for the animal as it affects their fitness and body condition (Dominoni, 2015).

*Lycalopex culpaeus* is a native mesocarnivore with a wide distribution range in South America, which is commonly found in agricultural lands (Escudero-Paez et al., 2019; Moreira-Arce et al., 2016; Simonetti et al., 2013). Its diet has been described as generalist and opportunistic (Carevic et al., 2019). For example, in the Chilean desert, the preys are mainly composed of arthropods, followed by reptiles and micromammals (Carevic et al., 2019). In the Andes of northern Chile, its diet consists of rodents, arthropods, camelids, birds, and reptiles (Lagos et al., 2021). But in a national park in the south of Chile, its diet corresponds principally to rodents followed by lagomorphs and birds (Zúñiga & Fuenzalida, 2016). According to this and, moreover, the exhaustive compilation made by Medel and Jaksic (1988) and Guntinas et al. (2021), *L. culpaeus* generalist diet is opportunistic, including what is available in the environment and among seasons.

An important food item for native carnivore species in Chile corresponds to the European hare (*Lepus europaeus*) (Castillo-Ravanal et al., 2021; Rubio et al., 2013; Zapata et al., 2005), an exotic lagomorph, abundant in Chilean agroecosystems. For example, it has been reported as part of the diet for the culpeo fox (*Lycalopex culpaeus*), the puma (*Puma concolor*), the lesser grison (*Galactis cuja*), and the Andean-Skunk (*Conepatus chinga*) (Buenavista &

Palomares, 2018; Guerisoli et al., 2021; Palacios et al., 2012; Rubio et al., 2013; Zúñiga et al., 2018).

It is known that native carnivores depend on natural area patches located within agricultural environments (Lyra-Jorge et al., 2011), as their activity tends to correlate with habitat structure features, such as tree density in native patches, shrub density, and soils rich in organic matter (Carvalho et al., 2011). Previous studies highlighted the importance of the quality of native patches and corridors for the presence, abundance, and activity (Davis et al., 2021; Fontúrbel et al., 2021; Shapira et al., 2008; Vilella et al., 2020) of native carnivores in agricultural landscapes, since they provide prey availability (Cervinka et al., 2013; Ferreira et al., 2018; Pereira & Rodriguez, 2010; Pita et al., 2009; Salek et al., 2009). Gálvez et al. (2021) found that *L. culpaeus* activity was insensitive to habitat structure such as forest cover, fragmentation, and land subdivision in an anthropogenic landscape scenario. However, *L. culpaeus* abundance was high in an agroecosystem with a high area of natural area around. In addition, the activity of *L. culpaeus* extensively overlapped with that of exotic prey in highly fragmentated scenarios, suggesting that carnivore's activity and foraging behavior depends on anthropogenic habitats (Gálvez et al., 2021). *Lycalopex culpaeus* habitat use and generalist diet make it a good study model to assessing the effect of agroecosystems in carnivore food sources, and daily activity patterns.

Central Chile is a biodiversity hotspot due to its high levels of endemism

(Myers et al., 2000) as it is highly threatened by land use change due to agricultural expansion (Armesto et al., 2010; Brooks et al., 2002). Accordingly, it is important to understand how these processes work and inform decision-makers regarding environmental management and agricultural practices. Thus, on this study we assessed the effect of natural area adjacent to agricultural habitats on the abundance and behavior of *Lycalopex culpaeus*. We hypothesized that: (1) higher amounts of native nearby vegetation affects the mesocarnivore behavior by maintaining their predominantly crepuscular-nocturnal activity pattern, (2) higher prey availability will positively affect the abundance of *L. culpaeus* in the agricultural landscape of central Chile, and (3) as natural area increases nearby agricultural plantations, *Lycalopex culpaeus* will positively respond by increase their abundance.

## MATERIALS AND METHODS

*Study area*

We conducted this study between the O'Higgins and Maule regions (32° to 35° S) in central Chile (Figure 1). The Chilean central valley is characterized by a heterogeneous landscapes with mosaics of intensive productive lands (the most important area for fruit production of high economic importance in Chile) and remnants of sclerophyllous forest interspaced (Luebert & Pliscoff, 2006) in public and private lands, along with semi-natural habitats.

*Study species*

The mesocarnivore *Lycalopex culpaeus* (Canidae) is a common South American fox distributed from Colombia to Tierra del Fuego (Iriarte & Jaksic, 2017; Lucherini, 2016). This species can be found from sea level until ~4800 m of elevation, and is considered as a habitat and diet generalist species (Carevic et al., 2019). Its wide distribution encompasses different habitat types, such as mountains, valleys, desert soils, thorny scrublands, forests and agricultural lands, and forest monocultures (Escudero-Paez et al., 2019; Moreira-Arce et al., 2016; Simonetti et al., 2013). The diet of *L. culpaeus* is predominantly carnivorous, with lagomorphs and small rodents as its main food sources. Birds, reptiles, arthropods, eggs, and fruits are often found in their feces (Carevic et al., 2019; Guzmán-Sandoval et al., 2007; Iriarte et al., 1989; Zúñiga & Fuenzalida, 2016). The available literature highlights that the European hare (*Lepus europaeus*), an exotic and invasive species in Chile, is one of the main food items for *Lycalopex culpaeus* (Castillo-Ravanal et al., 2021; Rubio et al., 2013). *Lycalopex culpaeus* activity is concentrated in crepuscular and nocturnal hours; however, diurnal activity peaks have also been recorded (Gálvez et al., 2021; Monteverde & Piudo, 2011; Salvatori et al., 1999).

*Selection of sampling sites*

Based on the 2020 geo-referenced Fruit Cadaster (ODEPA, 2021), we selected a total of 1,016 red apple and 11,433 sweet cherry orchards, all of them operated commercially at present. For each orchard, we calculated the proportional area of different land use within a 1 km-wide buffer polygon around it. We used the land use layer of Zhao et al. (2016). Then, we categorized each orchard depending on the area of the adjacent natural habitat, considering a 1 km radius buffer, hereafter Categories (Cat1 = 0-35%; Cat2 = 35-70%; and Cat3 = over 70%). Finally, we selected six 15 x 15 km landscapes, three for cherry (C2, C4, C5) and three for apple (A1, A2, A3) orchards (referred as landscapes hereafter) (Soto et al., 2023). Additionally, for each camera trap installed within the orchards, we estimated the percentage of natural vegetation (i.e., native forests and shrubland) in a 1-km ratio around each camera trap.

*Data collection and processing*

We monitored carnivores using infrared camera traps (Browning Strike Force Pro XD) a methodology that reduces observer interference (Kucera & Barrett, 2011). We conducted the monitoring between January 2021 to December 2021 using a total of 54 camera traps. We set three cameras on each of the three categories (i.e., Cat1, Cat2, Cat3), within each landscape replicate (i.e., A1, A2, A3, C2, C4, C5). Each camera was located randomly using the QGIS 3.20.2 *polygon research tool*, separated by a minimum of 500 m one from each other. At each sampling point, a camera trap was installed on a tree 30–40 cm high to record terrestrial wildlife activity. All camera traps were set facing southwards to avoid sunrise/sunset light overexposure. All camera traps were set up to record three images per trigger, with a delay of 10 s between consecutive shots. The cameras were relocated within the orchards every 60 days using QGIS 3.20.2 (Soto et al., 2023).

The photographs obtained were analyzed with NAIRA v.3 (Pulido et al., 2018), a software program designed to process images obtained with camera traps. The following metadata was automatically extracted from each photograph: code, day, month, year, and time of recording, and a database was created. The identification of the content of each photograph was made by visual observation by one observer, and manually recorded in the database. In photographs with animal presence, the species and number of individuals were recorded. In the case of unclear images, they were identified at the level of genus, family, or animal type (i.e., canid, bird, feline, rodent).

*Data analysis*

*Orchard selection*.- We first conducted a spatial autocorrelation analysis using PASSAGE v2 (Rosenberg & Anderson, 2011) to determine if our camera-trap data was autocorrelated using Geary’s correlogram, which measures the degree of spatial correlation between environmental variables across distance classes (Anselin, 1995; Mathur, 2015). We obtained Geary's correlogram for *L. culpaeus* with a Bonferroni corrected significance level of P = 0.516, meaning that out data was not significantly autocorrelated (Geary, 1954).

*Daily activity analysis*

All statistical analyses were conducted using the statistical software R 4.2.1 (R Core Team, 2022). As our study is focused on the activity patterns of *Lycalopex culpaeus* and the effect of the landscape, rather than population estimates, we used the number of records of the predator and the possible prey. We used the date and time of each photograph of *L. culpaeus* and their potential prey (native and exotic) to represent time in radians. With these data, we fitted the activity density kernels for each landscape (i.e., C2, C4, C5, A1, A2, A3) and for each type of category (i.e., Cat1, Cat2, Cat3). To study predator and potential prey activity patterns, we estimated Kernel density (Rowcliffe et al., 2014). Then, we performed pairwise comparisons in activity patterns using the $Dhat_4$ overlap coefficient (as recommended by Ridout and Linkie (2009)), which indicates the degree of overlap between two activity kernels. We conducted randomization procedures with 1000 permutations to test for the significance of comparisons. As the daily light hours changes during the year, we also separated these analyses by season of the year. Analyses were performed using the R packages 'activity' (Rowcliffe, 2022) and 'overlap' (Ridout & Linkie, 2009). To assess if the activity pattern of *L. culpaeus* differed among the Categories (Cat1, Cat2, Cat3), the Mardia-Watson-Wheeler test was performed using the ‘circular’ R package (Agostinelli & Lund, 2022). The Mardia-Watson-Wheeler test detects if two circular samples significantly differ from each other and gives us the test statistic, which is approximately distributed as a chi-squared (Batschelet, 1981).

To assess the difference of *L. culpaeus* activity pattern between the study agroecosystem and native areas, we obtained the records of *Lycalopex culpaeus* within the Rio Los Cipreses National Reserve located in the O'Higgins Region (34°27′54″S 70°27′18″O), which was used as a reference site. The data base of the "Program for photo monitoring conservation targets and threats in the Sistema Nacional de Areas Protegidas del Estado (SNASPE)" (CONAF, 2021) consists of camera trap records between 2017-2019, with a complete monitoring in one season (4 months) per year. The database contains a total of 11,676 records for *L. culpaeus*. We performed the Mardia-Watson-Wheeler test between the study crops and the reference site (Reserva Nacional Rio Los Cipreses).

During the camera trap installation in 2021, fieldwork was limited due to COVID-19 restrictions. Therefore, Spring season records were limited due to grass growing in front of the camera traps, which we could not remove due to the lockdown. This is the reason why the Spring season did not register foxes.

*Lycalopex culpaeus abundance*

To assess the effect of the natural habitat coverage on *L. culpaeus* abundance, we performed paired factor comparisons (i.e., Cat1, Cat2, Cat3) to the calculation of estimates and p-values. We used the R package 'lsmeans' (Lenth, 2016). We performed two analyses (1) the effect of adjacent natural habitat coverage on *L. culpaeus* abundance and (2) the relationship between fox abundance and prey availability, we fitted multiple Generalized Linear Mixed Effects Model (GLMM hereafter) with a Poisson zero-inflated error distribution (to account for data overdispersion). In the first analysis, we evaluated two models i) using natural habitat as a categorical variable (i.e., Cat1, Cat2, Cat3), and ii) as a continuous variable (percentage of natural area in the 1 km ratio around each camera trap) as a fixed factor, using fox abundance as response variable in both cases. In the second analysis, we used fox abundance as a response variable, and the combination of all potential prey and natural area categories or continuous as fixed factors. In both analyses, we used landscape as a random factor (Table 1). Because overdispersion of the data was detected, we used adjacent natural habitat as a continuous variable (Model 2, see Table 1) and fitted a GAMM analysis using fox abundance as response variable and adjacent natural habitat as fixed factor, with the landscape as random effect. We used the packages "glmmTMB" (Brooks et al., 2017), "pscl" (Jackman, 2020), "mgcv" (Wood, 2011) for these analyses. To assess the parsimony of our models (Aho et al., 2014; Burnham & Anderson, 1998) we ranked the models based on the Akaike Information Criterion (AIC), using "AICmodavg" package (Mazerolle, 2020). Additionally, we obtained the variance inflation factor (VIF), which is a function of the independent variables, and it measures the degree of collinearity between them, with values VIF<4, we assumed that there is no collinearity (Craney & Surles, 2002).

## RESULTS

We obtained 919 records of *L. culpaeus*, from which 163 occurred in Cat1, 226 in Cat2 and 530 in Cat3 (Table A2). *Lycalopex culpaeus* was present in every landscape, and in every category (i.e., Cat1, Cat2, Cat3), except for the A3 and C2 landscapes where foxes were recorded in Cat1/Cat3 and Cat3, respectively (Table 2).

Regarding *L. culpaeus* potential prey, the most abundant is the exotic hare *Lepus europaeus. Lepus europaeus* had a total of 102,592 records, of which 11,279 occurred in Cat1, 26,988 in Cat2, and 64,325 in Cat3. To assess other potential prey, as birds are part of the fox food source, we selected the second most abundant animal recorded, the native bird *Turdus falcklandii* (Passeriformes, Turdidae). *Turdus falcklandii* had a total of 12,618 records, of which 3,256 occurred in Cat1, 3,956 in Cat2 and 5,406 in Cat3.

### *Daily activity patterns*

*Lycalopex culpaeus* daily activity was mainly crepuscular and nocturnal in all habitat categories (Figure 2), concentrated between 18:00h and 07:00h. However, there were important diurnal peaks around 11:00 h in Cat1, and other smaller activity peaks during the day in all cases (Figure 3). As the day light hours changes considerably during the year, we decomposed the daily activity patterns according to seasons (i.e., autumn= March-June; winter= June-September; spring= September-December; summer= December-March) and according to the categories (Figure 4). In Cat3, the activity started at 18:00h during winter and autumn, and in spring and summer, just when the night begins. There is a different scenario in Cat1 and in Cat2, where the activity patterns show diurnal peaks. In Cat1, there is a diurnal peak during Summer at 12:00h, and in Cat2 there is a diurnal peak at 09:00 h during Winter.

The daily activity pattern of *L. culpaeus* within the agricultural orchards is responding to the near natural area, with the Cat1-Cat2 being different (Mardia-Watson-Wheeler test: W= 55.92, p-value < 0.001), as it is the Cat1-Cat3 (W= 29.91, p-value < 0.001). The comparison between Cat2-Cat3 showed no significant differences (W= 3.91, p-value = 0.1415). The same comparison of the activity pattern using the Categories and the Los Cipreses National Reserve shows different activity patterns between Cat1-Los Cipreses (W= 26.01, p-value < 0.001) and Cat2- Los Cipreses (W= 19.08, p-value < 0.001). When contrasting Cat3- Los Cipreses there was no difference (W= 2.41, p-value = 0.299), meaning there is no difference between those conditions regarding the fox activity. The activity pattern of *Lycalopex culpaeus* was mainly crepuscular- nocturnal in the native habitat of the Los Cipreses National Reserve (Figure 5).

The daily activity overlapping of *L. culpaeus* with each of its potential prey (Figure 6) showed high activity overlap between *L. culpaeus* and *Lepus europaeus*, with high index values (Dhat4) and statistically significant in all cases (p-value < 0.001). As it was expected considering that *T. falcklandii* is a diurnal bird, *Lycalopex culpaeus* and *Turdus falcklandii* presented low activity overlap index Dhat4 (Figure 6). The activity overlapping is higher between *L. culpaeus* and *L. europaeus* than between *L. culpaeus* and *T. falcklandii* (Figure 6), meaning that *L. culpaeus* and *L. europaeus* are both active at the same time. The analysis decomposition by season (Figures 7 to 10) shows the same crepuscular-nocturnal activity patterns for *Lycalopex culpaeus* and *Lepus europaeus*, and diurnal activity patterns for the bird *Turdus falcklandii*, and higher Dhat4 index for the fox and the hare as it happened in the one-year period analysis.

*Lycalopex culpaeus* abundance

The paired comparisons of *L. culpaeus* abundance between the categories revealed that the fox abundance is influenced by the natural area coverage, with Cat1 differing from Cat3, and Cat2 differing from Cat3 (p-value $<0.05$) (Figure 11). The natural area cover surrounding the orchards was important, both as categorical and continuous variable (Table 3). The category by itself is affecting positively the abundance of *L. culpaeus* (Model 1 estimate: $0.403 \pm 0.097$, p-value$<0.01$). In the Model 2 the natural area cover (expressed as the exact percentage of natural area within the buffer) affects the abundance of *L. culpaeus* positively (Model 2 estimate: $0.006 \pm 0.002$, p-value$<0.01$). As it is the potential prey that showed higher and significant overlap with the fox, the hare was the main potential prey we tested. In the Model 3 the effect of the hare itself indicates a significant positive effect on the fox relative abundance (Model 3 estimate: $9.58e\text{-}5 \pm 3.15e\text{-}5$, p-value$<0.01$). The Model 4 and the Model 5, that assessed the effect of the main possible prey and the environment, demonstrated the positive effect of both variables. Furthermore, the five mixed models exhibit a positive slope (Table 4), supporting the positive response of the fox to the prey and the environment natural area cover.

## DISCUSSION

In the one-year sampling*, L. culpaeus* was the only native carnivore recorded in the study area. Due to its habit as a habitat generalist and wide home range, it was expected to be found it in our agricultural landscape, as has been previously reported for other landscapes of human intensive use (Galvez et al., 2021; Lucherini, 2016; Zúñiga et al., 2018). Its ability to use these habitats can be explained by its generalist diet and its ability to change its foraging behavior, such as its activity patterns and food sources (Castillo-Ravanal et al., 2021; Sanglas & Palomares, 2022; Streicher et al., 2022; Zapata et al., 2005).

The European hare *L. europaeus* is a highly-invasive species worldwide (Bonino et al., 2010; Green et al., 2013). It was the most abundant vertebrate on the three categories of our study, with its higher numbers on those orchards with higher natural area cover (Cat3). Open spaces are often their preferred habitats; although, they show a high plasticity in their habitat use (Smith et al., 2005; Vidus-Rosin et al., 2012). In this case, those orchards surrounded mainly by natural area were their preferred habitat. So, even when orchards show low natural area cover and are mainly open spaces, they may not be able to sustain the different food items preferred by the animal, which consists of grasses, roots, branches, and other available herbs (Jennings et al., 2006; Reichlin et al., 2006).

The activity of *Lycalopex culpaeus* was crepuscular/nocturnal with few diurnal activity peaks (Figures 2 and 3). Diurnal peaks occurred in all categories of our study. However, the activity density in orchards of higher natural area showed less diurnal activity than those with lower natural area surrounding them. In the orchards with lower vegetation cover (i.e., Cat1), some diurnal peaks were equivalent to the relative abundance peaks occurring at night. However, Gálvez et al. (2021) described a cathemeral activity behavior for *L. culpaeus*. In native habitats *L. culpaeus* activity was mainly crepuscular/nocturnal (Monteverde & Piudo, 2011). Moreover, when comparing the activity pattern of *Lycalopex culpaeus* in our Cat3 with the Los Cipreses National Reserve, they were not significantly different. This is first evidence that supports that the larger availability of a native matrix is maintaining the original foraging behavior of *Lycalopex culpaeus*, which can be traduced to a less stressful environment for the animals.

According to our activity analysis, *L. europaeus* is the main possible prey that mostly overlaps its activity with *L. culpaeus* (Figure 6). They both concentrate their foraging and travel activity in twilight and nighttime periods (Gantchoff et al., 2013; Monteverde & Piudo, 2011). Even when it is an exotic source of food for *Lycalopex culpaeus*, *Lepus europaeus* has shown to be an in important food item for *Lycalopex culpaeus* and other native carnivores in Chile when in native and exotic habitats (Buenavista & Palomares, 2018; Palacios et al., 2012; Rubio et al., 2013). Disturbance of natural habitats has made these ecosystems more vulnerable to biological invasions, which became a critical problem for native biodiversity and agroindustry (Marvier et al., 2004; Paini et al., 2016). *L. europaeus* is an herbivore that has significant negative consequences for crops, being considered an important agricultural pest, but also for the natural regeneration of natural area (Huertas Herrera et al., 2022). Therefore, promoting a greater abundance of foxes in more complex landscapes could provide higher pest control services in agricultural landscapes.

The abundance of *L. culpaeus* in the study orchards responded positively to the percentage of natural area cover around them and to the abundance of the exotic hare *L. europaeus* (see Tables 3 and 4). Moreover, the natural area covers around the orchards was an important variable to the foxes, being their abundance significantly and positively related to area cover (Table 4), as found in Soto et al. (2023), where vertebrate fauna biodiversity responded positively to vegetation cover. *Lycalopex culpaeus* has high plasticity in the habitat use. However, and even when it is a generalist carnivore, they are being affected by the agricultural landscape conditions, that increases human activities and exotic fauna species as agriculture lands intensifies (Soto et al., 2023). Additionally, vertebrate diversity recorded in our study area increased with vegetation cover (Soto et al., 2023). This fact can be explained by the availability of resources of sites, as the habitat requirements vary among species (Holzkämper et al., 2006). The landscape heterogeneity provided by the native habitat surrounding the orchards must be playing an important role in resource availability (Fahrig et al., 2011). For example, the orchards located within intensively agricultural landscapes (i.e., Cat1) can provide almost only what the agricultural activity allows. In those orchards, the availability of refugees may also be a problem, as they are mainly limited to vegetative corridors. This scenario might be important to *L. culpaeus* and other native carnivores and mammals, as mammals depend and respond to the availability of different food options that can be affected by the spatial conditions such as, for example, the native understory in anthropogenic landscapes (Simonetti et al., 2013).

Ecosystem functioning rely on all organisms and their interactions working, and even when *L. culpaeus* inhabits our three orchards, our study area houses other native carnivores, and none of them was recorded by our camera traps. Meaning that these ecosystems do not serve as habitats for the other Chilean carnivores and that they are more sensitive organisms to habitat transformation (Ferreira et al., 2018). Our results strongly suggest that (1) Agroecosystems can contribute to maintaining carnivore populations when there is a certain amount of neighboring vegetation cover; (2) Agroecosystems with higher amount of vegetation cover are less stressful environments for *Lycalopex culpaeus*, as their activity patterns showed no difference with their activity patterns inside near a national reserve, and (3) Despite *Lepus europaeus* is an exotic and invasive species to Chile, it may be an important food item for the native fox, and it may be playing an important role as its prey, and orchards constitute suitable habitats that provide resources for this native carnivore.

Our study showed the importance of conserving remnants of natural area in agricultural landscapes to protect native fauna, especially carnivores that can trigger a trophic cascade. We hope that our results contribute as an input to decision-makers, producers, and public policies to the understanding that not all habitats are usable for native fauna, especially when those habitats are used only for productive vegetation as the ones of this study, and to promote agriculture practices and management that improve the use of crops by carnivores.

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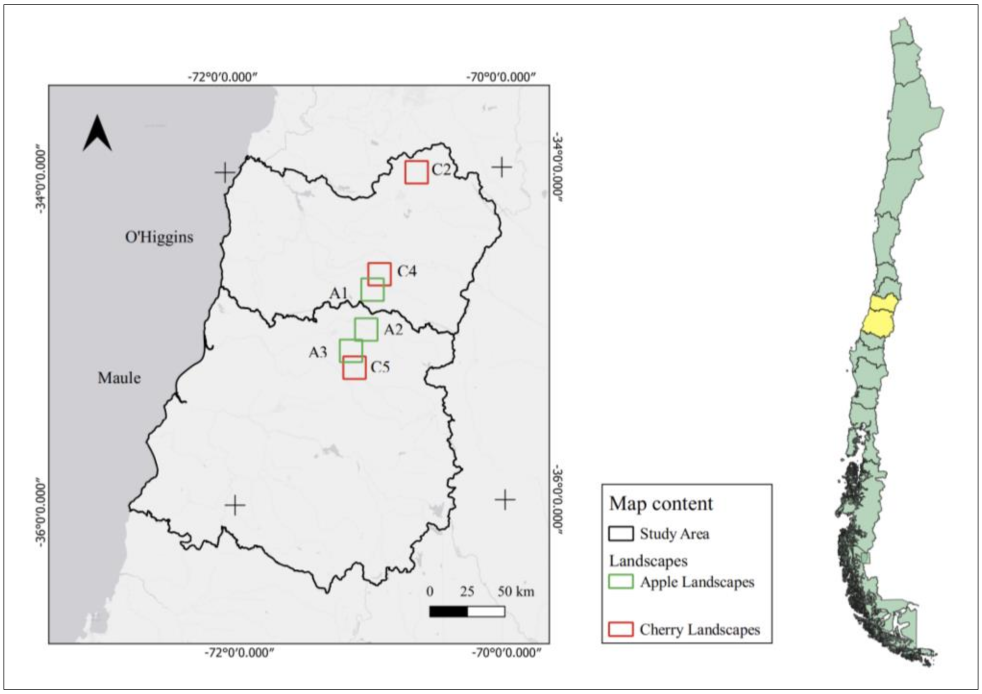


**Figure 1.** Study area located in the O'Higgins and Maule regions in Central Chile.

**Table 1**. VIF and AIC indices of the Mixed Models.

| ID Model | Model | VIF | AIC |
|---|---|---|---|
| 1 | (*L. culpaeus~Category*+(1 \| Landscape) | 1.00 | 2377.0 |
| 2 | (*L. culpaeus*~ Natural_area_cover+(1 \| Landscape) | 1.01 | 2375.8 |
| 3 | (*L. culpaeus~Lepus europaeus*+(1 \| Landscape) | 1.07 | 2364.9 |
| 4 | (*L. culpaeus~Lepus europaeus*+Category+(1 \| Landscape) | 1.28 | 1377.0 |
| 5 | (*L. culpaeus~L. europaeus*+ Natural_area_cover + (1 \| Landscape) | 1.27 | 1378.1 |

**Table 2.** *Lycalopex culpaeus* records in all our study Landscapes and Categories of natural area cover.

| Landscape | Category | N° records |
|---|---|---:|
| A1 | Cat1 | 6 |
| A1 | Cat2 | 155 |
| A1 | Cat3 | 101 |
| A2 | Cat1 | 10 |
| A2 | Cat2 | 0 |
| A2 | Cat3 | 49 |
| A3 | Cat1 | 27 |
| A3 | Cat2 | 0 |
| A3 | Cat3 | 17 |
| C2 | Cat1 | 0 |
| C2 | Cat2 | 0 |
| C2 | Cat3 | 119 |
| C4 | Cat1 | 83 |
| C4 | Cat2 | 23 |
| C4 | Cat3 | 129 |
| C5 | Cat1 | 36 |
| C5 | Cat2 | 15 |
| C5 | Cat3 | 55 |

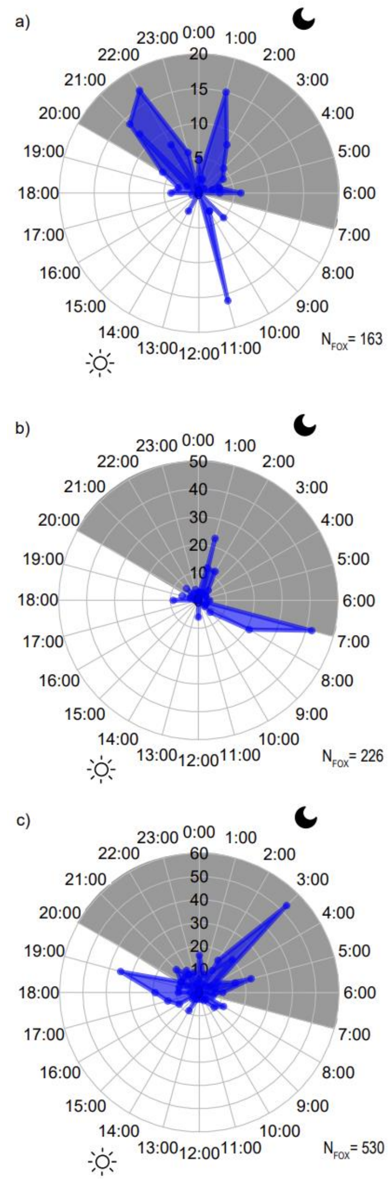


**Figure 2**. *Lycalopex culpaeus* activity patterns (blue shaded area) at the agroecosystem landscapes in the Categories (a) Cat1, (b) Cat2, (c) Cat3. Each circular plot depicts a 24-h clock, with concentric circles representing the number of records obtained via camera traps.

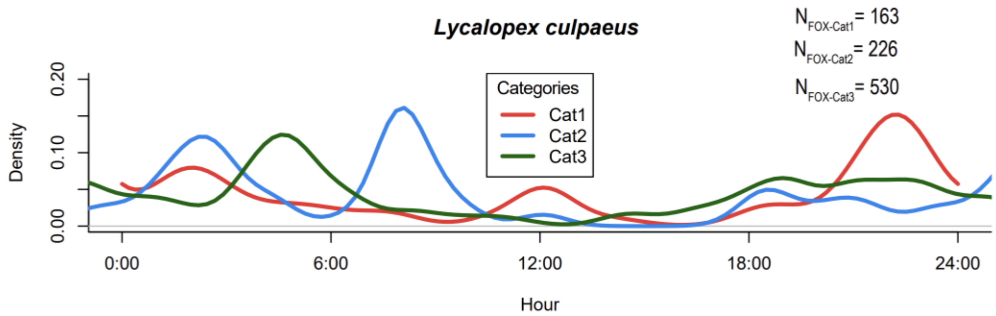


**Figure 3.** Comparison of the daily activity patterns of *Lycalopex culpaeus* between the Categories (depicted using kernel density functions).

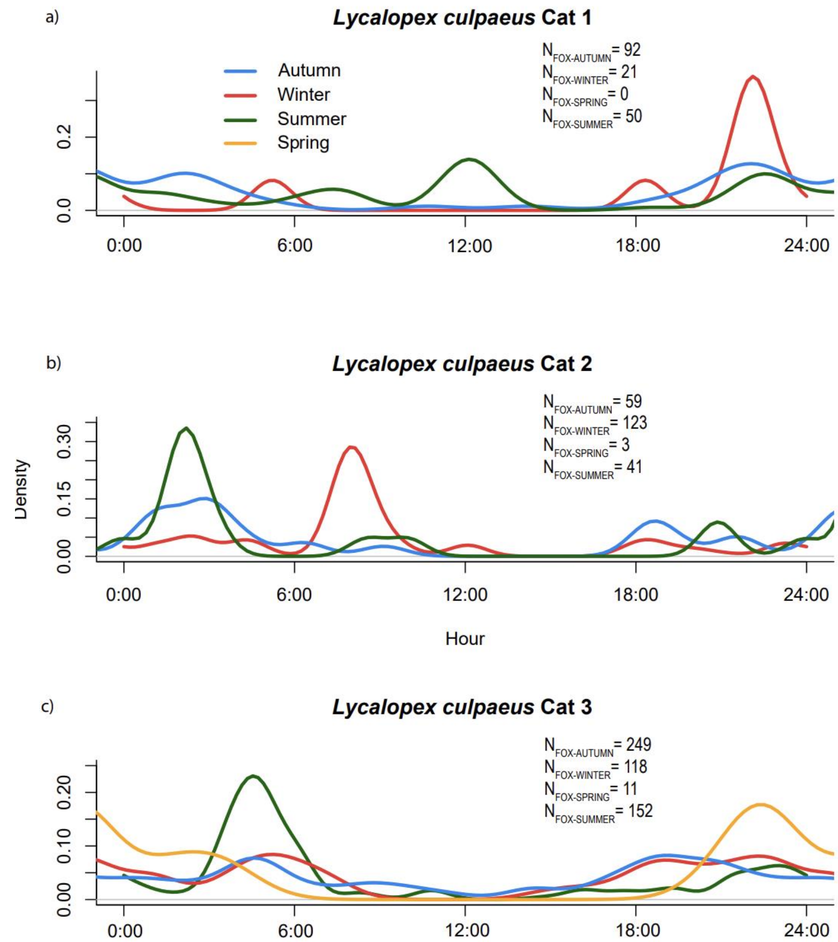


**Figure 4**. Comparison of the daily activity patterns of *Lycalopex culpaeus* between Seasons of the year for Chile in the Categories (depicted using kernel density functions) (a) Cat1, (b) Cat2, (c) Cat3.

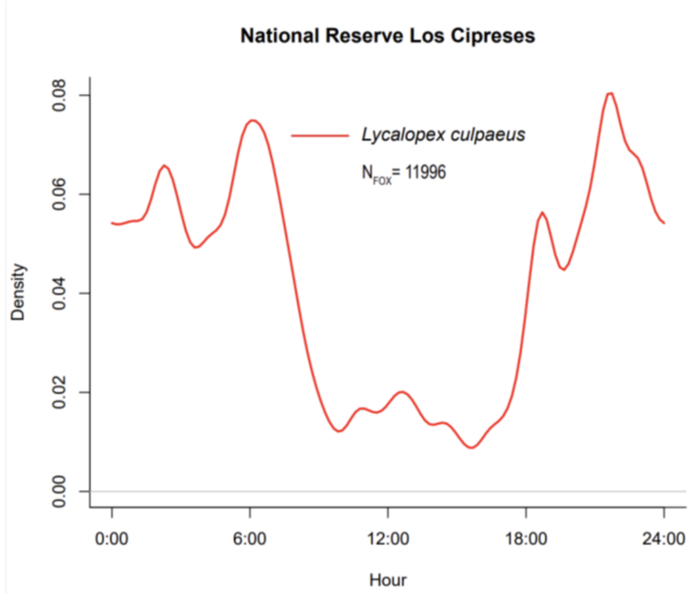


**Figure 5.** Daily activity pattern (depicted using kernel density functions) of the predator *Lycalopex culpaeus* (solid line) in the Los Cipreses National Reserve (CONAF 2021).

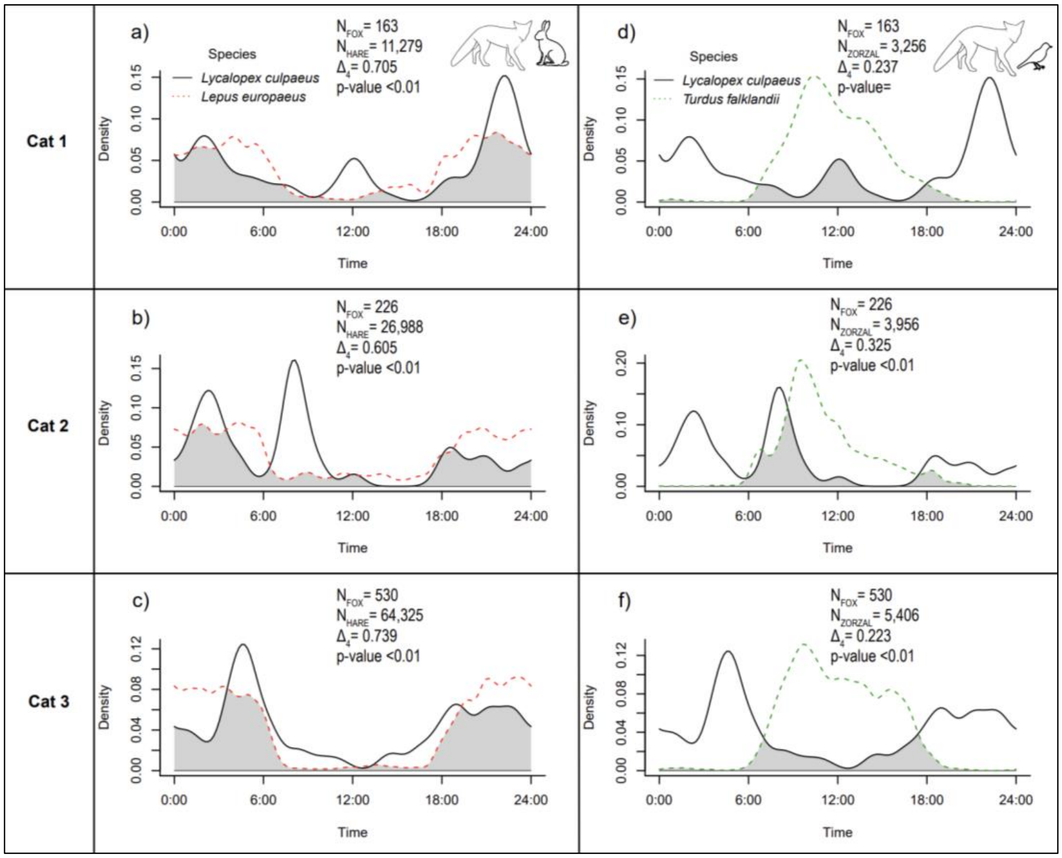


**Figure 6.** Comparison of the overall daily activity patterns (depicted using kernel density functions) between the predator *Lycalopex culpaeus* (solid line) and the two more abundant potential prey *Lepus europaeus* and *Turdus falcklandii* (dashed lines).

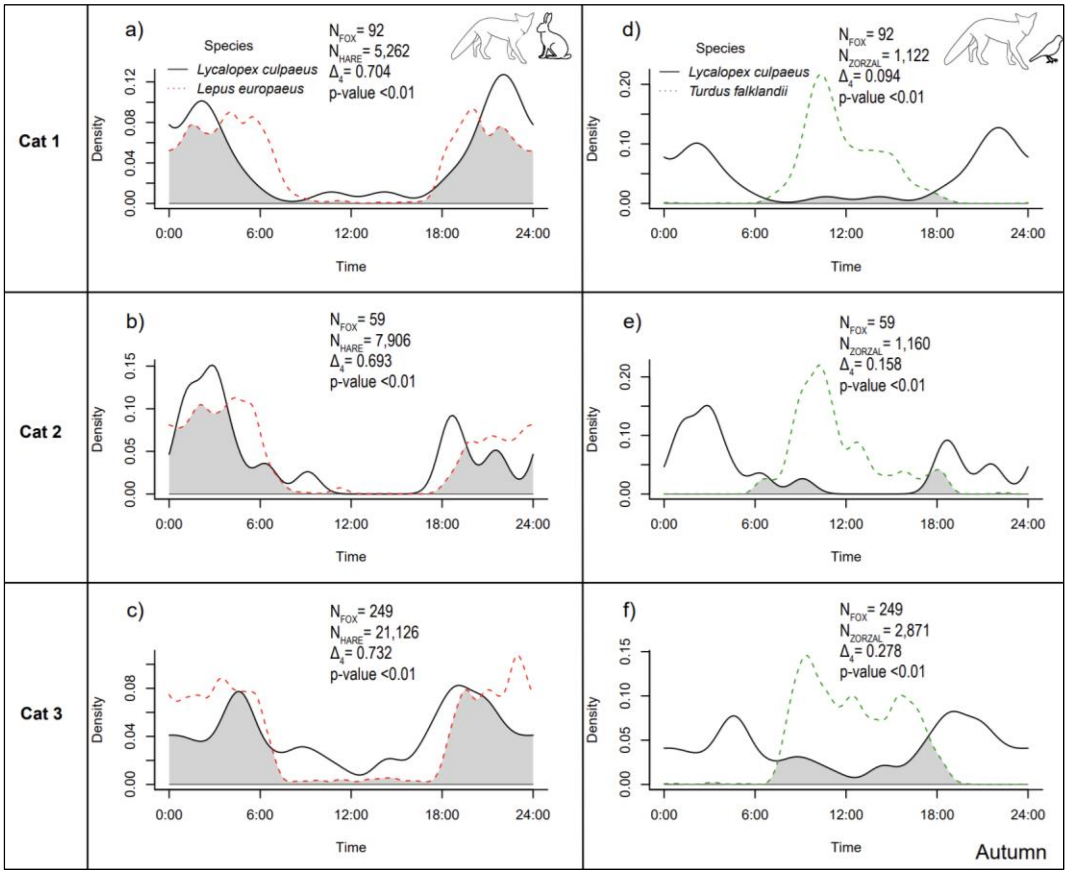


**Figure 7.** Autumn comparison of the overall daily activity patterns (depicted using kernel density functions) between the predator *Lycalopex culpaeus* (solid line) and the two more abundant potential prey *Lepus europaeus* and *Turdus falcklandii* (dashed lines).

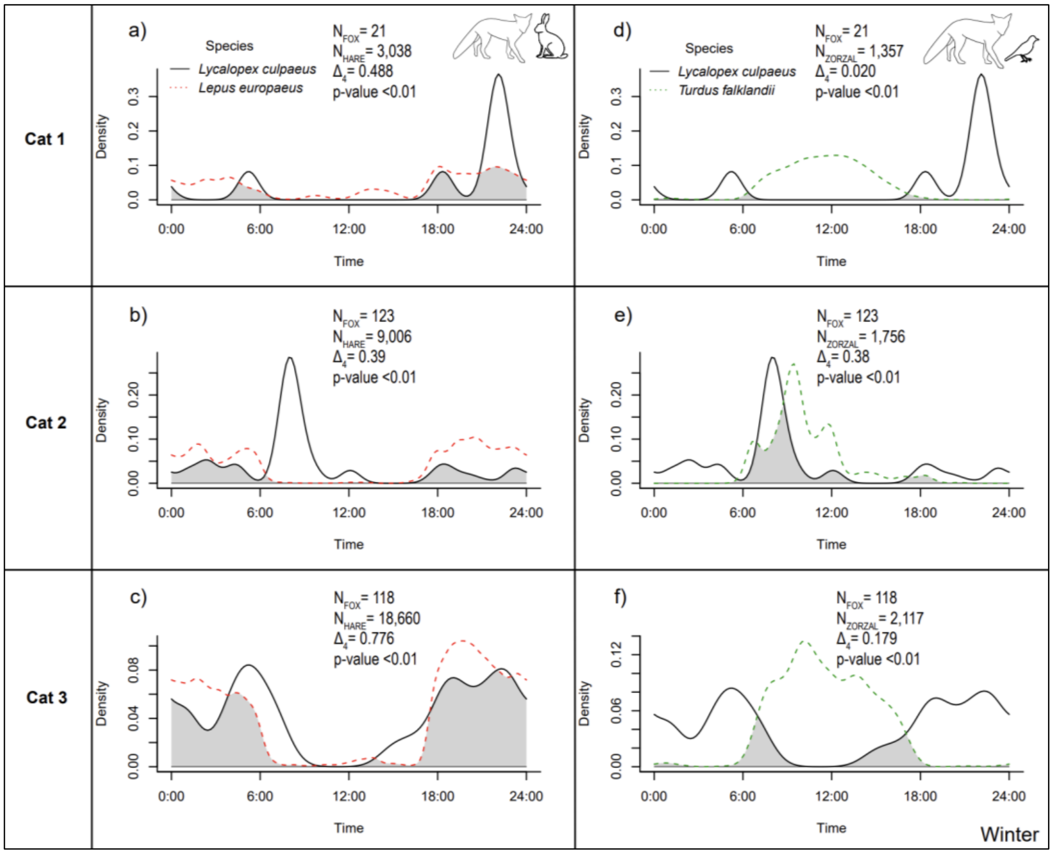


**Figure 8.** Winter comparison of the overall daily activity patterns (depicted using kernel density functions) between the predator *Lycalopex culpaeus* (solid line) and the two more abundant potential prey *Lepus europaeus* and *Turdus falcklandii* (dashed lines).

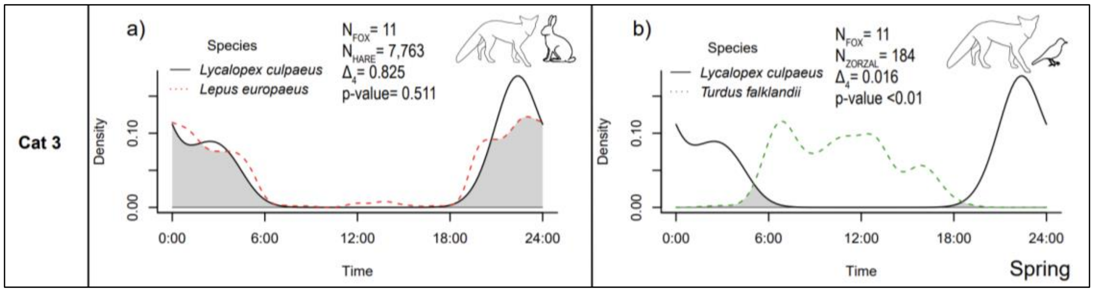


**Figure 9.** Spring comparison of the overall daily activity patterns (depicted using kernel density functions) between the predator *Lycalopex culpaeus* (solid line) and the two more abundant potential prey *Lepus europaeus* and *Turdus falcklandii* (dashed lines).

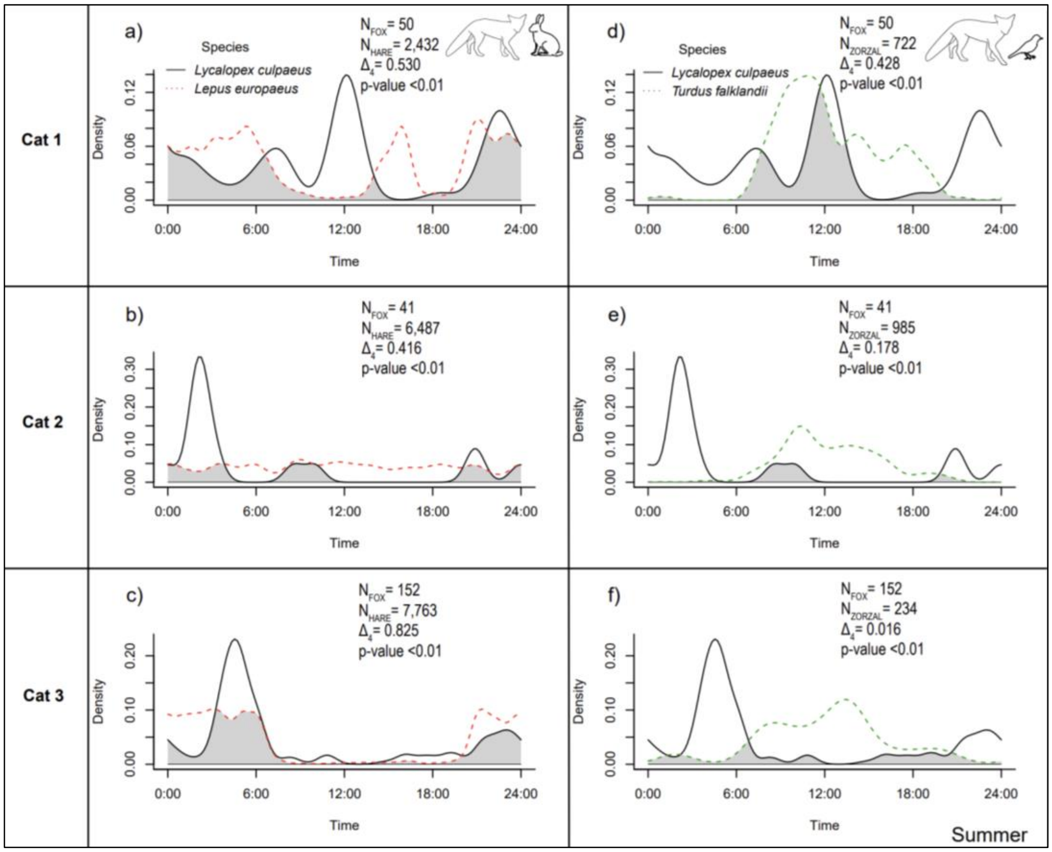


**Figure 10.** Summer comparison of the overall daily activity patterns (depicted using kernel density functions) between the predator *Lycalopex culpaeus* (solid line) and the two more abundant potential prey *Lepus europaeus* and *Turdus falcklandii* (dashed lines).

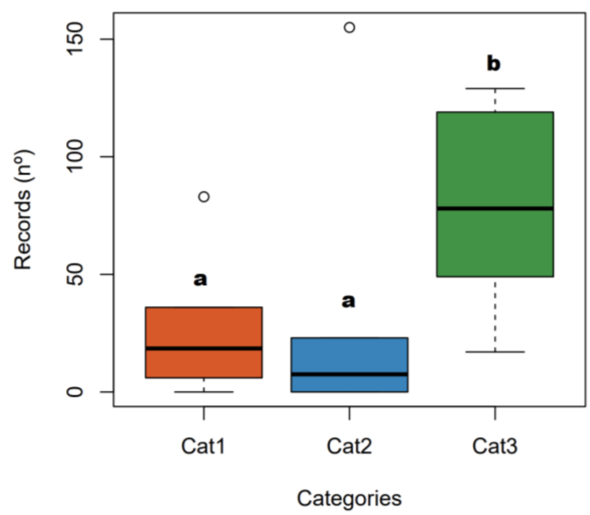


**Figure 11.** Number of *Lycalopex culpaeus* records among the landscape Categories (i.e., Cat1, Cat2, Cat3). Different letters indicate significant differences (p-value<0.05).

**Table 3.** Study principal GLMM formulas. (* p-value<0.05; *** p-value<0.01)

| Variable | Model 1 | Model 2 | Model 3 | Model 4 | Model 5 |
|---|---|---|---|---|---|
| Category | 0.403±0.097 *** | - | - | 3.37e-1±1.04e-1 *** | - |
| Natural area cover (%) | - | 0.006±0.002 *** | - | - | 0.039±0.24 * |
| Hare | - | - | 9.58e-5±3.15e-5 *** | 5.63±3.65e-5 * | 0.003±0.00 *** |

**Table 4.** GLMM analysis estimates.

| Model ID | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| Model 1 | 2.458 | 0.324 | 7.592 | <0.001 |
| Model 2 | 2.356 | 0.345 | 6.822 | <0.001 |
| Model 3 | 2.626 | 0.343 | 7.650 | <0.001 |
| Model 4 | 2.446 | 0.329 | 7.428 | <0.001 |
| Model 5 | 2.439 | 0.552 | 6.934 | <0.001 |