

Behavioral traits of the arboreal marsupial *Dromiciops gliroides* during *Tristerix corymbosus* fruiting season

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The importance of a frugivore's behavior and movement on seed dispersal patterns, although widely recognized, is sometimes difficult to obtain. This is particularly true for small and nocturnal animals that inhabit structurally complex environments, such as *Dromiciops gliroides*. We studied different behavioral traits of this species in its natural environment during the fruiting season of the mistletoe *Tristerix corymbosus*. Using videos recorded by camera traps, we obtained data regarding activity levels, time allocation, feeding patterns, and movement velocities of this frugivore. Our results showed that this small marsupial seemed to avoid moonlight, and to balance the costs generated by feeding during brightest nights (i.e., when more conspicuous to predators) feeds at higher rates than during less-illuminated nights. Feeding pattern analyses showed that *D. gliroides* can consume between 1 and 10 fruits per plant, but generally consumes 3 fruits. We also observed that the mean time needed for *D. gliroides* to extract and manipulate a fruit was 6 s. Time allocation analyses showed that, on average, individuals stayed on *T. corymbosus* and its hosts for 55 s, and allocate most of that time on feeding and moving within the mistletoe. Video analyses were demonstrated to be a useful sampling technique, which, in addition to allowing us to obtain information about activity patterns, also permitted us to assess fruit consumption patterns, visit lengths, and time allocation when visiting mistletoe. Moreover, video allowed us to understand the variability of movement velocities under different behavioral states. The information we provide here could be included into models to simulate seed dispersal in a more realistic and accurate way that incorporates not only spatial distribution of resources, but also detailed behavioral information of frugivores.

Key words: activity patterns, camera traps, fruit consumption, movement velocity, time allocation

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Seed dispersal is an important demographic event that has a strong influence on population dynamics and community structure by affecting key processes such as new habitat colonization, genetic differentiation, disease transmission, and interaction between different species (Nathan and Muller-Landau 2000; Levine and Murrell 2003). Particularly for animal-dispersed plants, the activity patterns and behavioral traits displayed by a frugivore define its efficiency as a dispersion vector (Spiegel and Nathan 2007). This dispersion efficiency includes not only the number of dispersed seeds, but also the fate of those seeds and their probability to survive after being dispersed. To study animal-mediated seed dispersal, the probability for a seed to be deposited at a certain distance from maternal plant can be estimated by combining information about a seed's passage time through the gut and the frugivore's movement over time (see Morales and Carlo 2006). This model is likely too simple and could lead to an overestimation of seed-dispersal effectiveness (Muller-Landau and Hardesty 2005;

Russo et al. 2006). Spatially explicit models (see Morales and Carlo 2006; Morales et al. 2012) that incorporate several aspects of frugivore behavior (e.g., Russo et al. 2006; Kays et al. 2011) could lead to a better understanding of the variability present in the dispersal process and could provide a more accurate tool to predict seed dispersal patterns of animal-dispersed plants.

Despite the recognized importance of the spatial distribution of seeds, our knowledge of the factors that lead to variation in patterns of seed deposition is limited. For instance, activity patterns of frugivores in space and time could significantly affect fruit deposition, and as a consequence influence seed fate and survival probability (e.g., Westcott et al. 2005). Behavior within activity periods may not be uniformly or randomly distributed (e.g., Milner and Harris 1999; Porter 2004), and the



time that a disperser spends on different activities or at different sites has strong impact on seed dispersal patterns, producing more- or less-clumped patterns according to how it distributes its available time (Kays et al. 2011). Considering that seed dispersal facilitates plant genotype movement and impacts genetic structure of plant populations (Westcott and Graham 2000), the assessment of movement velocities and fruit consumption patterns of frugivores may give important insights to understand and predict the effects of dispersal at the plant population level. When frugivores move faster through the landscape the possibility for seeds to be dispersed at distances farther from maternal plants increases and, as a consequence, may allow new habitats to be colonized. The timing of fruit consumption may influence the time of reproductive events of the plants they disperse (Rathcke and Lacey 1985; Primack 1987; Aizen 2003), and the number of fruits consumed per plant can strongly impact the genetic structure of plant populations.

The arboreal marsupial *Dromiciops gliroides* plays an important ecological role as a seed disperser of many native plant species (Amico et al. 2009), and apparently is the only effective seed disperser of the mistletoe *Tristerix corymbosus* in the temperate forest of southern South America (Amico and Aizen 2000; Amico et al. 2011), where mistletoe's fruits are green in color when ripe and hence inconspicuous to birds (Amico et al. 2011). This plant plays a key role in community structure and dynamics for 2 main reasons: as a hemiparasitic plant, it can affect the growth and survival of its hosts (Mathiasen et al. 1990) and has the potential to modify plant community structure (e.g., Pennings and Callaway 1996; Press and Phoenix 2005); and during winter, it is the only nectar resource for the endemic hummingbird *Sephanoides sephanioides* (Aizen 2003), which pollinates approximately 20% of the native woody plant genera in this forest during the summer (Aizen and Ezcurra 1998). Given the requirements of *T. corymbosus* for dispersal and the fact that it depends on a sole known disperser in temperate forests, variations in activity patterns, behavior, and movement of *D. gliroides* may strongly affect seed dispersal and eventually plant dynamics (Morales et al. 2012; Sasal and Morales 2013). Although the importance of the feeding patterns of this frugivore on seed dispersal success has been acknowledged, we still lack essential information about this unique species (Amico and Aizen 2000). The main objective of our paper is to generate relevant behavioral information of activity patterns, feeding behavior, time allocation, and movement velocities of *D. gliroides* that can be used to understand the factors and processes that influence seed dispersal of *T. corymbosus*.

MATERIALS AND METHODS

Study Site and Species

The study was conducted at the Parque Municipal Llao-Llao; a protected forest located 25 km west of San Carlos de Bariloche, Argentina (41°8'S, 71°19'W). This area belongs to the South American Temperate Forest of the Sub-Antarctic

biogeographical region (Mermoz and Martín 1986). The climate is cold-temperate with annual average precipitation and temperature of 1,800 mm and 9°C, respectively (Mermoz and Martín 1986). The forest has 2 differentiated strata: the canopy (> 15 m) dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis*, and an understory stratum (< 6 m) characterized by several species of shrubs, small trees, and bamboo (Aizen and Ezcurra 1998). In these forests *D. gliroides* is the most abundant small mammal, with estimated densities of more than 20 individual/ha (Rodríguez-Cabal et al. 2008; Fontúrbel et al. 2012). Spatially, activities of *D. gliroides* are concentrated in the understory stratum at least during austral summer and autumn, rarely including the arboreal stratum (Calzolari 2013). Temporally, at least in the Andean part of its distribution, this species is mostly inactive from late fall to early spring (Kelt et al. 1994). On the other hand, *T. corymbosus* presents an apparently uninterrupted flowering period that extends from March to December (i.e., austral winter), and a fruiting season that extends from austral summer to early fall (i.e., January–April/early May—Aizen 2003). In order to cover almost a whole season of interaction between the mistletoe and the marsupial, we conducted our fieldwork between January and May of 2011.

Sampling Protocol

To analyze activity and behavior of *D. gliroides* in its natural habitat, we used 8 motion-triggered infrared camera traps programmed to record during day and night. Four of these cameras were Moultrie Game Spy I-40 (Moultrie Feeders, Alabaster, Alabama) and were located pointing at branches connecting patches of *T. corymbosus* (hereafter “in-transit” cameras—see also Russo et al. 2006). These cameras can record short-length videos, and were programmed to record videos of 5-s maximum length. The other 4 cameras, which recorded videos of longer length, were placed in front of small trees parasitized by *T. corymbosus*, and aimed at the mistletoe (hereafter “mistletoe” cameras). Two of these cameras were Bushnell Trophy 119425C (Bushnell, Overland Park, Kansas), and the other 2 were Stealth Cam Unit IR (Stealth Cam, Grand Prairie, Texas). These 4 cameras were programmed to record videos of 60 s. We set all cameras to record videos with a resolution of 320 × 240 pixels per frame and 1-s response time. All cameras were checked and all videos were downloaded weekly from 4G memory cards. Each camera was placed at a fixed site, but removed and placed at a different location after 7 days without records of *D. gliroides*. During the beginning of the sampling, only 1 of the 8 cameras did not record any videos after 7 days, and was relocated to a new site. Afterward, the 8 cameras were located at a fixed position during the sampling period. Temperature data loggers (HOBO H8, with 23,520 eight-bit samples/readings storage capacity, and an operating range of temperatures from –20°C to 70°C) were placed at the location of camera traps and set to record information every 15 min.

Data Compilation

Videos with activity of *D. gliroides* were selected to extract information about activity patterns, time allocation, and feeding behavior (see an example in Supporting Information S1, B, DOI: 10.1644/13-MAMM-A-281.S1). From all videos with activity of *D. gliroides*, we recorded the date and time, environmental temperature, and moon phase. Moon-phase data was divided into 3 categories according to illumination levels: new-moon nights, half-moon nights, and full-moon nights. As descriptors of activity patterns we recorded the daily number of videos with activity of *D. gliroides* from in-transit and mistletoe cameras. To assess time allocation by *D. gliroides*, we extracted from each video recorded by mistletoe cameras the following information: time spent on *T. corymbosus* and its host (hereafter, “visit length”); and time spent on different activities, such as feeding, movement, and vigilance. For the analysis of feeding behavior we also collected from mistletoe videos: the total number of fruits of *T. corymbosus* consumed per visit to a plant, the total number of fruits consumed per branch, the location of fruit consumption (i.e., in situ consumption, when individuals fed in the same place where they extracted the fruit; or ex situ consumption, when individuals moved away from the extraction point to consume the fruit), and postural behavior while feeding. To estimate movement velocities, we identified on the videos: move length, which was defined by the distance between initial and ending points of a move; and move duration, which included the pauses on movements made to perform different activities, such as browsing, feeding, and vigilance. For move length measurement we identified the branches where each movement occurred and within a period of no more than 5 days after video recordings, we measured in the field the distance between starting and ending points of all moves (1-cm accuracy). With this information we estimated movement velocities separately for videos obtained from in-transit and mistletoe cameras.

To understand which factors affect activity, time allocation, and feeding behavior of *D. gliroides*, we considered different variables that might influence those patterns at different temporal scales (from during the day to during seasons). For instance, at the scale of one-half day, the daylight hours, we included time in the models, but as the number of minutes before sunrise, because that is the moment when this species begins its daily torpor. At the full-day scale, we assessed the effects of mean temperature and the coefficient of variation of temperature during the daily activity period of *D. gliroides* (see Fig. 1). For longer temporal scales, we included in the models moonlight intensity, season, and ripe fruit availability. The variable season was divided into 4 categories according to the extent of our sampling period: midsummer (from 21 January to 21 February), late summer (from 22 February to 21 March), early autumn (from 22 March to 21 April), and midautumn (from 22 April to 21 May). From Tiribelli (2014) we calculated the average number of ripe fruits available per plant. These data were collected from the same sampling site and season, and sampling consisted of counting the number of ripe fruits from 10 corymbs selected randomly from 23 *T. corymbosus*

plants, every 7 or 15 days from mid-December 2010 until May 2011. Lastly, we included into the models the site where cameras were located, because although we did not measure any characteristics, the mistletoe plants seemed to vary in traits such as height, size, connecting branches, and canopy cover (see Supporting Information S1, C).

Data Analysis

Activity levels.—The number of videos recorded per night was used as an indicator of activity levels. For this estimation, we used videos obtained from the 8 sites where we located the cameras. We performed multimodel selection through a likelihood ratio test to assess the possible effects of the following variables on activity patterns of *D. gliroides*: moonlight intensity, temperature, ripe fruit availability, season, and site where video was recorded. To model the excess of zeros in our data, a zero-inflated Poisson regression was fitted using the glmmADMB R package (Fournier et al. 2012; Skaug et al. 2013), and with day as random effect to consider variability among days (see Supporting Information S2, model 1, DOI: 10.1644/13-MAMM-A-281.S2). Also, in order to consider the temporal correlation between observations, we included in the model the number of videos recorded on the previous day as an explanatory variable. We standardized the variables to compare their coefficients.

Fruit consumption.—Feeding patterns of *D. gliroides* were described by the mean ($\pm SE$) number of fruits consumed and the mean ($\pm SE$) number of branches used for fruit consumption. We also estimated the time taken for extraction, manipulation, and consumption of fruits of *T. corymbosus*. During mistletoe video analysis we also identified the different body postures adopted during fruit consumption and different modes of fruit consumption. To assess if the number of fruits consumed by *D. gliroides* depended on the variables described above, we fitted generalized linear mixed models, assuming Poisson distribution with log link function (see Supporting Information S2, model 2), using lme4 R package (Bates et al. 2014). We selected the models with best fit, through a likelihood ratio test. We standardized the variables to compare their coefficients.

Visit lengths and time budgets.—To describe how *D. gliroides* employed its time when visiting *T. corymbosus*, we estimated the mean ($\pm SE$) for visit length and time spent on different activities. Moreover, to examine which variables affected visit lengths and activity budgets (i.e., the proportion of time spent feeding, browsing, moving, and on vigilance) of *D. gliroides*, we fitted Cox proportional hazards models (e.g., Fox 2002—see Supporting Information S2, model 3), using the survival R package (Therneau and Grambsch 2000; Therneau 2014). The variables included in the models were moonlight intensity, temperature, ripe fruit availability, season, site where video was recorded, and time before sunrise (in minutes). We selected the model with best fit. For this analysis we used the videos recorded from mistletoe cameras. We standardized the variables to compare their coefficients.

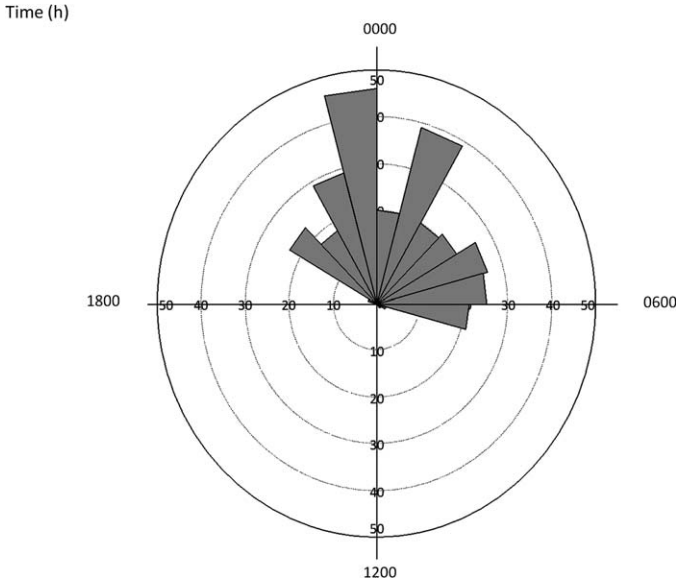


FIG. 1.—Rose diagram showing the number of videos of *Dromiciops gliroides* recorded per hour during the entire sampling period. Time (in hours) is on the axes, and circumferences represent the number of videos recorded.

Movement velocities.—We estimated the mean and 95% confidence interval for in-transit and mistletoe velocities, and fit a linear mixed-effects model to assess movement velocities when individuals performed different activities (i.e., browsing, feeding, movement, and vigilance) and at different times before sunrise (Supporting Information S2, model 4).

RESULTS

Dromiciops gliroides was the most abundant animal recorded by camera traps at night; from a total of 928 camera/day sampling effort we obtained 296 videos with activity of *D. gliroides* (209 mistletoe and 87 in-transit videos) and only 1 video of a rodent. We also detected 3 events of predation by domestic cats (*Felis silvestris*) on *D. gliroides* and 16 videos with the presence of cats surrounding the areas where this marsupial fed. During daylight, 36 videos recorded the activity of other animals, such as lizards and birds. The hummingbird *S. sephanioides* visiting *T. corymbosus* flowers was the most common species (28 videos), recorded just after dawn and very abundant at the end of the sampling season (in May).

Activity Levels

The activity of *D. gliroides* varied during the night (Fig. 1) and throughout the season. In January, the activity period was 7 h (from 2300 h to 0600 h), whereas in April and May it lasted 14 h (from 1900 h to 0900 h). On average, activity peaks occurred at a few hours after nightfall (at approximately 2300 h) and at a few hours before dawn (at approximately 0300 h). Also, activity patterns of this species seemed to vary through

the seasons, because at the beginning of the sampling season the number of videos recorded by all cameras was low, and increased markedly at the end of the austral summer (late March) and at the beginning of autumn (early April). During early May, activity levels seemed to decrease again and videos records became null after mid-May (Fig. 2).

The model to assess activity patterns with best fit considered the effects of moonlight intensity, coefficient of variation of temperature, ripe fruit availability, and season. The results showed that during new-moon nights, individuals were more active than during half- and full-moon nights. On average, during new-moon nights we expected to record almost twice the number of videos recorded during half-moon nights (Table 1; Fig. 3). When temperatures were more homogeneous *D. gliroides* was more active than during nights with more variable temperatures (Fig. 4). For example, for a night with an average coefficient of variation (and with all other variables at average values) we expected to record about 2.9 videos, but for nights with minimum coefficient of variation, the model predicts 10.8 records of activity (Table 1). Although we did not find evidence of the effect of ripe fruit availability on activity levels of *D. gliroides*, the model's fit significantly increases when we include this variable (Table 1; Fig. 3). Seasons seemed to have significant effects on this species' activity levels, with lower activity during mid- and late summer. For instance, under this model we expected to record 0.24 and 0.43 videos per day during mid- and late summer, respectively, and 2.66 and 1.34 during early and midautumn, respectively (see Table 1; Fig. 4).

Fruit Consumption

Dromiciops gliroides extracted between 1 and 10 fruits per visit to a mistletoe plant (Fig. 5). About half of the individuals consumed only 1 fruit per visit to a plant, and on average (\pm SE), individuals extracted 3 ± 2.14 fruits per visit. In 85% percent of the cases, individuals extracted fruits from only 1

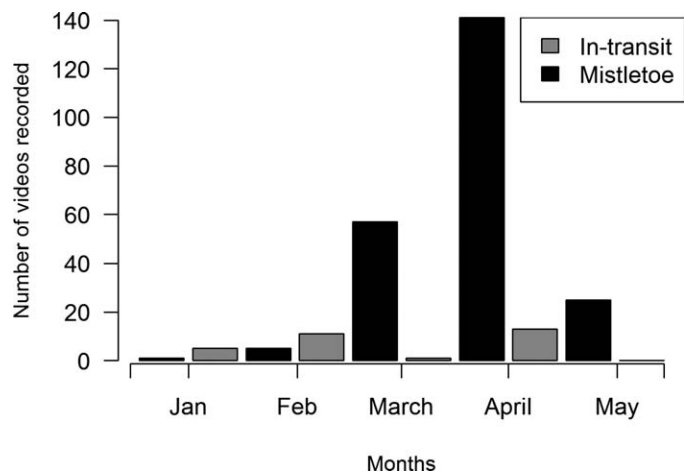


FIG. 2.—Bar plot showing the total number of videos of *Dromiciops gliroides* recorded from “in-transit” (gray bars) and “mistletoe” (black bars) cameras over the sampling period.

TABLE 1.—Estimates, *SEs*, 95% confidence intervals, and *P*-values for the generalized mixed-effect model fitted to assess activity patterns, with a zero-inflated Poisson distribution (*n* = 119 days). Detection parameter (*v*) was 0.2696 (*SE* = 0.057), and the model’s Akaike information criterion (AIC) and Bayesian information criterion (BIC) were 402.8 and 425.0, respectively. Boldface type indicates a *P*-value < 0.05. The likelihood ratio test between the model without ripe fruit availability (*df.* = 7, AIC = 413.6, BIC = 433.1) and with ripe fruit availability (*df.* = 8, AIC = 402.8, BIC = 425.0) showed a χ^2 -value of 12.8 and a *P*-value of 0.0003. *CV* = coefficient of variation.

Parameter	Estimate	<i>SE</i>	95% confidence interval		<i>P</i>
			Lower	Upper	
β_0	0.99	0.33	0.34	1.62	0.002
β_1 (New moon)	0.88	0.32	0.25	1.51	0.006
β_2 (Full moon)	0.10	0.34	-0.57	0.76	0.766
β_3 (<i>CV</i> _temperature)	-0.26	0.11	-0.47	-0.04	0.020
β_4 (Ripe_fruits)	0.07	0.02	-0.76	1.47	0.535
β_5 (Activity _{<i>t</i>-1})	0.35	0.57	0.02	0.12	0.004
β_6 (Midsummer)	-2.39	0.99	-4.34	-0.45	0.016
β_7 (Late summer)	-1.81	0.64	-3.09	-0.52	0.006
β_8 (Midautumn)	-0.68	0.64	-1.92	0.57	0.288

branch per visit (mean \pm *SE* = 2 \pm 0.88 branches). The highest fruit consumption rate occurred during March and April, which is consistent with higher activity levels during this time period (Fig. 3). Mean time (\pm *SE*) of fruit extraction–manipulation and consumption was 1 \pm 0.06 s and 5 \pm 0.17 s, respectively. Fruit processing is fast (extraction–manipulation and consumption takes, on average, no more than 7 s), which may allow processing a large number of fruits in a short period of time. We also observed that *D. gliroides* employed different body postures while feeding, including sitting, hanging from the hind limbs, and holding on with both the hind limbs and forelimbs (see Supporting Information S1, A). Moreover, the

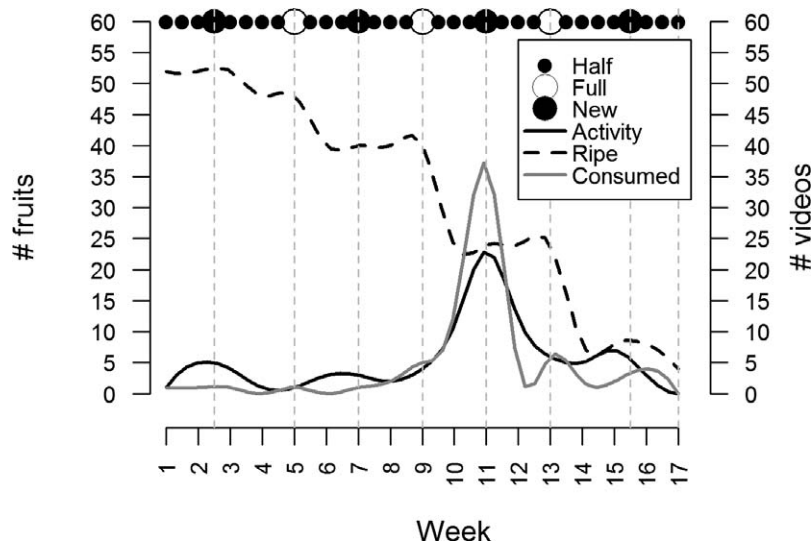


FIG. 3.—Plot showing the activity and fruit consumption patterns of *Dromiciops gliroides* through time and as a function of ripe fruit availability and moonlight intensity. The black solid line represents the number of videos recorded weekly, the black dashed line depicts the number of ripe fruits available weekly, and the gray line depicts the number of fruits consumed weekly. The vertical dashed lines (gray) represent the darkest and brightest periods.

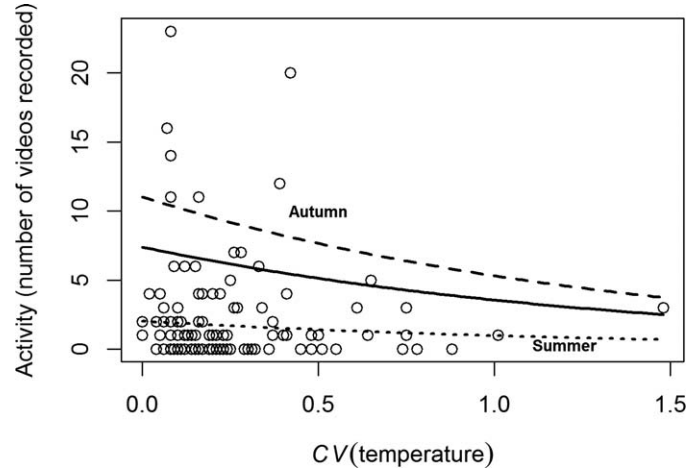


FIG. 4.—Plot showing the number of videos of *Dromiciops gliroides* recorded daily as a function of the coefficient of variation (*CV*) of temperature estimated for each day during the activity period (dark period of the day). The solid line is the average activity estimated from the model. The dashed lines represent the values of activity estimated for summer (which included mid- and late summer estimates) and autumn (which included early and midautumn estimates).

modes of fruit consumption identified in this work were in situ (when individuals consumed fruit in the same place of extraction) and ex situ (when individuals moved away from the extraction site to consume fruits in a different site). Examination of our data showed that the 26% of the fruits were consumed ex situ, approximately the 70% were consumed in situ, and only in 4% of the fruits extracted we were unable to determine the mode of fruit consumption.

The best-fit model for fruit consumption included moonlight intensity, coefficient of variation of temperature, season, and

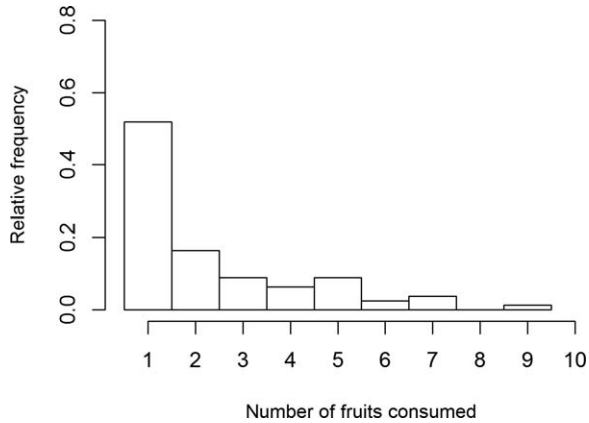


FIG. 5.—Histogram showing the relative frequency for the different number of fruits of *Tristerix corymbosus* consumed by *Dromiciops gliroides* per visit (i.e., video) to *T. corymbosus* trees in all camera-trap sites.

the number of fruits consumed on the previous day as explanatory variables. Including the number of fruits consumed on the previous day allowed us to include temporal autocorrelation in the model. The model did not show overdispersion in its residuals. Even though individuals are less active during full-moon nights, we found that they consumed more fruits per visit (Table 2). According to our model, we would expect *D. gliroides* to consume an average of 11.6 fruits per plant during full-moon nights, but only 3.5 and 7.1 fruits per plant during half- and new-moon nights, respectively. On the other hand, we would expect that individuals would consume fewer fruits at the end of the sampling season (i.e., midautumn [Table 2]). Models predicted an average of 0.15 and 0.48 fruits consumed per visit during mid- and late summer, and an average of 3.5 and 0.25 fruits during early and midautumn, respectively.

Visit Lengths and Activity Budgets

Video analysis ($n = 209$) showed that *D. gliroides* spent, on average ($\pm SE$), 55.35 ± 4.8 s visiting *T. corymbosus* plants. During the time that they remain on a plant, we recorded different activities, such as feeding (which included browsing, fruit extraction, and consumption), movement, and vigilance. The average times spent on those activities were 23 ± 1.1 s, 15.22 ± 1.5 s, and 5.56 ± 0.9 s, respectively. For visit-length and time-activity budgets the models with best fit included only moonlight intensities and site as explanatory variables. Results from visit length showed that, during new-moon nights, visit lengths by *D. gliroides* to mistletoe plants and their hosts were longer in comparison to half-moon nights (see Table 3). Also, we detected differences between sites, particularly for site 7 where visits were longer. The predicted visit lengths for new-moon nights and half-moon nights were 42 s and 36 s, respectively. Estimated visits for site 7 were almost 4 s longer than for the other sites. Cox proportional hazard models fitted to time budgets showed that the proportions of time that *D.*

TABLE 2.—Estimates, SEs, *P*-values, and 95% confidence intervals for the generalized mixed-effect model with Poisson distribution ($n = 119$ days) fitted for fruit consumption patterns. The model's Akaike information criterion and Bayesian information criterion were 292.7 and 311.8, respectively. Boldface type indicates a *P*-value < 0.05 .

Parameter	Estimate	SE	95% confidence interval		<i>P</i>
			Lower	Upper	
β_0	1.11	0.64	-1.01	0.58	0.477
β_1 (New moon)	0.76	0.72	-0.67	2.17	0.269
β_2 (Full moon)	1.18	0.67	0.11	2.51	0.007
β_3 (Consumption _{<i>t</i>-1})	0.09	0.04	0.03	0.17	0.005
β_4 (Midsummer)	-3.17	0.86	-4.85	-1.48	< 0.001
β_5 (Late summer)	-2.07	0.65	-3.05	-0.79	0.001
β_6 (Midautumn)	-1.72	0.67	-3.04	-0.40	0.010

gliroides spent on feeding, moving, or vigilance were not significantly related to moonlight intensity, and only the time spent moving and on vigilance was significantly higher for site 7. For instance, the models for moving and vigilance predicted that on site 7 individuals spent 3 s more on movement and 5 s more on vigilance in comparison to the other sites (see Table 3).

Movement Velocities

From video analysis, the estimated and 95% confidence interval for in-transit and mistletoe sites were: 23.6 m/min (17.0 m/min; 30.2 m/min) and 11.9 m/min (9.7 m/min; 14.6 m/min), respectively. The model fitted to assess if mistletoe movement velocities varied when individuals were involved in different behaviors showed that the highest velocities were when *D. gliroides* moved without performing any other activity, and that the lowest velocities were when feeding. Browsing and vigilance had shown similar velocities (see Table 4). The estimated velocity without performing any other activity was 21.33 m/min and the estimated velocity while feeding was 2.64 m/min. Also, *D. gliroides* moved faster earlier during the night. For every minute farther from sunrise, velocity increased by 2.7 m/min (see Table 4).

DISCUSSION

In this paper, we obtained information about activity patterns, time allocation, and feeding behavior on *T. corymbosus* fruits of *D. gliroides* using videos recorded with camera traps. Often, behavioral patterns are difficult to quantify under wild conditions (Westcott et al. 2005; Russo et al. 2006; McConkey and Chivers 2007), and this type of data is obtained from habituated animals. Nevertheless, for some types of organisms this is not possible because they are susceptible to observer presence, difficult to find or track because they inhabit under dense canopy, or move rapidly through the landscape, or a combination of these. Although this is the case for *D. gliroides*, the sampling technique that we used in this work was useful to obtain relevant behavioral information, such as the average time spent on different activities, the number of fruits

TABLE 3.—Estimates, *SEs*, *P*-values, and 95% confidence intervals for the Cox proportional hazard models fitted for visit length ($n = 169$, log-likelihood = -578.7), feeding ($n = 169$, log-likelihood = -198.5), moving ($n = 169$, log-likelihood = -440.8), and vigilance ($n = 169$, log-likelihood = -92.9). Boldface type indicates a *P*-value < 0.05.

Parameter	Estimate	SE	95% confidence interval		<i>P</i>
			Lower	Upper	
Visit lengths					
β_0	36.06	0.38	17.11	76.02	< 0.001
β_1 (New moon)	0.96	0.27	0.55	1.66	0.037
β_2 (Full moon)	5.54	0.48	1.60	7.89	0.723
β_3 (Site 4)	0.62	0.54	0.21	1.80	0.386
β_4 (Site 5)	1.73	0.36	0.84	3.56	0.136
β_5 (Site 7)	3.68	0.39	1.71	7.83	< 0.001
Feeding					
β_0	-0.82	0.39	-1.59	-0.04	0.03
β_1 (Site 4)	-1.25	0.67	-2.57	0.06	0.06
β_2 (Site 5)	-1.28	0.46	-2.18	-0.38	0.005
β_3 (site 7)	-0.69	0.46	-1.59	0.21	0.13
Moving					
β_0	-0.99	0.21	-1.41	-0.58	< 0.001
β_1 (New moon)	-0.20	0.26	-0.71	0.30	0.43
β_2 (Full moon)	-0.01	0.15	-0.30	0.28	0.94
β_3 (Site 4)	0.63	0.29	0.06	1.19	0.03
β_4 (Site 5)	0.58	0.20	0.19	0.97	0.03
β_5 (Site 7)	0.54	0.21	0.13	0.96	0.09
Vigilance					
β_0	-3.56	0.49	-4.52	-2.59	< 0.001
β_1 (New moon)	0.75	0.61	-0.45	1.94	0.21
β_2 (Full moon)	0.04	0.34	-0.63	0.71	0.89
β_3 (Site 4)	0.64	0.69	-0.72	2.00	0.36
β_4 (Site 5)	1.45	0.47	0.52	2.38	0.02
β_5 (Site 7)	1.70	0.49	0.73	2.68	< 0.001

consumed per plant, and movement velocities, from this unique species under natural conditions. Our general results showed that variability in activity patterns was related to moonlight intensity, temperature homogeneity, and season; feeding patterns were influenced by moonlight intensity and season; and time allocation was affected by moonlight intensity and site. Although we were not able to identify and differentiate among individuals it would be interesting to combine camera-trap video analysis with mark–recapture data and other complementary tools that allow individual identification from videos, in order to assess the possible effects of age, sex, and other traits (such as weight and fat reserves) on activity and feeding behavior. Our findings about activity patterns of *D. gliroides* may be used to guide mark–recapture and presence–absence studies conducted on this key species (e.g., Fontúrbel et al. 2010; Rodríguez-Cabal and Branch 2011), focusing the sampling effort during the periods of the season where individuals are more active. Moreover, movement velocities estimated through this sampling technique can be combined with movement data from other methods (such as thread spool—see Boonstra and Craine 1986; Nams 2005) to simulate this frugivore’s movement thorough landscape.

Activity of *D. gliroides* activity was not constant along the sampling period; data obtained from videos showed that

TABLE 4.—Estimates, *SEs*, *P*-values, and 95% confidence intervals for linear mixed-effect models fitted for movement velocities (number of observations = 232, number of groups = 57, Akaike information criterion = 617.75). Boldface type indicates a *P*-value < 0.05.

Parameter	Estimate	SE	95% confidence interval		<i>P</i>
			Lower	Upper	
β_0	1.57	0.19	1.27	1.87	< 0.001
β_1 (Feeding)	-0.96	0.17	-1.30	-0.62	< 0.001
β_2 (Movement)	1.25	0.15	0.94	1.55	< 0.001
β_3 (Vigilance)	-0.17	0.18	-0.53	0.19	0.152
β_4 (Time_before_sunrise)	0.001	0.01	0.0002	0.001	0.006

activity records of this species were low at the beginning of sampling season (early and midsummer) and almost null at the ending of sampling season (midautumn). This may be due to the fact that during early and midsummer, the diet of *D. gliroides* is composed mainly of insects and fleshy fruits from other plant species (Celis-Diez et al. 2012), so its activity could be focused on a different forest stratum or different plant species from where we located the cameras (i.e., understory stratum and on *T. corymbosus*). On the other hand, several studies have observed torpor and hibernation of this marsupial species under laboratory conditions (Bozinovic et al. 2004; Cortés et al. 2009; Nespolo et al. 2010). The fact that we recorded almost no activity by *D. gliroides* when environmental conditions started to become less favorable (i.e., toward mid- and late autumn) could be evidence of this energetic strategy under field conditions.

From all the factors that we examined, only moonlight intensity, coefficient of variation of temperature, and season showed significant effects on this species’ activity patterns. As expected for a small and nocturnal animal such as *D. gliroides*, activity was higher during darkest nights. This behavior is known as moonlight avoidance (e.g., Brown and Kotler 2004; Orrock et al. 2004; Berger-Tal et al. 2010; Kotler et al. 2010) and could generate variability in the temporal patterns of seed dispersal. During brighter nights *D. gliroides* is more conspicuous to predators, and feeding on a predictable resource such as fleshy fruits also increases the probability of being predated. In order to compensate for the cost associated with predation risk, this marsupial seems to consume higher quantities of *T. corymbosus* fruits during shorter visits. This pattern of fruit consumption and visit duration could lead to nonuniform seed dispersal over time, with periods of higher seed dispersal during brighter nights. Moreover, during these nights of shorter visits on *T. corymbosus* and its hosts the probability of a seed being dispersed close to the maternal plant could be lower, because *D. gliroides* tended to stay for shorter periods in comparison to darker nights. Our results also showed that the coefficient of variation of temperature seemed to affect activity patterns of this species, but the importance of this effect was apparently higher during autumn, when temperature became more heterogeneous.

The fruit consumption patterns of this marsupial could have important consequences on the genetic structure of populations of *T. corymbosus*. For instance, individuals generally

consumed 3 fruits per plant, whereas nearly 50% of their feces have between 4 and 14 seeds (Amico 2000). Those quantities imply that seeds from at least 2 different plants may be deposited on potential hosts. Another important aspect of feeding behavior of *D. gliroides* was that the peak of activity matches with the peak of fruit consumption (i.e., between late summer and early autumn). Aizen (2003) proposed a hypothesis stating that winter flowers should be favored because of the temporal overlap between the mistletoe fruiting period and its disperser's period of higher activity. But contrary to our expectations, although ripe fruit availability increased the goodness of fit of the activity patterns model we did not detect a significant effect of this variable on activity, visit length, or feeding behavior of *D. gliroides*. In fact, the greatest fruit consumption rates seemed to occur during the ripening period of the spring flowers, which ripen faster than winter flowers, as well as during late summer or early autumn when there are few ripe fruits. This could be explained by the fact that the fruiting period of *T. corymbosus* spans multiple seasons (see Aizen 2003) and is a predictable resource in space and time for *D. gliroides*. It is possible that during early and midsummer, this generalist disperser feeds on insects and fleshy fruits from other plant species (Celis-Diez et al. 2012) that are more time-restricted in comparison to fruits of *T. corymbosus*. Another possible explanation may be related to differential nutritional contents of fruits that ripen under differential climatic conditions. For instance, Aizen (2003) noted that fruits that became ripe in early summer came from flowers that opened during winter and ripening occurred slowly and under harsh environmental conditions. On the other hand, fruits ripe during the activity peak of *D. gliroides* came from spring flowers and ripening occurred quickly and under more favorable weather conditions. Is possible that, if the ripening process occurs under different environmental conditions, the fruits produced could have different sugar content or flavor (Paull and Jung Chen 2000), and these differences could be detected by this marsupial. This fact can be related to seed fate, because more severe environmental temperatures also can influence the survival probabilities of seeds dispersed during different moments of the fruiting period. For instance, seeds dispersed during late March and early April had lower survival probabilities than seeds dispersed early in the fruiting season (G. Amico, Laboratorio Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue, pers. comm.), but this could be compensated for by the higher activity levels and fruit consumption rates of *D. gliroides* during this period.

From video analysis we were able to identify different behavioral states of *D. gliroides* while visiting *T. corymbosus*. This marsupial spent most of its time feeding and moving, and allocated less time to vigilance. The way that this species allocated time for different behaviors often depended on moonlight or site. The sites selected for camera locations had different structural characteristics, such as height where *T. corymbosus* was located, size, number of connecting branches, and canopy cover. Also, by locating

camera traps on different types of sites (i.e., in transit and mistletoe) we were able to estimate velocities while individuals were in different behavioral states (see Morales et al. 2004). In-transit velocities could be considered as the fastest velocities when *D. gliroides* is moving through the understory stratum. Considering that mistletoe velocities were significantly slower than in-transit velocities, the probability of a seed being dispersed at certain distance from the maternal plant could be quite different if this marsupial is moving through a site with higher mistletoe density, or through a site with different connectivity among mistletoes. For this same plant–frugivore system, Morales et al. (2012) empirically tested the effects of conspecific fruiting plant neighborhoods, crop sizes, and plant accessibility on fruit removal rates and seed dispersal distances of *T. corymbosus*. For instance, they found that plants located in denser neighborhoods had greater fruit removal and shorter mean dispersal distances than more isolated plants and that larger crop size resulted in larger fruit removal rates and smaller probabilities of longer distance dispersal. All the small-scale information obtained in this work about behavior and movement patterns of *D. gliroides* could contribute to the development of more realistic seed dispersal models that link organisms' behavior to plant population and community dynamics (Morales et al. 2010).

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SUPPORTING INFORMATION

SUPPORTING INFORMATION S1.—Photos and video.

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SUPPORTING INFORMATION S2.—Models.

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