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Species-specific effects of moonlight on insectivorous bat activity in central Chile

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Moonlight intensity influences the activity patterns of bats. Some bat species reduce their activity levels during brighter nights, a phenomenon known as "lunar phobia." While lunar phobia of bats has been extensively studied in tropical regions, the same is not the case of bats in temperate regions. By using acoustic detectors, we examined differences in the activity of insectivorous bats on nights with different moonlight intensity in an agricultural landscape of central Chile. We also examined the hourly activity patterns throughout the night and how these varied between full and new moon nights. All bat species modified their activity based on the moonlight intensity; however, their effects were species-specific. The activity of *Lasiurus varius*, *L. villosissimus*, *Myotis chiloensis*, and *Histiotus montanus* was lower during bright nights, while *Tadarida brasiliensis* was the only species whose activity was higher during bright nights. Hourly activity throughout the night differed between full moon nights and new moon nights in most bat species. During full moon, bats concentrated their activities in the early hours of the nights; a more homogeneous activity pattern was exhibited during new moon night. Our study demonstrates that moonlight affects the activity of bats in Chile, a factor that should be considered when studying bats.

Key words: acoustic monitoring, Chiroptera, lunar phobia, moonlight intensity, time activity

La intensidad de la luz de la luna influye sobre los patrones de actividad de los murciélagos. Algunas especies reducen sus niveles de actividad durante las noches más brillantes, un fenómeno conocido como "fobia lunar." Si bien esos efectos se han estudiado ampliamente en las especies de murciélagos de las regiones tropicales, pocos estudios han evaluado la respuesta de los murciélagos en las regiones templadas. Mediante el uso de detectores acústicos, examinamos las diferencias en la actividad de los murciélagos insectívoros entre noches con diferentes intensidades de la luz de la luna en un paisaje agrícola de la zona central de Chile. También examinamos la actividad temporal a lo largo de la noche y cómo ésta varía entre noches de luna llena y luna nueva. Todas las especies de murciélagos modificaron su actividad en función de la intensidad de la luz de la luna; sin embargo, sus efectos fueron especie-específicos. La actividad de *Lasiurus varius*, *Lasiurus villosissimus*, *Myotis chiloensis*, e *Histiotus montanus* fue menor durante las noches más claras, mientras que *Tadarida brasiliensis* fue la única especie cuya actividad fue mayor en las noches claras. La actividad por hora a lo largo de la noche difirió entre las noches de luna llena y las de luna nueva en la mayoría de las especies de murciélagos. Durante la luna llena, los murciélagos concentraron su actividad durante las primeras horas de la noche, mostrando una actividad más homogénea a lo largo de la noche en luna nueva. Nuestro estudio indica que la luz de la luna es un factor que afecta la actividad de los murciélagos en Chile, y por lo tanto debe ser considerado al realizar estudios de murciélagos.

Palabras clave: actividad temporal, Chiroptera, fobia lunar, intensidad de la luz lunar, monitoreo acústico

The activity patterns of bats can vary, both spatially and temporarily, in response to various environmental factors, including wind speed, temperature fluctuations, and rainfall (Hayes 1997; Voigt et al. 2011; Kronfeld-Schor et al. 2013; Leuchtenberger et al. 2018). In addition, bats have been known to alter their behavior and activity with changes in the intensity of the moonlight (Morrison 1978). During bright nights, some species of bats modify their foraging behavior, either by selecting vegetative strata of denser coverage, or by reducing their activity levels, a phenomenon known as "lunar phobia" (Morrison 1978; Saldaña-Vázquez and Munguía-Rosas 2013), patterns that seem to be associated with avoiding an increased risk of predation (Esberard 2007; Lima and O'Keefe 2013).

However, responses to lunar illumination are species-specific. For species of aerial insectivorous bats that use echolocation as an orientation system, wing morphology, body size, and flexibility in the use of habitats, all can be determining features (Appel et al. 2017). Species with long, narrow wings, adapted to rapid flight in open spaces or above the canopy (Norberg and Rayner 1987; Schnitzler and Kalko 2001) appear to be less susceptible to predators and therefore can forage more safely on illuminated nights (Holland et al. 2011). Likewise, bat species that use multiple habitats during foraging, such as forest interiors, vegetation borders, and open areas, move through a gradient of vegetation cover density (Mancina 2008), which makes them more tolerant to changes in illumination. These species therefore may be less affected by variations in the intensity of moonlight (Rydell 1991; Breviglieri 2011).

A recent review suggests that lunar phobia is more common in bat species of tropical regions than those of temperate regions, due to the high diversity of predators and high proportion of slow-flying species in tropical areas (Saldaña-Vázquez and Munguía-Rosas 2013). However, the shortage of studies conducted in temperate latitudes limits the generality of this hypothesis. We therefore carried out a study to evaluate the response of aerial insectivorous bats to variation in moonlight illumination in the temperate zone.

The central zone of Chile is characterized by a mild climate, with a fauna of bats dominated by insectivorous species that capture their prey in flight (Canals and Cattan 2008; Rodríguez-San Pedro et al. 2016). Several studies undertaken in the country have examined the patterns of activity and habitat use of a number of different bat species (Rodríguez-San Pedro and Simonetti 2013a, 2015; Meynard et al. 2014; Rodríguez-San Pedro et al. 2018, 2019). These studies have, however, been limited to the first 4 h of nighttime activity. Due to the role that insectivorous bats play in the region's crops as pest insect controllers (Boyles et al. 2011; Kunz et al. 2011; Rodríguez-San Pedro et al. 2020), their conservation in agricultural landscapes is of importance to farmers. Having information on the temporal activity patterns of insectivorous bats is relevant for the planning and design of research and monitoring programs for their populations and associated ecosystem services.

In this study, we examined differences in the activity of insectivorous bats between nights with different moonlight intensity in a vineyard system of central Chile. In addition, we examined hourly activity throughout the night and how it varied between bright (full moon) and dark (new moon) nights. Considering that moonlight may affect bats, in most cases adversely (Saldaña-Vázquez and Munguía-Rosas 2013), we hypothesized that negative responses would occur on brighter nights. We therefore predicted a decline in bat activity under such conditions. Given that moonlight intensity also varies throughout a single night, we further hypothesized that hourly bat activity throughout the night would vary between bright and dark nights, as documented by Mello et al. (2013) and Appel et al. (2017). We therefore predicted that bat activity would be more uniform on dark nights, while on bright nights, the activity would be concentrated at the beginning of the night.

Materials and Methods

Study area.—The study area was an agricultural landscape dominated by vineyards, located in Huelquen, commune of Paine, Santiago Metropolitan Region, Chile (33°48.412′S, 70°39.086′W to 33°51.960′S, 70°35.352′W). Although to a lesser extent, the area also contains horticultural, cereal, and fruit crops; as well as small patches of native vegetation (scrubland and sclerophyllous forest), forest plantations of exotic species (*Pinus* sp. and *Eucalyptus* spp.), and urbanized or semiurban areas. The climate of the region is temperate pluviseasonal Mediterranean according to the Köppen climate classification, with most rainfall concentrated in the winter season, June–August. The mean annual precipitation is ca. 360 mm and mean annual temperature ca. 15°C (Luebert and Pliscoff 2017).

Bat activity and moonlight intensity.—The study was carried out between October 2017 and February 2018, corresponding to the spring and summer seasons of the southern hemisphere. Activity of bats was recorded inside the vineyards, in seven acoustic monitoring points separated from each other at a minimum distance of 1.0 km. At each monitoring point, an automatic full-spectrum bat detector (Song Meter SM4BAT-FS) was used, with an SMM-U1 ultrasonic omnidirectional microphone (Wildlife Acoustics, Maynard, Massachusetts) located at an approximate height of 4.5 m above ground level, in consideration of the flight height of bat species in our study area. Detectors were programmed to passively and continuously record the activity of the bats throughout the night, starting at sunset (between 2000 and 2050 h) and ending at dawn (between 0600 and 0659 h), for a total of 10 h of recording per night. Detectors were set with a 256-kHz sample rate, 16-kHz digital high-pass filter, and 18-dB trigger level. We used a 3.0-s trigger window to capture calls prior to the initial trigger. At each sampling point, the activity of the bats was monitored for a minimum of 17 and a maximum of 25 nights, across the entire lunar cycle (waning, new, waxing, and full, moon), resulting in a total of 143 sampling nights and 1430 h of recording.

The acoustic records obtained were visualized and analyzed using the Avisoft-SASLab Lite program (Avisoft Bioacoustics, Germany) with a Hanning window.

Spectrograms were made of consecutive Fast Fourier Transforms (FFTs) with a 75% overlap. The allocation of the calls to each species was done manually, comparing the acoustic parameters of the calls recorded at each sampling point with those stored in a validated reference call library for bats in central Chile (Rodríguez-San Pedro and Simonetti 2013b; Rodríguez-San Pedro et al. 2016). An activity index for each species was estimated by counting the number of echolocation passes recorded per night for each sampling point. For the analysis of hourly activity, this index was estimated as the number of bat passes per hour in each night per sampling plot. A bat pass was defined as a recording of 15 s maximum in which two or more pulses emitted by a bat were identified. The bat species were named following the nomenclature proposed by Burgin et al. (2018).

To evaluate the effects of moonlight intensity on bat activity, the full gradient of the moon's illumination percentage, i.e., 0–100% of the moon's illumination, was considered. Data of the percentage of illumination of the moon were obtained using the Moonphase 3.3 software (Tingstrom 2009) for each sampling period. To examine differences in hourly activity between nights with different moonlight intensity (dark and bright), nights were categorized in two contrasting phases: dark nights (those with 0–20% of moonlight intensity) and bright nights (those with 80–100%). Sixteen dark nights and 25 bright nights were included in the analysis.

Canopy cover can influence the lunar luminosity in a habitat, with potential effects on bat activity. All sampling points in our study were inside vineyard crops, in open canopy sites. We therefore assumed that the effect of lunar luminosity on bat activity was similar among points sampled. Cloud presence was assessed by the accumulated rainfall data from the Climatological Station in Huelquen, Paine. Rainfall data were used for estimation of cloudy nights. Rainfall data comprised measures at 1-h intervals between October 2017 and February 2018. Following Appel et al. (2017, 2019), nights were considered "cloudy" when rainfall ranged from 0.1 to 10 mm per hour. Nights with these characteristics did not exceed 4% of the total of nights during our sampling period and were not considered in the analyses.

Statistical analyses.—The relationship between bat activity and moonlight intensity was evaluated using a generalized linear mixed model (GLMM) with a Poisson distribution controlled by overdispersion, in the "lme4" package of R (Bates et al. 2013); the variance explained (R^2) was obtained as described by Nakagawa and Schielzeth (2013). We used the number of bat passes per night for each of the bat species as a response variable, and the gradient of the moon's illumination percentage (0–100%) as the predictor variable. Each sampling point was included in the model as a random factor. To examine the variation in hourly activity (number of bat passes per hour after sunset) of bats between full moon nights and new moon nights, a two-sample Kolmogorov–Smirnov Z-test was used. The statistical programs used for analyses were R version 3.6.1 (R Core Team 2015) and SPSS Statistics 23.0 (SPSS Inc., Chicago, Illinois).

Results

A total of 10,038 echolocation passes were recorded, of which 99.6% (10,001 passes) could be identified and attributed to one of the six species registered in the study area: *Tadarida brasiliensis* (7,768 passes), *Lasiurus villosissimus* (719 passes), *Myotis chiloensis* (676 passes), *Lasiurus varius* (561 passes), *Histiotus montanus* (254), and *Histiotus macrotus* (23; Table 1). Due to the low number of echolocation passes registered for *H. macrotus*, this species was not included in the analyses.

Lasiurus varius, *L. villosissimus*, *M. chiloensis*, and *H. montanus* showed a negative response to the moonlight intensity, significantly decreasing their activity during nights with greater lunar illumination (Fig. 1; Table 2). In contrast, activity levels of *T. brasiliensis* increased significantly with moonlight intensity (Fig. 1; Table 2).

Hourly activity throughout the night differed between bright and dark nights for *L. villosissimus* (Z = 1.789, P = 0.003), *M. chiloensis* (Z = 2.012, P = 0.001), and *H. montanus* (Z = 1.565, P = 0.015), but not for *L. varius* (Z = 1.342, P = 0.055) and *T. brasiliensis* (Z = 0.894, P = 0.400). On both bright and dark nights, *L. varius* concentrated their activity during the first 2 h after sunset, gradually decreasing their activities toward the end of the night (Fig. 2). *Tadarida brasiliensis* also concentrated their activity at the beginning of the night in both phases, although activity tended to be more homogeneous throughout the night during dark nights (Fig. 2). During bright nights, *L. villosissimus* and *H. montanus* concentrated their activity in the first 2 h after sunset, followed by a marked decrease in activity until the end of the night, while *M. chiloensis* showed two activity

Table 1.—Total number of bat species echolocation passes (mean ± *SE*) recorded per night in each lunar phase. New moon nights were considered those with moonlight percentage between 0% and 20%, waxing or waning (21–79%), and full moon nights (80–100%). Data were collected in a vineyard landscape in Huelquen, Paine, Santiago Metropolitan Region, central Chile, between October 2017 and February 2018.

	Full moon		New moon		Waxing or waning moon	
	Sum	Mean ± *SE*	Sum	Mean ± *SE*	Sum	Mean ± *SE*
Lasiurus varius	154	3.55 ± 1.91	228	5.73 ± 2.44	179	3.32 ± 2.08
Lasiurus villosissimus	145	2.92 ± 0.74	349	8.58 ± 2.86	225	4.75 ± 2.04
Myotis chiloensis	79	1.71 ± 0.78	358	8.75 ± 3.68	239	4.32 ± 3.29
Histiotus montanus	46	0.76 ± 0.21	131	3.32 ± 1.02	77	1.52 ± 0.73
Tadarida brasiliensis	3,744	64.12 ± 11.85	1,739	44.73 ± 16.51	2,285	42.37 ± 8.60

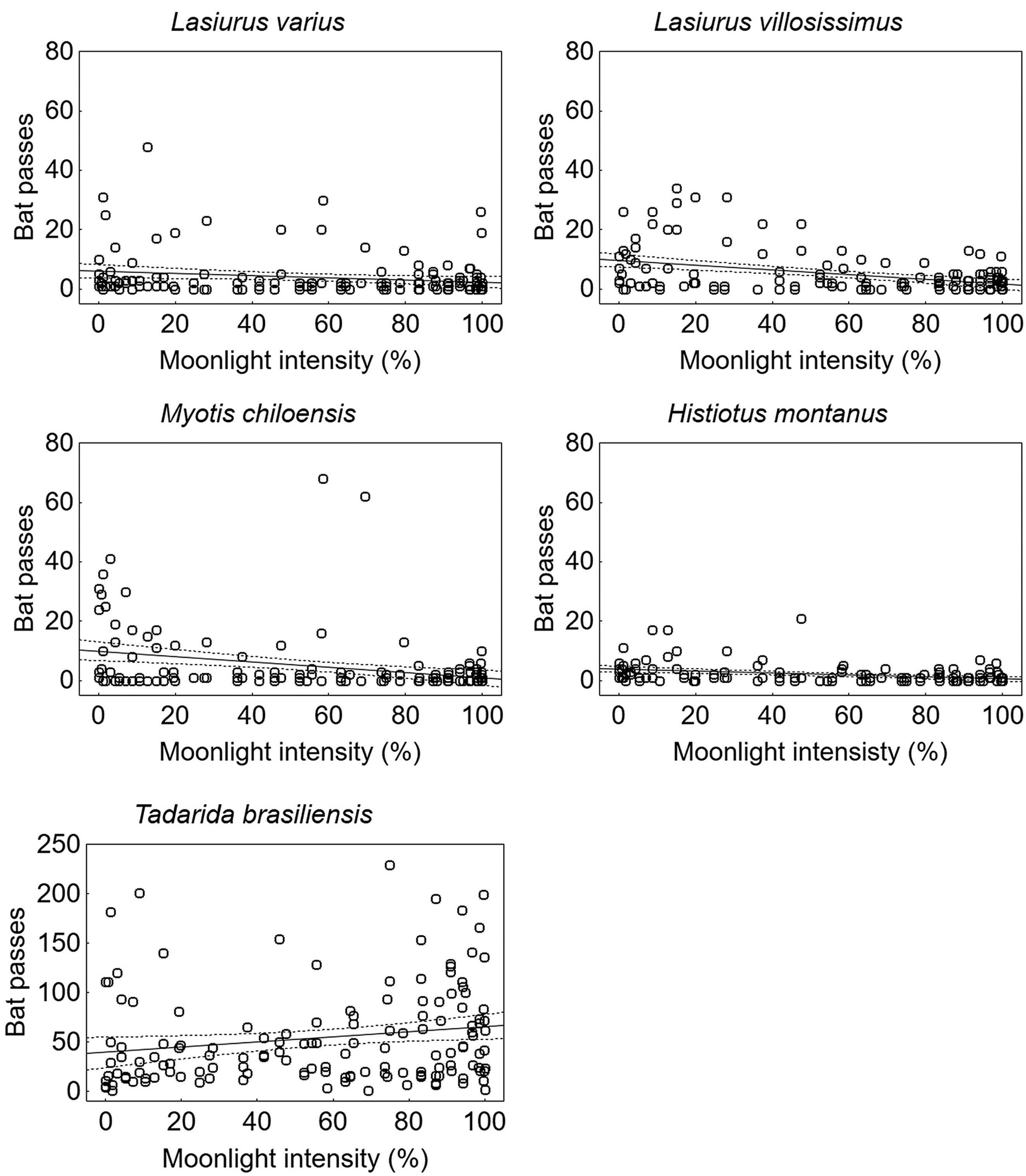

Fig. 1.—Relationship between bat activity and the percentage of illumination of the moon. Each point corresponds to the average of bat passes recorded per sampling night for five species of insectivorous bats. The solid line represents the regression line; the dashed lines denote the 95% confidence interval. Data were collected in a vineyard landscape in Huelquen, Paine, Santiago Metropolitan Region, central Chile, between October 2017 and February 2018.

peaks at beginning and the end of the night (Fig. 2). During dark nights, the activity of *L. villosissimus* remained constant throughout the night, while *H. montanus* and *M. chiloensis* showed bell-shaped activity patterns with a peak in the middle of the night (Fig. 2).

Discussion

The variation in bat activity patterns due to the effect of moonlight is a phenomenon documented in different parts of the world (Fenton et al. 1977; Lang et al. 2006; Esberard 2007), although it mostly has been described for species from tropical

Table 2.—Results of generalized linear mixed models (GLMMs) showing the relationships between the activity of five insectivorous and the percentage of illumination of the moon in 143 sampling nights. The R^2 values represent the variance explained by the model. The asterisk (*) indicates significant differences ($P < 0.05$). Data were collected in a vineyard landscape in Huelquen, Paine, Santiago Metropolitan Region, central Chile, between October 2017 and February 2018.

Bat species	Moonlight %		
	R^2	Z	P
Lasiurus varius	0.98	−2.69	0.007*
Lasiurus villosissimus	0.99	−9.35	< 0.001*
Myotis chiloensis	0.99	−10.78	< 0.001*
Tadarida brasiliensis	0.99	12.95	< 0.001*
Histiotus montanus	0.99	−7.59	<< 0.001*

regions, with very few records in temperate environments (see review in Saldaña-Vázquez and Munguía-Rosas 2013). Our results demonstrate that intensity of moonlight illumination influences the foraging activity of insectivorous bats in central Chile, a temperate zone. All bat species modified their activity based on intensity of moonlight; however, the effects of moonlight illumination were species-specific. These results are consistent with studies on bats in other temperate regions (Fenton et al. 1977; Adam et al. 1994; Ciechanowski et al. 2007), which leads us to hypothesize that this is not an uncommon phenomenon outside the tropics, contrary to the suggestion of Saldaña-Vázquez and Munguía-Rosas (2013). However, it has been suggested that the phenomenon of lunar phobia cannot be generalized across all species of insectivorous bats because the behavior varies depending on species and conditions (Appel et al. 2017). This pattern is consistent with the species-specific response observed in our study.

Lunar phobia in bats appears to be principally associated with an increase in perceived risk of predation (Fenton et al. 1977; Saldaña-Vázquez and Munguía-Rosas 2013) due to enhanced visibility on the part of predators under more illuminated conditions (Lima and O'Keefe 2013). Likewise, moonlight also may reduce the availability of bat prey. More light could mean prey detecting and evading its predator with more ease. Studies evaluating the density of prey available to insectivorous bats have reported a negative relationship between moonlight intensity and insect activity (Lang et al. 2006). Different species are affected in different ways depending on their degree of tolerance to moonlight intensity, which in turn depends on their ability to escape predators (Saldaña-Vázquez and Munguía-Rosas 2013). Contrary to most species in our study, *T. brasiliensis* significantly increased its activity with increasing moonlight. This finding is consistent with that reported for other insectivorous bats (Karlsson et al. 2002; Rogers et al. 2006; Roeleke et al. 2018; Musila et al. 2019) and could be explained by the eco-morphology of this species. Fast-flying species with long, narrow wings, such as *T. brasiliensis*, are less maneuverable but also potentially less exposed to predation than slow-flying species, characterized by shorter and broader wings, such as *M. chiloensis* and *H. montanus* (Norberg and Rayner 1987; Canals et al. 2005). On the other hand, the response of bats to changes in moonlight intensity may be related to flexibility in the use of habitats by different species (Hecker and Brigham 1999; Mancina 2008; Saldaña-Vázquez and Munguía-Rosas 2013; Roeleke et al. 2018). *Tadarida brasiliensis* is a species of generalist habits adapted to foraging in multiple habitats, which makes it more tolerant of changes in illumination and therefore is not affected by changes in moonlight. In contrast, *L. villosissimus*, *L. varius*, *M. chiloensis*, and *H. montanus* are species that forage close to vegetation, along edges, and are associated with forested habitats (Ossa and Rodríguez-San Pedro 2015; Rodríguez-San Pedro et al. 2016). For these species, specialization to forests would limit the range of variation in terms of coverage density in which they move, which makes them less tolerant to changes in illumination and therefore to being more affected by lunar phobia.

As expected, the overnight temporal activity varied between bright and dark nights for most bat species in our study. All species began their activity immediately after sunset, specifically during the first 2–3 h of the nights, regardless of the moon phase. They then decreased their activity toward the end of the night on bright nights or kept it constant throughout the night on dark nights. This early onset of foraging activity may be associated with the availability of some of bat insect prey (Arndt et al. 2018). The local bat assemblage in our study was dominated by generalist predators, such as the free-tailed bat (*T. brasiliensis*), which feeds on insects of different orders, including Lepidoptera, Coleoptera, Diptera, Hemiptera, and Hymenoptera (Lee and McCraken 2005; Gamboa and Díaz 2018; Rodríguez-San Pedro et al. 2020). Other species, such as *L. varius*, *L. villosissimus*, and *M. chiloensis*, feed on many species of moths, which represent an important fraction of their diet (Hickey et al. 1996; Clare et al. 2009; Kunz et al. 2011; Rodríguez-San Pedro et al. 2020). The activity of Diptera is concentrated in the early hours of the night (Jones and Rydell 1994), whereas Lepidoptera show a bimodal pattern, being more active in the early and late hours of the night (Meyer et al. 2004). This could potentially explain the bimodal nocturnal activity pattern observed in *M. chiloensis* during full moon nights. A foraging activity in the middle of the night, although it does not completely coincide with the activity of the insects, may represent a trade-off between the availability of resources and the risk of predation (Thies et al. 2006). *Lasiurus villosissimus*, on the other hand, shows a clear preference for being active during the early hours of the night in bright nights and homogeneously active throughout the night on dark nights. Differences in temporal activity throughout the night between moon phases are consistent with the pattern found in insectivorous bats in Africa (Fenton et al. 1977), where on bright nights their foraging activity is concentrated in the early hours of the night with the absence of a second feeding period. On darker nights, the successful search for food by these bat species improves, concentrating their activity in the middle of the night (Fenton et al. 1977; Elangovan and Marimuthu 2001). However, it is worth mentioning that the reasons for the variation in the patterns of temporal activity of bats are not clear,

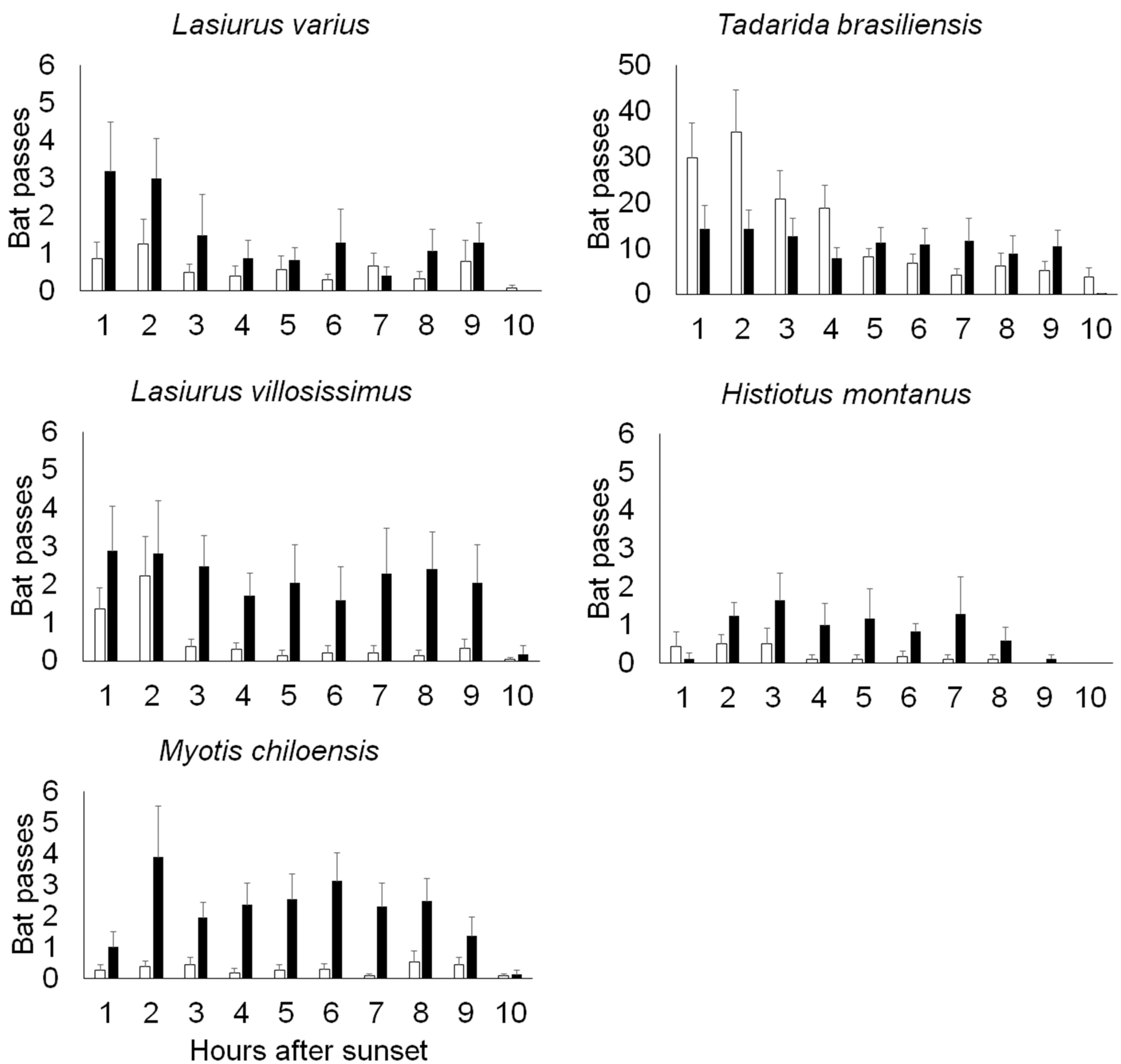

Fig. 2.—Hourly activity of five species of insectivorous bats on bright nights (white bar) and dark nights (black bar). Dark nights (n = 16) were considered those with moonlight percentage between 0% and 20%, and bright nights (n = 25) those between 80% and 100%. The bars represent the average of bat passes per hour and the vertical lines are the standard errors per hour. Data were collected in a vineyard landscape in Huelquen, Paine, Santiago Metropolitan Region, central Chile, between October 2017 and February 2018.

and may be multifactorial, including the abundance of insects, weather conditions, and social or other factors (Hayes 1997). Appel et al. (2019) observed a variation of hourly activity between nights with rain and nights without rain. On the other hand, it is important to highlight that within a single night, luminosity may vary (e.g., the moon may rise at the beginning or hours after sunset), which also could affect behavior throughout the night (Appel et al. 2017).

Artificial light pollution is an increasing environmental global problem affecting bats (Stone et al. 2015; Schoeman 2016; Russo et al. 2019). The occurrence of lunar phobia in Chilean bats may have implications for how bat species will be affected by increasing light pollution in the future. The light intensity under a full moon on a bright night is at most ca. 0.3 lx (Kyba et al. 2017), which is 100 times lower that the light intensity of a modern streetlamp (30 lx—Musila et al. 2019). For those bat species that significantly decreased their activity on full moon, it herefore also would be expected that they might avoid artificial lights such as streetlights. In contrast, those bat species that were not affected or increased their activity with the intensity of the moonlight, as was *T. brasiliensis* in our study, probably are able to tolerate increasing light pollution.

We showed that moonlight affects the activity of insectivorous bats in temperate regions, and therefore should be considered when undertaking a study on bats. We propose that species inventories be conducted during new moon nights, during which the highest activity of bats is recorded, in order to generate more complete inventories. It also is necessary to consider the temporal activity of different species, and sample throughout the night. The results of our study are a contribution to the knowledge about the ecology of these five species of bats, which makes it possible to improve the design of the future studies, by adjusting sampling schedules to activity patterns.

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