A matter of time: Temporal partitioning facilitates coexistence between coyotes (Canis latrans) and gray foxes (Urocyon cinereoargenteus) in temperate forests of Mexico.

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Research Article

1 **A matter of time: Temporal partitioning facilitates coexistence between coyotes (*Canis latrans*) and gray foxes**

2 **(*Urocyon cinereoargenteus*) in temperate forests of Mexico.**

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ABSTRACT

Sympatric species reduce competitive interactions by segregating their ecological niche as a strategy that promotes coexistence. Two main dimensions in which niche differentiation occurs are spatial and temporal axes. Thus, describing the spatiotemporal patterns of sympatric species help us better grasp how species coexist. In Mexico, coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) are sympatric and widely distributed, and information about their temporal and spatiotemporal interactions is needed to explain their coexistence. As an approach to exploring the coexistence between these species in a temperate forest, we pose the following question: Is there temporal or spatiotemporal segregation between sympatric coyotes and gray foxes? We aimed to evaluate indicators of ecological niche segregation through two approaches: *i*) temporal partitioning, measuring the levels and overlap of daily activity patterns; and *ii*) spatiotemporal partitioning, through temporal co-occurrence analysis and time-to-encounter analysis. In 2018, we used a camera trap network ($n = 43$) to measure spatiotemporal patterns of coyotes and gray foxes. We found that coyotes showed a diurnal daily activity pattern while gray foxes were nocturnal, the overlap was low (49%), and daily activity levels varied significantly as coyotes remained active during slightly higher levels of proportion of the circadian cycle (60%) compared with the gray foxes (37%). We found a temporal co-occurrence random pattern (not aggregation/segregation pattern) between species and no avoidance behavior between coyotes and gray foxes was displayed, according to the time-to-encounter analysis. In general, we did not detect segregation patterns between species at the spatiotemporal level, but we found strong evidence of important temporal activity segregation patterns between coyotes and gray foxes as a mechanism that facilitates sympatry, and which likely complements the ecological strategy of coexistence between these species in temperate forests at the southern of the Sierra Madre Occidental, Mexico.

KEYWORDS

Activity pattern, camera-traps, canids, co-occurrence, coexistence, niche segregation.

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53   Understanding processes that maintain the structure of ecological communities is crucial for wildlife

54   conservation programs (Glen and Dickman 2005; Vellend 2016). Interspecific competition is an important species

55   interaction factor that structures ecological communities (Rosenzweig 1966; Sommer and Worm 2002) and can take

56   two forms: interference and exploitative competition (Case and Gilpin 1974; Schoener 1983). Interference

57   competition can be considered one of the main factors determining intraguild relationships among mammalian

58   species belonging to the order Carnivora (Rosenzweig 1966; Palomares and Caro 1999; Linnell and Strand 2000).

59   These competitive interactions are usually more intense among sympatric species with similar ecological niches

60   (MacArthur and Levins 1967; Morin 1999); therefore, the strategy to promote their coexistence is niche segregation

61   to minimize competition (MacArthur and Levins 1967; Pianka 1969; Schoener 1974a).

62   Ecological niche segregation has mainly been studied in terms of three axes: spatial, trophic, and temporal

63   (Pianka 1973; Schoener 1974a). Potential competition between sympatric species is largely determined by spatial

64   niche segregation (Kitchen et al. 1999; Palomares and Caro 1999; Grassel et al. 2015) because the development of

65   interactions between species that share the same distribution area involves accessibility to the resources found there

66   (Schoener 1974a; Sih 2005). However, more attention has been given recently to the temporal niche due to the

67   availability of new technology, such as camera traps and accelerometers, for defining the temporal activity patterns

68   of wild animals (Sanchez-Ferrer et al. 2016; Zimmermann et al. 2016; Frey et al. 2017). Temporal segregation is

69   important to reduce competitive interactions (Schoener 1974b; Kronfeld-Schor and Dayan 2003) because species can

70   reduce intraguild competition and predation risk by minimizing temporal overlap with ecologically similar species or

71   with sympatric predators (Carothers and Jaksić 1984). Consequently, spatiotemporal niche partitioning research

72   enables a better understanding of the coexistence mechanisms among wildlife species (Sommer and Worm 2002;

73   Kronfeld-Schor and Dayan 2003; Watabe et al. 2022). Therefore, we intend to evaluate the spatial and temporal axes

74   of the ecological niche of two sympatric species, in order to quantitatively determine their segregation to elucidate

75   how their coexistence occurs.

76   In Mexico, coyotes *(Canis latrans)* and gray foxes (*Urocyon cinereoargenteus*) are abundant and widely

77   distributed; both species are sympatric throughout much of their distribution range in the country (Servín and Chacón

78   2014; Servín et al. 2014a). Both species belong to the same taxonomic family (*Canidae*) and have similar feeding

79 habits (Bekoff 1977; Fritzell and Haroldson 1982). Studies of intraguild interactions between coyotes and gray foxes

80 have mainly focused on spatial and trophic axes of their ecological niches. The studies about spatial niche

81 interactions have found both absence (Neale and Sacks 2001; Chamberlain and Leopold 2005; Rodríguez-Luna et al.

82 2021a) and presence (Fedriani et al. 2000; Farías et al. 2012) of spatial segregation between species. However,

83 temporal niche interactions between coyotes and gray foxes have received scarce attention and are poorly

84 understood. We lack a comprehensive understanding of spatiotemporal niche partitioning between coyotes and gray

85 foxes which can potentially explain the coexistence of the species in areas where they are sympatric. Therefore, in

86 this study we analyzed information generated during 2018 in a temperate forest in the Sierra Madre Occidental of

87 Durango, Mexico, to determine and evaluate the temporal and spatiotemporal use patterns of both canids. We

88 hypothesized that the temporal and spatiotemporal niche segregation between coyotes and gray foxes acts as an

89 ecological mechanism that facilitates coexistence between both species.

90   MATERIALS AND METHODS

91 **Study area**

92   We carried out the fieldwork in the mountain region on the buffer area of La Michilía Biosphere Reserve

93 (MBR), municipality of Súchil, Durango, Mexico; between the coordinates 23°21'00"–23°28'00" N and

94 104°09'00"–104°21'00" W (Figure 1). The MBR is located on the southeastern of the Sierra Madre Occidental and

95 covers *ca*. 70,000 ha, with altitudes that range between 2000 and 2985 masl (Halffter 1978). In the MBR sub-humid

96 temperate (Cw) climate predominates, average annual rainfall fluctuates between 700 to 900 mm, and the mean

97 annual minimum and maximum temperatures are 2°C (in winter) and 22°C (in summer), respectively (Gadsden and

98 Reyes-Castillo 1991; INEGI 2017). Dominant vegetation types in the MBR are the coniferous forest (*Pinus* spp.)

99 and oak forest (*Quercus* spp.), with areas of natural grasslands (*Bouteloua* spp.), xerophilous scrubs (dominated by

100 two species: *Arctostaphylos pungens* and *Acacia schaffneri*), and transition zones for these types of vegetation where

101 dominant species vary depending on altitude, geomorphology, and microclimatic conditions (González-Elizondo et

102 al. 1993).

103 **Camera traps survey**

104   During 2018, we considered four biological seasons described for both species for the implementation of the

105 camera traps survey (Servín and Huxley 1995; Smith et al 1981): breeding (January–March 15), gestation (March

106   16–April 30), pup-rearing (May 1–July 31), and dispersal or pups' independence (August 1–December 31). At the

107   end of each season, we checked the camera traps, downloaded the images, and replaced the batteries. We set and

108   geo-referenced 43 infrared-triggered camera trap sites (Cuddeback[TM] mod E3 Long Range, WI, USA, and

109   Bushnell[TM] mod HD Essential, KS, USA), we determined the spatial arrangement of the camera traps sites based on

110   the average home range size of focal species (Rovero and Spitale 2016) in the study area: for coyotes 12.20 ± 1.74

111   km^2 (Servín and Huxley 1995; Rodríguez-Luna et al. 2021a) and for gray foxes 5.30 ± 0.67 km^2 (Servín et al. 2014a;

112   Rodríguez-Luna et al. 2021a). As a result, camera traps were distributed at an average distance of 1.14 ± 0.20 km

113   between them, considering a regular grid (Figure 1). During the fieldwork, we placed camera traps sites at locations

114   with signs of wildlife presence to maximize the capture probability of the target species (Zimmerman and Rovero

115   2016) and we attached the camera traps to trees at 30–60 cm above ground level. We programmed all camera traps

116   to be active 24 hours a day and to burn three images for each trigger, with a 60 s of delay between them. We

117   recorded the species, time, date, and camera trap site for all images. To maintain statistical independence, we

118   considered as independent events all photographic records of the same species when multiple individuals appeared in

119   the same image or when they were ≥ 30 min apart (Ridout and Linkie 2009).

120   **Data analysis**

121   Factors affecting species interactions may differ depending on the temporal scales; therefore, we evaluated

122   temporal and spatiotemporal niche partitioning through multiple analytical methods (*sensu* Watabe et al. 2022). We

123   evaluated the temporal niche partitioning through the overlap of daily activity patterns and daily activity levels

124   (Ridout and Linkie 2009; Rowcliffe et al. 2014). Besides, we evaluated the spatiotemporal niche partitioning based

125   on: *i*) temporal co-occurrence analysis (Veech 2013), a method that allows evaluating the spatiotemporal responses

126   of species focusing on the date rather than the time of the day by using detection and non-detection data (Watabe et

127   al. 2022); and *ii*) time to encounter analysis (Karanth et al. 2017), which evaluates data with multiple temporal scales

128   (e.g., hours, days, weeks; Watabe et al. 2022) and is conditional on observed space use and temporal activity patterns

129   of the focal species, and thus allows to infer fine-scale behavioral segregation/aggregation patterns (Karanth et al.

130   2017; Balme et al. 2017).

131   *Overlap of daily activity patterns and daily activity levels*. In the tropics the clock time of sunrise and

132   sunset changes slightly over the year, depending on the distance from the equator and time of year; however,

133   behavior timing should be recorded relative to these events to avoid biased conclusions (Nouvellet et al. 2012).

134   Thus, we used solar time rather than clock time to analyze daily activity patterns. To account for successive changes

135   in the solar position throughout the year, we corrected the clock time of each photographic record with reference to

136   the solar time, according to its specific geographical position and date (*sensu* Nouvellet et al. 2011). Sunrise and

137   sunset times for each survey day were established using information from the United States Naval Observatory

138   (USNO; https://aa.usno.navy.mil/). We considered: *i*) sunrise and sunset, when the geometric center of the sun was

139   on the horizon; *ii*) twilight, as the average duration of this period throughout the 365 days of the year in the study

140   area, so morning twilight was 1.32 ± 0.07 h before sunrise and evening twilight was 1.32 ± 0.07 h after sunset; *iii*)

141   daylight period, the time span between sunrise and sunset; and *iv*) night period, the time span that occurred after the

142   end of evening twilight until morning twilight (Seidelmann and Wilkins 2006). We classified the records as diurnal

143   if they were obtained during daylight hours; nocturnal, if they were obtained during the night period; or, crepuscular,

144   if they were obtained during morning or evening twilight. To determine the main activity period over 24 hours, we

145   counted the number of independent photographic records obtained for each period of the day for the entire sample.

146   We performed a chi-square goodness of fit test (McDonald 2014) to test the null hypothesis of no difference in the

147   number of observations in each period of the day. When necessary, we performed a *post hoc* chi-square goodness of

148   fit test.

149   To represent daily activity patterns, we convert solar time to radians and represented data using circular

150   statistics. We estimated the daily activity patterns of focal species as a probability density function using kernel

151   density estimation, and then we adjusted the sunrise, noon, and sunset to $\pi/2$, π, and $3\pi/2$, respectively (Ridout and

152   Linkie 2009). Daily activity level, defined as the proportion of a 24-hour daily cycle during which animals appeared

153   to be active, was equal to the area under the capture rate curve (Rowcliffe et al. 2014). We determined interspecific

154   temporal overlap using the delta coefficient Δ, which acquires values between 0 (no overlap between density curves)

155   and 1 (complete overlap; Ridout and Linkie 2009). We considered the overlap proportion of daily activity patterns

156   "low" when $\Delta \leq 0.50$ (i.e., partitioning), "moderate" when $0.50 < \Delta \leq 0.75$, and $\Delta > 0.75$ as "high" (Monterroso et al.

157   2014). Due to the large number of records obtained for both species, we estimated the specific overlap coefficient

158   through the Δ_4 method, which more robustly estimates overlap for samples ≥ 75 registers (see Ridout and Linkie

159   2009), and we calculated 95% confidence intervals (CI) for each Δ value using the bootstrap method with 10,000

160   repetitions. To statistically evaluate daily activity patterns data, we performed a Rao's spacing test of uniformity to

161   test whether each underlying distribution appears to deviate from circular uniformity (Rao 1976); we used a non-

162   parametric Mardia-Watson-Wheeler test (MWW) to assess interspecific and intraspecific variation and to determine

163   whether two circular distributions differ significantly from each other (Batschelet 1981), and we performed a Wald

164   test on chi-square distribution to test for significant differences in the activity levels of each pair of distributions

165   (Rowcliffe et al. 2014).

166   *Temporal co-occurrence analysis*. We used camera trap data to test for statistically significant temporal co-

167   occurrence patterns between coyotes and gray foxes by using a matrix containing the detection-non-detection data

168   per night at each camera site for each species (Veech 2013). This method determines the probability (P_j) that the

169   observed frequency of co-occurrence of two species at exactly j sites is less than (P_{lt}), greater than (P_{gt}), or not

170   different from the expected frequency (species occurred independently from each other; Griffith et al. 2016). We

171   calculated the observed co-occurrence rate for each species by dividing the number of detections for one species by

172   the total number of nights at each j site, and we calculated the expected co-occurrence by multiplying the observed

173   co-occurrence rate of one species, the observed co-occurrence rate of other one species, and the total number of

174   nights at each j site; then we compared calculated expected co-occurrence to the number of observed co-occurrence

175   (Veech 2013; Watabe et al. 2022). Thus, $P_{lt} < 0.05$ indicates negative species associations (i.e., partitioning), $P_{gt} <$

176   0.05 indicates positive species associations (i.e., co-occurrence), and p values ≥ 0.05 of these parameters indicates

177   random species associations (i.e., species occurred independently from each other; Veech 2013; Griffith et al. 2016).

178   *Time to encounter analysis*. Following Karanth et al. (2017), we used multi-response permutation

179   procedures (MRPP) to assess the overall behavioral segregation between coyotes and gray foxes. To do this, we

180   analyzed the entire data from 2018. Multiple captures of the same individual less than 1 min apart were collapsed

181   into a single record (Balme et al. 2017).   For every coyote detection record, we calculated the minimum time to the

182   subsequent gray fox encounter and vice versa, we obtained the expected statistical distributions of the time to

183   encounter by assigning encounter times to the camera trap sites in 10,000 random permutations. Subsequently, we

184   compared the random permutations with the observed median of the minimum time to encounter. We calculated the

185   p values as the proportion of times that the observed median was larger than the medians of the random permutations

186   (Li et al. 2018). Under the assumption of species independence, obtaining a larger time to encounter than expected

187   suggests spatiotemporal segregation between species, while a shorter time to encounter suggests species

188   spatiotemporal aggregation (Karanth et al. 2017; Balme et al. 2019).

189   We used R version 4.0.2 software (R Core Team 2022) for all statistical analyses, considering a significance

190   level $\alpha = 0.05$. We used "overlap" (Ridout and Linkie 2009), "activity" (Rowcliffe 2022), "circular" (Agostinelli

191   and Lund 2022), and "cooccur" (Griffith et al. 2016) R packages to estimate daily activity patterns and overlap,

192   activity levels, circular statistical analyses, and temporal co-occurrence, respectively. Whenever necessary, we

193   reported the mean ± SD values of those parameters.

194   **RESULTS**

195   Throughout the year 2018, we obtained a total sampling effort of 11,814 camera trap-days. We obtained a

196   total of 1569 independent records for both species combined throughout the entire study: 1041 records for coyotes

197   and 528 records for gray foxes. We presented a detailed description of independent records obtained for both species

198   per biological season in Table 1.

199   **Overlap of daily activity patterns and daily activity levels**

200   For coyotes, we obtained 602 (57.83%) diurnal records, 313 (30.07%) nocturnal records, and 126 (12.10%)

201   crepuscular records. Record frequency across the periods throughout the 24 h varied significantly ($\chi^2_{(2)} = 331.47$, $p <$

202   0.001); diurnal records were greater than expected by chance (*post hoc* $\chi^2_{(1)} = 25.52$, $p < 0.001$). For gray foxes, we

203   obtained 37 (7.01%) diurnal records, 409 (77.46%) nocturnal records, and 82 (15.53%) crepuscular records. As in

204   the previous case, record frequency across the periods throughout the 24 h varied significantly ($\chi^2_{(2)} = 468.44$, $p <$

205   0.001); nocturnal records were greater than expected by chance for the comparison (*post hoc* $\chi^2_{(1)} = 159.28$, $p <$

206   0.001).

207   Overall daily activity pattern for coyotes was not uniform (Rao's test; $U = 158.75$, $p < 0.001$), it displayed

208   two activity peaks (bimodal) during the daylight period which occurred after sunrise and before sunset; coyotes

209   showed lesser activity at noon and during the night period, shortly after midnight (Figure 2). Regarding gray foxes,

210   the overall daily activity pattern was not uniform (Rao's test; $U = 203.02$, $p < 0.001$) and it was also bimodal, with

211   two main activity peaks: the first one -which was greater- occurred during the night period before morning twilight,

212   and the second one occurred at the end of evening twilight and the beginning of night period; gray foxes drastically

213   restricted its activity during daylight period (Figure 2). The overall daily activity patterns from both species differed

214   significantly (MWW; $W = 373.83$, *d. f.* = 2, $p < 0.001$), and their overlap index was $\Delta_4 = 0.49$ (CI; 0.45–0.53), which

215   we classified as low (Figure 2). Overall daily activity levels of coyotes were Act = 0.60 (CI; 0.52–0.67); they were

216   higher and differed significantly (Wald test; Dif. = 0.23, W = 22.44, $p < 0.001$) from those of gray foxes: Act = 0.37

217   (CI; 0.31–0.42). That is, we detected an important segregation in the temporal niche between both species.

218   For both species, data distribution for the daily activity patterns was not uniform for any of the biological

219   seasons (Table 1). On one hand, coyotes displayed slight variations across biological seasons; in general, the first

220   activity peak remained shortly after sunrise, while the second one was variable before sunset and around evening

221   twilight (Figure 3). There was no evidence of significant differences between the daily activity patterns of coyotes

222   among breeding, gestation, and dispersal seasons; however, the pup-rearing season showed significant differences

223   compared with the rest of the biological seasons (Table 1; Figure 3). In the case of gray foxes, there was no evidence

224   of significant differences among daily activity patterns throughout biological seasons (Table 1; Figure 3); regardless

225   of the biological season, the first activity peak occurred during the nocturnal period before morning twilight, while

226   the second activity peak showed slight variation between the end of the evening twilight and a short time before

227   midnight (Figure 3). The overlap of daily activity patterns between both species was intermediate during breeding

228   season (Δ_4 = 0.56; CI 0.48–0.65), but it was low during all other biological seasons (Figure 4): gestation, Δ_4 = 0.50

229   (CI 0.43–0.59); independence-dispersal, Δ_4 = 0.47 (CI 0.41–0.54); and pup-rearing, Δ_4 = 0.44 (IC 0.36–0.51). Daily

230   activity levels for coyotes ranged from Act = 0.48 (CI 0.35–0.63) to Act = 0.61 (CI 0.47–0.71), while for the gray

231   foxes they ranged from Act = 0.35 (CI 0.25–0.42) to Act = 0.40 (CI 0.31–0.43; Table 2). For both species, there

232   were no significant differences in the comparison of intraspecific daily activity levels among biological periods;

233   however, there were interspecific significant differences because, in general, coyote's daily activity levels were

234   higher than those estimated for gray foxes (Table 2).

235   **Temporal co-occurrence**

236   Probabilistic co-occurrence analyses showed that the observed frequency of co-occurrence of coyotes and

237   gray foxes was not different from the expected frequency, both for the overall data and most of the biological

238   seasons; this indicated that both species co-occurred independently of each other (random pattern) except in dispersal

239   season when the co-occurrence pattern was positive (Table 3).

240   **Time to encounter**

241   We observed a minimum time to encounter median of 21.56 days (n = 867) for gray foxes after the

242   detection of coyotes (i.e., coyotes-gray foxes), and a median of 7.37 days (n = 449) for coyotes after the detection of

243   gray foxes (i.e., gray foxes-coyotes). In both cases, the observed time to encounter median and the medians of the

244   random permutations did not differ significantly: coyotes-gray foxes, $p = 0.74$; and gray foxes-coyotes, $p = 0.52$

245   (Figure 5). Therefore, no behavioral fine-scale spatiotemporal segregation was detected.

<div align="center">

DISCUSSION

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247   Intensive sampling with camera traps provided plentiful information for a detailed understanding of the

248   spatiotemporal interactions between coyotes and gray foxes by examining mechanisms by which these sympatric

249   species coexist in temperate forests. Through the temporal partitioning approach, we found low activity overlap and

250   therefore temporal segregation pattern between coyotes and gray foxes (Figure 2). In contrast, through the

251   spatiotemporal approach, neither co-occurrence nor segregation patterns between species were detected by the

252   temporal co-occurrence analyses (Table 3) and we even found that these species lacked avoidance behavior

253   according to the time-to-encounter analysis (Figure 5). In conclusion, we found that ecological segregation occurred

254   in the temporal niche of coyotes and gray foxes, and not in the spatiotemporal niche; therefore, temporal segregation

255   presents itself as a mechanism that facilitates the coexistence between these species.

256   Coyotes have been described to exhibit multiple periods of activity throughout the day with mainly

257   crepuscular and nocturnal activity along its distribution range (Bekoff 1977; Andelt and Gipson 1979; Andelt 1985;

258   Gese et al. 1996; Gese and Bekoff 2004; Young et al. 2006; Servín et al. 2014b). However, here we determined that

259   the daily activity pattern of coyotes was predominantly diurnal (Figure 2), therefore daily activity pattern appears to

260   be context dependent. Daily activity patterns change seasonally, or in response to human disturbance and

261   persecution (Kitchen et al. 2000). In places with significant human presence, coyotes tend to be mainly nocturnal to

262   reduce encounters with humans, whereas in places with limited or no anthropogenic disturbance coyotes tend to be

263   more active during the daylight period (List 1998; Kitchen et al. 2000; McClennen et al. 2001; Way et al. 2004;

264   Lendrum et al. 2017). We thus consider that the diurnal activity pattern of coyotes in the study area reflects the

265   positive effect of conservation programs implemented in the MBR-protected area, where anthropogenic activities are

266   limited, and the human presence is reduced. Additionally, the diurnal activity patterns displayed by the sampled

267   coyotes can be explained by the mesopredator release effect (Crooks and Soulé 1999; Prugh et al. 2009). For

268   instance, mesopredators can develop behavioral adaptations that include an expansion of their daily activity patterns

269   in the absence of top predators (Hudgens and Garcelon 2011). This behavioral adaptation by coyotes has been

270   demonstrated in areas where wolves (*Canis lupus*) have been reintroduced, as they represent dominant predators

271   (Switalski 2003). Thus, in places where both canids coexist, the daily activity patterns of coyotes turn to be

272   predominantly nocturnal (Arjo and Pletscher 1999) to avoid competitive interactions and the risk of mortality

273   associated with wolves (Atwood and Gese 2008; Merkle et al. 2009; Miller et al. 2012). An important factor to

274   consider in our study is that coyotes do not have to avoid competitive interactions with two top predators that have

275   been extirpated from the temperate forests in the MBR region: the Mexican gray wolf (*Canis lupus baileyii*) and the

276   black bear (*Ursus americanus*) both extirped in the 1970s (Ceballos and Navarro 1991; Delfín-Alfonso et al. 2011).

277   However, it is not possible to probe this hypothesis because there is no available data on the daily activity patterns of

278   these species before the extirpation. When we analyzed seasonally, daily activity patterns of coyotes were similar

279   during three of the four biological periods and there was no evidence of significant differences among breeding,

280   gestation, and dispersal seasons. However, during the pup-rearing season, the daily activity pattern of coyotes was

281   significantly different from the daily activity patterns of the rest of the seasons because the coyotes displayed their

282   highest rate of diurnal activity of the year (Figure 3). The increase in diurnal activity during this period is related to

283   reproductive behavior; namely: females entering oestrus, triggering the active search for a mate, courtship behavior,

284   large increase in aggressive behavior, long-distance traveling displayed to provide enough food for pup rearing

285   (Bekoff 1977; Bekoff and Wells 1980; Sevín et al. 2003).

286   The daily activity pattern of the gray foxes was nocturnal (Figure 2), as has been reported for this species

287   throughout its distribution in North America (Fritzell and Haroldson 1982; Harrison 1997; Fedriani et al. 2000;

288   Fuller and Cypher 2004; Farías et al. 2012; Servín and Chacón 2014; Gómez-Ortiz et al. 2019). Evidence supporting

289   the nocturnal activity pattern of gray foxes shows that the presence and abundance of superior competitors limit gray

290   fox abundance and daily activity pattern frame (e.g., Crooks and Soulé 1999; Henke and Bryant 1999; Hudgens and

291   Garcelon 2011). We observed that daily activity patterns of gray foxes were consistent throughout the biological

292   seasons and there was no evidence of substantial changes (Figure 3), even though slight variations were observed in

293   activity peak around evening twilight between periods.

294   The overlap between the daily activity patterns of coyotes and gray foxes was low (Figure 2), which

295   indicates temporal niche segregation. Although overall temporal niche segregation between both canids was

296   incomplete, it was evident during the daylight period. If we consider that the size of the species involved in the

297   competition process determines the results of competitive interactions, then larger carnivores will dominate smaller

298 carnivores (Polis et al. 1989; Donadio and Buskirk 2006; Wallach et al. 2015). Therefore, gray foxes avoid lethal

299 encounters with coyotes through temporal niche segregation, because coyotes can kill sympatric species of foxes to

300 reduce interspecific competition (Cypher and Spencer 1998; Sovada et al. 1998; Kitchen et al. 1999; Farías et al.

301 2012; Cherry et al. 2016). We found a similar species overlap in daily activity throughout almost all biological

302 seasons (Figure 4), except in the breeding season when the overlap was intermediate (56%). During breeding season

303 both species are actively searching for mates and courtship behaviors that may promote temporal overlap are taking

304 place (Bekoff 1977; Bekoff and Wells 1986; Servín et al. 2003). On the other hand, during the pup-rearing season,

305 the lowest overlap proportion (44%) was shown, when both canids are dedicated to caring for and feeding their litters

306 and females spend a greater amount of time around their dens, traveling with pups across their home ranges

307 (Nicholson et al. 1985; Bekoff and Wells 1980; Servín and Huxley 1995; Chamberlain and Leopold 2002; Gese and

308 Bekoff 2004; Fuller and Cypher 2004; Servín et al. 2003).

309 Overall daily activity levels of the coyotes far exceeded those of the gray foxes. The proportion of the day

310 that coyotes remain active was 60% (14.40 h) in contrast to gray foxes which was 37% (8.88 h) of the day. The

311 coyote daily activity level estimated here was within the range reported for the species (38%–67%) in Eastern

312 Connecticut (O'Connor and Rittenhouse 2017). In contrast, the daily activity levels of gray foxes that we estimated

313 were much lower than the values reported for Southern California (56%–60%) estimated by radiotelemetry (Farías et

314 al. 2012). Differences in daily activity levels between both species constitute a behavioral response by gray foxes to

315 avoid agonistic encounters with coyotes. By avoiding activity during the daylight period and therefore spending less

316 time active, gray foxes have a lower probability of agonistic encounters with coyotes and thus can reduce intraguild

317 predation.

318 Our study represents the first attempt to describe fine-scale spatiotemporal segregation between coyotes and

319 gray foxes. We demonstrated that coyotes and gray foxes co-occurred independently of each other (random co-

320 occurrence pattern) and neither spatiotemporal partitioning pattern nor avoidance behavior was shown by the species

321 in the temperate forests under the current study (Table 3; Figure 5). Our findings coincide with broader-scale spatial

322 interaction patterns since the absence of spatial segregation between both species was demonstrated with

323 radiotelemetry data (i.e., Neale and Sacks 2001; Chamberlain and Leopold 2005; Rodríguez-Luna et al. 2021a).

324 However, it is important to note that there is also evidence of clear spatial segregation patterns between both species

325 that are explained by interference competition since gray foxes spatially avoided coyotes as a means of decreasing

326 predation risk (Fedriani et al. 2000; Farías et al. 2012).

327   Although we did not identify all factors involved, coexistence between coyotes and gray foxes can be also

328 facilitated by segregation among different ecological niche dimensions. Ecological segregation strategies include

329 differentiated habitat use (Neale and Sacks 2001; Rodríguez-Luna et al. 2021a), differences in prey type,

330 consumption frequency, and niche breadth (trophic segregation; Delibes et al. 1989; Fedriani et al. 2000;

331 Cunningham et al. 2006; Rodríguez-Luna et al. 2021b).

332   Our findings about the spatiotemporal interactions between coyotes and gray foxes provide evidence that

333 the temporal niche segregation represents one of the main ecological strategies that facilitate their coexistence and

334 therefore promotes their sympatry in the temperate forests of Mexico.

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541

543   **Table 1.** Rao's spacing test of uniformity and intraspecific–interspecific variations in daily activity patterns of

544   coyotes and gray foxes among biological periods in 2018, evaluated by Mardia-Watson-Wheeler test (MWW), in

545   temperate forests in La Michilía Biosphere Reserve (MBR), Durango, México.

		Coyotes				Gray foxes			
		Breeding $n = 213$	Gestation $n = 252$	Pup-rearing $n = 341$	Dispersal $n = 235$	Breeding $n = 80$	Gestation $n = 100$	Pup-rearing $n = 88$	Dispersal $n = 260$
		Rao's test $U = 164.91$ $p < 0.001$	Rao's test $U = 151.03$ $p < 0.001$	Rao's test $U = 160.61$ $p < 0.001$	Rao's test $U = 171.65$ $p < 0.001$	Rao's test $U = 220.69$ $p < 0.001$	Rao's test $U = 215.62$ $p < 0.001$	Rao's test $U = 205.12$ $p < 0.001$	Rao's test $U = 211.08$ $p < 0.001$
Coyotes	Breeding	---							
	Gestation	$W = 2.19$ $p = 0.33$	---						
	Pup-rearing	$W = 20.45$ $p < 0.001*$	$W = 8.03$ $p = 0.02*$	---					
	Dispersal	$W = 3.66$ $p = 0.16$	$W = 1.10$ $p = 0.58$	$W = 14.54$ $p < 0.001*$	---				
Gray foxes	Breeding	$W = 63.55$ $p < 0.001*$	$W = 59.67$ $p < 0.001*$	$W = 101.45$ $p < 0.001*$	$W = 71.28$ $p < 0.001*$	---			
	Gestation	$W = 47.94$ $p < 0.001*$	$W = 55.53$ $p < 0.001*$	$W = 100.90$ $p < 0.001*$	$W = 67.48$ $p < 0.001*$	$W = 3.51$ $P = 0.17$	---		
	Pup-rearing	$W = 54.40$ $p < 0.001*$	$W = 64.25$ $p < 0.001*$	$W = 97.69$ $p < 0.001*$	$W = 75.88$ $p < 0.001*$	$W = 0.83$ $P = 0.66$	$W = 1.31$ $P = 0.52$	---	
	Dispersal	$W = 84.50$ $p < 0.001*$	$W = 102.82$ $p < 0.001*$	$W = 204.90$ $p < 0.001*$	$W = 121.97$ $p < 0.001*$	$W = 1.08$ $P = 0.58$	$W = 1.46$ $P = 0.48$	$W = 1.23$ $P = 0.54$	---

546   Sample size is denoted with n symbol. The degrees of freedom for all MWW tests were equal to 2. *Significant

547   differences ($\alpha = 0.05$) are indicated in bold.

548

549   **Table 2.** Wald test for intraspecific and interspecific variations in activity levels of coyotes and gray foxes in 2018

550   among biological periods in temperate forests in La Michilía Biosphere Reserve (MBR), Durango, México.

		Coyotes				Gray foxes			
		Breeding Act = 0.48 (0.35–0.63)	Gestation Act = 0.61 (0.47–0.71)	Pup-rearing Act = 0.52 (0.41–0.64)	Dispersal Act = 0.57 (0.44–0.66)	Breeding Act = 0.40 (0.27–0.44)	Gestation Act = 0.35 (0.25–0.42)	Pup-rearing Act = 0.35 (0.25–0.43)	Dispersal Act = 0.40 (0.31–0.43)
Coyotes	Breeding Act = 0.48 (0.35–0.63)	---							
	Gestation Act = 0.61 (0.47–0.71)	$W = 1.95$ $Dif = -0.13$ $p = 0.16$	---						
	Pup-rearing Act = 0.52 (0.41–0.64)	$W = 0.18$ $Dif = -0.04$ $p = 0.67$	$W = 1.20$ $Dif = 0.09$ $p = 0.27$	---					
	Dispersal Act = 0.57 (0.44–0.66)	$W = 0.94$ $Dif = -0.09$ $p = 0.33$	$W = 0.27$ $Dif = 0.04$ $p = 0.60$	$W = 0.37$ $Dif = -0.05$ $p = 0.54$	---				
Gray foxes	Breeding Act = 0.40 (0.27–0.44)	$W = 0.91$ $Dif = 0.08$ $p = 0.34$	$W = 8.16$ $Dif = 0.22$ **$p < 0.01*$**	$W = 2.78$ $Dif = 0.12$ **$p = 0.05*$**	$W = 5.80$ $Dif = 0.17$ **$p = 0.01*$**	---			
	Gestation Act = 0.35 (0.25–0.42)	$W = 2.18$ $Dif = 0.13$ $p = 0.14$	$W = 11.70$ $Dif = 0.26$ **$p < 0.001*$**	$W = 5.13$ $Dif = 0.17$ **$p = 0.02*$**	$W = 9.06$ $Dif = 0.22$ **$p < 0.01*$**	$W = 0.56$ $Dif = 0.04$ $p = 0.45$	---		
	Pup-rearing Act = 0.35 (0.25–0.43)	$W = 2.00$ $Dif = 0.12$ $p = 0.16$	$W = 10.99$ $Dif = 0.26$ **$p < 0.001*$**	$W = 4.73$ $Dif = 0.16$ **$p = 0.03*$**	$W = 8.43$ $Dif = 0.21$ **$p < 0.01*$**	$W = 0.45$ $Dif = 0.04$ $p = 0.50$	$W = 0.01$ $Dif = -0.01$ $p = 0.95$	---	
	Dispersal Act = 0.40 (0.31–0.43)	$W = 0.90$ $Dif = 0.08$ $p = 0.34$	$W = 9.10$ $Dif = 0.21$ **$p < 0.01*$**	$W = 3.03$ $Dif = 0.12$ **$p = 0.05*$**	$W = 6.54$ $Dif = 0.17$ **$p = 0.01*$**	$W = 0.01$ $Dif = -0.04$ $p = 0.92$	$W = 0.89$ $Dif = -0.05$ $p = 0.34$	$W = 0.71$ $Dif = -0.05$ $p = 0.71$	---

551   Activity level is denoted by "Act" and 95% confidence intervals are shown in parentheses. *Significant differences

552   ($\alpha = 0.05$) are indicated in bold.

553

554   **Table 3.** Co-occurrence probabilistic analysis between coyotes and gray foxes, for 2018 overall data and by

555   biological seasons, in temperate forests in La Michilía Biosphere Reserve (RBM), Durango, Mexico.

Comparison level	Observed co-occurrence	Expected co-occurrence	P_{lt}	P_{gt}	Pattern
Overall	33.00	32.98	1.00	0.99	Random
Biological season					
Breeding	14.00	12.10	0.94	0.18	Random
Gestation	6.00	6.00	0.67	0.66	Random
Pup-rearing	9.00	7.40	0.97	0.19	Random
Dispersal	28.00	23.60	0.99	**0.001***	Positive

556   P_{lt} and P_{gt} represents respectively the probability that the two species would co-occur at a frequency smaller and

557   greater than the observed frequency. $P_{lt} < 0.05$ indicates partitioning, $P_{gt} < 0.05$ indicates co-occurrence, and p

558   values ≥ 0.05 of these parameters indicates that species occurred independently from each other (random pattern).

559   *Significant differences ($\alpha = 0.05$) are indicated in bold.

560

FIGURE CAPTIONS

562   **Fig. 1** Camera-traps arrangement (black squares) in La Michilía Biosphere Reserve (MBR), Durango, Mexico. MBR

563   buffer zone is denoted with black solid line, MBR core zone is denoted with black dashed line, and contour lines (15

564   m) are denoted with thin gray solid lines

565   **Fig. 2** Daily activity patterns and overlap (dark grey area) between coyotes (yellow line) and gray foxes (light gray

566   line) in 2018 in temperate forests in La Michilía Biosphere Reserve (MBR), Durango, Mexico. Confidence intervals

567   (95%) of the Δ_4 overlap index value are indicated in parentheses. The light gray area indicates morning and evening
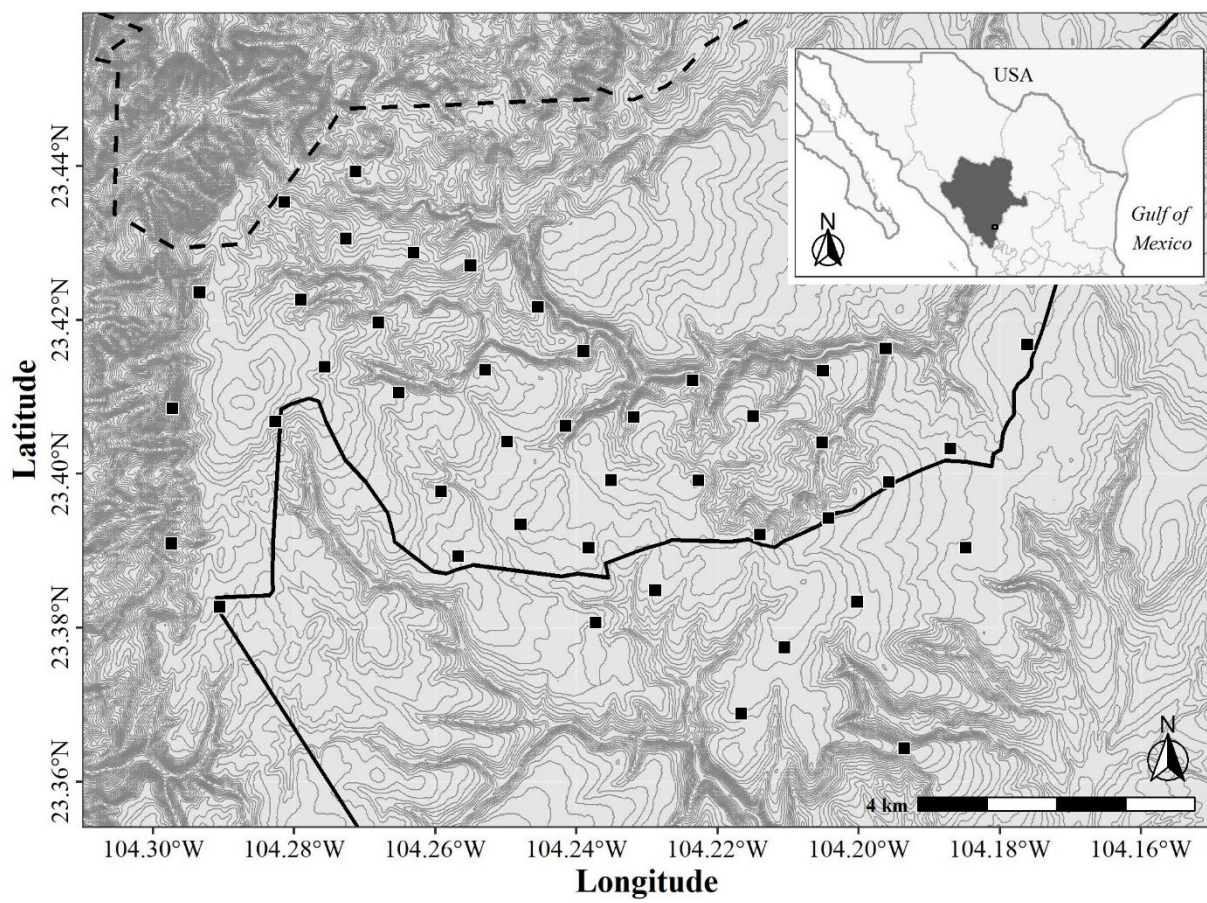
568   twilight periods

569   **Fig. 3** Daily activity patterns of coyotes (a) and gray foxes (b) through biological seasons in 2018 in temperate

570   forests in La Michilía Biosphere Reserve (MBR), Durango, Mexico. Light gray area indicates morning and evening

571   twilight periods

572   **Fig. 4** Daily activity patterns and overlap (dark grey area), through biological seasons in 2018, between coyotes

573   (yellow line) and gray foxes (light gray line) in temperate forests in La Michilía Biosphere Reserve (MBR),

574   Durango, Mexico. Biological seasons are denoted as follows: a) breeding, b) gestation, c) pup-rearing, and d)

575   dispersal

576   **Fig. 5** Multi response permutation procedures (MRPP) for time-to encounter analysis between coyotes and gray

577   foxes in 2018 in temperate forests in La Michilía Biosphere Reserve (MBR), Durango, Mexico. Coyotes-Gray foxes

578   (a) represents that gray foxes were detected after coyotes, and Gray foxes-Coyotes (b) represents the opposite case.

579   The number of the observed time-to-encounter is denoted with n. The dashed vertical lines represent the observed

580   median minimum time-to-encounter between the two species, while the rug plot represents the 10,000 medians of the

581   random permutations and the area under the curve represents the distribution estimated from them. The p-values

582   indicate the proportion of times the randomly generated median values was larger than the observed median
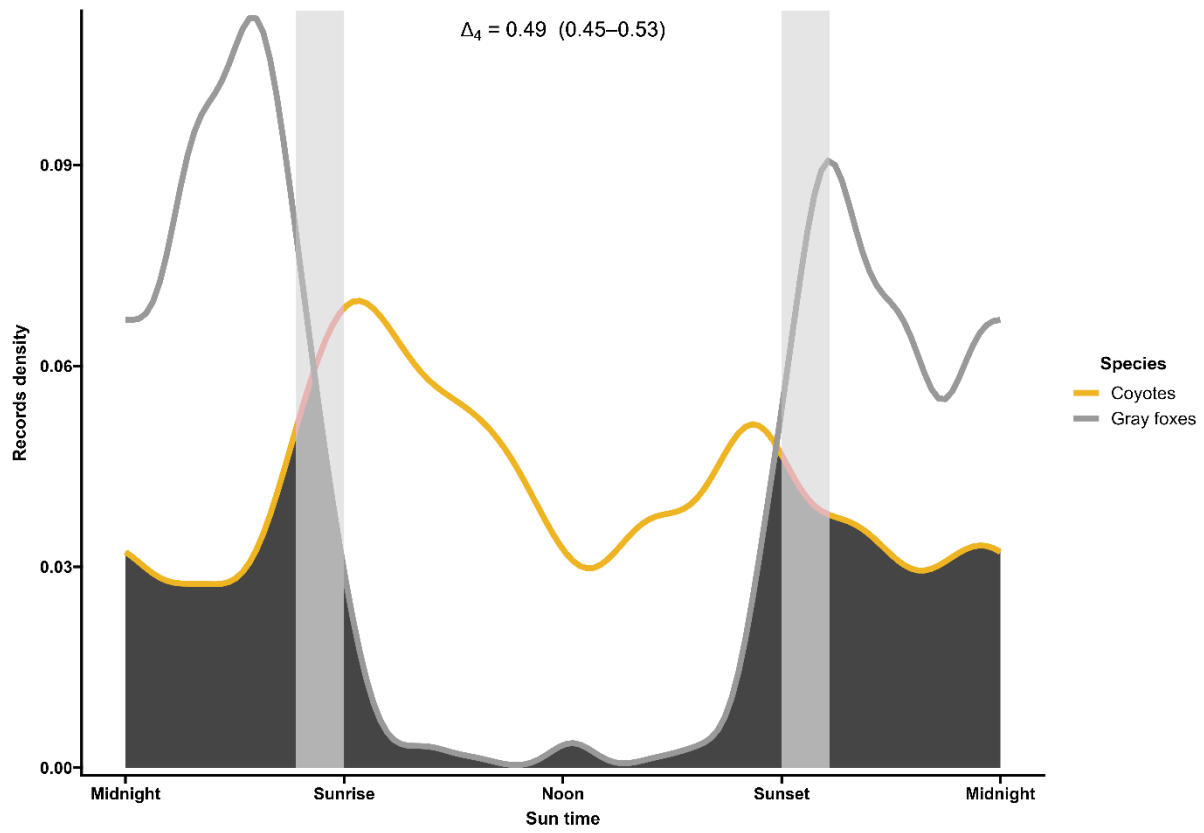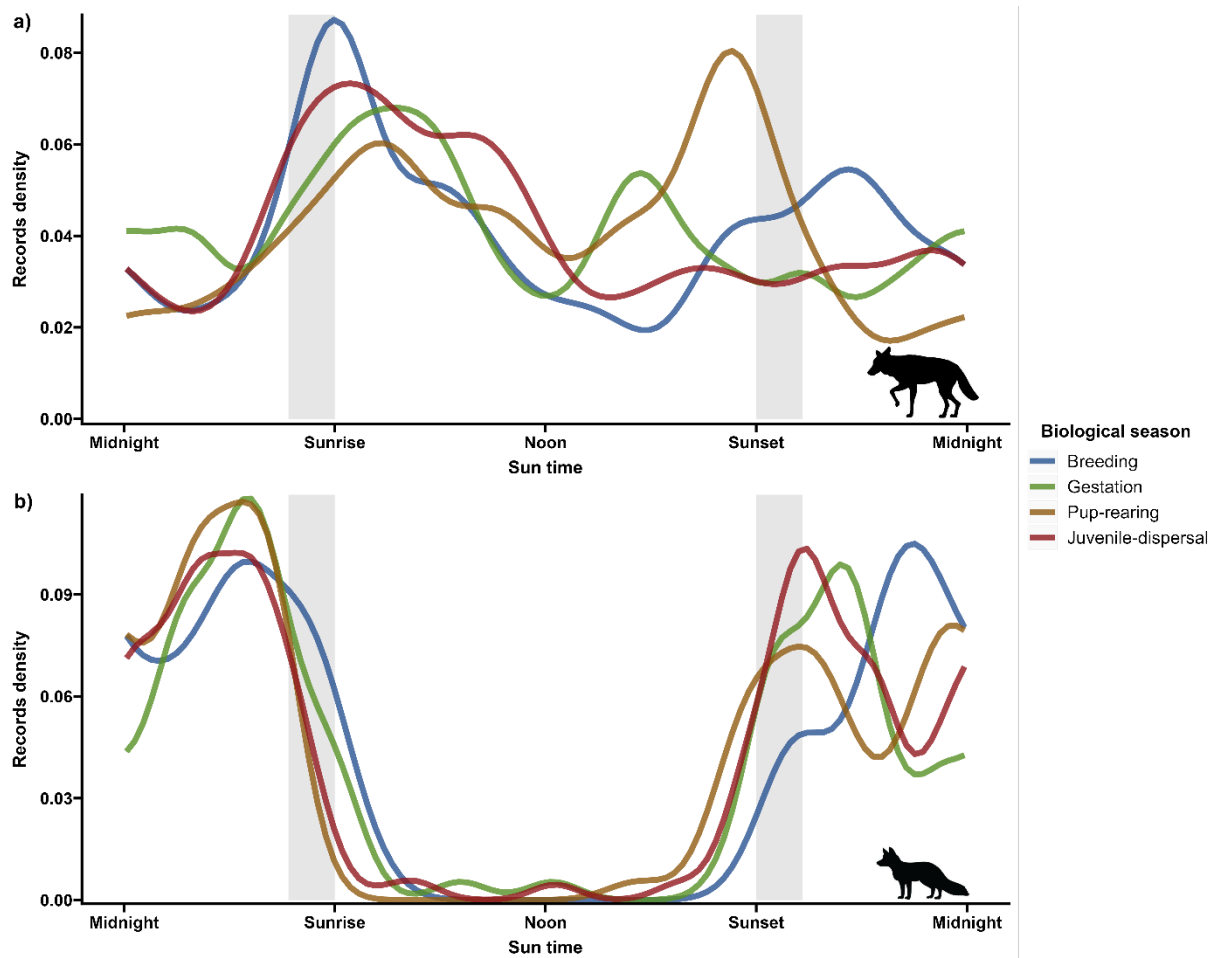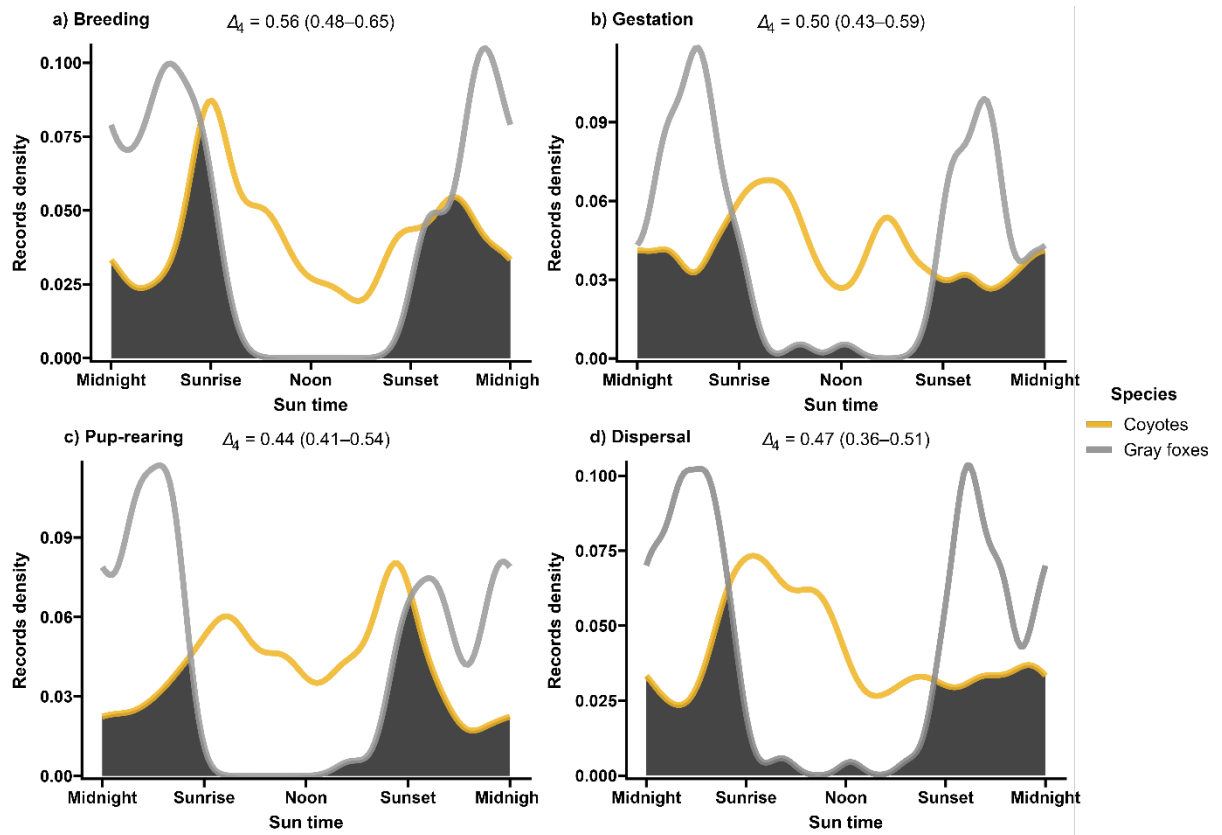
583

FIGURES

586   **Fig. 1**

587

$\Delta_4 = 0.49 \ (0.45\text{–}0.53)$

588

589   **Fig. 2**

590

591

Fig. 3

593

a) Breeding $\Delta_4 = 0.56\ (0.48–0.65)$

b) Gestation $\Delta_4 = 0.50\ (0.43–0.59)$

c) Pup-rearing $\Delta_4 = 0.44\ (0.41–0.54)$

d) Dispersal $\Delta_4 = 0.47\ (0.36–0.51)$

Species
Coyotes
Gray foxes

594

595   **Fig. 4**

596

30

a) Coyotes-Gray foxes

b) Gray foxes-Coyotes

p = 0.74
n = 867

p = 0.52
n = 449

Simulated probability

Days

597

598   **Fig. 5**

31