

Daily patterns of activity of passerine birds in a Magellanic sub-Antarctic forest at Omora Park (55°S), Cape Horn Biosphere Reserve, Chile

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Abstract Ecosystems in the sub-Antarctic region can be subjected to extreme weather conditions year-round. Little data exist that show any relationship between climatic variables and activity patterns of passerine birds, despite the fact that weather patterns can have a dramatic influence on the foraging strategies of these birds in different seasons. Passerine birds must balance the risk of starvation and the risk of predation in accordance with variation in environmental variables. The goal of this study was to determine the relationship of season, habitat type and weather patterns with the daily activity patterns of three diurnal passerine bird species from different trophic guilds. Unlike most low-latitude passerine species, the three passerine bird species in Omora Park on Navarino Island do not show strict adherence to a bimodal activity pattern; instead, these birds show a variety of activity patterns throughout the year that differ by trophic guild and habitat

type. These modifications in activity patterns may be an adaptation to minimize the risk of predation and starvation in the face of temperature-dependent food availability.

Keywords Daily activity · Passerines · Cape Horn · Trophic guild · Starvation–predation

Introduction

Daily activity patterns of birds, related to foraging and territorial displays, are affected by biotic variables such as competition (Newton 1998a), predation (Newton 1998b; Cimprich et al. 2005; Trnka and Prokop 2006), food availability (Pepper et al. 2000; Blake and Loiselle 2009), habitat type (Terborgh et al. 1990) and phylogenetic constraints and abiotic variables such as climatic conditions (Boyes and Perrin 2010). These have significant impacts on bird activity patterns, both at the spatial level such as habitat and landscape scales (Blake and Loiselle 2009) and the temporal level such as daily, seasonal and annual scales (Salinas-Melgoza and Renton 2005; Latta et al. 2011). In particular, daily activity patterns in passerine birds are strongly influenced by food availability and predator activity. Generally, feeding activity and territorial display of birds are concentrated during the early morning and the late afternoon and reduced around midday (Aschoff 1966; Morton 1967a; Dann and Aschoff 1975; Bednekoff and Houston 1994; McNamara et al. 1994), resulting in a bimodal activity pattern. It has been hypothesized that this bimodal pattern has multiple causalities related to food availability (Hutto 1981; Polo and Bautista 2006), avoidance of higher temperatures at midday, especially in warm areas (Morton 1967b; Ricklefs and Hainsworth 1968; Jacquet and Launay 1997; Brandt and Cresswell 2009), and

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maintaining a trade-off between avoiding starvation and predation risk (McNamara et al. 1994; MacLeod et al. 2005b). These bimodal patterns have been described mainly for birds in the Northern Hemisphere and in tropical and Mediterranean regions of the Southern Hemisphere (Robbins 1981; Boyes and Perrin 2010; Maruyama et al. 2010). Furthermore, this bimodal pattern variation has been described according to season; bimodal patterns with peaks in the morning and in late in the afternoon occurred for bird species in summer (Burger 1976; Skirvin 1981 in USA; Cullen 1974 in the Arctic; Pizo and Simão 1997 in South America; Trnka et al. 2006 in Slovakia) and winter (McNamara et al. 1994 in England, Canada and USA, including Alaska). It has also been demonstrated that some birds can modify their daily activity patterns according to environmental conditions, changing from bimodal to unimodal patterns and vice versa (Bas et al. 2007; Low et al. 2008 in temperate forests of Europe). Also, daily activity of birds can vary according to habitat type. For example, temperature, solar radiation and light levels are higher in exposed habitats such as low shrublands compared to closed habitats such as dense evergreen forests. All these factors can change the prevailing bimodal daily activity pattern described for birds (references in Morton 1967a; Burger 1976; McNamara et al. 1994). Preliminary studies in temperate and sub-Antarctic forests in the Southern Hemisphere indicate that the bimodal pattern of daily activity in birds is less marked, and they tend to be active throughout the day (Rozzi et al. 2006).

Four hypotheses have been offered to explain the modifications in patterns of daily activity by passerine bird species:

1. *Level of food availability* When moderate-to-high food levels exist, foraging can be interrupted during the day to minimize predation risk and the pattern is thus bimodal. In contrast, an amodal or flat pattern appears when food availability is low and passerine birds are forced to forage continuously throughout the day (McNamara et al. 1994, 2005). Alternatively, an amodal pattern can be explained by the risk-spreading hypothesis (Houston et al. 1993) where birds spread out their mass gain foraging throughout the entire day when mass-dependent effects are not important and foraging interruptions are negligible.
2. *Type of food eaten* Activity of insectivorous birds depends on insect activity, which is strongly influenced by temperature and light levels that are higher during midday, generating a strong unimodal pattern (Lewis and Taylor 1964; Low et al. 2008). In contrast, no influence on seed- or fruit-eating birds is expected.
3. *Breeding season* A unimodal pattern is prevalent in summer as a result of feeding of chicks overcoming the influence of other risks and then transitioning to bimodal in winter (Low et al. 2008).
4. *Temperature and light levels* Bird activity is reduced at midday, which decreases metabolic expenditure on days with high temperatures, generating a bimodal pattern during summer (Lima 1988; McNamara et al. 1994). In contrast, on cold short winter days, birds feed intensively throughout the day, showing a midday peak of activity (McNamara et al. 1994).

The effect of the availability and type of food, breeding season, temperature, daylight levels and habitat types on daily activity patterns of birds may be stronger at higher latitudes, due to lower temperatures, more snowfall and marked seasonal variation in daylight hours. The magnitude of the effect of all these variables on birds may limit their ability to obtain resources, depending on the quantity and diversity of these resources and time and effort exerted by birds to acquire them (McNamara et al. 2005; Møller et al. 2008; Schoech and Hahn 2008; Yom-Tov and Geffen 2011). Although empirical data are scarce to understand fully the relationship between environmental conditions and the patterns of daily activity, we can expect birds to exhibit marked changes in their daily activity pattern at high latitudes according to the availability and type of food, breeding season, climatic conditions and habitat type, based on results found with passerine bird species in high latitudes of the Northern Hemisphere.

The goal of this study is to investigate the daily activity patterns of three passerine bird species, one insectivorous, one frugivorous and one omnivorous that inhabit the southernmost forests of the planet, the Magellanic sub-Antarctic forests at Omora Park in the Cape Horn Biosphere Reserve, Chile. We particularly focus on seasonal changes and contrast the patterns of daily activity in two types of dominant habitats—dense evergreen forests and shrublands. We discuss whether activity patterns can be related to availability and type of diet that bird species consume, their breeding season, temperature, solar radiation and daylight hours, by contrasting these variables in exposed and closed habitats.

Methods

Study area

This study is part of the long-term bird-banding program conducted in Omora Park (54°57'S, 67°39'W), located 3 km west of Puerto Williams on the northern coast of Navarino Island, Cape Horn Biosphere Reserve, Chile (Fig. 1, Rozzi et al. 2003, 2006; McGehee et al. 2004). The park constitutes the southernmost site of the International

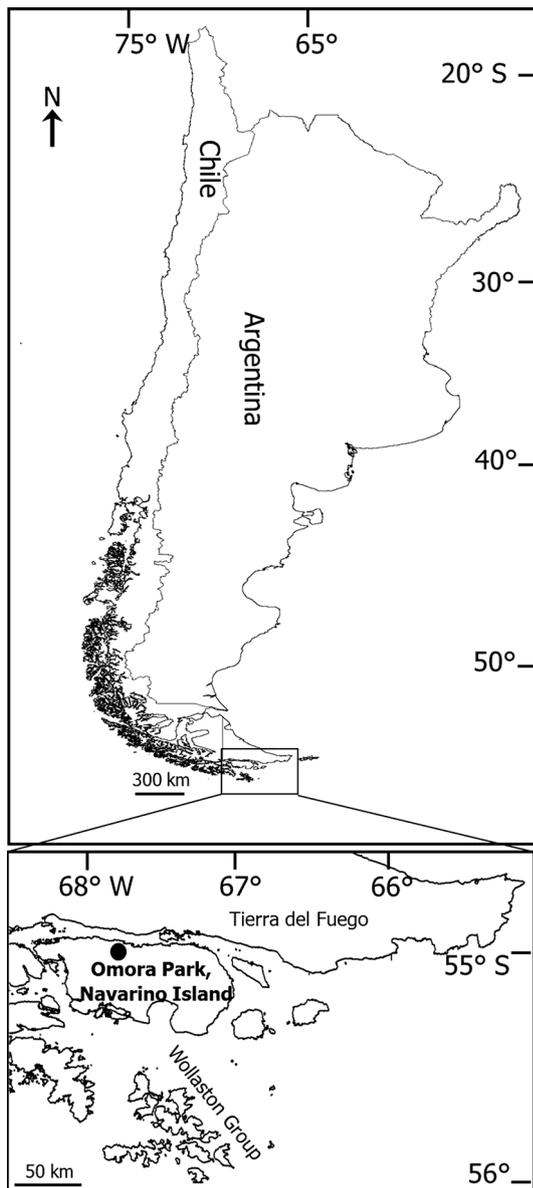


Fig. 1 Map of southern South America and the studied area in Omora Park, Navarino Island

Long Term Ecological Research Network (ILTER, Rozzi et al. 2012). The park protects 1,088 ha of Magellanic sub-Antarctic forests dominated by evergreen stands of *Nothofagus betuloides* and *Drimys winteri* and by deciduous forests of *N. pumilio* and *N. antarctica* (Ippi et al. 2009). These are the closest forest ecosystems to Antarctica (1,000 km north of the Antarctic Peninsula, Rozzi et al. 2012). The forest bird community is subjected to strong seasonality and contrasting climatic conditions in temperature, rainfall, snowfall and daylight hours between summer and winter seasons. However, oceanic conditions attenuate the seasonal temperature fluctuations, providing an environment that contrasts strongly with Northern

Hemisphere temperate or boreal forests (Rozzi et al. 2012). Annual precipitation reaches approximately 412 mm, and the mean annual temperature is 6.3 °C. In summer (January), the mean temperature is 12.8 °C and the index of solar radiation is 179.3 w m^{-2} . In winter (July), these values are 2.4 °C and 23.2 w m^{-2} , respectively. The study was conducted in the lower areas of Omora Park where habitats include secondary and primary *Nothofagus* and *Drimys* forests and anthropogenic shrubland composed of *Berberis buxifolia*, *Chiliodrimum diffusum*, *Ribes magellanicum* and *Embothrium coccineum* (Brown et al. 2007).

Climatic conditions

We compared daily temperature, solar radiation, wind speed pattern and daylight hours (from time of sunrise to time of sunset) for every day in summer (January, February, March 2012) and winter seasons (June, July, August 2011), of Navarino Island, along with the sum of precipitation for the season. The climate conditions are very special in the area, different than the nearby scenario in Antarctica and different than its counterpart in the Northern Hemisphere at the same latitude because of the ocean influence that regulates climate, contrary to what occurs in the Northern Hemisphere with vast land areas without nearby sea. Data for daylight hours were obtained from the Chilean Navy Hydrographic Service at Puerto Williams Station (<http://www.shoa.cl/index.htm>). The climatic conditions were obtained from the database of the Omora Park LTSER Chile Meteorological Station, operating since summer 2010. We took all available values in an interval between 05:00–22:00 h local time for each day of the months considered (winter $n = 92$ days, summer $n = 91$ days). Temperature and wind speed in a habitat exposed to solar radiation (shrubland) and one protected from solar radiation (forest) were measured hourly during all days of sampling during the summer and winter of 2011 using a Kestrel 2500[®] anemometer. To determine the climatic conditions in both habitat types, we calculated Δ values (differences between values) for temperatures and wind speed between data obtained in the two sites and data obtained in the LTSER Meteorological Station for the same time. This enabled us to control the hourly weather conditions for the area at the time that we obtained the measures on the sites. Climatic data are presented as mean \pm SD.

Since our data for bird captures are for the years 2004, 2005 and 2006 (see below) and we have confident climatic data for Navarino Island only since 2010, we reviewed the temperature and rainfall data of the Centro Austral de Investigaciones Científicas (CADIC) for 2004, 2005 and 2006 of Meteorological Station at city of Ushuaia, 45 km north of Navarino Island, to detect any anomaly in patterns

of climatic conditions for the area in the sampling period. We did not consider wind conditions for the analyses as the two stations are located in sites with different wind conditions.

Bird activity

The activity pattern of birds can be described by their capture rates using mist-nets, a method widely used in studies of distribution, abundance and activity of birds (Remsen and Good 1996; Bibby et al. 1998; Blake and Loiselle 2001). The advantage of this method is that captures with mist-nets better reflect bird activity compared to techniques more appropriate for abundance estimates such as point counts (Remsen and Good 1996; Jiménez 2000). Mist-nets are relatively easy to use and avoid misidentification that depends on the auditory and visual skills of the observer (Karr 1981; Remsen and Good 1996; Derlindati and Caziani 2005). Daily activity patterns of birds were estimated using the database of the banding program. We assumed that capture rate provides a good estimator of activity level for all three species considered. Extensive bird captures were conducted with mist-nets during summer (January–March) and winter (June–August) daylight hours for 2004, 2005, 2006 and summer 2011. Sampling periods included at least nine to ten consecutive hours with data taken beginning at dawn, including one hour that is perceived by the human eye as darkness. Captures were conducted at two sites representative of two habitat types within the Omora Park: shrubland (exposed to direct solar radiation) and dense evergreen forest (unexposed to direct solar radiation). We obtained data for 31 and 35 days in shrubland and forest habitats, respectively, in summer, and 17 and 20 days, respectively, in winter. Total effort included 730 h for all 103 days of sampling. Almost all data were recorded by only one trained person in charge of the monitoring of birds, covering a daily effort of nine to 10 h of fieldwork in winter and 10–14 h in summer.

Birds were sampled continuously for 3 days each month in each habitat type in all sampled seasons. It has been shown that birds become familiar with the nets after sampling for more than three consecutive days (Zakaria and Rajpar 2010). We used 5–6 ground level mist-nets (6 to 12 wide \times 2.6 m high, 30 mm mesh, 50 cm above ground) 30 m apart from each other. Sites (forest and shrubland) were 500 m apart to increase capture independence (Barlow and Peres 2004). Nets were located randomly with respect to topography, locations of fruiting plants, tree fall gaps or other factors that might influence capture rates (Blake and Loiselle 2001). All captured birds were banded with a numbered aluminum band and then released. For the analyses, we excluded recaptures that occurred within the same sampling period of 3 days because some individuals

were more susceptible to fall into the net twice, overestimating the capture data.

Species by trophic group

To evaluate the relationship between diet type and activity of birds, we chose the three most captured species that have differences in their diet, on the basis of the type of food consumed (Blake and Loiselle 2001), literature accounts (Goodall et al. 1951; Martínez and González 2004; Brown et al. 2007; McGehee and Eitniear 2007), qualitative analyses of fecal samples in the field (Rozzi et al. unpublished data) and field observations: (1) the Thorn-tailed Rayadito *Aphrastura spinicauda* (Furnariidae) that feeds primarily on insects captured both in flight and in foliage, branches and logs; (2) the frugivorous/granivorous Patagonian Sierrafinch *Phrygilus patagonicus* (Emberizidae); and (3) the omnivorous White-crested Elaenia *Elaenia albiceps* (Tyrannidae), which has a mixed diet composed of fruits, seeds and insects. These three species represented 83 % of all captures, with 43, 25 and 15 %, respectively. The White-crested Elaenia is a migratory species that arrives to the area of study during the middle of the austral spring.

Statistical analyses

Data for climatic conditions were compared between sites for the variables' temperature, wind speed, solar radiation, Δ temperature and Δ wind speed with mean \pm SD.

We performed a Poisson Generalized Lineal Model (GLM)-type ANCOVA for all three bird species to relate capture to environmental variables (hour, season and habitat) controlling for the effect of capture effort (m^2 of net per hour of exposure). GLM were used with logarithmic link function (log link), including interactions between independent variables. GLM are robust to unbalanced designs (Quinn and Keough 2002).

We performed all analyses with STATISTICA version 7 (StatSoft, Inc., Tulson, OK). Descriptive statistics are presented as mean \pm SD (standard deviation) and range.

Results

Climatic conditions

On Navarino Island, the highest temperatures were reached nine (12.2 °C) and seven (4.2 °C) hours after dawn in summer and winter, respectively (Table 1; Fig. 2). Daylight extended for 17 h during summer (05:00–22:00 h local time) and for 8 h in winter (08:00–17:00 h local time). Solar radiation was greater in summer than in winter (Table 1), with maximum recorded 8 and 6 h after dawn in

Table 1 Weather conditions between 05:00 AM and 22:00 PM for Puerto Williams in June, July and August 2011 (winter) and January, February and March 2012 (summer) obtained from Omora Park LTSER Chile Meteorological Station

	Summer (n = 1,639)	Winter (n = 1,656)
Temperature (°C)	9.6 ± 3.8 (−1.1–22.9)	2.1 ± 2.8 (−5.1–10.4)
Wind (km h ^{−1})	2.6 ± 1.5 (0–7.5)	1.6 ± 1.3 (0–7.3)
Radiation (w m ^{−2})	216 ± 231 (0–1,083.3)	44.1 ± 77.9 (0–417.3)
Rainfall (mm)	105.6	86.2

All variables are shown as mean ± SD and range, except rainfall which is sum of all values (winter n = 92 days, summer n = 91 days)

summer (481 w m^{−2}) and winter (154 w m^{−2}) (Fig. 2). Wind speed also showed differences between seasons (Table 1), reaching maximum values 8 and 6 h after dawn in summer (3.4 km h^{−1}) and winter (2 km h^{−1}), respectively (Fig. 2). Rainfall was higher in summer than in winter (Table 1). Temperature and rainfall conditions for Ushuaia were similar between years and similar to Puerto Williams (Table 2). The mean Δ of temperature was greater for shrubland habitat than in forest in summer, but the sites were similar in winter. Mean Δ of wind speed was greater in forest than in shrubland in both seasons (Table 3).

Daily activity pattern of birds in Omora Park

We had got 285 captures of Thorn-tailed Rayaditos, 487 of Patagonian Sierra-finches and 164 of White-crested Elaenias in the sampling period. Captures made during the breeding season considered the time interval from the incubation period until the time where juveniles were independent of their parents. Time, season and habitat parameters related to bird activity differed between species (Table 4).

Thorn-tailed Rayadito

Rates of capture of this species varied significantly by hour, season and habitat. Captures were significantly higher in summer and in the forested habitat (Table 4). In the forest, daily activity patterns were concentrated around midday both in summer and winter (Fig. 3), but with constant activity during the evenings. In the shrubland, captures fluctuated throughout the day in both seasons, exhibiting a trimodal pattern in summer and a bimodal pattern in winter (Fig. 3), with large hourly variance.

Patagonian Sierra-finch

Rates of capture varied significantly between hour and season, and there was interaction between hour, season and

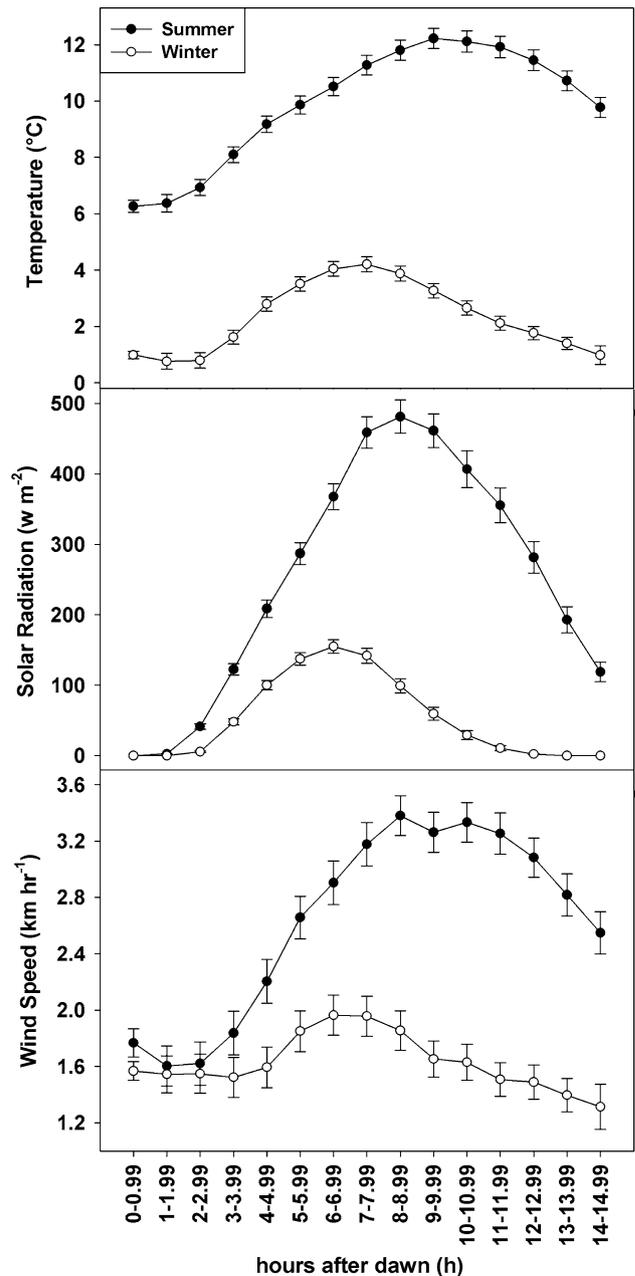


Fig. 2 Daily pattern of temperature, solar radiation and wind speed for winter (mean ± SE, 92 days from June to August 2011) and summer (91 days from January to March 2012) recorded at the meteorological station of the Long Term Socio-Ecological Research Site (LTSER Chile) in Omora Park

habitat (Table 4). More individuals were captured in shrubland than in forest, but principally during summer and in the first part of the day. In shrubland during summer, the rate of capture reached its maximum in the early morning and then decreased throughout the day, while in winter the daily pattern was bimodal. In the forest, activity patterns were not significantly different between seasons and these were bimodal both in summer and winter (Fig. 4).

Table 2 Temperature and rainfall conditions for Ushuaia in June, July and August (winter) and January, February and March (summer) of 2004, 2005 and 2006, obtained from the Centro Austral de Investigaciones Científicas (CADIC) Meteorological Station in the city of Ushuaia, 45 km at north of Navarino Island

	Year	Summer	Winter
Temperature (°C)	2004	10.6 ± 1.5	2.5 ± 0.8
	2005	9.5 ± 1.6	1.5 ± 1.4
	2006	9.8 ± 0.7	2.1 ± 0.7
Rainfall (mm)	2004	98.6	82.8
	2005	144.6	69.7
	2006	162.8	188.6

Data are shown as mean ± SD, except rainfall which is the sum of all values (winter $n = 92$ days, summer $n = 91$ days)

Table 3 Mean Δ of temperatures and wind for shrubland and forest for summer (January–March 2011) and winter (June–August 2011)

	Season	Shrubland	Forest
Δ Temperature (°C)	Summer ($n = 193$)	0.7 ± 1.5	-0.4 ± 1.2
	Winter ($n = 83$)	0.2 ± 1.2	0.3 ± 1.4
Δ Wind speed (km h^{-1})	Summer ($n = 193$)	-0.9 ± 1.4	-1.2 ± 1.1
	Winter ($n = 83$)	-1.0 ± 1.0	-1.4 ± 1.0

Negative and positive numbers indicate that site values were lower or higher than the weather values for the area, respectively
 n number of hours

White-crested Elaenia

Captures of this species showed no significant differences between hour and habitat but were higher in shrubland (Table 4; Fig. 5). In the forest and shrubland, captures did not vary significantly throughout the day, showing a fluctuating daily pattern; however, there were captures during the morning and late in the afternoon (Fig. 5).

Discussion

During daylight hours, birds can reduce starvation risk by foraging intensively at the beginning of the day, storing up energy reserves and minimizing the chance of starving due to foraging opportunity lost later in the day (Bednekoff and Houston 1994; McNamara et al. 1994) because of variations in climatic conditions, disturbance or random variation in the food supply (MacLeod et al. 2005a). In contrast, by delaying foraging activity as late as possible until the end of the day, an individual can avoid carrying extra mass that will reduce its escape ability if it encounters a predator by being able to fly faster and/or being more maneuverable,

thereby reducing its predation risk for most of the day (MacLeod et al. 2005a, 2005b). There is empirical evidence showing birds regulating their diurnal mass gain by the following patterns: (a) the largest mass gain is acquired during first hours of the day in winter to compensate great metabolic expenditure due to short time span availability; (b) bimodal outside the breeding season (pre- or post-breeding), where birds show a trade-off between starvation and predation risks; and (c) constant in the breeding season when starvation–predation risk trade-off no longer seems to drive mass gain behavior, and instead, birds forage and gain mass throughout the entire day when they try to maximize their breeding success (McNamara et al. 1994; MacLeod et al. 2005a, 2005b). When breeding, birds forage throughout the day to satisfy their demands for both the offspring and themselves (MacLeod et al. 2005a). However, availability of mobile invertebrate food items varies throughout the day, and therefore, foraging patterns of insectivorous birds depend on this availability. Activity of mobile invertebrates is strongly linked to ambient temperature and light levels (Lewis and Taylor 1964); thus, these usually display a peak during midday hours (Low et al. 2008). Therefore, when foraging is temperature dependent (i.e., temperature-dependent food-availability hypothesis), birds should exhibit a foraging pattern centered at midday, modified by other factors such as predation (Low et al. 2008).

Activity patterns of three passerine bird species of Navarino Island varied according to breeding season, habitat type, food availability, time of the day and the food requirements of the species. Our study identified the occurrence of amodal, bimodal, trimodal, declining and fluctuating activity patterns, which can be driven by food availability, temperature or the presence of predators. The effect of heat stress during midday would not define the activity pattern of these three passerine bird species on Navarino Island is in contrast to that documented for tropical species (Gilardi and Munn 1998; Cameron 2005; Boyes and Perrin 2010), because Thorn-tailed Rayadito activity during the summer season was high in the exposed shrubland where temperatures were high.

Daily activity patterns of birds in Omora Park

The three bird species on Navarino Island had variable activity patterns that differed throughout the day, depending on species, hour, season and habitat.

Patagonian Sierra-finch

In general, frugivorous birds forage over predictable but low energetic content food items. If foraging is continuous in the absence of disturbances such as predation and bad

Table 4 Poisson Generalized Lineal Model-type ANCOVA for bird captures and its relationship with environmental variables (hour, season and habitat), controlling for the effect of capture effort

Variables	Effect	<i>df</i>	Wald	<i>P</i>	Deviance
Patagonian Sierra-finch					2.11
<i>n</i> = 654	Intercept	1	67.63	<0.001	
	Effort	1	0.31	0.57	
	Hour	8	100.14	<0.001	
	Season	1	14.51	0.001	
	Habitat	1	<0.001	0.99	
	Hour × habitat	8	90.64	<0.001	
	Hour × season	8	4.94	0.76	
	Habitat × season	1	0.07	0.79	
Hour × season × habitat	8	43.84	<0.001		
Thorn-tailed Rayadito					1.14
<i>n</i> = 654	Intercept	1	<0.001	0.99	
	Effort	1	1.42	0.23	
	Hour	8	50.99	<0.001	
	Season	1	13.89	<0.001	
	Habitat	1	47.17	<0.001	
	Hour × habitat	8	10.60	0.22	
	Hour × season	8	9.94	0.27	
	Habitat × season	1	0.52	0.47	
Hour × season × habitat	8	9.97	0.27		
White-crested Elaenia					0.89
<i>n</i> = 558	Intercept	1	17.76	<0.001	
	Effort	1	5.62	0.01	
	Hour	12	20.76	0.05	
	Habitat	1	1.74	0.19	
	Hour × habitat	12	6.69	0.87	

Significant *P* values ($\alpha \leq 0.05$) are shown in italics

n number of hours of sampling

weather conditions, the activity pattern should depend on energy gain. As the gain is low, birds should forage intensively during early daylight hours and activity should decrease progressively during the day until they fulfill the energetic requirements that allow them to compensate the metabolic expenditure at night (McNamara et al. 1994). This scenario appears to occur in summer in the shrubland habitat: Patagonian Sierra-finches consuming grains, seeds and fruits forage mainly in the morning and decline drastically around midday, showing little activity during the rest of the day. Shrubland habitats provide large amounts of berries available for passerine birds during late summer (Parrish 1997; Suthers et al. 2000; Bonter et al. 2008). Individuals of this trophic guild concentrate their activity in the morning, consuming highly predictable items quickly to satisfy their energetic requirements and avoiding predation the risk present in this habitat by seeking cover and using it as a refuge to rest during the rest of the day, thus minimizing energy expenditure (MacLeod et al. 2005a, 2005b). The refuge effect is a refinement of the starvation–predation risk trade-off hypothesis that allows an animal to escape to a zero predation risk environment (MacLeod

et al. 2005a, 2005b), such as dense fashine (*C. diffusum*) at ground level and low-canopy firebush (*E. coccineum*) where flocks of Patagonian Sierra-finch were frequently found resting (McGehee and Eitniear 2007). Low predation risk at ground level is assumed in the absence of native terrestrial predators in the island (Rozzi et al. 2010) as opposed to the Northern Hemisphere where strong predation pressure can be exerted by wolves *Canis lupus* (Spaulding et al. 1998) and arctic foxes *Alopex lagopus* (Anthony et al. 2000; Liebezeit and Zack 2008). Using this diurnal foraging strategy, as a result of greatest food availability during the summer, the Patagonian Sierra-finch would gain mass during the first half of the day, thereby minimizing starvation risk (Bednekkoff and Houston 1994; McNamara et al. 1994; MacLeod et al. 2005a, 2005b). Few Patagonian Sierra-finches were found in the forest during the day in summer; they had a relatively constant activity pattern with an increase in the afternoon. The very low captures show that this habitat offers low food availability for this species, although it breeds both in dense forest and open shrubland.

The activity pattern became bimodal in winter in both habitats; thus, birds must balance food acquisition and

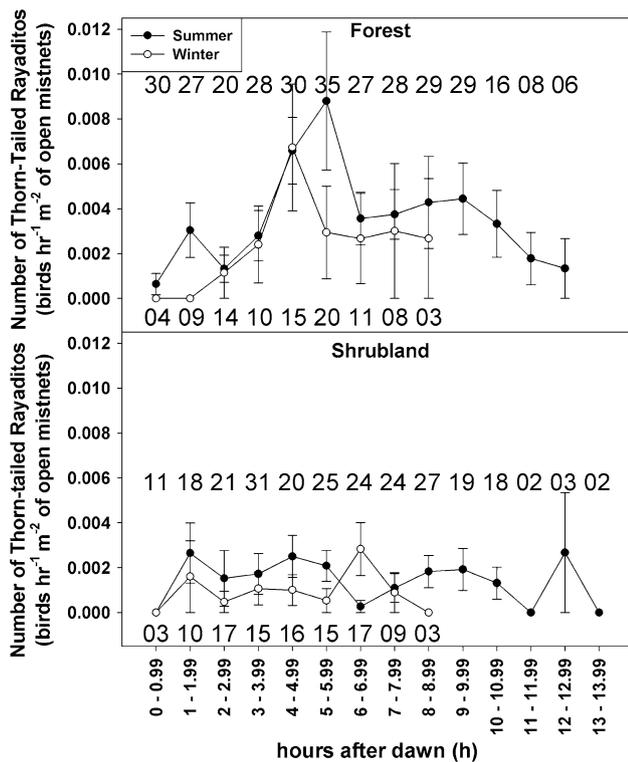


Fig. 3 Standardized daily captures of Thorn-tailed Rayadito (mean \pm SE of birds $\text{h}^{-1} \text{m}^{-2}$ of open mist-nets) in summer and winter, in forest and shrubland habitats on Omora Park, Navarino Island. Numbers within the box represent number of days sampled (top = summer, bottom = winter)

predator avoidance. Survival conditions during winter can be extreme for these birds, because weather conditions change quickly, food sources and potential refuges are covered by snow, especially in exposed habitats, and predation risk may be higher due to the dense shrub vegetation cover at ground level. The patterns found are consistent with the starvation–predation trade-off hypothesis postulated for winter seasons.

Thorn-tailed Rayadito

Theoretically, birds of the insectivorous trophic guild show daily activity patterns according to the activity of invertebrates. In the forest habitat of Navarino Island in summer, the Thorn-tailed Rayaditos displayed an activity pattern concentrated mainly around midday, when the highest temperature occurs with high activity and abundance also expected for invertebrates (Lewis and Taylor 1964; Avery and Krebs 1984; Low et al. 2008). For insectivorous birds, activity would be driven by availability of invertebrates predicted by the temperature-dependent food-availability hypothesis (Low et al. 2008) to maximize breeding success. During summer, both risks of predation and starvation are lower in the forest, because the canopy offers

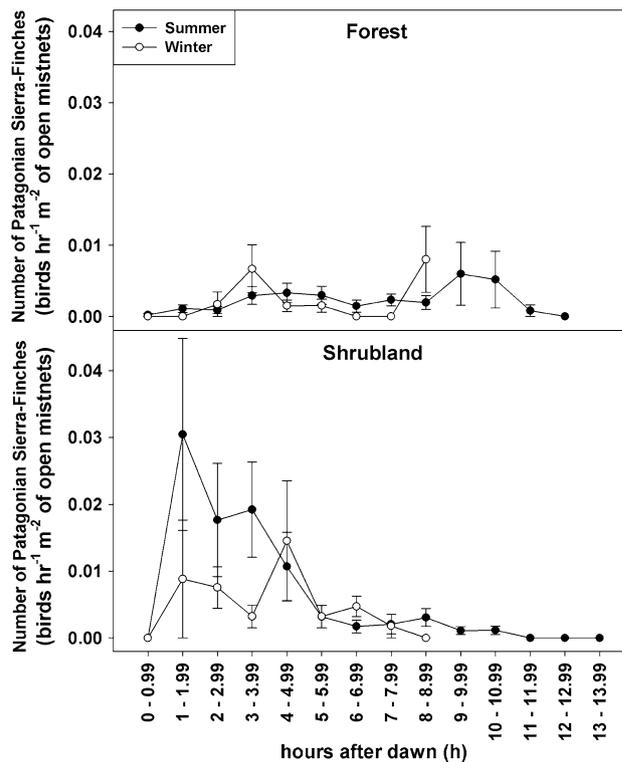


Fig. 4 Standardized daily captures of Patagonian Sierra-finch (mean \pm SE of birds $\text{h}^{-1} \text{m}^{-2}$ of open mist-nets) in summer and winter, in forest and shrubland habitats in Omora Park, Navarino Island. Refer to Fig. 3 for sample sizes

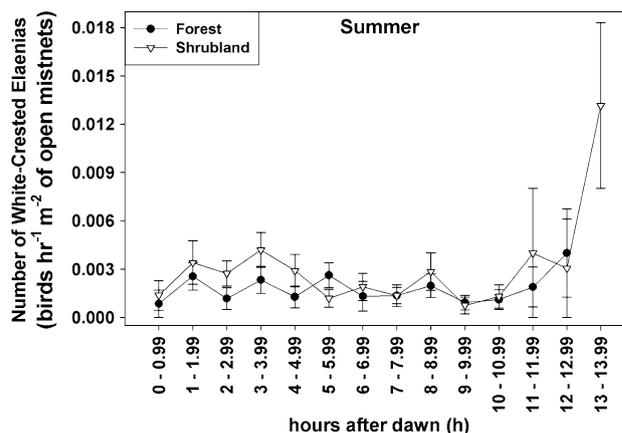


Fig. 5 Standardized daily captures of White-crested Elaenia (mean \pm SE of birds $\text{h}^{-1} \text{m}^{-2}$ of open mist-nets) in summer and winter, in forest and shrubland habitats in Omora Park, Navarino Island. Refer to Fig. 3 for sample sizes

protection against most diurnal raptors and insects are active throughout the day (Brown et al. 2007). This has been the evolutionary scenario (prior to the arrival of the North American mink) that could explain the unimodal pattern of activity in this habitat during summer, a pattern

that is closer to the ones described for other northern latitude forest regions (MacLeod et al. 2005a, 2005b; Low et al. 2008; Cresswell et al. 2009). In winter, the unimodal activity pattern in the forest habitat may be related to the shorter daylight time and solar radiation, which would force birds to consume food as quickly as possible to recover body mass lost at night, which must be recovered during the first daylight hours through intense foraging activity (Lees 1948). The forest still offers protection from predators because of the presence of evergreen tree species.

In the exposed shrubland habitat, activity changed from a trimodal pattern in summer to a bimodal pattern in winter; birds probably depend on the mobility of invertebrates but also avoid predation and starvation risks for their offspring and themselves (Low et al. 2008). The trimodal pattern in summer differs from other studies, which suggest that food availability determines activity pattern and mass gain during the breeding season (MacLeod et al. 2005a, 2005b; Low et al. 2008; Cresswell et al. 2009). Because parents when rearing nestlings often perform close to their energetic limit to maximize food delivery to their offspring, insectivorous birds in exposed habitats of Navarino Island would interrupt their foraging strategy by trading off food availability with starvation and predation risks. Birds even show a third peak of activity, possibly to gather the necessary amount of food to satisfy energetic demands and reduce predation risk. The trimodal pattern would be related to the lower number of captures throughout the day in shrubland, although it is not possible to assess the predation pressure parameter with the differences in food availability in either habitat with our data. The expected bimodal pattern occurred in shrubland in winter, where as in frugivorous birds activity would be affected by starvation and predation risks. The activity pattern described for Thorn-tailed Rayadito is similar to that found in other insectivorous species such as the Northern Wheatear *Oenanthe oenanthe* (Low et al. 2008).

White-crested Elaenia

Omnivorous birds that are able to exploit different dietary items can modify their food consumption pattern according to availability, predictability and food energetic contents to satisfy the energetic requirements of their offspring, as in the Blackbird *Turdus merula* (MacLeod et al. 2005a). White-crested Elaenias showed no significant differences between hours and habitats in summer. Although not significant, in the shrubland habitat, the pattern of activity was high during the first 5 h of the day, then declined and later showed a peak in the afternoon, after 15–16 h local time, reflecting that individuals may deal with the risk of predation during midday in this exposed habitat.

The amodal pattern found in the forest is consistent with the risk-spreading hypothesis (Houston et al. 1993), with birds spreading out their mass gain foraging throughout the entire day when mass-dependent effects and foraging interruptions are not important (MacLeod et al. 2005a, 2005b). Furthermore, this behavior would be favored by the ability to exploit different dietary items during the day the benign climatic conditions that occur during the warm season and the protection provided by the forest canopy against predators (Cimprich et al. 2005).

Species may be flexible in their foraging strategies, and thus, care must be taken when generalizing activity patterns, not only among species but also among populations of the same species (Low et al. 2008). Understanding the mechanisms underlying the avoidance of starvation and predation risks in passerine birds requires an analysis of the diurnal mass gain pattern (MacLeod et al. 2005a, 2005b). This would allow an assessment of the ability to manipulate the body mass gain during the day as a tool to improve survival in birds due to problems in resource availability (MacLeod et al. 2005a, 2005b) and would also allow assessment of the effects of temperature increases at a global scale on mass gain patterns of bird populations (Cresswell et al. 2009).

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