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Response of mesocarnivores to anthropogenic landscape intensification: activity patterns and guild temporal interactions

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Carnivores face important anthropogenic threats in agricultural areas from habitat loss and fragmentation, disturbance by domestic free-roaming dogs and cats, and direct hunting by humans. Anthropogenic disturbances are shifting the activity patterns of wild animals, likely modifying species interactions. We estimated changes in the activity patterns of the mesocarnivore guild of agricultural landscapes of the La Araucanía region in southern Chile in response to land-use intensification, comparing intra- and interspecific activity patterns at low and high levels of forest cover, fragmentation, and land ownership subdivision. Our focal species comprise the güiña or kod-kod (*Leopardus guigna*), two fox species (*Lycalopex culpaeus* and *L. griseus*), a skunk (*Conepatus chinga*), and one native mustelid (*Galictis cuja*), in addition to free-roaming dogs (*Canis lupus familiaris*) and cats (*Felis catus*) and their main mammalian prey species (i.e., Rodentia and Lagomorpha). In 23,373 trap nights, we totaled 21,729 independent records of our focal species. Our results show tendencies toward nocturnality at high land-use intensification, with potential impacts on species fitness. Nocturnal mesocarnivores decreased their diurnal/crepuscular activity, while cathemeral activity shifted to nocturnal activity at high land-use intensification, but only when in sympatry with a competitor. High land-use intensification decreased the activity overlap between native and domestic mesocarnivores but increased the overlap between native mesocarnivores. High intensification also reduced overlap with prey species. Notably, foxes displayed peaks of activity opposing those of dogs, and plasticity in activity pattern when in sympatry with dogs, such as strategies to avoid encounters. We stress the need to suppress the free-roaming and unsupervised activity of dogs to mitigate impacts of high land-use intensification on mesocarnivores.

Key words: activity pattern, agricultural landscapes, camera traps, free-roaming dogs, intraguild competition, land-use intensification, *Leopardus guigna*, mesocarnivores, temporal segregation

Los carnívoros enfrentan importantes amenazas antropogénicas en áreas agrícolas, amenazas provenientes de la pérdida y fragmentación de hábitat, perturbación por perros y gatos domésticos y caza directa por humanos. Las perturbaciones antropogénicas están cambiando los patrones de actividad de los animales silvestres, probablemente modificando las interacciones entre especies. Estimamos los cambios en los patrones de actividad del gremio de mesocarnívoros en paisajes agrícolas de la región de La Araucanía, en el sur de Chile, en respuesta a la intensificación del uso de la tierra, comparando los patrones de actividad intra- e interespecíficos en niveles bajos y altos de cobertura de bosque, fragmentación y subdivisión en la cantidad de propietarios de la tierra. Nuestras especies focales comprendieron a la güiña (*Leopardus guigna*), dos especies de zorros (*Lycalopex culpaeus* y *Lycalopex griseus*), el chingue (*Conepatus chinga*), y el quique (*Galictis cuja*), además de perros (*Canis lupus familiaris*) y gatos (*Felis catus*) de movimiento libre, y asimismo las principales presas mamíferas (es decir, Rodentia y Lagomorpha). Totalizamos 21,729 registros independientes de nuestras especies focales en 23,373 noches-trampa. Nuestros resultados muestran tendencias hacia la nocturnidad en alta intensificación del uso de la tierra, con potenciales impactos en el fitness de las especies. Los mesocarnívoros nocturnos disminuyeron su actividad diurna/crepuscular, mientras que los catemerales cambiaron hacia una actividad más nocturna a mayor intensificación del uso de la tierra, pero solo estando en simpatría con un competidor. Una alta intensificación del uso de la tierra disminuyó la superposición de actividad entre mesocarnívoros nativos y domésticos, mientras que aumentó la superposición entre nativos. Adicionalmente, la alta intensificación redujo la superposición con especies presa. Notablemente, los zorros mostraron picos de actividad opuestos a los de los perros y plasticidad en su patrón de actividad cuando en simpatría con esta especie, tales como puedan ser medidas para evitar encuentros. Hacemos hincapié en la necesidad de eliminar el movimiento libre y sin supervisión de los perros para mitigar los impactos de la intensificación del uso de la tierra en los mesocarnívoros.

Palabras clave: cámaras trampa, competición intra-gremial, intensificación del uso de la tierra, *Leopardus guigna*, mesocarnívoros, paisajes agrícolas, patrones de actividad, perros de movimiento libre, segregación temporal,

Growing anthropogenic pressure resulting from major land-use changes is one of the greatest threats to terrestrial biodiversity around the world (Sala et al. 2000). Land-use change for agriculture causes habitat loss and fragmentation, contributing to biodiversity extinction and defaunation in almost all ecosystems (Fischer and Lindenmayer 2007), with profound impacts on their functions (Young et.al. 2016). The increase in subdivision of land ownership in rural areas also is of growing concern for biodiversity conservation (Hansen et al. 2005). Anthropogenic pressure in the form of habitat fragmentation from land-use change can affect the biology, genetics, and interspecific interactions, of species (Henle et al. 2004). Some species, such as carnivorous mammals, are more sensitive than others to these alterations due to their life histories, wide-ranging behavior, and low densities (Crooks 2002; Prugh et al. 2009). These mammals face important anthropogenic threats that include habitat loss and fragmentation (Crooks 2002; Henle et al. 2004), disturbance by free-roaming domestic cats and dogs, and direct hunting by humans (Treves and Karanth 2003; Inskip and Zimmermann 2009; Marchini and Macdonald 2012; Bonacic et al. 2019), all factors related to human encroachment and the increase in subdivision of land ownership (Gálvez et al. 2018).

Given their high trophic level, carnivores play an important ecological role in controlling herbivore populations (Ripple and Beschta 2006; Bruno and Cardinale 2008). The decline or disappearance of carnivore populations has cascade effects and can generate top-down changes in biodiversity (Prugh et al. 2009). The role of mesocarnivores in the function and dynamics of ecosystems becomes pivotal because of their abundance and diversity of ecological niches (Prugh et al. 2009; Roemer et.al. 2009). Mesocarnivores are mid-trophic level predators with body weights of 1 – 15 kg (Gehrt and Clark 2003). Despite their potential importance, these species are poorly known in their occurrence, trends, and activity periods, highlighting our need to further understand community-level interactions of this carnivore guild (Roemer et.al. 2009).

Community-level interactions occur at temporal, spatial, and trophic dimensions of species activity. Segregation by species in any of these dimensions can contribute to their coexistence (Emmons 1987; Aranda and Sánchez-Cordero 1996; Fedriani et al. 2000; Núñez et al. 2002; Harmsen et al. 2009). These three dimensions (time, space, and diet) are viewed as mediators of biological interactions (Kronfeld-Schor and Dayan 2003). Predators also often synchronize their activity to coincide with that of their main prey (Mendes Pontes and Chivers 2007; Romero-Muñoz et al. 2010). Prey specialization usually forces predators to be active at different periods, thereby facilitating coexistence (Scognamillo et al. 2003). By studying activity patterns of the different species, it is possible to understand certain biological processes and how species address their needs of food acquisition, thermoregulation, and danger avoidance (Downes 2001). And, to understand the interaction mechanisms among species, it is necessary to compare their activity patterns (Foster et al. 2013; Ross et al. 2013; Delibes-Mateos et al. 2014; Hernández et al. 2015; Biggerstaff et al. 2017), which are shifting worldwide as a result of anthropogenic disturbances (Gaynor et al. 2018).

In light of the foregoing, we assessed changes in the activity patterns of the understudied mesocarnivore guild of agricultural landscapes of the La Araucanía region in southern Chile in response to anthropogenic landscape modification. Our focal guild of mesocarnivores share several niche dimensions. They overlap in their habitat use (Zapata et al. 2005; Rubio et al. 2013; Moreira-Arce et al. 2016; García et al. 2020) and in parts of their diets (Ebensperger et al. 1991; Freer 2004; Correa and Roa 2005; Zapata et al. 2005; Zúñiga et al. 2005; Silva-Rodríguez and Sieving 2011), and there is some evidence of their temporal overlap in other study areas (Zúñiga et al. 2016). Moreover, they interact with introduced carnivores that have been observed to affect native carnivores, both directly (Kasper et al. 2009; Silva-Rodríguez et al. 2010; Castillo et al. 2011; Romero et al. 2019) and indirectly (Acosta-Jamett et al. 2011; Mora et al. 2015; García et al. 2020).

We compared activity patterns relative to land-use intensification measured as the percentage of native forest cover, degree of fragmentation, and subdivision of land ownership (hereafter subdivision) at the species and community level. We also evaluated the effect of land-use intensification on activity patterns of predator–prey systems. Our main hypothesis was that high land-use intensification forced native mesocarnivores to increase their nocturnal activity and decrease their diurnal activity. As native mesocarnivores would tend to be more nocturnal, we expected that their activity overlap would also increase as land intensification increased. We also predicted that overlap of native mesocarnivores with domestic mesocarnivores and their prey would decrease as land-use intensification increased, as consequences of temporal partitioning.

Materials and Methods

Study area.—Our research took place in La Araucanía Region of southern Chile, on the northern edge of the South American temperate forest ecoregion (39°15′S, 71°48′W—Armesto et al. 1998), part of the Chilean winter rainfall–Valdivian forests biodiversity hotspot (Myers et al. 2000; Arroyo et al. 2006). Native vegetation consisted of forests dominated by deciduous and perennial species of beech (*Nothofagus*—Luebert and Pliscoff 2006). Our study area covered the agricultural valleys of La Araucanía Region from the central valley, characterized by intensive agriculture (cereals, cattle, and fruit orchards) and urban settlements, toward the Andes, characterized by a less intensive agricultural use with extensive livestock production and timber, which provided a land-use intensity gradient. Survey sites were all below 600 m and surrounded by patches of continuous forest on steep slopes and by protected areas (> 800 m). Forest cover varied in the study area, ranging from irregular mosaics of forests in the central valley to continuous stretches of native forest at higher elevations in the Andes (Miranda et al. 2015). Between 1983 and 2007, valleys in the Andes have increased in forest cover with reduced fragmentation but have had an increase in ownership subdivision (Petitpas et al. 2017).

Terrestrial mammalian mesocarnivores of the study area were güiña or kodkod cat (*Leopardus guigna*), Andean or culpeo fox (*Lycalopex culpaeus*), gray fox (*L. griseus*), lesser-grisson (*Galictis cuja*), and Molina's hog-nosed skunk (*Conepatus chinga*), along with exotic species such as the American mink (*Neovison vison*) and domestic species such as free-roaming dogs (*Canis lupus familiaris*) and domestic cats (*Felis catus*). Two introduced lagomorphs, *Lepus europaeus* and *Oryctolagus cuniculus*, comprised important prey items for the guild. The only large carnivore occurring in the entire area is the puma (*Puma concolor*).

Sampling design.—Sampling was carried out using camera traps to obtain photographic records of the mesocarnivores and their prey. Potential sampling units were defined by positioning a 4 km^2 grid over the area aiming to represent the gradient of forest habitat fragmentation < 600 m caused by agriculture and human settlements. Size of the sampling units was determined by the estimated home range of the güiña in a previous study (Gálvez et al. 2018). We assumed that this was appropriate for the other mesocarnivores due to the large size of the home range of güiña and that the temporal dimension rather than spatial was being evaluated. A total of 145 sampling units were selected randomly from a grid of 230 cells, of which 73 were in forest and cropland mosaic of the central valley and 72 were in the less fragmented forest agricultural landscapes of the Andes (Fig. 1). Sampling took place in four 90 – 100-day sessions (summer 2012, spring 2013, summer 2013, and summer 2014), which should not have induced clock time bias (Nouvellet et al. 2012). The Andean valleys were sampled during all seasons, and the central valley was sampled in the last three. To cover all sampling units within each season, camera traps were rotated in four blocks and were active 20 days at each location. Two camera traps (Bushnell Trophy Cam 2012) were used per sampling unit and acted as a single observer. They were located at 100 – 700 m from each other and at least 1.5 – 2 km from the cameras of adjacent sampling units.

Interspecific interactions.—Donadio and Buskirk (2006) suggested that taxonomic and spatial similarities among species, as well as similarities in size and prey, determine intensity and form of biological interactions that occur between them. Based on evidence of observed interference competition, exploitation competition, similarities in size, and predator – prey interactions reported in the scientific literature (Table S1 in Supplementary Data SD1), we established species comparisons to examine the partitioning and overlap in temporal activity in the mesocarnivore guild and the mammalian prey (Fig. 2).

Data analysis.—We used independent detections at each sampling unit to evaluate the activity patterns of mesocarnivores and their prey in the study area. As a conservative approach, we considered independent records to be those with 60 min between detections of the same species at the same sampling unit (Ridout and Linkie 2009). Activity patterns of each mesocarnivore and prey (at the Order level for the latter) were estimated non-parametrically using "kernel density" (Ridout and Linkie 2009). The independent photographic records of the species were considered a random sample with a continuous distribution (i.e., time of day) over a 24-h period and were used to estimate a probability density function (hereafter PDF) or activity pattern (Linkie and Ridout 2011). PDFs were only generated when there were ≥ 50 independent records (Monterroso et al. 2014). To use our entire data set, we first evaluated intraspecific differences of activity pattern between our four sampling sessions (summer 2012, summer 2013, spring 2013, and summer 2014). No significant difference activity patterns were found (compareCkern test; see below) for our native focal species that could impair our interpretations. To assess the influence of land-use intensification, we separated species records into high and low categories of land-use intensification and analyzed: (1) each species' general activity pattern and intraspecific comparisons between categories of land-use intensification; (2) overall overlap of mesocarnivores' interspecific activity patterns, and overlap comparisons between categories of land-use intensification; and (3) overall activity pattern overlap between mesocarnivores and their potential prey, and overlap comparisons between categories of land-use intensification. For (2), we also compared intraspecific activity curves in sympatric and allopatric condition between competitor species (e.g., *L. guigna* activity in sites with and without *F. catus* detections), both for overall data and for each category of land-use intensification. This last comparison should provide evidence of avoidance due to competition and indicate the conditions in which it is intensified. The stages of analysis were structured as follows:

1. Activity patterns at the general level. We calculated the activity patterns of our focal species using our whole data set. Following Gómez et al. (2005), records were classified as diurnal, nocturnal, or crepuscular. We then classified species as diurnal (< 10% of records at night), nocturnal (> 90% of records at night), mainly diurnal (10 – 30% of records at night), mainly nocturnal (70 – 90% of records at night), crepuscular (50% of observations during crepuscular phase),

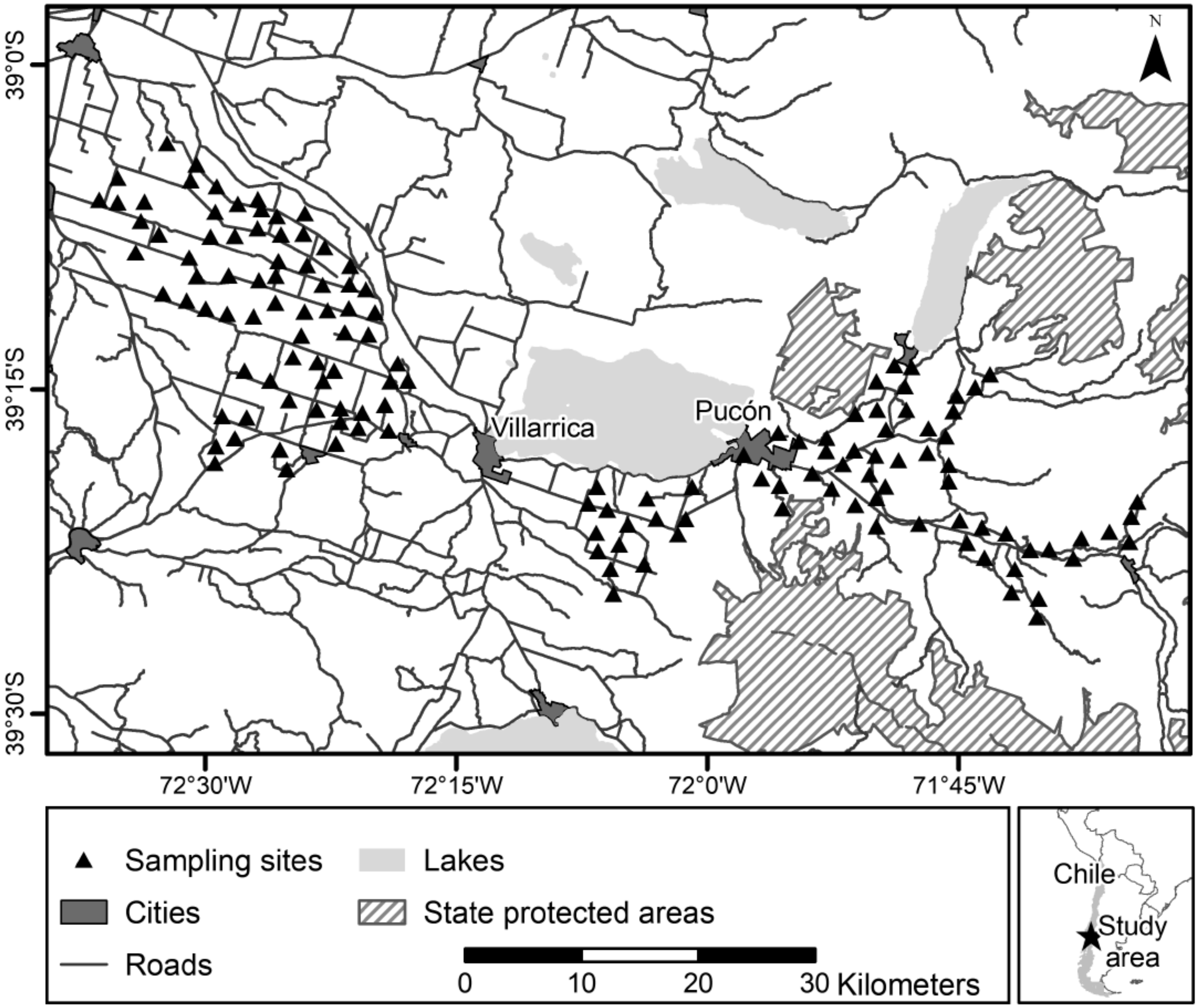


Fig. 1.—Study area in the La Araucanía Region of southern Chile. Sampling units were located through a gradient of land-use intensification from the central valley (72°30′W) to Andean valleys (71°45′W), the latter surrounded by protected areas.

or cathemeral (intermittent activity throughout 24 h). We used exact sunrise and sunset times for record classification (NOAA 2017). Given we were interested in comparing prey activity at a coarse level with mesocarnivore activity, we merged records of mammalian prey species at the order level as Lagomorphs or Rodents. We were confident in representation of lagomorphs because they only comprise two species, and for Rodents, we assumed that photographs were a good proxy to the activity of the entire rodent community (De Bondi et al. 2010).

2. Activity patterns by category of land-use intensification. To estimate the influence of land-use intensification on the activity patterns of the mesocarnivore guild, we analyzed its variation taking three uncorrelated landscape variables (Gálvez et al. 2018): forest cover as a proxy to habitat loss; number of forest patches as a proxy to the degree of fragmentation; and land ownership subdivision as a coarse filter of anthropogenic pressure. Metrics for each of these habitat variables were generated for 300-ha sampling units around the midpoint between cameras. We selected sampling units to be used in this analysis according to extreme values (relatively high and low) for each of the three landscape variables, based on two criteria: (1) minimum and maximum ranges observed for each variable in the set of sampling units; and (2) a minimum of 75 records for each species in the selected ranges (except in the case of high fragmentation where a minimum of 64 records was used for the *F. catus* species; Supplementary Data SD2). Based on these criteria, the following values were set as low and high for the three variables: low forest cover < 20%, high forest cover > 50%; low fragmentation < 20 patches/300 ha, high fragmentation > 60 patches/300 ha; low subdivision < 20 landowners/300 ha, and high subdivision > 60 landowners/300 ha. Although these ranges were relative to the landscape studied, they were within the medium-high and medium-low categories of level

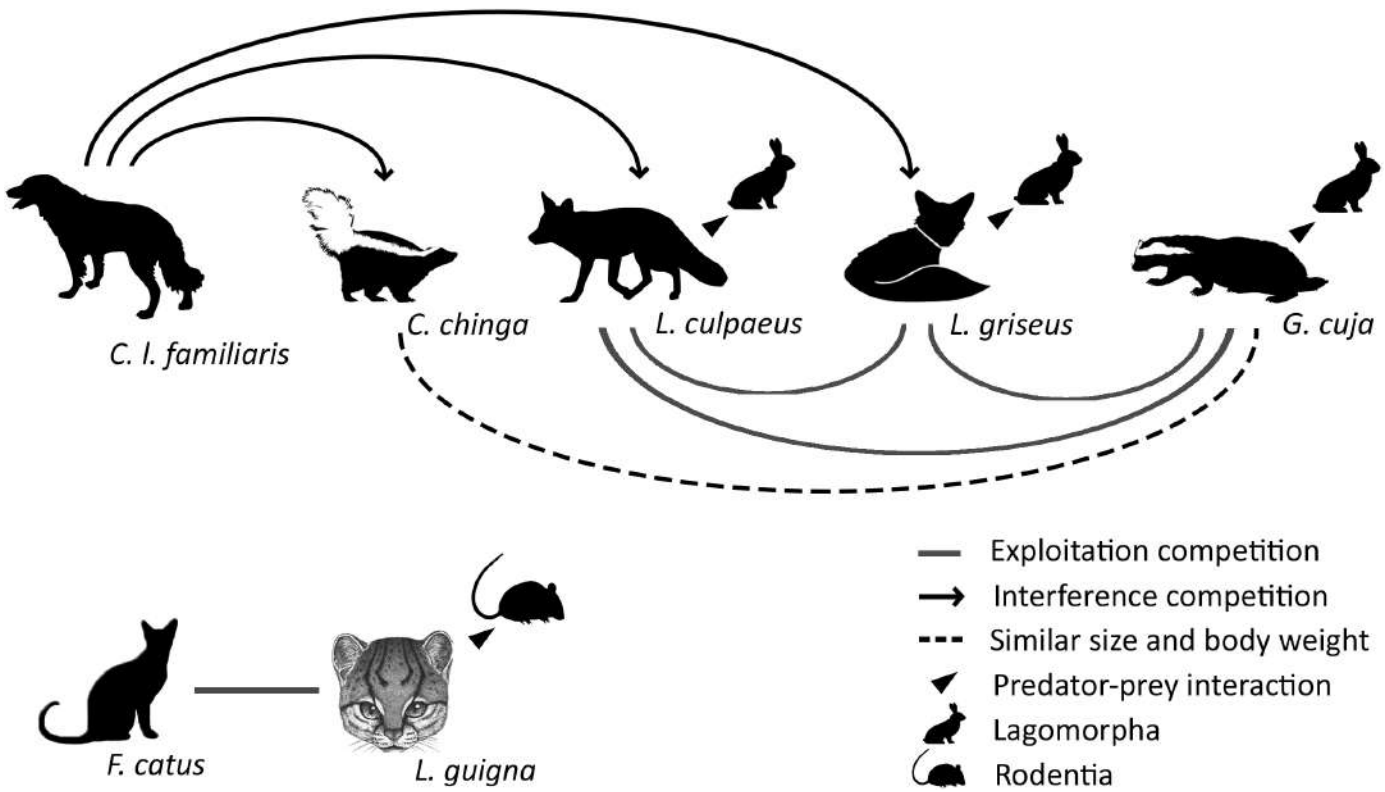


Fig. 2.—Depiction of known species interactions as the basis for temporal activity comparisons of the mesocarnivore guild and their mammalian prey in agricultural landscapes of La Araucanía Region, Chile. Comparisons are based on niche overlap and observed interactions described in the literature (Table S1 in Supplementary Data SD1 gives references). All species sharing an interaction were compared with their temporal activity pattern.

of modification of a landscape in terms of forest cover (Fischer and Lindenmayer 2007). After the ranges for each variable had been determined, Probability Density Function plots were generated for each species in each category of land-use intensification and compared.

3. Inter- and intraspecific comparisons of activity patterns. After PDFs had been generated for each species at the general level and for each level of land-use intensification, pairs of intra- and interspecific activity patterns were compared, and the overlap coefficient (Δ) was estimated (Ridout and Linkie 2009). This coefficient ranged from 0 (no overlap) to 1 (complete overlap) and was obtained by taking the minimum of the density functions of the two cycles being compared at each time point (Monterroso et al. 2014). Following Meredith and Ridout (2017), the $\hat{\Delta}_4$ estimator was used when the smallest sample in each comparison had ≥ 75 observations; otherwise, the $\hat{\Delta}_1$ estimator was used. Analysis was carried out in R 3.2.1 (R Development Core Team 2015) with the "overlap" package (Meredith and Ridout 2017). For each of the comparisons, 95% *CI* were calculated for $\hat{\Delta}$, using 10,000 bootstrap repetitions for each distribution (Meredith and Ridout 2017).

We considered a strong overlap when $\hat{\Delta} > 0.8$ approximately, and $\hat{\Delta} < 0.5$ was considered low (Lynam et al. 2013; Allen et al. 2018). We used the function compareCkern() from the package Activity v.1.3 (Rowcliffe et al. 2014) with 10,000 bootstrap iterations to test the probability that two activity curves come from the same distribution (Havmøller et al. 2020). We interpreted statistically significant differences when overlap was strong due to fine-scale differences in activity curves enabled by the high density of our data.

Results

Over the 4 sampling sessions, we surveyed for 23,373 trap nights, totaling 21,729 independent records of our focal guild (Table 1). The lowest number of records corresponded to *N. vison* and *G. cuja*; thus, the former was eliminated from subsequent analysis, and the latter was only considered for comparisons in which ≥ 50 observations were available.

Activity patterns and intraspecific overlap.—The most nocturnally active species were *L. guigna* and *C. chinga*, with more than 70% of records being nocturnal and ~20% to the twilight phases (Table 2). Both species of *Lycalopex* were cathemeral, showing intermittent activity throughout the 24-h cycle. Similarly, *F. catus* was considered a cathemeral species because 60% of its observations were at night and 23% during the day. *Canis l. familiaris* was found to be mainly diurnal, with 68% of observations during the day and less than 15% at night. Finally, 94% of observations of *G. cuja* occurred during the day.

Differences of activity patterns by species at different land-use intensification categories were mostly non-significant and with moderate to high overlaps in almost all cases (Fig. 3). Only *L. guigna*, *F. catus*, and *C. chinga* showed significant differences between curves at contrasting categories. The small

Table 1.—Number of independent records (≥ 1 h) by species and land-use intensification category. Samples analyzed with Δ1 estimator[a] (50 ≤ records < 75) and Δ4 estimator (records ≥ 75), or not analyzed[b] (records < 50) are shown.

Species	Total records	Low forest cover	High forest cover	Low fragmentation	High fragmentation	Low land subdivision	High land subdivision
Mesocarnivores							
Leopardus guigna	924	559	120	155	344	241	97
Conepatus chinga	800	512	78	100	250	158	152
Lycalopex culpaeus	905	378	99	198	178	307	130
Lycalopex griseus	979	408	250	265	378	385	163
Canis l. familiaris	1,157	585	164	251	318	369	394
Felis catus	386	127	79	97	64[a]	96	138
Galictis cuja	51[a]	35[b]	4[b]	6[b]	19[b]	9[b]	5[b]
Neovison vison	7[b]	0[b]	3[b]	0[b]	0[b]	4[b]	0[b]
Prey							
Rodentia	14,056	6,928	1,681	2,943	3,418	2,951	3,884
Lagomorpha	2,464	1,457	171	564	630	688	1,062

Table 2.—Activity pattern classification[a] for the mesocarnivore guild in agricultural landscapes of La Araucanía Region. Species were classified either as diurnal (< 10% of records at night), nocturnal (> 90% of records at night), mainly diurnal (10–30% of records at night), mainly nocturnal (70–90% of records at night), crepuscular (50% of observations during crepuscular phase), or cathemeral (intermittent activity throughout 24 h).

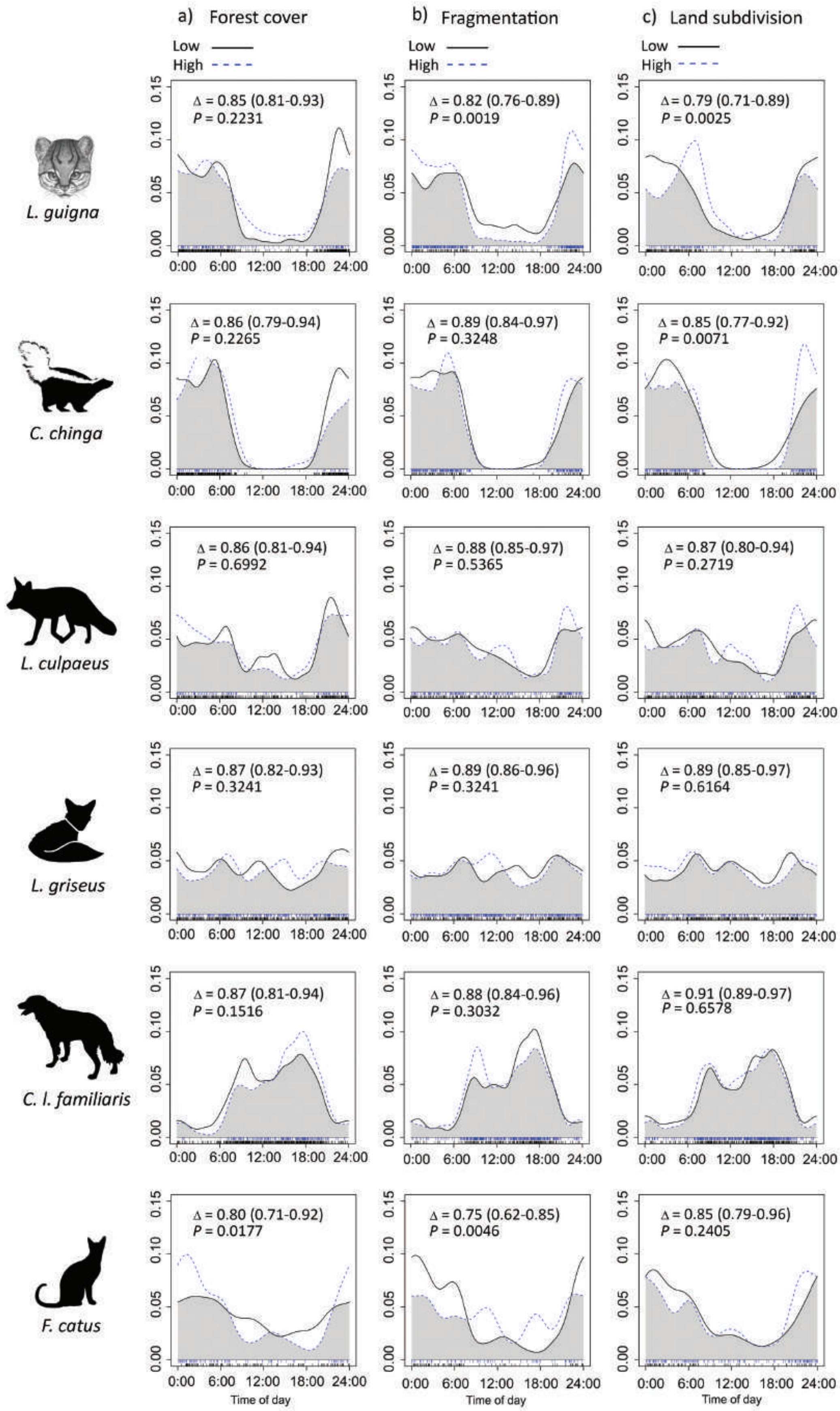
Species	Nocturnal (%)	Diurnal (%)	Crepuscular (%)	Activity classification
Leopardus guigna	71.5	10.7	17.7	Mainly nocturnal
Conepatus chinga	79.0	1.5	19.5	Mainly nocturnal
Lycalopex culpaeus	56.2	29.3	14.5	Cathemeral
Lycalopex griseus	42.1	40.4	17.5	Cathemeral
Canis l. familiaris	13.2	67.9	18.8	Mainly diurnal
Felis catus	62.4	23.3	14.2	Cathemeral
Galictis cuja	2.0	94.1	3.9	Diurnal

[a]Crepuscular is 1 h before sunrise to 1 h after sunrise and 1 h before sunset to 1 h after sunset; diurnal and nocturnal are from daytime and nighttime intervals in between crepuscular times, respectively.

felid *L. guigna* had higher nocturnal peaks of activity at high fragmentation and higher diurnal activity when fragmentation was low. In highly subdivided landscapes, *L. guigna* reduced nocturnal activity but showed a concentration of activity during crepuscular hours (i.e., 0600–0700 h). In the case of *F. catus*, differences were observed at contrasting levels of fragmentation. This domestic feline showed higher nocturnal activity in landscapes with low fragmentation but almost a cathemeral pattern at high fragmentation with two peaks during the day (morning and afternoon). In turn, *C. chinga* reduced crepuscular activity and concentrated nocturnal activity when subdivision increased.

Activity overlap among mesocarnivores.—At the general level, all comparisons of activity among the mesocarnivore species were significantly different (Fig. 4a). Overlap in activity patterns ranged from as low as 13% between *C. chinga* and *G. cuja* to as high as 87% between *L. culpaeus* and *L. griseus*. *Leopardus guigna* showed a strong overlap with *F. catus* ($\hat{\Delta} = 0.83$, 95% $CI = 0.79 – 0.88$), with the latter being more diurnal and the former more nocturnal. At only 27%, the overlap between *C. l. familiaris* and *C. chinga* was very low because *C. chinga* was active mainly at night and the canid during the day. Due to the concentrated diurnal activity of *G. cuja*, overlap was low with all other native mesocarnivores, such as the cathemeral activities of both *Lycalopex* species and mainly nocturnal activity of *C. chinga*. Similarly, mainly diurnal activity of *C. l. familiaris* overlapped to a low extent with activity of *L. culpaeus* and *L. griseus*. Peaks and decreases of activity of foxes also clearly followed patterns opposite to the diurnal peaks of *C. l. familiaris*. Overlap of cathemeral activity of the *Lycalopex* species was high, although *L. griseus* showed higher diurnal activity and *L. culpaeus* presented more accentuated peaks of activity. Furthermore, no differences were observed between sympatric and allopatric activity patterns with competitors except for *L. griseus* (Fig. 5a). *Lycalopex griseus* modified patterns toward more diurnal activity in presence of *G. cuja* (also diurnal) and a reduction in diurnal-crepuscular activity and higher nocturnal activity in the presence of *C. l. familiaris*.

Interspecific activity overlap within each category of land-use intensification showed moderate to high values, except for *C. chinga* and *C. l. familiaris* (Fig. 6); however, between low and high categories of land-use intensification, activity overlap changed in most species comparisons (i.e., 9 out of 15 species pairs being compared) with an overall tendency to reduce overlap with domestic species at higher intensification (Fig. 6). Furthermore, there were significant changes in *L. griseus* activity between sympatry and allopatry with *C. l. familiaris* (Fig. 5a). Both *Lycalopex* species showed an increase in overlap at high intensification, but patterns differed due to shifts in peak activities. For example, at high forest cover, *L. griseus* showed higher diurnal activity with a lower overlap than at low forest cover. In turn, overlap increased at low forest cover with a decrease in diurnal activity and differentiated peaks throughout the cathemeral pattern. Nevertheless, at low forest cover, significant differences emerged in the activity of *L. griseus* in sympatry with *L. culpaeus* with a marked increase in diurnal


a) Forest cover
b) Fragmentation
c) Land subdivision
Low
High
L. guigna
Δ = 0.85 (0.81-0.93) P = 0.2231
Δ = 0.82 (0.76-0.89) P = 0.0019
Δ = 0.79 (0.71-0.89) P = 0.0025
C. chinga
Δ = 0.86 (0.79-0.94) P = 0.2265
Δ = 0.89 (0.84-0.97) P = 0.3248
Δ = 0.85 (0.77-0.92) P = 0.0071
L. culpaeus
Δ = 0.86 (0.81-0.94) P = 0.6992
Δ = 0.88 (0.85-0.97) P = 0.5365
Δ = 0.87 (0.80-0.94) P = 0.2719
L. griseus
Δ = 0.87 (0.82-0.93) P = 0.3241
Δ = 0.89 (0.86-0.96) P = 0.3241
Δ = 0.89 (0.85-0.97) P = 0.6164
C. l. familiaris
Δ = 0.87 (0.81-0.94) P = 0.1516
Δ = 0.88 (0.84-0.96) P = 0.3032
Δ = 0.91 (0.89-0.97) P = 0.6578
F. catus
Δ = 0.80 (0.71-0.92) P = 0.0177
Δ = 0.75 (0.62-0.85) P = 0.0046
Δ = 0.85 (0.79-0.96) P = 0.2405
0.00 0.05 0.10 0.15
0:00 6:00 12:00 18:00 24:00
Time of day

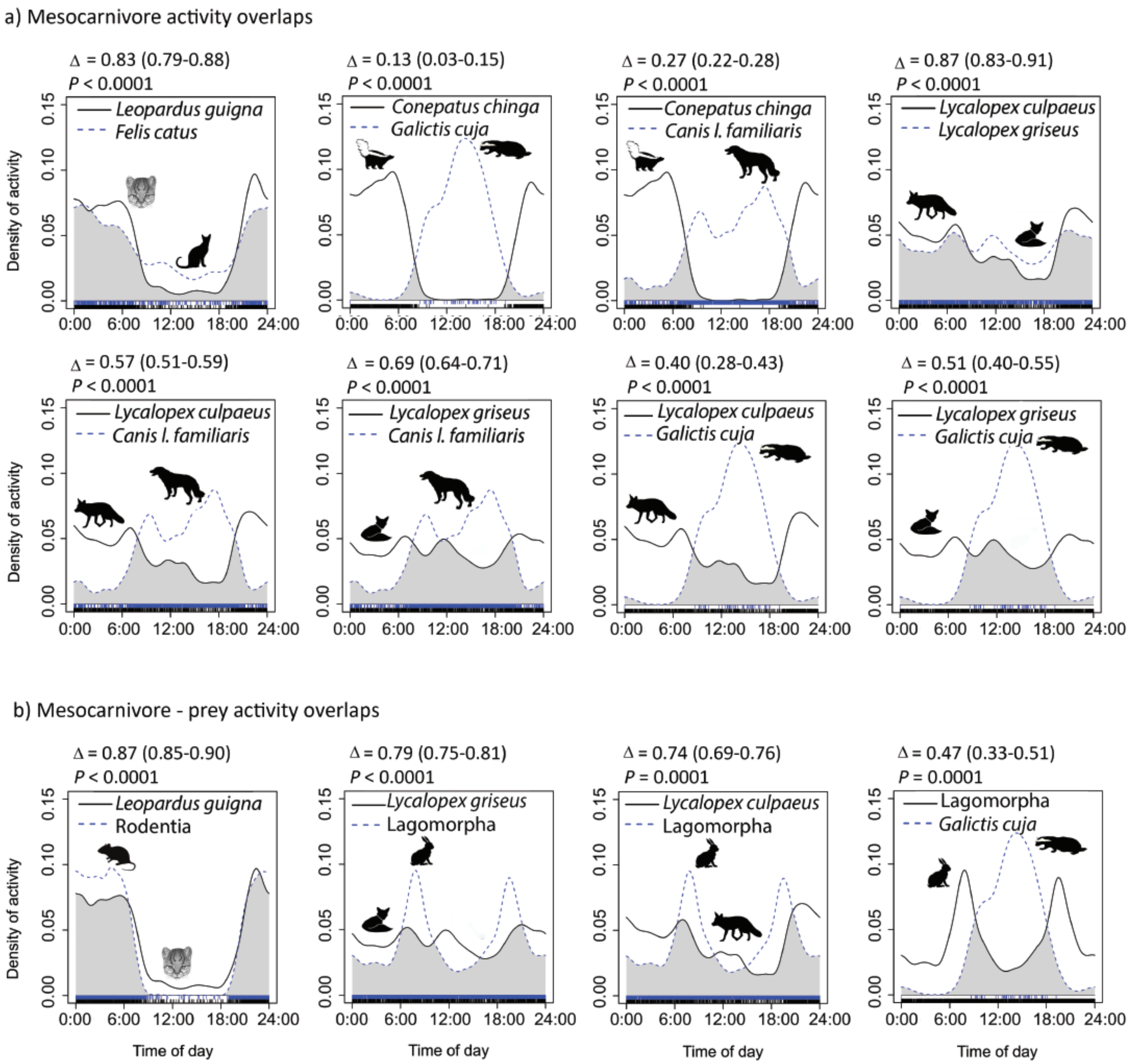


Fig. 4.—Estimated activity patterns and overlap (Δ) between mesocarnivores and between mesocarnivores and their potential prey using all records. The overlap of activity density curves (overlap coefficient Δ, in addition to 95% *CI*) and *P*-values from compareCkern() test are shown for each comparison. Independent records are displayed tick marks along the x-axis of the plot.

activity and reduction of nocturnal activity (Fig. 5b). In turn, *L. culpaeus* decreased diurnal activity at low forest cover and in sympatry with *L. griseus*.

Patterns between both *Lycalopex* species increased overlap at high subdivision with no significant differences between them. Differences between *L. guigna* and *F. catus* rose to higher levels with changes in diurnal activity. When forest cover was high, *L. guigna* showed greater diurnal activity very similar to that of *F. catus*; however, at low forest cover, significant differences appeared because *L. guigna* reduced its diurnal activity while *F. catus* increased it. A similar pattern was observed at sites with higher fragmentation, with *L. guigna* reducing diurnal activity. At high subdivision, differences also appeared due to shifts in peaks by *L. guigna*. Activity peaks of

Fig. 3.—Estimated activity patterns of the mesocarnivore guild for: (a) forest cover (low: 20%, high: 50%); (b) fragmentation (low: 30 patches/300 ha, high: 60 patches/300 ha); and (c) subdivision (low: 20 owners/300 ha, high: 60 owners/300 ha). The overlap of activity density curves (overlap coefficient Δ, in addition to 95% *CI*) and *P*-values from compareCkern() test are shown for each comparison. Independent records are displayed as tick marks along the x-axis of the plot.

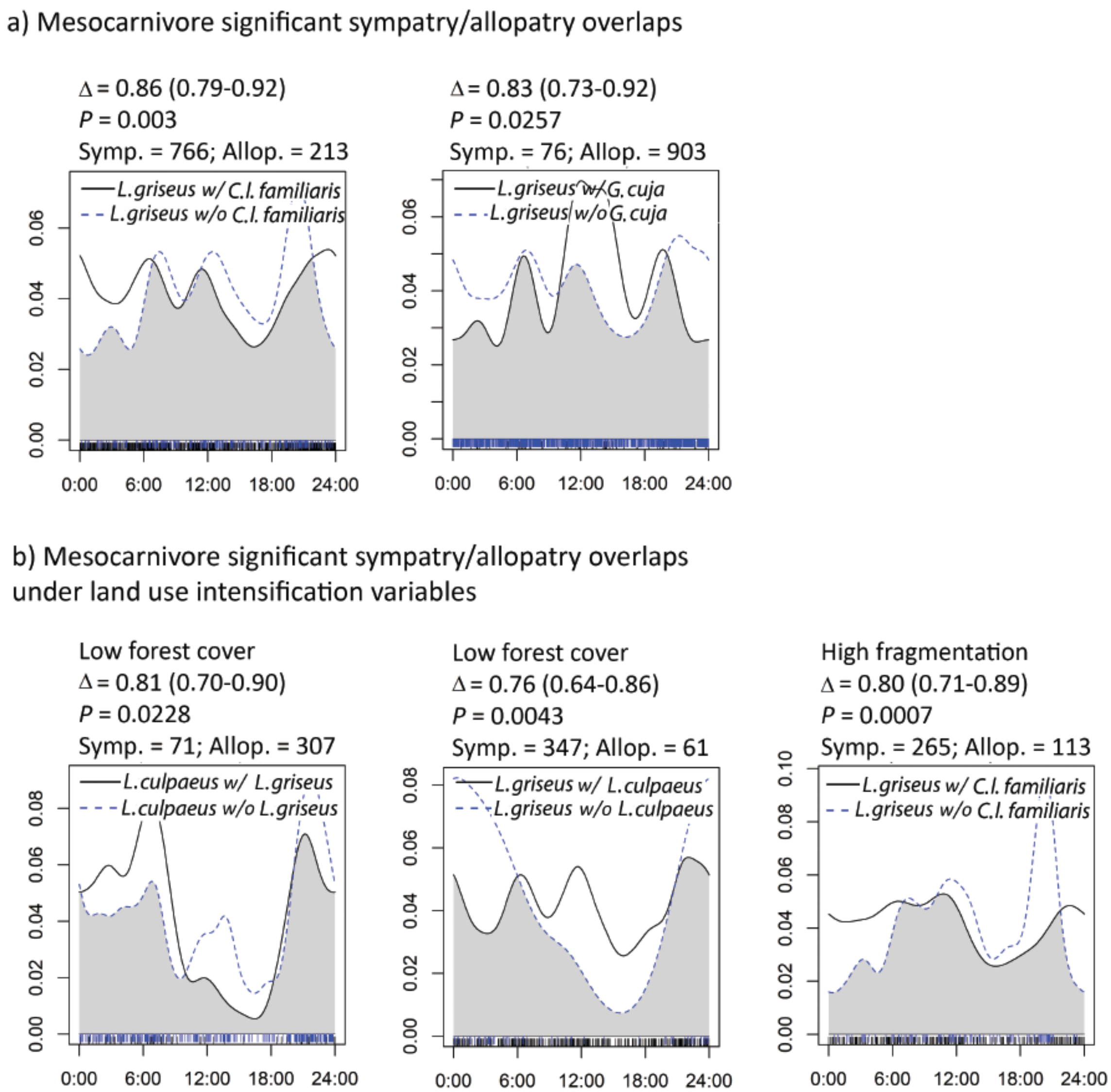


Fig. 5.—Estimated intraspecific overlap (Δ) of mesocarnivores' activity between sympatric and allopatric conditions with competitors with (a) overall data and for (b) each land-use intensification category. We show the sample size for sympatry and allopatric conditions, the overlap and confidence intervals (Δ), and *P*-value of compareCkern() test (p). We only show comparisons considered statistically significant. For all results, see Tables S2 and S3 in Supplementary Data SD1.

foxes varied among land-use intensification levels, but changes in overlap with domestic dogs were moderate (Fig. 6). Patterns of opposite activity peaks between foxes and dogs were accentuated with higher intensification, particularly for *L. culpaeus.* Overlap between *L. culpaeus* and *C. familiaris* was higher at low forest cover, and *L. griseus* showed a decrease in overlap at low forest cover and high subdivision with shifts toward nocturnal peaks or reduction in diurnal activity. Furthermore, *L. griseus* shifted patterns when in sympatry with domestic dogs at highly fragmented sites by increasing its nocturnal activity and reducing its diurnal and crepuscular activity peaks (Fig. 5b).

Activity overlap between mesocarnivores and their potential prey.—At the general level, comparisons of mesocarnivores with their potential prey showed low to high overlap of activity curves and significant differences for all pairs of species (Fig. 4b). High overlap was observed between activity patterns of *L. guigna* and rodents, although rodents were not detected during daylight hours. Lagomorphs presented two peaks of activity in the twilight phases, which resulted in a moderate-high overlap of temporal activity with *L. griseus* (cathemeral) and *L. culpaeus* (cathemeral) and low overlap with *G. cuja* (diurnal). Comparisons at different land-use intensification categories showed an overlap of > 70% in all activity curves among mesocarnivores and their prey but were all statistically different, except for *L. culpaeus* and lagomorphs, when forest cover was high (Fig. 6). Shifts in activity patterns at intensification level depended on the type of prey. Both *Lycalopex* species overall decreased their overlap with lagomorphs as intensification increased. In particular, *L. culpaeus* showed differences with lagomorphs at low forest cover, but at high forest cover, no differences were observed due to the prey species not

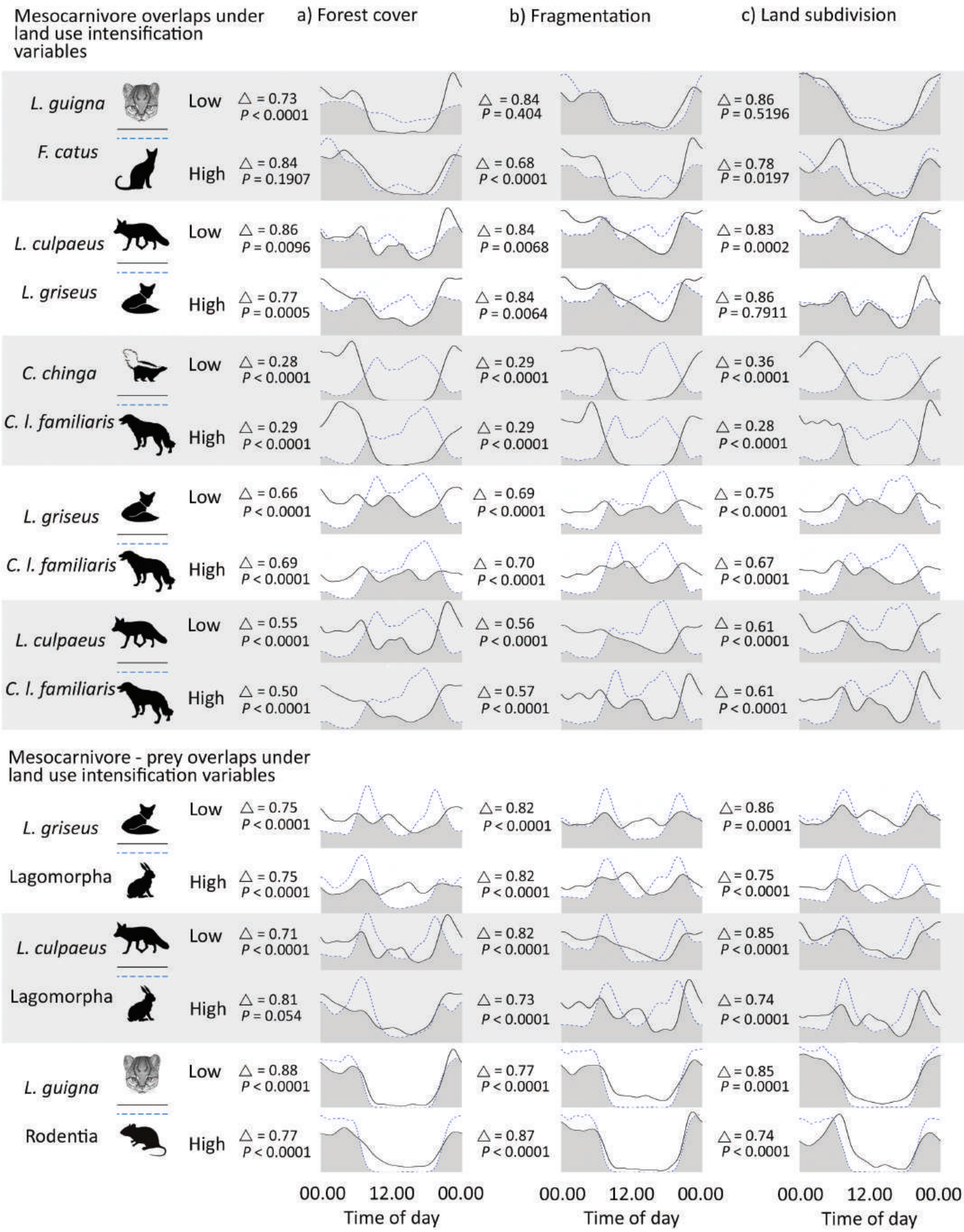


Fig. 6.—Estimated activity patterns and overlap (Δ) between the mesocarnivore species and their potential prey for each land-use intensification category: (a) forest cover (low: 20%, high: 50%); (b) number of patches (low: 30 patches/300 ha, high: 60 patches/300 ha); and (c) land ownership subdivision (low: 20 owners/300 ha, high: 60 owners/300 ha). The graphs are simplified versions of activity patterns due to the number of comparisons (for full details of graphs see Supplementary Data SD1). Estimated *P*-values from compareCkern() test are shown for each comparison.

showing two distinct peaks of activity. Furthermore, overlap in temporal activity of *L. guigna* and rodents decreased only at higher intensification for the subdivision variable, always close to $\Delta = 0.8$ although all were significantly different. The main differences arose from the fact that rodents remained nocturnal in all categories, but *L. guigna* showed some diurnal activity, which was more prevalent at lower land-use intensification. Overlap in all activity curves of the predator–prey comparisons showed a decrease at higher subdivision of land.

Discussion

Mesocarnivores undoubtedly play important roles in ecosystem functions (Prugh et al. 2009; Roemer et al. 2009; Williams et al. 2018), and their continued occurrence in landscapes under increasing intensification requires our attention (Roemer et al. 2009; Farias and Jaksic 2011). Temporal patterns can shift due to competition (Harrington et al. 2009; Cunningham et al. 2019), resource availability (Schmidt 1999; Weckel et al. 2006; Foster et al. 2013), predation risk (Ross et al. 2013), and human illumination (Hoffmann et al. 2018), among others (Presley et al. 2009; Davimes et al. 2017; Diete et al. 2017; Lendrum et al. 2017). Shifts in temporal patterns can have varying consequences such as unnecessary energy expenditure potentially reducing fitness (Kronfeld-Schor and Dayan 2003; Hut et al. 2012) or risk of intra- or interspecific interference that can result in death (Berger and Gese 2007). Our results show tendencies toward nocturnality at high land-use intensification, but the type of shift in activity within the 24-h cycle depends on species biological circadian rhythms and the magnitude of interspecific competition. For species considered nocturnal such as *L. guigna* and *C. chinga*, high levels of modification presented a decrease of diurnal/crepuscular activity that might reduce access to food resources or time spent on other behavioral activities (e.g., territorial roaming, reproduction, etc.). For cathemeral mesocarnivores (e.g., foxes), there was a shift to nocturnal activity at high land-use intensification but only when in sympatry with a competitor. Furthermore, at high land-use intensification, overlap in activity between native and domestic mesocarnivores generally decreased, while overlap between native mesocarnivores generally increased. High intensification also reduced overlap with prey species. Consequently, reduction of diurnal/crepuscular activity, higher interspecific overlap and competition, and reduced overlap with prey species as land-use intensification increases, could have implications for the survival of mesocarnivores in human-dominated landscapes.

Activity patterns and intraspecific overlap.—The mesocarnivore guild showed a diverse range of activity patterns from primarily nocturnal to diurnal and cathemeral behavior. Most of native species had their peak activity at dusk or night, except for *G. cuja* being the only diurnal species. Observed activity patterns of wild mesocarnivores were similar to those documented in the literature and, in the case of domestic species, patterns are attributed mostly to matching human activity (Supplementary Data SD1). Moreover, differences of activity between levels of land-use intensification were observed for nocturnal species but not for cathemeral species such as foxes. The primarily nocturnal activity pattern observed for *L. guigna* parallels previous studies in other areas (Delibes-Mateos et al. 2014; Hernández et al. 2015); however, more diurnal detections were observed in landscapes with greater forest cover or low fragmentation, as reported for protected areas (Zúñiga et al. 2016). *Leopardus guigna* seems resilient to habitat disturbances and hunting pressure (Gálvez et al. 2018), but here we show that land-use intensification is reducing its diurnal activity, which implies a reduction in access to prey such as diurnal birds. This reduction in diurnal activity is either due to direct factors of intensification (e.g., low habitat cover for refuge during daytime) or perhaps indirectly as a response to low bird abundance or activity (Delibes-Mateos et al. 2014; Figueroa et al. 2018). The activity pattern of *C. chinga* also was primarily nocturnal, with crepuscular activity but almost no diurnal detections. This behavior is consistent with previous studies (Donadio et al. 2001; Kasper et al. 2009); however, at high subdivision, crepuscular activity was significantly reduced, potentially decreasing time spent on key behavioral activities such as foraging, territorial roaming, dispersal, reproduction, etc. (Kasper et al. 2009; Castillo et al. 2014). *Conepatus chinga* prefers open habitat; thus, loss of forest cover might promote its presence (Iriarte and Jaksic 2017), but subdivision of land might increase threats such as domestic dogs and humans.

Activity overlap among mesocarnivores.—Mesocarnivores overlapped their temporal activity to different extents, but ecologically and taxonomically similar species overlapped at greater amounts. For example, activities of both feline species strongly overlapped (Fig. 4). The high overlap between *L. guigna* and *F. catus* could imply a high probability of encounters and exploitation competition for resources such as prey. Nevertheless, analyses of sympatry and allopatry suggest that interference competition is not causing changes in activity patterns of *L. guigna*, possibly indicating less temporal plasticity of *L. guigna* or fine-scale spatial segregation (Soto and Palomares 2015), low interference interaction between the species at encounter (either due to tolerance or attraction), or that *L. guigna* is not subordinate to domestic cats. In any case, the high overlap between these mesocarnivores could have implications for *L. guigna*. Cats with poor care from their owners have been shown to prey more on wild nocturnal vertebrates in southern Chile (Silva-Rodríguez and Sieving 2011), and small mammals were found in 37.6% of their scats. Prey included the native rodents *Abrothrix* sp., *Irenomys tarsalis*, and *Olygoryzomys longicaudatus*, and the native nocturnal marsupial *Dromiciops gliroides,* all of them also preyed upon by *L. guigna* (Freer 2004; Correa and Roa 2005). In landscapes with low levels of fragmentation and high forest cover, activity patterns of these felines were similarly close (Fig. 5), and the overlap decreased with high land-use intensification. This decrease mostly was explained by the lower diurnal activity of *L. guigna*, which could be a response to avoid diurnal threats from human activity. The similarity between activity patterns and co-occurrence of the two felines is concerning given the interspecific transmission of diseases by contact, such feline immunodeficiency virus and feline leukemia virus (Mora et al. 2015).

Of concern is the moderate to high overlap in activity between dogs and both *Lycalopex* species, in addition to the latter's apparent response to dog activity. Noticeably, both *Lycalopex* species had opposite diurnal peaks of activity with dogs, particularly *L. culpaeus* with high land-use intensification, although its overlap with dogs remained similar despite higher intensification. For *L. griseus*, the overlap with dogs tended to decrease with higher land-use intensification, while diurnal activity decreased and nocturnal activity increased when in sympatry with dogs, which supports avoidance behavior toward dog activity. Our results show that this pattern occurs mainly in highly fragmentated landscapes (Fig. 5b), but it also might arise in high land subdivision; samples in allopatry were too few to conduct analyses (i.e., dogs were too common in high land subdivision; Table S3 in Supplementary Data SD1). Dogs have been documented persecuting and killing foxes in Chile (Silva-Rodríguez et al. 2010). Attacks by dogs were the main reason for admission of foxes into wildlife rescue and rehabilitation centers in Chile due to animal interactions (Romero et al. 2019). Moreover, rural and urban dogs are reservoir and transmitters, from either direct contact or feces, of diseases such as canine distemper with outbreaks in fox populations in central Chile (Acosta-Jamett et al. 2011) and increasing presence of sarcoptic mange (Montecino-Latorre et.al. 2020). Domestic dogs also showed low activity pattern overlap and no changes at different levels of land-use intensification with *C. chinga*, which could indicate a low probability for both species to encounter. Nonetheless, dogs have been observed killing *C. chinga* in other areas (Kasper et al. 2009; Castillo et al. 2011). Because *C. l. familiaris* also was observed to be active at night, it is unknown if their nocturnal activity and the encounter rate between the species is enough to affect *C. chinga*'s population growth rate by dog persecution and predation. For the guild, the encounter rate between domestic dogs and native species could be high given the observed overlap in activity and the high abundance of domestic dogs in Chile (Astorga et al. 2015). Thus, the negative interaction between domestic dogs and native mesocarnivores, and the potentially high encounter rates, highlight the importance of responsible ownership of dogs.

As expected, the overlap in activity between *L. culpaeus* and *L. griseus* increased with higher land-use intensification, both for lower forest cover and higher land subdivision. Higher overlap could be a problem for these species, given the avoidance evidence observed, which could arise from higher interference competition (Mills et al. 2019). The two species changed their activity pattern in sympatry when forest cover was low (Fig. 5b), with more nocturnal and less diurnal activity for *L. culpaeus* and more diurnal and less nocturnal activity for *L. griseus.* These canids share most of their diets (Ebensperger et al. 1991; Jiménez et al. 1996; Iriarte and Jaksic 2017; Muñoz-Pedreros et al. 2018) and were observed to segregate spatially (Jiménez et al. 1996; Moreira-Arce et al. 2016). They might naturally coexist by hunting and foraging at the same hours but in different areas (Jiménez et al. 1996; Zúñiga et al. 2009; Murphy and Ruth 2010; Moreira-Arce et al. 2016), but when habitat is reduced, their competition might intensify and force them to modify their activity patterns. In low forest cover conditions, this could be the case, but in other conditions, the possibility to segregate temporally might be compromised by other constraining factors, such as higher human and dog activity during the day in highly fragmentated habitats and subdivided landscapes. Diets of these two foxes also overlap with the native mustelid *G. cuja* (Ebensperger et al. 1991; Correa and Roa 2005; Zapata et al. 2005), but evidence of interference competition and avoidance was not found, given the low level of detections of the mustelid to make comparisons and to the unexpectedly higher diurnal activity of *L. griseus* when in sympatry with it.

Activity overlap between mesocarnivores and their potential prey.—All species of mesocarnivores overlapped to a moderate-high extent with their prey ($\hat{\Delta} > 0.74$; Fig. 4), except for *G. cuja*, which overlapped only moderately with lagomorphs. This was to be expected given this mustelid usually uses a different hunting strategy because it can enter rabbit burrows (Miller and Rottmann 1976), which is more effective when these small mammals are inactive. *Lycalopex culpaeus* and *L. griseus* often overlapped strongly with lagomorphs under different land-use intensification. Lagomorphs have become an important prey item to native foxes because they have with high biomass (Zúñiga et al. 2008; Poo-Muñoz et al. 2014; Muñoz-Pedreros et al. 2018). In general, overlap between foxes and lagomorphs decreased with higher land-use intensification and particularly with contrasting levels of subdivision. Nocturnal activity of lagomorphs was lower in these environments, which could be a response to the increase in nocturnal activity of foxes or other factors reducing their activity making them less available for as prey. Temporal activity of *L. guigna* also overlapped strongly with its rodent prey, particularly with high fragmentation and reduced forest cover. Daytime detections of *L. guigna* were less frequent in high land-use intensification, likely because of avoidance from diurnal human activity threats, making it more nocturnal and thus overlapping its activity more with other nocturnal species. Nocturnal rodent abundance also could influence this behavior because they proliferate in agricultural lands (Stenseth et al. 2003; Benedek and Sîrbu 2018). Nevertheless, at high subdivision, their overlap decreased due to reduced güiña nocturnal activity, possibly making rodents less available for predation. Even though we are unable to provide a thorough explanation to the complex shifts in activity patterns of prey species, it is likely that modification of activity overlap between predators and their prey has consequences in fitness due to lower probability of encountering prey (Ramesh et al. 2012; Delibes-Mateos et al. 2014).

We provide new insights in the temporal behavior of the understudied mesocarnivore community of agricultural landscapes in southern Chile and fine-tune explanations of land-use intensification impacts that can be used in other aggregate systems around the world to study mesocarnivores. Our study suggests that land-use intensification is triggering subtle community-level shifts in activity patterns of native mesocarnivores that constrict temporal niche breadth during the 24-h cycle with potential impacts on species fitness (Kronfeld-Schor and Dayan 2003; Hut et al. 2012; Sévêque et al. 2020). Our results also serve as evidence for the need to suppress activities of free-roaming dogs; that is: they should be tethered or kept in enclosures to mitigate the impacts of high land-use intensification on mesocarnivores. For a more complete view of community dynamics in these landscapes under increasing human pressure, a better understanding is needed on the spatial segregation of the mesocarnivore guild and prey availability along a land-use intensification gradient. In particular, multi-season studies of the occurrence and abundance of these species should be carried out to determine their currently unknown population trends.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Includes Table S1 with details of the references used to make Fig. 2. It also includes: Tables S2 and S3 with detailed results from sympatric/allopatric analyses; all plots of comparisons that are summarized in Fig. 6; and supplementary discussions of intraspecific results.

Supplementary Data SD2.—Number of records observed for each species in each range for the three landscape variables studied.

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