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Spatiotemporal interactions of predators and prey of a neotropical mammal community in southern Mexico

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35 **Abstract**

36 Predator-prey interactions are one of the central themes in ecology due to their importance as a
37 key mechanism in structuring biotic communities. In the predator-prey systems, the no-trophic
38 interactions, such as persecution and avoidance, have more impact on ecosystems than the
39 trophic ones. We analyze the spatiotemporal relations between prey and predators of a
40 community of medium and large-size mammals in a tropical region. We analyzed time data
41 series of camera-trap data. The observed data of time lags among occurrences of pairs of species
42 were compared with random data using the Bootstrap method. We generate a network of co-
43 occurrences to describe the significant spatiotemporal patterns between predators and prey and
44 used the kernel density estimator to analyze the overlap of daily activity patterns themy. We
45 found 26 predator-prey interactions ($p < 0.05$), which involved 14 species. The results suggest that

prey perceives the risk of predation and display avoidance behavior both spatially and temporally which is consistent with fear theory. Predators may be deploying opportunistic and / or intermittent foraging strategies to reduce prey mobility caused by previous predation encounters. This study provides a new approach to understand the interactions between predators and prey through camera-trapping or similar data of spatiotemporal co-occurrences.

Introduction

Predator-prey interactions have received considerable attention (Krebs 1972; Clinchy et al. 2012) due to their importance as a key mechanism in structuring biotic communities (Suraci et al. 2016; Brown 2019; Gaynor et al. 2019). Reviews on the topic have provided a better understanding in both theoretical and empirical areas, showing these relationships influence the demographic dynamics of populations, through processes of dependent regulation (Rosenzweig & Macarthur 1963; Berryman 1992; Jost et al. 1999; Gaynor et al. 2019) modulating trophic chains and configuring ecosystems (Suraci et al. 2016).

In the predator-prey systems, it has been observed that indirect interactions play an important role in communities (Preisser et al. 2005; Preisser & Bolnick 2008; Clinchy et al. 2012), influencing the dynamics of ecosystems more than the direct interactions themselves (Preisser et al. 2005; Peckarsky et al. 2008). Indirect interactions are mediated by a third element left by one of the species, as a result search and avoidance behaviors can emerge (Endler 1986; Brown 2019), in a variate of temporal and spatial scales (Lima & Dill 1990). For instance, indirect interactions can occur from cues left by predators, which may include spraying urine, scraping, calls, and odors left during the territory defence and foraging walks (Rabinowitz & B. G. Nottingham 1986; Palomares et al. 2018); The prey when perceiving the cues of the predator develop survival strategies, such as changes in movement and foraging patterns (Preisser et al.

2005; Clinchy et al. 2012). When the risk of predation is perceived by the prey in their feeding areas or home ranges, a "landscape of fear" occurs, therefore, potentially dangerous places or times are avoided (Laundré et al. 2010; Clinchy et al. 2012; Brown 2019). In these situations, prey must deal with the trade-offs between the risk of predation and the consumption of sufficient and quality food (Lima & Dill 1990; Bouskila & Blumstein 1992; Suselbeek et al. 2014; Gaynor et al. 2019; Smith et al. 2019). From a predator point of view, there is a "landscape of opportunity", and changes in prey densities will force predators to move to the areas where the prey is, in order to increase the rate of encounters, predation, and consumption (Gaynor et al. 2019).

The search and avoidance behaviors of predator and prey, respectively, can be species-specific and vary at multiple spatiotemporal scales, therefore, different approaches are required to study them (Gaynor et al. 2019; Niedballa et al. 2019). Camera-trapping has been an effective method to study ecological aspects of ground-dwelling birds and mammals allowing for the recording of a large amount of data with very little interference in the behavior of the species (O'Connell, A. F., Nichols, J. D., and Karanth 2010). One of the lines of research carried out with this technique, is the processes underlying interspecific interactions, such as the predator-prey systems in the temporal and spatial dimensions (Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares 2012; Sollmann 2018)). In the spatial dimension, the approaches to identify spatial segregation between predators and prey have used models of occupation of one or two species and correlation tests; using occupation models, they have found that the abundance of prey is positively associated with the occurrence of predators (Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares 2012; Padilla-Gómez 2018). Other studies have integrated models of occupation and temporal overlap to measure spatial and temporal segregation between species, respectively, improving the

92 understanding of the regulatory mechanisms of predator-prey systems, showing, in general, that
93 when there is a high overlap in one of the two dimensions (space or time) in the other dimension
94 a segregation occurs (Carter N.Jasny, M., Gurung, B., Liu 2015; Gutiérrez-González & López-
95 González 2017; Yang et al. 2018; Pudyatmoko 2019). Although a high spatial-temporal overlap
96 between predators and prey has also been observed, suggesting a high dependence of the
97 predator on the prey (Dias et al. 2019). Regarding predator species, it is known that there is
98 competitive exclusion, which indicates that the coexistence of two species with identical
99 ecological niches is not possible (Gause 1934) and one of them, the subordinate species, will
100 show a segregation in one of the axes to facilitate coexistence (Amarasekare 2003). At the
101 temporal dimension, temporal overlap of daily activity between pairs of species has been
102 measured by fitting circular models to the data obtained with camera-traps (which record the
103 time an animal is photographed) (Sollmann 2018). With this approach it has been observed that
104 predators adjust their daily activity schedules to those of their main prey (Foster et al. 2013;
105 Herrera et al. 2018; Sollmann 2018), whereas the prey tries to avoid the predators' peak activity
106 times (Suselbeek et al. 2014).

107 A few studies have investigated the time intervals between the occurrence of predators and prey
108 observed in camera-traps to explore spatiotemporal avoidance and search to infer indirect
109 interactions(Sollmann 2018). Parsons et al. (2016) calculated time intervals between prey events
110 with and without the passage of a predator, finding that prey species temporarily avoid coyotes
111 (*Canis latrans*), dogs (*Canis lupus familiaris*), and humans, but not the sites where they co-occur.
112 Karanth et al. (2017) contrasted times between events of species pairs against random intervals,
113 finding that the dhole (*Cuon alpinus*), leopard (*Panthera pardus*) and tiger (*Panthera tigris*)

displayed a higher spatial and temporal overlap when prey densities were low, while combined spatiotemporal overlap was minimal.

In this work, we use two mathematical tools: matrices and networks to infer search and avoidance behaviors between predators and prey. The objectives of this work are two: 1) to analyze the spatiotemporal co-occurrence of prey and predators of a community of mammals of medium and large-sized in a tropical region of southern Mexico. We hypothesized that prey would avoid predators in the spatial and temporal dimensions, as a strategy to minimize the risk of predation (Gaynor et al. 2019). In turn, we predict that predators will occur at sites where potential prey previously occurred, following a search behavior (Endler 1986). 2) To analyze the overlap of diel activity patterns between species pairs. In this case, we assumed that predators synchronize their activity with that of their prey (Carrillo, E., Fuller, T. K., & Saenz 2009; Foster et al. 2013; Herrera et al. 2018) but not among them, since the coexistence of two species with identical ecological niches is not possible (Gause 1934).

The region where the present study was carried out is relatively conserved; the camera-trap stations were placed in community conservation areas, the records of domestic animals and humans are scarce, consequently our findings may show natural / conserved interactions between species and reflect the proper functioning of the ecosystem. Changes in these patterns may be indicative of disturbed ecosystems with consequences for evolutionary and ecosystem services.

Methods

Study area

The Chinantla is a region located in the state of Oaxaca, southern Mexico (17.317 and 18.164 N and -95.567 and - 96.699 W, Fig. 1). It has a heterogeneous topography, with elevation ranges

136 from 50 to 3,100 m (Van Der Wal 1999). The climate is warm humid in the lowlands and
137 temperate humid in the highlands (INEGI, 2000). This region is recognized as hyper-rainy
138 because rainfall reaches 4,500 mm per year (Meave et al. 2006). Natural vegetation includes
139 rainforest, cloud montane forest, and pine-oak forest (INEGI, 2015). The Chinantla region has
140 the third largest tropical rainforest in Mexico (CONANP 2005). Land tenure is mainly
141 communal, followed by ejidos (a system of communal land tenure) and private property; there
142 are areas voluntarily designated for conservation (ADVC), of social initiative but with
143 government recognition, that protect 58,765,785 ha of conserved forests (CONANP-Chinantla
144 Office) (Fig. 1). Specifically, this study was carried out in 18 communities in the municipalities
145 of San Miguel Soyaltepec, Santa María Jacatepec, San Juan Bautista Valle Nacional, San Felipe
146 Usila, San José Chiltepec and Santiago Jocotepec.

147 Data collection

148 Between 2011 and 2014, 130 camera-trap stations were installed in the Chinantla region. The
149 camera-trapping samplings were carried out in collaboration with indigenous communities and
150 representatives of the National Commission for Protected Areas (CONANP). Sites for trap
151 camera stations were selected based on the presence of wildlife evidence, and also near fruit trees
152 and water bodies (Swann et al. 2011). The cameras were placed at a height of 30-40 cm above
153 the ground, they were tested to verify their correct functioning, and they were programmed to
154 work 24 hours and with the minimum delay time between the photographs; care was taken not to
155 use daylight savings time. Each of the stations was geo-referenced. The cameras were spaced
156 between 100-1,000 m and remained in the field up to 131 days with an average of 34 days. The
157 photographs obtained at each station were organized in folders with their names and geographic
158 coordinates. A data base was created from the photographic records and associated data, with the

159 following information: municipality, town, station, camera ID, camera brand, installation date,
160 remotion date, latitude, longitude, altitude, type of vegetation, station ID, species recorded,
161 photograph or video, digital photograph ID, day, month, year, time, sex of the species and
162 observations. For data analysis, we only used the photographs that were considered independent
163 events: consecutive photographs separated by 24 hrs. We use the records of terrestrial species
164 and of all those considered potential prey for the three main predators in the region, *Panthera*
165 *onca*, *Puma concolor* and *Leopardus pardalis*.

166 Data analysis

167 The analysis of the time intervals between the occurrence of predators and prey was approached
168 spatially and temporally, following the model of Niedballa et al. (2019), in which it is assumed
169 that species i is not affected by species j , while species j has two possibilities to avoid interaction
170 with species i , the absence of the species, or the change in its activity peaks. Additionally, we
171 consider attraction, in which species i is attracted to species j (search behavior).

172 Spatiotemporal co-occurrence of predators and prey

173 We used a mechanistic approach similar to that of Karanth et al. (2017) to analyze the time
174 intervals between the occurrence of two species (predators-prey and predator-predator). The data
175 of the observed species by site and day were used to build a three-dimensional matrix that is
176 formed by 14 bidimensional matrices of size 1492 x 130. Each bidimensional matrix corresponds
177 to one observed species, whose rows are the days and their columns are the camera-trap stations.
178 Each two-dimensional matrix A satisfies that the input $A_{ij} = 1$ or $A_{ij} = 0$, depending on whether
179 or not the species was observed on a certain day i and a certain station j respectively, in other
180 words, the matrix A is of presence / absence. When adding the bidimensional matrices A and B

181 associated to the species e_A and e_B , respectively, we will obtain a value of 2 in the simultaneous
182 appearances, i.e. $(A + B)_{ij} = A_{ij} + B_{ij}$, we call this step species e_A versus species e_B
183 coincidences. To determine on which days in a fixed station, the species e_B (e. g. predator) passes
184 after the species e_A (e. g. prey) did it, we time lag occurrences from 1 to 20 days. This involves
185 computationally limiting the matrix A to rows from 1 to $1492 - k$, where k is the number of time
186 lag days, and the matrix B to the rows from k to 1492. When the sum of both limited matrices in
187 a position (i, j) is 2 tell us that the species e_A was observed on a certain day and the species e_B is
188 observed k days after, we call this step coincidences with time lags. We chose 20 days because it
189 is the maximum time that a feline scent remains (David Smith *et al.* 1989).

190 We define co-occurrence as the presence of the specie e_A at certain station certain day x and the
191 presence of the specie e_B at the same station the day $x + k$, where k is a unique value from 0 to
192 20.

193 By using the absolute frequency, i. e., the number of total co-occurrences in each of the 21
194 studied days (the same days plus 20 days of time lag), a species-species file was constructed
195 indicating the co-occurrence of each species e_A with every specie e_B and the frequency by 21
196 days.

197 Once the species-species file was constructed, we used the Bootstrap method to identify
198 significant co-occurrences, which consists of random resampling the data and obtaining the p-
199 value of the real sample against the randomized data. In this case, considering the observed dates
200 and days in which each camera-trap worked and the number of times that a certain species was
201 observed according to the presence / absence data (probability of presence in calendar days i. e.
202 independent events), 100 random tridimensional matrices of size $1492 \times 130 \times 14$ were

203 generated. As well as we did to the three-dimensional matrix constructed with the observed data,
204 to each of these 100 matrices we apply the steps 1) the species e_A versus species e_B coincidences
205 and 2) coincidences with time lags. The result of these steps was kept in 100 files, where each
206 pair of species and the absolute frequency of their co-occurrences for 21 days are saved.

207 To obtain the p-value of the co-occurrence between e_A and e_B in a fixed day k , where k takes
208 integer values between 0 and 20 the following formula was used:

$$209 \quad p(e_A, e_B, k) = \frac{1 + \sum H(s \geq s_0)}{N + 1}$$

210 where s_0 is the observed number of co-occurrences between e_A and e_B in the observed data on the
211 studied day, s is the observed number of co-occurrence between e_A and e_B for each evaluated
212 random matrix, $H(s \geq s_0)$ returns a 1 if the inequality is satisfied and a 0 if not, $\sum H(s \geq s_0)$ is
213 the number of times the inequality $s \geq s_0$ is satisfied and $N = 100$ (Davidson and Hinkley, 1997).
214 Once the p-value was obtained, the values where $p(e_A, e_B, k) < 0.05$ are taken, this means that we
215 can reject, in our hypothesis test, the null hypothesis (no co-occurrence or avoidance) and accept
216 the alternative hypothesis (co-occurrence). Hereinafter every time that we say co-occurrence, we
217 are saying that the interaction between the pair of species in a given day in the observed data has
218 p-value < 0.05 .

219 The programs developed to analyze the data were implemented in Octave (Eaton et al., 2019).
220 Octave allows the use of matrices naturally and also allows the graphing of the data. To visualize
221 the co-occurrences, we created a spatiotemporal co-occurrence digraph, composed by vertices
222 and directed edges (network), where a vertex (circle) represents a species and a directed edge

(arrow) that leaves one vertex and reaches another indicates that the first one follows the second one.

The network was implemented in Python (Rossum 1995), and the algorithm uses the libraries: networkx, matplotlib, pyplot and pandas to create a digraph G. The vertex size is the relative abundance index (IAR) which was obtained with the following formula: $IAR = (\text{independent events of each species} / \text{trap days}) * 100$. The thickness of the arrow indicates the statistical significance; a thicker arrow implies a smaller p-value. The color of the arrow represents the first appearance of a significant interaction between the species, i.e. the first day among the 21 days in which the co-occurrence hypothesis is accepted $p(e_A, e_B, k) < 0.05$ (Supplementary material 1).

Overlapping daily activity patterns

Independent events of species throughout the study were used to measure the degree of overlap in the activity patterns among pairs of species. We fit a smooth circular curve with the kernel density method to quantify overall activity levels of the species (Meredith M. 2017). The degree to which the species pair curves overlap serve as an index of similarity (Sollmann 2018). The analysis was performed with the Overlap package (Meredith M. 2017). As a smoothing parameter, a value of $h = 1$ was used, suitable for small samples (Ridout & Linkie 2009; Sollmann et al. 2012). Observed time was adjusted to solar time according to the Müller (1995).

Results

A total of 26 species of medium and large-sized mammals were recorded during the course of the study. For the spatiotemporal analysis, 14 not arboreal species with more than 20 records were selected (*Didelphis*, *Philander opossum*, *Dasypus novemcinctus*, *Dasypus procta mexicana*,

245 Cuniculus paca, Sylvilagus, Leopardus pardalis, Puma concolor, Panthera onca, Eira barbara,
246 Nasua narica, Procyon lotor, Pecari tajacu and Mazama temama).

247 Spatiotemporal co-occurrence of predators and prey

248 We found a total of 166 interactions between pairs of species of which 80 are significant co-
249 occurrences. The 14 species co-occur with at least one other species, either on the same day or in
250 any of the 20 days of time lag. In specific, all the predator-prey co-occurrences are 26 (Fig. 2).

251 The spatiotemporal co-occurrence network shows that predators are generally not searching for
252 prey, but apparently prey are displaying avoidance behavior. P. onca had co-occurrences with
253 nine species (eight potential prey and one competitor), only one suggests a seeking behavior:
254 $p(P. onca, P. tajacu, 17 \text{ days}) = 0.049$. Prey of P. onca showed avoidance, once P. onca occurs at
255 one site, seven other possible prey passed after at least seven days: $p(P. onca, N. narica, 7 \text{ days})$
256 $= 0.049$, $p(P. onca, D. mexicana, 12 \text{ days}) = 0.009$, $p(P. onca, C. paca, 14 \text{ days}) = 0.039$, $p(P.$
257 $onca, Didelphis, 14 \text{ days}) = 0.049$, $p(P. onca, P. tajacu, 15 \text{ days}) = 0.009$, $p(P. onca, P. opossum,$
258 $13 \text{ days}) = 0.019$, and $p(P. onca, Sylvilagus, 5 \text{ days}) = 0.049$. On the other hand, three species
259 co-occurred with P. concolor, two species showed avoidance behavior: $p(P. concolor, D.$
260 $mexicana, 19 \text{ days}) = 0.009$, and $p(P. concolor, P. opossum, 7 \text{ days}) = 0.019$; whereas one
261 species suggested a tolerance behavior: $p(P. concolor, E. barbara, \text{same day}) = 0.019$. Similar to
262 P. onca, P. concolor occurred several days later than P. tajacu: $p(P. tajacu, P. onca, 17) = 0.049$.

263 In the case of L. pardalis, avoidance was observed by its main prey: $p(L. pardalis, D.$
264 $novemcinctus, 11 \text{ days}) = 0.029$, $p(L. pardalis, D. mexicana, 14 \text{ days}) = 0.009$, and $p(L. pardalis,$
265 $C. paca, 18 \text{ days}) = 0.049$. Other species rarely predated by L. pardalis, also occurred several
266 days after the pass of the feline: $p(L. pardalis, P. tajacu, 11 \text{ days}) = 0.019$ and $p(L. pardalis, M.$

temama, 12 days) = 0.049. On the other hand, *L. pardalis* was found at the same site several days after prey occurred: $p(D. mexicana, L. pardalis, 7 \text{ days}) = 0.019$, $p(D. novemcinctus, L. pardalis, 18 \text{ days}) = 0.009$, and $p(D. marsupialis, L. pardalis, 19 \text{ days}) = 0.039$. *E. barbara* appears to be tolerant to the *L. pardalis* presence: $p(L. pardalis, E. barbara, \text{same day}) = 0.009$.

Regarding to co-occurrence among predators, we found *P. concolor* passed after *P. onca* with a small difference in days: $p(P. onca, P. concolor, 3 \text{ days}) = 0.029$; whereas once that *P. concolor* passed *P. onca* did not occur. Noticeably, we found *L. pardalis* and *P. concolor* co-occur on the same day: $p(L. pardalis, P. concolor, \text{same day}) = 0.019$; Fig. 2).

Overlapping daily activity patterns

The highest daily temporal overlap was found to occur between the predators, *P. onca* and *P. concolor* and *L. pardalis* (both $\Delta=0.83$), followed by *L. pardalis* and *C. paca* ($\Delta=0.80$). In particular, the overlaps between *P. onca* and its prey were moderate, with values ranging from $\Delta=0.41$ with *N. narica* to $\Delta=0.75$ with *C. paca*. On the other hand, *P. concolor* presented overlap values $\Delta > 0.7$ with *Didelphis* and *C. paca* (Table 1; Supplementary material 1). *L. pardalis* showed the highest overlap with *C. paca*. $\Delta= 0.80$, *Sylvilagus* $\Delta= 0.79$, *Didelphis* $\Delta= 0.75$, and *D. novemcinctus* $\Delta= 0.70$ (Table 1; Supplementary material 2).

Discussion

Spatiotemporal co-occurrence of predators and prey

There is a debate about whether the presence-absence data allow us to make inferences about interactions (Blanchet et al. 2020), we recognize that there are multiple factors influencing these relationships, such as abundance fluctuations or habitat features. However, in this study, we

288 propose the use of different methods as: the tridimensional matrix representation of the data, the
289 bootstrap method to identify spatiotemporal interactions in the search and avoidance phase of the
290 predator-prey system in neotropical ecosystems and a visual tool to show co-occurrences. As a
291 result, we identify six important findings.

292 First, we found prey co-occurs many days after predators passed. For instance, *N. narica*, *C. paca*
293 and *P. tajacu* occurred in the same site 7, 14 and 15 days after *P. onca*, respectively; *Dasyprocta*
294 *mexicana* occurred 19 days after *P. concolor*; and *D. mexicana* and *C. paca*, occurred 14 and 18
295 days after *L. pardalis*, respectively. These findings can be explained from the “ecology of fear”,
296 which proposed the risk of predation is perceived by prey, and they in response display
297 antipredatory avoidance behaviors, occurring in these cases, many days after the predator pass
298 (Clinchy et al. 2012; Brown 2019).

299 Second. Overall, we found predators did not show a search behavior, since they were not
300 recorded in the same stations where their prey passed, neither on the same day, nor on
301 subsequent days as had been predicted; with the exception of the pairs *P. tajacu*-*P. onca*, *P.*
302 *tajacu*-*P. concolor*, *D. mexicana*-*L. pardalis*, *D. novemcinctus*-*L. pardalis* and *D. marsupialis*-*L.*
303 *pardalis*, for which predator occurrence was many days later (>seven days). One explanation
304 may be that predators hunt by opportunistic encounters, as has been suggested before (Emmons
305 1987; Romero-Muñoz, A., Maffei, L., Cuéllar, E., & Noss 2010) instead of following a particular
306 prey clue. Another non-exclusive explanation is that predators perform an intermittent foraging
307 (Dias et al. 2019), in which individuals implement a search for prey in two phases: 1) intensive
308 search in several sites and 2) rapid movements among sites. In the intensive search phase, the
309 predator visits particular sites where it is more likely to find prey and lead an attack (O.
310 Bénichou, C. Loverdo, M. Moreau 2011; Murakami & Gunji 2017). The movement phase is

311 generally performed quickly, with a low probability of encounters, but it allows traveling long
312 distances. If the predator performs this kind of foraging, the predator will forage for a short time
313 in different areas within its territory and thus prevents the prey in these areas displayed migratory
314 behaviors, so that the foraged areas will almost always have prey availability.

315 Third. Our research revealed that the overlap of the activity patterns of *P. onca*, *P. concolor* and
316 *L. pardalis* with their prey was low in the case of *N. narica*, moderate with *M. temama*, *D.*
317 *novemcinctus*, *P. tajacu*, and high with *C. paca*. These contrasts in activity overlaps have been
318 reported in other studies (Rabinowitz & B. G. Nottingham 1986; Chinchilla 1997; Estrada-
319 Hernández 2008; Harmsen et al. 2009; de Oliveira & Pereira 2014). In the case of *P. onca* and *P.*
320 *concolor*, it has been suggested that the activity patterns are synchronized with those of their prey
321 (Foster et al. 2013), however, asynchronization has been observed more frequently in studies
322 with camera-traps (Romero-Muñoz, A., Maffei, L., Cuéllar, E., & Noss 2010; Herrera et al.
323 2018). For these two large predators whose diet is versatile, asynchronization with a greater
324 number of prey species seems to be a better hunting strategy than synchronization with a single
325 species (Romero-Muñoz, A., Maffei, L., Cuéllar, E., & Noss 2010). In the case of the two main
326 prey of the medium-sized predator *L. pardalis*, we found an asynchronization with *D. mexicana*
327 ($\Delta=0.45$) but synchronization with *C. paca* ($\Delta=0.80$). It has been observed that the agoutis, such
328 as *D. mexicana*, concentrate its activity at times of low risk of predation, especially when there is
329 more food availability (Suselbeek et al. 2014). Meanwhile the high overlap activity of *L. pardalis*
330 with *C. paca* suggests a seeking behavior.

331 Fourth. We found tolerance between two predators, *L. pardalis* and *P. concolor*, since they
332 occurred in the same places, in a few days of difference and at high synchrony in their daily
333 activity pattern. Therefore, our findings contradict the findings that *P. concolor* is a dominant

334 species over *L. pardalis* (Elbroch & Kusler 2018), at least in the spatial and temporal dimension.
335 In addition, a review of studies of activity patterns among the two species in Central and South
336 America reported overlaps between 0.61 and 0.73, suggesting that these species overlap in
337 activity behaviors (Santos et al. 2019). In contrast, studies of feeding habits of these two species
338 show a low (Chinchilla 1997; Martins, R., Quadros, J., & Mazzolli 2008; Gómez-Ortiz et al.
339 2015) or moderate overlap in the prey they consume (Moreno et al. 2006; Giordano et al. 2018),
340 and rarely high, probably as a consequence of the habitat condition (Tirelli et al. 2019). The
341 partition of the food niche of both species can explain the coexistence at the temporal and spatial
342 scales found in this study. Moreno et al. (2006) suggest that *L. pardalis* and *P. concolor* fit the
343 energetic model proposed by Carbone (2002) which indicates that small predators (<21.5 kg)
344 predate prey smaller than 45% of their mass, and large predators (> 21.5 kg) are capable of
345 consuming prey greater than 45% of their mass. Consequently, *P. concolor* and *L. pardalis* are
346 exploiting the same sites at the same times in search of prey of different size classes: *P. concolor*
347 for large prey and *L. pardalis* for small prey (Sunquist & Sunquist 2019). Future studies of the
348 feeding habits of these species in the region will be able to complete the panorama of coexistence
349 between both felids.

350 Fifth. We found high intra-guild spatiotemporal tolerance of the pairs of carnivores *L. pardalis*-*E.*
351 *barbara*, *P. concolor*-*L. pardalis* and *P. concolor*-*E. barbara*, which co-occurred on the same day
352 or in very close days in the same places. The co-occurrence of these pairs was cyclical, i. e., the
353 passage of one was followed by the passage of the other. A similar pattern, between *L. pardalis*
354 and *E. barbara* was found by Massara et al. (2018) in the Atlantic forest, where *L. pardalis* did
355 not influence the spatial distribution of *E. barbara*. However, de Oliveira and Pereira (2014)
356 found that *P. concolor* and *L. pardalis* exert a strong impact on the assembly of small carnivores,

among which are *E. barbara*, which has been reported in the diet of these felines. The tolerance of felines towards the mustelid is explained by the low overlap in the pattern of daily activity that occurred between them, while the felines were nocturnal, the mustelid was mainly diurnal, which reduces the probability of encounters and possible predation.

Six. The two larger predators in the region, *P. onca* and *P. concolor*, are active at the same times of the day, overlapping in their diel activity patterns ($\Delta=0.89$), but they occur with a time lag in the same place. It was recorded that *P. concolor* is the one that occurs after *P. onca* (three days later), suggesting a temporal segregation not measured previously. The high temporal overlap between both felids has been explained from the spatial segregation (Foster et al. 2013; Herrera et al. 2018). In this regard, it has been pointed out (in 65% of 25 studies reviewed) that *P. onca* temporarily or spatially displace *P. concolor* (Elbroch & Kusler 2018). However, in eight neotropical forests of South America, it was found that *P. onca* does not influence the habitat use of *P. concolor*, and although they presented a moderate temporal overlap, the activity peaks of *P. concolor* seem to avoid the hours of highest activity of *P. onca* (Santos et al. 2019). For the apparent spatial and temporal partition observed among carnivores, it has been proposed that prey abundance is more important than intra-guild interactions (Santos et al. 2019). In contrast, other studies have indicated that both felines are active at the same times (Foster et al. 2013), both during the day and at night; this strategy achieves greater availability of prey with different activity patterns (Romero-Muñoz, A., Maffei, L., Cuéllar, E., & Noss 2010). In the Caatinga of Brazil (Astete et al. 2017) and in an arid environment in northern Mexico (Gutiérrez-González & López-González 2017) both spatial and temporal coexistence has been found, the researchers explain, that this happens as a consequence of habitat conditions and abundance of prey.

In conclusion, this study explores spatiotemporal patterns in the avoidance and search phases in the predator-prey system using time series and ecological networks. In this way, as far as we know, we provide a complementary method to current methods to infer interactions between species, such as: the occupancy models of two-species and the temporal overlap of daily activity patterns (Sollmann et al. 2012; Sollmann 2018). Two-species occupancy models work with a dominant and a subordinate species, assuming that the subordinate will have a lower probability of occupation in the presence of the dominant one (Richmond, O. M., Hines, J. E., & Beissinger 2010), and the overlap methods analyze pair of species activity patterns throughout the 24 hr cycle. Our approach analyzes the encounter times between species to measure the time intervals between the occurrence of one species and another at the same site in a different way. An advantage of the ecological networks used here is that it is feasible to analyze interactions between more than two species, for example, to test whether the presence of species A followed by species B increases the probability of species C passage or avoidance and gives a panoramic view of the behaviour of the interactions. Future studies on times for encounters and ecological networks can be directed to accommodate imperfect detection and to distinguish patterns between habitats (Gorini, L., Linell, JD, May, R., Panzachi, M., Boitani, L., Odden, M., Nilsen 2011; Morueta – Holme et al. 2016). Also it is of interest the reduction of the time intervals, instead of using 1 day, as in this study, using intervals of for example 4, 8 or 12 hrs. to obtain a finer pattern in the predator and prey search and avoidance phases. Although this will strongly depend on the amount of data obtained per station.

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639 Table 1. Daily temporal overlap between predators and prey in the Chinantla region, Mexico.

640 Delta value and 95% confidence intervals in parentheses.

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	<i>P. onca</i>	<i>P. concolor</i>	<i>L. pardalis</i>
<i>P. concolor</i>	0.83 (0.77-0.96)		
<i>L. pardalis</i>	0.80 (0.69-0.91)	0.83 (0.76-0.94)	
<i>N. narica</i>	0.41 (0.30-0.50)	0.41 (0.29-0.51)	0.34 (0.21-0.40)
<i>E. barbara</i>	0.41 (0.27-0.55)	0.41 (0.27-0.53)	0.35 (0.18-0.46)
<i>D. marsupialis</i>	0.72 (0.56-0.82)	0.72 (0.59-0.83)	0.75 (0.60-0.84)
<i>P. tajacu</i>	0.55 (0.46-0.65)	0.57 (0.48-0.64)	0.51 (0.39-0.55)
<i>M. temama</i>	0.61 (0.44-0.73)	0.58 (0.39-0.70)	0.54 (0.34-0.70)
<i>D. mexicana</i>	0.52 (0.40-0.62)	0.51 (0.39-0.59)	0.45 (0.34-.64)
<i>C. paca</i>	0.75 (0.63-83)	0.77 (0.67-0.87)	0.80 (0.72-0.90)
<i>S. floridanus</i>	0.76 (0.59-0.83)	0.77 (0.65-0.87)	0.79 (0.67-0.89)
<i>D. novemcinctus</i>	0.65 (0.49-0.79)	0.69 (0.53-0.83)	0.70 (0.64-0.93)

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