



Temporal variation of daily activity on pollinator and frugivorous birds simultaneously interacting with a specialized mistletoe

Victoria P. Fernández¹ · Francisco E. Fontúrbel¹

Received: 19 January 2021 / Accepted: 10 May 2021
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Abstract

Different interactions occur simultaneously, affecting the ecological and evolutionary outcome of the species within a community. Mutualisms are particularly relevant for maintaining and generating biodiversity, and among them, pollination and seed dispersal play a central role in plant regeneration. Due to its parasitic life-form and ecological specialization, mistletoes provide a good study system to assess the effects of simultaneous interactions in the wild. We used the highly specialized mistletoe *Tristerix aphyllus*, its pollinator (the hummingbird *Sephanoides sephanioides*), and its seed disperser (the mockingbird *Mimus thenca*) to assess their daily activity patterns during a flowering-fruiting overlap period. Given that both bird species are diurnal, we expect them to have different visitation times despite using different resources. Using camera traps, we found that both species have different daily activity patterns (overlap index $\hat{\Delta}_4 = 0.83$, $p < 0.001$). While *M. thenca* had a narrow activity period early in the morning, *S. sephanioides* had a wider activity range. We also found that the temporal variation of those activity patterns might be related to resource availability, as the number of flowers has decreased ($F_{2,52} = 13.85$, $p < 0.001$) over time, while the number of ripe fruits has increased ($F_{2,52} = 5.16$, $p = 0.009$) over time. Our results show that having different activity patterns could be a coexistence mechanism among bird species interacting with the same plant but exploiting different resources. Thus, taking activity patterns into account can provide a better understanding of ecological processes involving multiple interactions taking place simultaneously in the community.

Keywords Central Chile · Plant phenology · Pollination · Resource availability · Seed dispersal · *Tristerix aphyllus*

Introduction

Ecological interactions influence species' abundance, distribution, phenotype, and genotype as they interact simultaneously with many counterparts (Strauss & Irwin, 2004). Among those interactions, mutualisms—and particularly pollination and seed dispersal—play a central role in the generation and maintenance of biodiversity (Bascompte, 2019; Bascompte et al., 2003) as they determine plant reproduction and regeneration. Both pollination and seed dispersal mutualisms result from complex coevolutionary processes that make asymmetric and diffuse interactions quite common in nature (Bascompte & Jordano, 2007; Bascompte et al., 2006). Thus, we can expect that even specialized species

would interact with more than one mutualist counterpart simultaneously, which may vary on its effectiveness (Schupp et al., 2017). Thus, mutualist species with redundant ecological roles within the community may be competing for shared resources, which can influence their phenology, distribution, and behavior. Besides, plants can simultaneously interact with different mutualist (e.g., pollinators and seed dispersers), which use different resources but may visit the plant at the same time.

Mistletoes provide a good study system to assess simultaneous interactions in the wild (Fontúrbel, 2020), as they are aerial parasitic plants that depend on host plants with which they establish antagonist interactions (Martínez del Río et al., 1996), and biotic vectors for pollination and seed dispersal with which they establish mutualistic interactions (Watson, 2004). Despite being capable of interacting with a wide range of animals (Arruda et al., 2012; Fadini et al., 2018; Lucero et al., 2014), birds are often involved in mistletoe–animal interactions (Watson & Rawsthorne, 2013). Also, it is common for mistletoes to have extended flowering and

✉ Francisco E. Fontúrbel
fonturbel@gmail.com

¹ Instituto de Biología, Facultad de Ciencias, Pontificia Universidad Católica de Valparaíso, Av. Universidad 330, 2373223 Valparaíso, Chile

fruiting periods, with unusual phenologies such as winter-flowering (Aizen, 2003) that make them a keystone resource in forests and woodlands worldwide because they provide food resources (i.e., nectar and fleshy fruits) for animals during scarcity periods (Watson, 2001). Thus, a temporal overlap between flowering and fruiting periods is a common consequence of such extended phenology.

While mistletoes are relatively more dependent on biotic vectors than most nonparasitic flowering plants, the range of interactions asymmetry with the interacting animals is very variable (Guerra & Pizo, 2014; Vazquez & Aizen, 2004), ranging from low asymmetry in highly specialized systems to high asymmetry when generalist animals are involved (Aizen, 2003; Watson, 2013; Watson & Rawsthorne, 2013). This issue opens interesting questions in community ecology regarding the coexistence mechanisms on animal species simultaneously interacting with mistletoes. The temporal overlap between flowering and fruiting will result in the simultaneous use of mistletoe resources by pollinator and frugivore species, leading to inter-guild competition, which is less understood than the intra-guild competition. Such inter-guild competition would be negligible in those cases in which different taxonomic groups are involved (e.g., a diurnal pollinator bird and a nocturnal frugivorous mammal: Aizen, 2003), but when it takes place among phylogenetically close species (e.g., diurnal birds), the overlap may be substantial depending on resource availability and its temporal variation, but our knowledge about such ecological phenomena remains limited.

We used a highly specialized mistletoe (*Tristerix aphyllus*) to fill this knowledge gap that presents flowering-fruiting temporal overlap and is pollinated and dispersed by two diurnal bird species. While those species do not share resources, they may interfere with each other visiting the mistletoe at the same time. Therefore, we hypothesized that: (1) both mutualists will concentrate their visits to the mistletoes at different times, and (2) the temporal variation on daily activity patterns of each mutualist will be influenced by changes in resource availability over time. To test these hypotheses, we conducted a camera-trap assessment and examined animal daily activity patterns along 3 months of overlap between mistletoe flowering and fruiting.

Materials and methods

Study site

We conducted this study at the Reserva Nacional Las Chinchillas (31° 30' S 71° 06' W), a public, protected area of central Chile, located ~300 km northwards from Santiago. This area has a semiarid Mediterranean-type climate with a thermal range of 5 °C in winter and 30 °C in summer.

Annual precipitation is 167 mm (mean value from 1974 to 1999), mainly concentrated in the winter. Drought events are frequent in this zone (Jaksic, 2001).

Study system

We focused this study on the holoparasitic mistletoe *Tristerix aphyllus* (Loranthaceae) and its mutualists. This mistletoe is a good example of ecological specialization as they depend on a few cacti host species (*Echinopsis chiloensis* and *Eulychnia acida* are the most frequent hosts) and two animal vectors for pollination and seed dispersal (Medel et al., 2002). On the one hand, *T. aphyllus* is pollinated by the Green-backed Firecrown (*Sephaniodes sephaniodes*, Trochilidae), a generalist hummingbird with a wide latitudinal distribution in Chile (Acosta et al., 2020). Most of the mistletoe pollination is performed by *S. sephaniodes* with occasional visits of some pollinator insects (Medel, 2000). On the other hand, *T. aphyllus*' fruits are dispersed by the Chilean Mockingbird (*Mimus thenca*, Mimidae). This medium-sized bird swallows the whole fruit and defecates intact seeds, acting as an effective seed disperser (Martínez del Río et al., 1996). Although *M. thenca* is the main seed dispersal vector for this mistletoe, other frugivorous birds pay occasional visits to the infructescences (Lucero et al., 2014), but we ignore if those birds act as effective seed dispersers or simply as pulp consumers. During this study, we recorded 72 visitation events of other bird species (*Diuca diuca*, *Phrygilus gayi*, *Pseudasthenes humicola*, and *Leptasthenura aegithaloides*), representing 5.45% of the total camera trap records. Therefore, we kept only *S. sephaniodes* and *M. thenca* records for analyses as the other bird species had very low sample sizes, precluding us from conducting any formal analyses. In this case, both pollination and seed dispersal interactions are highly asymmetric (i.e., the plant is highly dependent on the animal, but the animal is little dependent on the plant), as the mistletoe depends more on the animal mutualists than they depend on the mistletoe (Fontúrbel, 2020; Guerra & Pizo, 2014). Both *S. sephaniodes* and *M. thenca* populations are resident in the study area. Furthermore, *T. aphyllus*—as most mistletoes—presents an extended phenology (March to November) in which flowering and fruiting have a temporal overlap of about 3 months (July to September; Medel, 2000). Flowering goes from March to August (with a peak between May and June) with some scant flowers in September, while fruiting goes from May to November (with a peak between July and September; Medel et al., 2002).

Data collection

We conducted a camera-trap assessment on 24 *T. aphyllus* individuals from July to September 2013, representing a total sampling effort of 2160 camera-days. We set infrared camera

traps (Bushnell model Trophy Cam 2011, with 5-megapixel resolution) in front of *E. chiloensis* individuals infected by *T. aphyllus* (Lucero et al., 2014). We georeferenced our camera traps using a Garmin GPSMAP 62 s device (location error ≤ 5 m). Our cameras were separated at least 50 m from each other and operated in photographic mode with a 1-min delay between shots to reduce the probability of capturing duplicate records. Camera traps are a cost-effective approach to assess pollination and seed dispersal interactions involving vertebrates (Fontúrbel et al., 2015), as they have minimum observer interference and have long autonomy periods (Burton et al., 2015). Camera traps are also an effective tool to assess daily activity patterns as they collect information throughout the day and stamp the exact time and date in the photographs (Fontúrbel et al., 2021).

Part of the camera-trap information was published by Lucero et al. (2014), focused on the diversity of frugivorous species interacting with *T. aphyllus*, but hummingbird and activity data were not published. Thus, we reprocessed the original camera-trap dataset to extract hour and date information from the photographs reporting *S. sephaniodes* and *M. thenca* visits to *T. aphyllus* individuals. We also quantified *T. aphyllus* flowers and fruits' availability on a monthly basis at the 24 focal mistletoes assessed. We counted total and ripe fruits (but we only used ripe fruits for analysis purposes). In this mistletoe, ripe fruits are easy to distinguish because of their pale pink-white color (Medel et al., 2002).

Statistical analyses

To assess whether the number of flowers and ripe fruits varied over time, we used one-way ANOVA tests (assessing flowers and ripe fruits separately), followed by Tukey a posteriori tests to determine pairwise differences among sampling months. Then, we used the geographic coordinates of each focal mistletoe to conduct spatial correlation tests for the number of flowers and ripe fruits using the Moran index (I); we used ten distance classes of an equal number of observations (but we reported only the global result), we calculated the significance of this index after 999 permutations. We assessed the spatial autocorrelation for each sampling month. We conducted spatial autocorrelation tests using The PASSaGE2 software (Rosenberg & Anderson, 2011).

We extracted time and date information from all the photographic records in which we recorded *S. sephaniodes* or *Mimus thenca* visits. Once we had the information systematized, we converted time figures to radians to estimate daily activity density kernels for each bird species. Kernel density estimators are a nonparametric method to estimate a given random variable's probability density function using a smoothing process (Fontúrbel et al., 2021). In this regard, kernel estimators have been widely used to assess animal activity based on camera-trap information (Rowcliffe et al.,

2014). After obtaining individual kernel estimators, we compared those daily activity patterns using the $\hat{\Delta}_4$ overlap coefficient (following Ridout & Linkie, 2009), which indicates the degree of overlap between two activity kernel functions to test the null hypothesis that both functions have the same distribution. We tested the significance of those comparisons using 1000 permutations. Then, we repeated this analysis, examining sampling months individually (we were unable to estimate a kernel function for September using the hummingbird data as it had only five records). We performed activity analysis in R 3.6.3 (R Development Core Team, 2020) using the packages 'overlap' (Ridout & Linkie, 2009) and 'activity' (Rowcliffe, 2019) and the R code provided in this repository: <https://github.com/fonturbel-lab/AnimActivity>

Data availability

Original data are available from the *figshare* digital repository: <https://doi.org/10.6084/m9.figshare.13607279>

Results

We found that flower and ripe fruit availability changed during the camera-trap monitoring assessment (Fig. 1). Flower availability was significantly variable among months ($F_{2,52} = 13.85$, $p < 0.001$), showing an important reduction in August and September. Contrarily, ripe fruit availability was similar between July and August but have significantly increased in September ($F_{2,52} = 5.16$, $p = 0.009$). During July 7.0% of the fruits were ripe, while 4.4% of the fruit were ripe in August, but 35.6%

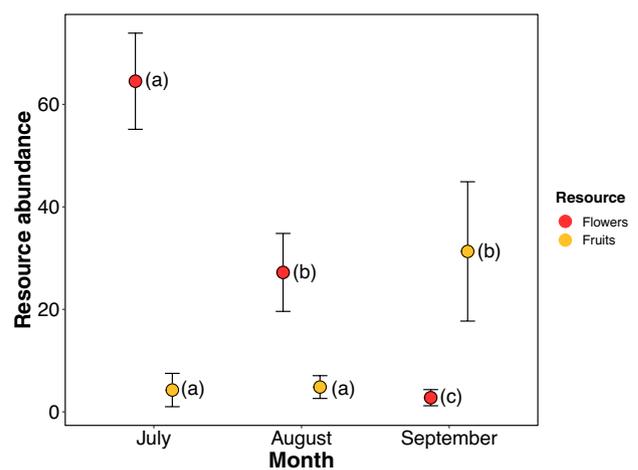


Fig. 1 Temporal variation on *Tristerix aphyllus* flower and ripe fruit availability per month. Vertical bars represent one standard error to each side of the mean. Different letters denote significant differences after ANOVA and Tukey a posteriori tests

in September, showing a ripening peak at the end of our monitoring period. We detected no spatial autocorrelation for the number of flowers (July: Moran's $I = -0.08$ $p = 0.63$; August: $I = -0.06$ $p = 0.26$; September: $I = 0.26$ $p = 0.19$) nor for the number of fruits (July: $I = -0.04$ $p = 0.83$; August: $I = -0.06$ $p = 0.39$; September: $I = -0.08$ $p = 0.06$).

From our camera-trap assessment, we obtained 953 records for the pollinator hummingbird *Sephaniodes sephaniodes* (Table S1) and 295 records for the frugivorous mockingbird *Mimus thenca* (Table S2). Examining overall activity for both mutualist bird species (Fig. 2), we found that the daily activity patterns of *S. sephaniodes* and *M. thenca* were significantly different ($\hat{\Delta}_4 = 0.83$, $p < 0.001$). Even though both species are diurnal, they visit *T. aphyllus* plants at different times. Particularly, *S. sephaniodes* had a wider activity range while *M. thenca* showed a narrower activity peak early in the morning. Analyzing these results by month, we found that activity patterns were significantly different between *S. sephaniodes* and *M. thenca* in both July ($\hat{\Delta}_4 = 0.79$, $p = 0.003$; Fig. 3a) and August ($\hat{\Delta}_4 = 0.77$, $p < 0.001$; Fig. 3b).

Then, we examined the temporal variation in daily activity patterns within each mutualist bird interacting with *T. aphyllus*. Comparing *S. sephaniodes* daily activity, we found a significant difference between July and August ($\hat{\Delta}_4 = 0.86$, $p < 0.001$; Fig. 4a), in which we observe more hummingbird activity during July when flowers were more abundant. Then, comparing *M. thenca* daily activity (Fig. 4b), we found no significant differences between July and August ($\hat{\Delta}_4 = 0.90$, $p = 0.496$), showing very similar kernel density functions, while we found significant differences between August and September ($\hat{\Delta}_4 = 0.80$, $p = 0.044$).

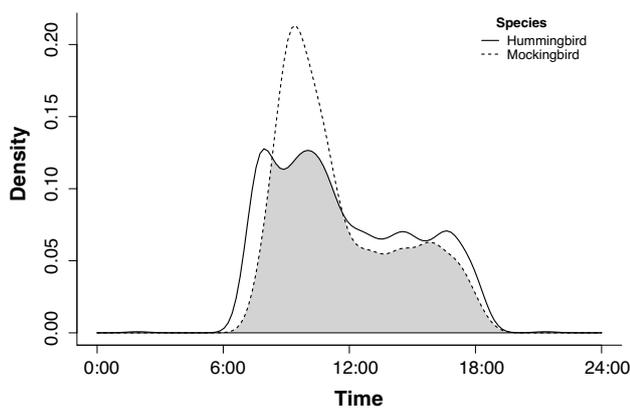


Fig. 2 Comparison of the overall daily activity patterns (depicted using kernel density functions) between the pollinator hummingbird *Sephaniodes sephaniodes* (solid line) and the frugivorous mockingbird *Mimus thenca* (dashed line). The shaded area represents the coefficient of overlap

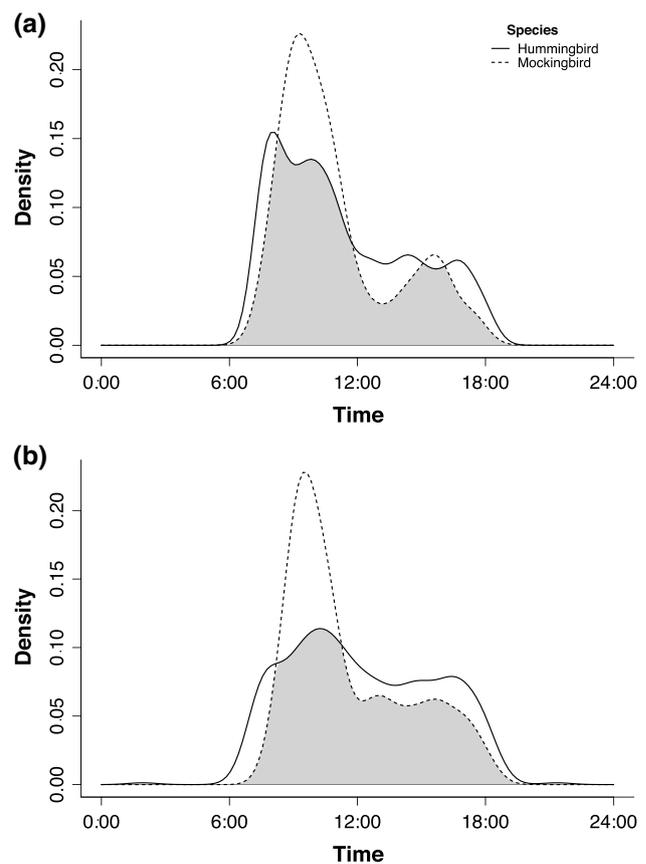


Fig. 3 Comparison of the monthly daily activity patterns (depicted using kernel density functions) between the pollinator hummingbird *Sephaniodes sephaniodes* (solid line) and the frugivorous mockingbird *Mimus thenca* (dashed line) during **a** July and **b** August. The shaded area represents the coefficient of overlap

Discussion

Our results showed that while both are diurnal birds, *S. sephaniodes* and *M. thenca* showed different daily activity patterns when visiting *T. aphyllus* mistletoes (Fig. 2). Those activity patterns change over time along with resource availability (i.e., flowers and ripe fruits; cf. Figures 1 and 3). While feeding on different resources, both bird species visit the mistletoes looking for food during the day (particularly in the morning.) However, *M. thenca* consistently showed a narrower activity peak of much activity early in the morning, but *S. sephaniodes* had a wider activity range along the day (see Figs. 2 and 3). Also, temporal changes in resource availability seem to affect daily activity patterns, particularly during September, when *S. sephaniodes* showed a significant change in its visitation hours from July to August and had only five visits during September, following the reduction in the number of available flowers. Contrarily, *M. thenca* showed a significant change in its daily activity pattern

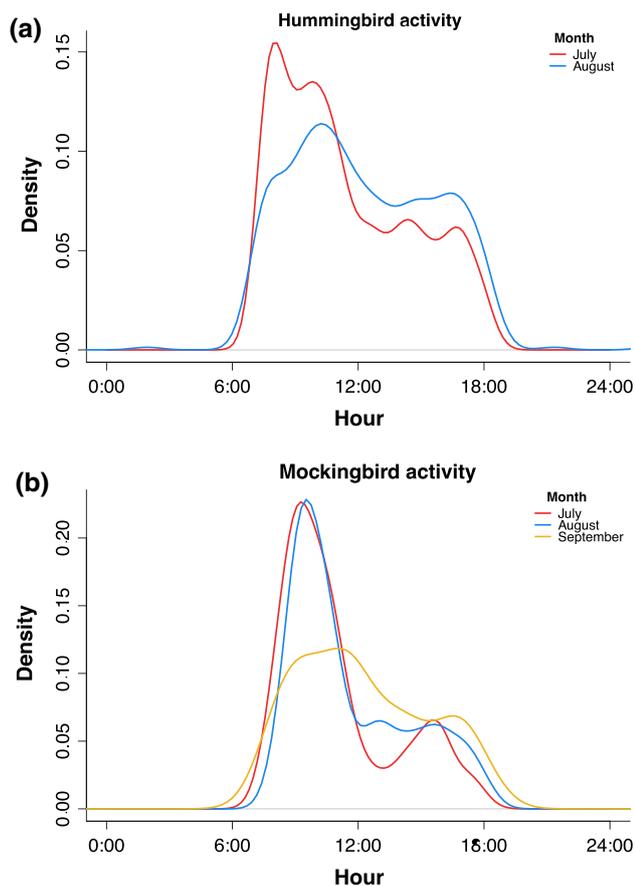


Fig. 4 Comparison of the monthly daily activity patterns (depicted using kernel density functions) for **a** the pollinator hummingbird *Sephaniodes sephaniodes* and **b** and the frugivorous mockingbird *Mimus thenca*

in September, coinciding with the fruit ripening peak (*cf.* Figures 1 and 4).

Both *S. sephaniodes* and *M. thenca* were reported to be territorial and defend feeding sites from their conspecifics (Ewald, 1985; González-Gómez & Vásquez, 2006; González-Gómez, Ricote-Martinez, et al., 2011; Medel et al., 2002; Pavan et al., 2020). This is particularly relevant for *S. sephaniodes*, which is known to be an aggressive territorial species (particularly the males) that actively defend their feeding territories (Wolf & Hagen, 2012), as they are capable of memorizing resource locations and nectar replenishing times (González-Gómez et al., 2014). Therefore, *M. thenca* may be restricting its visits to *T. aphyllus* to those periods between nectar replenishing in which *S. sephaniodes* reduces its visits to the mistletoes, but we need further studies to test this hypothesis. This outcome is more evident during September, as *M. thenca* activity pattern shows an important change when flowering is almost over and fruit ripening increases by sevenfold (Fig. 1). Originally *Mimus thenca* was pointed as the sole seed disperser of *T. aphyllus* (Martínez del Río et al., 1996;

Medel, 2000), but camera-trap evidence showed that other frugivore birds (*Diuca diuca*, *Phrygilus gayi*, *Pseudasthenes humicola*, and *Leptasthenura aegithaloides*) also feed on mistletoe fruits. However, its visitation frequency is very low (5.45% of the total visitation events), and its effects upon *M. thenca* or *S. sephaniodes* daily activity patterns may be negligible (Lucero et al., 2014). Both *S. sephaniodes* and *M. thenca* are territorial birds, showing intraspecific aggression to defend feeding territories (Medel et al., 2002). However, to date, no study has reported interspecific aggression between these two bird species while feeding on *T. aphyllus*, but given the overlap of flowering and fruiting, we cannot discard that daily activity patterns are not only influenced by resource availability but also by the presence of the other species.

While both bird species are generalist, *S. sephaniodes* energetic constraints and cognitive abilities are major determinants of its foraging behavior, and its aggressive behavior varies with ambient temperature (González-Gómez, Vasquez, et al., 2011). On the contrary, *M. thenca* has lower ecological constraints, and its generalist frugivore habits allow them to establish a different relationship with other frugivores and plant species within the community (Reid & Armesto, 2011). Nonetheless, from the plant perspective, the interaction with *M. thenca* might be more relevant as it plays a fundamental role in reaching viable hosts to allow recruitment (Medel, 2000; Medel et al., 2004). We need future studies to assess the consequences of *S. sephaniodes* and *M. thenca* daily activity patterns on *T. aphyllus* reproductive output, comprising the whole flowering and fruiting periods.

Detailed studies on animal daily activity patterns provide valuable information to understand ecological processes within the community (e.g., Fontúrbel et al., 2021; Rodríguez-Gómez & Fontúrbel, 2020). Examining daily activity patterns and their temporal variation provides a better understanding of ecological processes involving multiple interactions and their consequences at the community level (Strauss & Irwin, 2004), going further than only examining visitation rates (usually collected in discrete periods). In this regard, we can take advantage of modern approaches, such as camera traps, to study ecological interactions in the wild (e.g., Fontúrbel et al., 2015, 2017). Due to camera trap versatility, minimum observer interference, and the possibility of assessing many sampling units simultaneously for long periods, comprising the whole flowering and fruiting periods, we can now get more realistic activity estimates and draw more robust conclusions.

Conclusions

We found that *S. sephaniodes* and *M. thenca* visited *T. aphyllus* mistletoes at different times, corroborating our first hypothesis. We also found that activity patterns within each

mutualist bird species had a significant temporal variation along with resource availability, corroborating our second hypothesis. Such temporal variation is likely to be influenced by the temporal variation in flower and ripe fruit availability, which is more evident in September when flowering was almost over and fruit ripening has a significant increase, as *S. sephaniodes* drastically reduces its visitation events, but *M. thenca* widens its daily activity range.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42974-021-00050-x>.

Acknowledgements R. Cares, P. Cares, N. Peña, and F. Lucero assisted in the field. F. Lucero assisted with the raw camera-trap data processing. R. Medel and C. Botto arranged the 2013 fieldwork with funding of the FONDECYT projects 11090086 and 1120155, who authorized the reuse of raw camera trap data for this study. Comments from two anonymous reviewers helped us to improve the manuscript. Camera traps used were previously acquired with resources from the Rufford Foundation (Grant 10621-1 to FEF). The Chilean Forestry Corporation (CONAF) authorized access to the study site and provided lodging facilities.

Authors' contributions FEF conceived the ideas and designed the methodology. FEF collected field data. VF processed field data. VF and FEF analyzed data. VF led manuscript writing with contributions of FEF.

Funding No funding was received to assist with the preparation of this manuscript.

Data Availability Figshare digital repository: <https://doi.org/10.6084/m9.figshare.13607279>

Code availability Not applicable.

Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval Not applicable.

Consent to participate Not applicable.

References

- Acosta, I., Cabanne, G. S., Noll, D., González-Acuña, D., Plissock, P., & Vianna, J. A. (2020). Patagonian glacial effects on the endemic Green-backed Firecrown, *Sephanoides sephaniodes* (Aves: Trochilidae): Evidence from species distribution models and molecular data. *Journal of Ornithology*. <https://doi.org/10.1007/s10336-020-01822-4>
- Aizen, M. A. (2003). Influences of animal pollination and seed dispersal on winter flowering in a temperate mistletoe. *Ecology*, *84*, 2613–2627. <https://doi.org/10.1890/02-0521>
- Arruda, R., Fadini, R. F., Carvalho, L. N., Del-Claro, K., Mourão, F. A., Jacobi, C. M., Teodoro, G. S., van den Berg, E., Caires, C. S., & Dettke, G. A. (2012). Ecology of neotropical mistletoes: An important canopy-dwelling component of Brazilian ecosystems. *Acta Botânica Brasileira*, *26*, 264–274. <https://doi.org/10.1590/S0102-33062012000200003>
- Bascompte, J. (2019). Mutualism and biodiversity. *Current Biology*, *29*, R467–R470. <https://doi.org/10.1016/j.cub.2019.03.062>
- Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology and Systematics*, *38*, 567–593. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>
- Bascompte, J., Jordano, P., Melian, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences USA*, *100*, 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Bascompte, J., Jordano, P., & Olesen, J. M. (2006). Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, *312*, 431–433. <https://doi.org/10.1126/science.1123412>
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., & Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, *52*, 675–685. <https://doi.org/10.1111/1365-2664.12432>
- Ewald, P. W. (1985). Influence of asymmetries in resource quality and age on aggression and dominance in Black-Chinned hummingbirds. *Animal Behaviour*, *33*, 705–719. [https://doi.org/10.1016/S0003-3472\(85\)80001-4](https://doi.org/10.1016/S0003-3472(85)80001-4)
- Fadini, R. F., Fischer, E., Castro, S. J., Araujo, A. C., Ornelas, J. F., & de Souza, P. R. (2018). Bat and bee pollination in *Psittacanthus* mistletoes, a genus regarded as exclusively hummingbird-pollinated. *Ecology*, *99*, 1239–1241. <https://doi.org/10.1002/ecy.2140>
- Fontúrbel, F. E. (2020). Mistletoes in a changing world: A premonition of a non-analog future? *Botany*, *98*, 479–488. <https://doi.org/10.1139/cjb-2019-0195>
- Fontúrbel, F. E., Jordano, P., & Medel, R. (2015). Scale-dependent responses of pollination and seed dispersal mutualisms in a habitat transformation scenario. *Journal of Ecology*, *103*, 1334–1343. <https://doi.org/10.1111/1365-2745.12443>
- Fontúrbel, F. E., Orellana, J. I., Rodríguez-Gómez, G. B., Tabilo, C. A., & Castaño-Villa, G. J. (2021). Habitat disturbance can alter forest understory bird activity patterns: A regional-scale assessment with camera-traps. *Forest Ecol Manag*, *479*, 118618. <https://doi.org/10.1016/j.foreco.2020.118618>
- Fontúrbel, F. E., Salazar, D. A., & Medel, R. (2017). Increased resource availability prevents the disruption of key ecological interactions in disturbed habitats. *Ecosphere*, *8*, e01768. <https://doi.org/10.1002/ecs2.1768>
- González-Gómez, P. L., Madrid-Lopez, N., Salazar, J. E., Suárez, R., Razeto-Barry, P., Mpodozis, J., Bozinovic, F., & Vásquez, R. A. (2014). Cognitive ecology in hummingbirds: The role of sexual dimorphism and its anatomical correlates on memory. *PLoS ONE*, *9*, e90165. <https://doi.org/10.1371/journal.pone.0090165>
- González-Gómez, P. L., Ricote-Martinez, N., Razeto-Barry, P., Cotoras, I. S., & Bozinovic, F. (2011). Thermoregulatory cost affects territorial behavior in hummingbirds: A model and its application. *Behavioral Ecology and Sociobiology*, *65*, 2141–2148. <https://doi.org/10.1007/s00265-011-1222-2>
- González-Gómez, P. L., & Vásquez, R. A. (2006). A field study of spatial memory in Green-Backed Firecrown hummingbirds (*Sephanoides sephaniodes*). *Ethology*, *112*, 790–795. <https://doi.org/10.1111/j.1439-0310.2006.01223.x>
- González-Gómez, P. L., Vásquez, R. A., & Bozinovic, F. (2011). Flexibility of foraging behavior in hummingbirds: The role of energy constraints and cognitive abilities. *The Auk*, *128*, 36–42. <https://doi.org/10.1525/auk.2011.10024>
- Guerra, T. J., & Pizo, M. A. (2014). Asymmetrical dependence between a Neotropical mistletoe and its avian seed disperser. *Biotropica*, *46*, 285–293. <https://doi.org/10.1111/btp.12112>

- Jaksic, F. M. (2001). Ecological effects of El Niño in terrestrial ecosystems of western South America. *Ecography*, *24*, 241–250. <https://doi.org/10.1034/j.1600-0587.2001.240301.x>
- Lucero, F., Botto-Mahan, C., Medel, R., & Fonturbel, F. E. (2014). New insights on the mistletoe *Tristerix aphyllus* (Loranthaceae): interaction with diurnal and nocturnal frugivorous species. *Gayana Bot*, *71*, 270–272. <https://doi.org/10.4067/S0717-66432014000200010>
- Martínez del Río, C., Silva, A., Medel, R., & Hourdequin, M. (1996). Seed dispersers as disease vectors: Bird transmission of mistletoe seeds to plant hosts. *Ecology*, *77*, 912–921. <https://doi.org/10.2307/2265511>
- Medel, R. (2000). Assessment of parasite-mediated selection in a host-parasite system in plants. *Ecology*, *81*, 1554–1564. [https://doi.org/10.1890/0012-9658\(2000\)081\[1554:AOPMSI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1554:AOPMSI]2.0.CO;2)
- Medel, R., Botto-Mahan, C., Smith-Ramirez, C., Mendez, M. A., Ossa, C. G., Caputo, L. N., & Gonzales, W. L. (2002). Quantitative natural history of a host-parasite relationship: The *Tristerix*-cactus system in semiarid Chile. *Revista Chilena De Historia Natural*, *75*, 127–140.
- Medel, R., Vergara, E., Silva, A., & Arroyo, M. K. (2004). Effects of vector behavior and host resistance on mistletoe aggregation. *Ecology*, *85*, 120–126. <https://doi.org/10.1890/03-0261>
- Pavan, L. I., Jankowski, J. E., & Hazlehurst, J. A. (2020). Patterns of territorial space use by Shining Sunbeams (*Aglaeactis cupripennis*), tropical montane hummingbirds. *Journal of Field Ornithology*, *91*, 1–12. <https://doi.org/10.1111/jfo.12321>
- R Development Core Team (2020). R: A language and environment for statistical computing, reference index version 3.6.3. Foundation for Statistical Computing, Vienna, Austria
- Reid, S., & Armesto, J. J. (2011). Interaction dynamics of avian frugivores and plants in a Chilean Mediterranean shrubland. *Journal of Arid Environments*, *75*, 221–230. <https://doi.org/10.1016/j.jaridenv.2010.10.002>
- Ridout, M. S., & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, *14*, 322–337. <https://doi.org/10.1198/Jabes.2009.08038>
- Rodríguez-Gómez, G. B., & Fonturbel, F. E. (2020). Regional-scale variation on *Dromiciops gliroides* occurrence, abundance, and activity patterns along a habitat disturbance gradient. *Journal of Mammalogy*, *101*, 733–741. <https://doi.org/10.1093/jmammalgyaa022>
- Rosenberg, M. S., & Anderson, C. D. (2011). PASSaGE: Pattern Analysis, Spatial Statistics and Geographic Exegesis. Version 2. *Methods in Ecology and Evolution*, *2*, 229–232. <https://doi.org/10.1111/j.2041-210X.2010.00081.x>
- Rowcliffe, J. M., Kays, R., Kranstauber, B., Carbone, C., & Jansen, P. A. (2014). Quantifying levels of animal activity using camera trap data. *Methods in Ecology and Evolution*, *5*, 1170–1179. <https://doi.org/10.1111/2041-210x.12278>
- Rowcliffe M (2019). Activity: Animal Activity Statistics. R package version 1.2. <https://CRAN.R-project.org/package=activity>
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2017). A general framework for effectiveness concepts in mutualisms. *Ecology Letters*, *20*, 577–590. <https://doi.org/10.1111/ele.12764>
- Strauss, S. Y., & Irwin, R. E. (2004). Ecological and evolutionary consequences of multispecies plant-animal interactions. *Annual Review of Ecology Evolution and Systematics*, *35*, 435–466. <https://doi.org/10.1146/annurev.ecolsys.35.112202.130215>
- Vazquez, D. P., & Aizen, M. A. (2004). Asymmetric specialization: A pervasive feature of plant-pollinator interactions. *Ecology*, *85*, 1251–1257. <https://doi.org/10.1890/03-3112>
- Watson, D. M. (2001). Mistletoe—A keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics*, *32*, 219–249. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114024>
- Watson, D. M. (2004). Mistletoe: A unique constituent of canopies worldwide. In M. D. Lowman & H. B. Rinker (Eds.), *Forest Canopies* (2nd ed., pp. 212–223). Academic Press.
- Watson, D. M. (2013). The relative contribution of specialists and generalists to mistletoe dispersal: Insights from a Neotropical rain forest. *Biotropica*, *45*, 195–202. <https://doi.org/10.1111/j.1744-7429.2012.00905.x>
- Watson, D. M., & Rawsthorne, J. (2013). Mistletoe specialist frugivores: Latterday “Johnny Appleseeds” or self-serving market gardeners? *Oecologia*, *172*, 925–932. <https://doi.org/10.1007/s00442-013-2693-9>
- Wolf, C., & Hagen, E. (2012). Aggressive interactions of firecrowns (*Sephanoides* spp.; Trochilidae) during the breeding season on Robinson Crusoe Island, Chile. *Ornitología Neotropical*, *23*, 545–553.