ORNITOLOGÍA NEOTROPICAL
(2017) 28: 191–199

ORIGINAL ARTICLE

Sociedad de Ornitología Neotropical

ARTHROPODS IN THE DIET OF THE BIRD ASSEMBLAGE FROM A FORESTED RURAL LANDSCAPE IN NORTHERN CHILOÉ ISLAND, CHILE: A QUANTITATIVE STUDY

César E. Muñoz[1,2] · Silvina Ippi[1,3] · Juan L. Celis-Diez[4] · Daniel Salinas[1] · Juan J. Armesto[1,2,5]

[1] Instituto de Ecología y Biodiversidad (IEB), 7800003 Santiago, Chile.

[2] Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, 8331150 Santiago, Chile.

[3] CRUB Universidad Nacional del Comahue-CONICET, Quintral 1250, 8400 Bariloche, Río Negro, Argentina.

[4] Escuela de Agronomía, Pontificia Universidad Católica de Valparaíso, Casilla 4-D, 2260000 Quillota, Chile.

[5] Cary Institute of Ecosystem Studies, Millbrook, New York 12545, USA.

E-mail: Juan L. Celis-Diez · juan.celis@pucv.cl

Abstract · Knowledge of bird diets is important to understand population fluctuations and the persistence of bird communities in changing landscapes. However, there is a general lack of quantitative information about the composition of bird diets at the community level in the Neotropics. Although consumption of fruits and seeds by birds has been well documented for forest ecosystems in southern South America, consumption of arthropods has received less attention, despite their relevance in bird diets. Here we describe and evaluate the presence and diversity of arthropods consumed by members of different dietary guilds of the avian community from temperate forests and rural landscapes in northern Chiloé Island, Chile (42°S). We estimated the proportion of arthropods consumed by all bird species captured using mist nests in a mixed rural landscape, and identified arthropods at the order level, based on remains contained in bird droppings. In addition, we estimated trophic diversity for those bird species with the highest number of samples. Arthropod remains were prevalent in dropping contents for nearly all sampled species (17 out of 18 captured species), indicating that arthropod consumption is broadly distributed in the avian assemblage. The insectivorous Chilean swallow (*Tachycineta leucopyga*) had the highest average number of arthropods per sample but the lowest arthropod diversity. On the contrary, the highest arthropod diversity in droppings corresponded to the insectivorous House Wren (*Troglodytes aedon*). The omnivorous species, Austral Blackbird (*Curaeus curaeus*) and White-crested Elaenia (*Elaenia albiceps*) consumed mainly Coleoptera. Finally, arthropod orders found in droppings varied among bird species from the same and between dietary guilds.

Resumen · Artrópodos en la dieta del ensamble de aves que habitan el paisaje rural del norte de la Isla de Chiloé, Chile
La información sobre los distintos componentes de la dieta de aves resulta relevante para entender las variaciones poblacionales y la subsistencia de comunidades ante la modificación del paisaje. Sin embargo, a la fecha, falta información cuantitativa sobre la composición de la dieta a nivel comunitario en el Neotrópico. A pesar de que el consumo de frutas y semillas por aves ha sido bien documentado para los ecosistemas templados del sur, el consumo de artrópodos ha recibido menos atención a pesar de su relevancia en la dieta de las aves. En este trabajo describimos y evaluamos la diversidad de artrópodos en la dieta de miembros de distintos gremios tróficos de la comunidad de aves de los bosques templados del sur de Sudamérica en el norte de la Isla de Chiloé, Chile (42°S). Para cada especie de ave capturada, estimamos la composición y la diversidad trófica de artrópodos en la dieta en base al análisis de heces. Registramos el consumo de artrópodos en 17 de las 18 especies capturadas, sugiriendo que el consumo de artrópodos está ampliamente distribuido en la comunidad de aves analizada. La Golondrina chilena (*Tachycineta leucopyga)*, especie insectívora, tuvo el mayor número de artrópodos promedio por muestra y, a la vez, la menor diversidad de órdenes de artrópodos en su dieta. Por el contrario, el Chercán (*Troglodytes aedon*), especie insectívora, registró la mayor diversidad de artrópodos consumidos. Entre las especies omnívoras, tanto el Tordo (*Curaeus curaeus*) como el Fio-fio (*Elaenia albiceps*), consumieron principalmente coleópteros. Finalmente, los órdenes de artrópodos registrados variaron entre aves pertenecientes al mismo gremio así como también entre distintos gremios tróficos.

Key words: Dietary guild · Insectivorous birds · Omnivorous birds · Trophic diversity

Receipt 14 July 2016 · First decision 6 October 2016 · Acceptance 9 August 2017 · Online publication 21 August 2017

Communicated by Kaspar Delhey

INTRODUCTION

Information on what birds eat in a given environment at a given time is important to understand the interactions that give rise to community composition and structure (MacArthur 1954), and to explain population fluctuations. Land cover changes, habitat loss, and fragmentation are important drivers of changes in populations and resource supplies (Willson et al. 1994, Milesi et al. 2002, Sekercioglu et al. 2002, Saunders et al. 1991). Hence, knowledge of bird diets is relevant to infer the response of local bird assemblages to changing landscapes. In this context, feeding habits can be best understood by examining bird positions within feeding guilds (e.g., Jaksic & Feinsinger 1991, Lopez de Casenave 2001).

A feeding guild has been defined as a group of species that exploit the same class of environmental resources in a similar way (Root 1967, Simberloff & Dayan 1991). The study of bird diets in the field, along with the identification of dietary guilds, can have ecological and conservation relevance. For example, understory insectivorous birds can be highly sensitive to habitat degradation and fragmentation, as habitat disruption strongly affects their food supplies (Sekercioglu et al. 2002, 2004; Powell et al. 2015). Additionally, when insectivorous birds are experimentally excluded from a given habitat, insect damage to plants increases (e.g., Koh 2008, Michel et al. 2014), with cascading effects on other ecological processes (Karp & Daily 2014). For example, in *Nothofagus pumilio* (Nothofagaceae) forests, bird exclusion increases foliar damage and decreases leaf size, which illustrates the indirect effects of birds on plants (Mazía et al. 2009).

Arthropods are an important component of the diversity of forest ecosystems (Mattson 1977), and despite their relevance in the diet of forest birds (Jaksic & Feinsinger 1991), there is a lack of quantitative information regarding the prevalence of arthropods in the diet of birds from southern temperate forests, particularly in rural areas subject to rapid land cover change. Anecdotal or quantitative information on the diet of single species (e.g., Correa et al. 1991, Estades 2001, Tomasevic 2004, Ojeda & Chazarreta 2006), as well as data about fruit consumption by temperate forest birds (Armesto et al. 1987, Amico & Aizen 2005, Orellana et al. 2014) are now available, however we still lack quantitative information on the prevalence of other food items, such as terrestrial arthropods (see Grigera 1976, 1982). In the present article, we describe and quantify the consumption of arthropods for 18 species of the 24 birds belonging to the terrestrial bird assemblage associated with a rural landscape (Díaz et al. 2005), characterized by a mixture of remnant forests fragments, shrubs and pastures, in northern Chiloé Island, Chile.

METHODS

Study area and data collection. Fieldwork was conducted in Senda Darwin Biological Station, located in northern Chiloé Island, Lake district, Chile, 10 km N of the city of Ancud (41°53'S, 73°39'W) (Carmona et al. 2010). We sampled birds from October 2010 to March 2012, as part of the long-term bird-monitoring program of the Chilean Long-Term Socio Ecological Research Network (LTSER-Network; see Carmona et al. 2010, Gaxiola et al. 2014). The landscape mosaic in this area includes riparian, secondary, and old-growth evergreen forest remnants (80–400 years old), surrounded by a matrix of secondary shrubland and anthropogenic pastures (Aravena et al. 2002).

Ten mist nets (6–12 m x 2.6 m; 30 and 60 mm mesh, respectively) were set up in three sites, separated from each other by about 600 m. Minimum distances among mist nets within each of the three sites varied between 6 to 42 m (mean ± SD = 19.89 ± 10.51). Mist nets were deployed along the edges between forest and shrubland, or in shrublands with presence of scattered trees, and remained open between sunrise and midday (see Ralph et al. 1996). The long-term bird-monitoring program involves capturing and banding birds for individual identification, following the procedures established by the Servicio Agrícola y Ganadero, Chile (i.e., National Agriculture and Livestock Service). Bird droppings were obtained from the bags where birds were kept until they were ringed, usually less than five minutes, as we tried to minimize handling time. This methodology allowed us to describe the food contents of bird guts with a particular focus on arthropods, for comparison with previous research in southern Chile (e.g., Brown et al. 2007). The procedures did not seem to harm the birds (Carlisle & Holberton 2006).

Single droppings from each individual bird were stored in paper bags at room temperature and then taken to the lab for analysis. To separate body remains of arthropods, droppings were dissolved in 70% ethanol (Ralph et al. 1985). Body parts were examined under a binocular microscope (Nikon model SMZ800N) to assign arthropods to taxonomic categories and to estimate the number of arthropods in each dropping. To aid in the taxonomic identification of arthropods, remains were photographed with a Nikon D300 camera connected to the microscope. Whenever possible, depending on the remaining parts, arthropods present in droppings were identified to order, using available taxonomic keys (Borror et al. 1989, Peña 2006). In the case of the vegetal components of droppings, such as seeds and plant tissues, these were identified only as "plant material." Some of this vegetable material was highly degraded, making identification uncertain, and hence plant material was classified into subcategories.

Data analyses. For each bird dropping, we recorded i) the taxonomic order of every arthropod prey, ii) the number of arthropod orders present in each dropping, and iii) the total number of arthropods identifiable in each dropping. To estimate the number of individual arthropods consumed, we followed the method proposed by Rosenberg & Cooper (1990), which consists of counting arthropod remains in each dropping, and estimating from this count the minimum number of arthropods ingested. Additionally, we compared the proportion of arthropod orders found in droppings collected for every bird species.

To compare the diversity of arthropods consumed among bird species, we selected species having at least more than three droppings with arthropod remains and with more than 50% of the remains identifiable at the order level (Table 1). This procedure produced a subsample of seven bird species for comparisons of arthropod diversity. For each species in this subsample, we estimated the diversity of arthropod orders present in each dropping using the Brillouin (1965) formula (H_B), which is a modified Shannon's index (Hurtubia 1973, Grigera 1982). This index considers the total number of droppings as a finite sample:

$$H_B = (1/N) (\ln N! - \Sigma \ln Ni!),$$

where N is the number of different arthropod orders in the dropping and Ni is the number of arthropods identified in each dropping.

After calculating H_B value for each dropping, we estimated an average diversity of arthropod prey items (mean H_B) for each of the seven bird species, considering the entire sample of droppings with identifiable arthropods for that species. In addition, we calculated the accumulated trophic diversity (H_BK_z), using the following procedure: For each of the seven bird species, we randomly selected an "initial dropping" (i.e., arbitrarily termed dropping number 1) and calculated its H_B. We then added a second dropping, and calculated H_B again, now pooling droppings 1 and 2. We continued to do this until we completed the total sample of droppings for the selected bird species, thus obtaining its accumulated trophic diversity (Hurtubia 1973). This information provided us with a more precise estimate of trophic diversity for each species when compared with the mean H_B, since considering the average does not represent the entire trophic diversity of the sampled individuals, and each dropping potentially contains a nonrandom sample of preys (Pielou 1975).

Finally, for each species we plotted its accumulated trophic diversity (H_BK_z) *vs.* the total number of droppings with identifiable arthropod orders (K), thus performing a rarefaction analysis (see Supplementary material; Hurtubia 1973).

RESULTS

Data description. Overall, we analyzed 204 droppings from 176 different individual birds, including 18 species from the rural landscape mosaic of forests and shrublands, belonging to 12 families (Table 1). Based on the existing literature for the study region (Jaksic & Feinsinger 1991; Rozzi et al. 1996a, 1996b; Amico & Aizen 2005), species were classified as belonging to the insectivorous (n = 8, 44.4%), omnivorous (n = 7, 38.9%), and granivorous (n = 3, 16.7%) guilds (Table 1). Considering all droppings in our sample, 73% were obtained during the Austral breeding season (October to February), and the remaining during the Austral fall and winter (March to August) when birds were less active. Two bird species, White-crested Elaenia (*Elaenia albiceps*) and Thorn-tailed Rayadito (*Aphrastura spinicauda)* were the most common birds captured in mist nets (n = 51 and 49, respectively). These two bird species accounted for 25% and 24% of all droppings collected, respectively, and for 20.6% and 23.7% of the droppings containing identifiable arthropod remains (Table 1). The Chilean Swallow (*Tachycineta leucopyga*) presented the highest average number of individual arthropods per dropping (13.6), followed by the Austral Blackbird (*Curaeus curaeus)* with four arthropods per sample (Table 1).

Only samples obtained from two bird species belonging to the granivorous guild contained arthropod remains; these were Black-chinned Siskin (*Spinus barbatus*) and Patagonian Sierra-finch (*Phrygilus patagonicus)*. However, the poor quality of invertebrate remains in their droppings made it impossible to identify arthropod orders (Table 1).

Arthropod diversity in the birds' diet. Overall, seven orders of Arthropoda were identified from droppings collected for the sampled bird assemblage in rural landscapes. These include the orders Coleoptera, Orthoptera, Hymenoptera, Hemiptera, Lepidoptera, Araneae, and Plecoptera (Table 2). Seven bird species had more than three dropping with arthropod remains that were identifiable at the order level (Table 3). These seven bird species included two omnivores and five insectivores (Table 3). Droppings of *E. albiceps* and *C. curaeus,* the two omnivores, contained 76% and 100% arthropods, respectively (Table 1). Droppings of insectivorous birds, *T. leucopyga*, House Wren (*Troglodytes aedon*), Des Murs's Wiretail (*Sylviorthorhynchus desmursii*), *A. spinicauda*, and Tufted Tit-Tyrant (*Anairetes parulus*) contained 98–100% arthropods (Table 1). Flattening of the rarefaction curves (see Supplementary material) indicated that for six out of seven bird species, the diversity of arthropod preys was well represented in the sample. The rarefaction curve did not reach an asymptote for *A. parulus* and hence the diversity of arthropod orders will not be discussed further for this species.

The orders of arthropods found in droppings varied among bird species that were classified in the same guild, and also between guilds. For example, within the insectivorous guild, *A. spinicauda* preyed primarily on Aranae and Hymenoptera, while other insectivorous birds, such as *T. leucopyga* and *T. aedon*, primarily consumed Hemiptera, and *A. parulus* preyed on Coleoptera. Among the omnivorous species, *C. curaeus* and *E. albiceps* mainly consumed Coleoptera (Table 2).

The highest (1.36) and the lowest (0.89) accumulated diversity of arthropods (H_BK_z) occurred in droppings from *T. aedon* and *T. leucopyga*, respectively,

Table 1. Composition of arthropod prey from droppings collected from 18 bird species captured with mist nets in the rural landscape of Senda Darwin Biological Station, Chiloé Island, Lake district, Chile, between October 2010 and March 2012. Dietary guild assignments are based on Jaksic & Feisinger (1991), Rozzi et al. (1996a, 1996b), and Amico & Aizen (2005). N is the total number of droppings per species and K is the number of droppings with identifiable arthropods remains (Order level). IN = Insectivorous, OM = Omnivorous, GR = Granivorous. *uncertainty in the identification of plant material.

Bird species	Family	Diet guild	Droppings with arthropods (% [N])	Droppings with plant material (% [N])	Mean number of arthropods per dropping (K)
Veniliornis lignarius	Picidae	IN	100.0 (1)	0.0 (1)	6.0 (1)
Sephanoides sephaniodes	Trochilidae	OM	100.0 (1)	0.0 (1)	2.0 (1)
Aphrastura spinicauda	Furnariidae	IN	98.0 (49)	4.1 (49)	1.4 (31)
Sylviorthorhynchus desmursii	Furnariidae	IN	100.0 (13)	30.8 (13)	3.2 (11)
Leptasthenura aegithaloides	Furnariidae	IN	100.0 (3)	33.3 (3)*	2.0 (3)
Tachycineta leucopyga	Hirundinidae	IN	100.0 (16)	12.5 (16)*	13.6 (16)
Troglodytes aedon	Troglodytidae	IN	100.0 (10)	20.0 (10)	3.9 (10)
Elaenia albiceps	Tyrannidae	OM	76.5 (51)	60.8 (51)	1.3 (27)
Xolmis pyrope	Tyrannidae	OM	50.0 (6)	50.0 (6)	1.2 (2)
Anairetes parulus	Tyrannidae	IN	100.0 (20)	5.0 (20)	1.8 (16)
Scelorchilus rubecula	Rhynocryptidae	OM	100.0 (1)	100.0 (1)	1.0 (1)
Pteroptochos tarnii	Rhynocryptidae	OM	100.0 (1)	0.0 (1)	8.0 (1)
Scytalopus magellanicus	Rhynocryptidae	IN	100.0 (2)	0.0 (2)	1.5 (2)
Spinus barbatus	Fringillidae	GR	33.3 (3)	100.0 (3)	0.0 (0)
Sicalis luteola	Thraupidae	GR	0.0 (1)	100.0 (1)	0.0 (0)
Turdus falcklandii	Turdidae	OM	35.3 (17)	94.1 (17)	0.4 (4)
Phrygilus patagonicus	Thraupidae	GR	50.0 (2)	100.9 (2)	0.0 (0)
Curaeus curaeus	Icteridae	OM	100.0 (7)	28.6 (7)	4.1 (5)

both members of the insectivorous guild (Table 3). These values were similar to the highest and lowest diversity values recorded for the two members of the omnivorous guild, 1.20 for *E. albiceps* and 0.95 for *C. curaeus*. The two species with the lowest accumulated arthropod diversity (H_BK_Z) in their diets, *T. leucopyga* and *C. curaeus*, have traditionally been classified in separate guilds (see Table 1); insectivores and omnivores, respectively (Jaksic & Feinsinger 1991, Rozzi et al. 1996b). For these two species, more than 60% of the droppings contained remains of a single arthropod order, Hemiptera in the case of *T. leucopyga* and Coleoptera in the case of *C. curaeus* (Table 2).

DISCUSSION

We provide evidence here that 17 bird species captured in mist nets consumed a large number and wide variety of arthropods, including at least seven arthropod orders. The bird assemblages captured correspond to 75% of the bird diversity recorded by Díaz et al. (2005) in the rural environment of Chiloé. The sample of arthropods found in droppings accounted for 63.6% of the main arthropod orders described in a survey for southern South American temperate forests (Díaz et al. 2012). Moreover, arthropods were recorded in droppings from the two granivorous bird species captured in mist nets, which agrees with observations made by Escobar & Vukasovic (2001) for *S. barbatus*.

Previous studies of birds in South American temperate forests had revealed that the majority of species are dietary generalists (McGehee 2007). Examples include the Fire-eyed Diucon (*Xolmis pyrope)* and *E. albiceps*, both members of the Tyrannidae, which are usually assigned to the insectivorous guild but can also be major frugivores in South American temperate forests (Armesto et al. 1987, Amico & Aizen 2005, Bravo et al. 2015), in addition to frequent nectar feeders in the case of *E. albiceps* (Smith-Ramírez & Armesto 1998).

The order Coleoptera is the most abundant group of arthropods in terms of biomass and diversity in remnant forests from the study area (Arias et al. 2008, Díaz et al. 2012). Our results showed that *E.*

Table 2. Proportion of different arthropod orders identified in droppings of birds captured with mist nets in the forest-scrubland mosaic of the rural landscape in Senda Darwin Biological Field Station, Chiloé Island, Lake district, Chile. Dietary guild assignments are based on Jaksic & Feisinger (1991), Rozzi et al. (1996a, 1996b), and Amico & Aizen (2005).

Diet guild	Species	Proportion of arthropods						
		Coleoptera	**Hymenoptera**	**Hemiptera**	**Orthoptera**	**Lepidoptera**	**Araneae**	**Plecoptera**
Insectivorous	*Veniliornis lignarius*	0.33	0.50	0	0	0	0.17	0
	Aphrastura spinicauda	0.03	0.29	0.01	0.04	0.21	0.41	0
	Sylviorthorhynchus desmursii	0.10	0.48	0.02	0.14	0	0.26	0
	Leptasthenura aegithaloides	0	0	0	0.67	0	0.33	0
	Tachycineta leucopyga	0.23	0.11	0.64	0	0	0.01	0.005
	Troglodytes aedon	0.15	0.18	0.36	0.18	0	0.13	0
	Anairetes parulus	0.40	0.20	0.20	0.06	0.03	0.11	0
	Scytalopus magellanicus	0	0.33	0	0	0	0.67	0
Omnivorous	*Sephanoides sephaniodes*	0.50	0	0	0	0	0.50	0
	Elaenia albiceps	0.38	0.24	0	0	0.29	0.09	0
	Xolmis pyrope	0.33	0.33	0	0	0.33	0	0
	Scelorchilus rubecula	0	0	0	1	0	0	0
	Pteroptochos tarnii	0.25	0	0	0.63	0	0.13	0
	Turdus falcklandii	0.57	0	0	0.14	0.29	0	0
	Curaeus curaeus	0.62	0.10	0	0.17	0.03	0.07	0

Table 3. Arthropod diversity in droppings of the seven bird species with more than three droppings containing arthropods, and > 50% of arthropod remains identifiable at the order level (see methods), captured using mist nets in the rural landscape of Senda Darwin Biological Field Station, Chiloé Island, Lake district, Chile. Dietary guild assignments are based on Jaksic & Feisinger (1991), Rozzi et al. (1996a, 1996b), and Amico & Aizen (2005).

Diet guild	Species	Number of droppings	Diversity index (H_B)	
			Mean H_B	H_BK_z (accumulated)
Insectivorous	*Tachycineta leucopyga*	16	0.39	0.89
	Aphrastura spinicauda	31	0.14	1.24
	Sylviorthorhynchus desmursii	11	0.22	1.15
	Troglodytes aedon	10	0.39	1.36
	Anairetes parulus	16	0.21	1.31
Omnivorous	*Elaenia albiceps*	27	0.08	1.20
	Curaeus curaeus	5	0.45	0.95

albiceps and *C. curaeus* consumed a higher proportion of Coleoptera than any other arthropod order, and both species are classified as omnivores according to guild assignments (Jaksic & Feinsinger 1991, Rozzi et al. 1996b). In fact, *E. albiceps* showed the same feeding habit in forests from Nahuel Huapi National Park, Argentina (Grigera 1982). Particularly, in the case of *C. curaeus*, more than 60% of droppings contained coleopteran remains. Additionally, *A. parulus* consumed a higher proportion (40%) of Coleoptera than any other bird species included in the same insectivorous guild (range, 3–23%). In contrast, droppings from the aerial insectivore *T. leucopyga* contained 64% remains of Hemiptera. Our analysis indicates that birds consume a broad diversity of arthropods and that arthropods constitute a high percentage of the diet of omnivores, highlighting their relevance in the study area.

The diversity of arthropods (H_BK_Z) present in droppings of seven bird species analyzed in greater detail showed slight differences. The species showing the lowest value of trophic diversity was the insectivore *T. leucopyga*, which could be explained by a greater foraging specialization, as it has morphological adaptations that improve capture and consumption of insects in flight. Such adaptations include high maneuverability and broad bills with modified bristle feathers (Turner 2004). Specialization on a single group of arthropods had previously been reported for another species of *Tachycineta*, the Violet-green Swallow (*T. thalassina*) in Oregon, U.S.A. (Garlick et al. 2014). Alternatively, specialization on a single group of arthropod preys can also be a consequence of the greater relative abundance of this prey item in the environment. In the latter case, the bird species would have an opportunistic feeding behavior (Mengelkoch et al. 2004).

The insectivore *T. aedon* presented the highest arthropod diversity in its droppings. This result is consistent with findings by Guinan & Sealy (1987) in rural sites of Manitoba, Canada, where wrens consumed most of the available invertebrate taxa. In our study area, *T. aedon* occurs exclusively in shrublands and forest edges (Rozzi et al. 1996a, Díaz et al. 2005), which are highly heterogeneous habitats where a great diversity of arthropods can be found.

Avian dietary composition often exhibits regional and temporal variability in a single bird species (Ainley et al. 1996). An example of this in southern temperate rainforests is the case of nectar consumption from flowers of *Embothrium coccineum* (Proteaceae) by *E. albiceps*, which varies geographically between the western and eastern side of the Andes, in Chile and Argentina, as well as across seasons (Smith-Ramírez & Armesto 1998, Chalcoff et al. 2012). The frequency of arthropods in the diet of this species also varies. Using the same data collection methods, Brown et al. (2007) found that Diptera was the most common prey order in sub-Antarctic forests of the Cape Horn Biosphere Reserve at 55°S; however, this prey was absent from individuals of the same species sampled in the rural environments of Chiloé Island (present work). Such regional differences in prey consumption might depend on behavioral differences, as well as plastic response to the availability of different food sources, and could explain differences in the dietary guild assignment, depending on diverse studies (see Jaksic & Feinsinger 1991; Rozzi et al. 1996a, 1996b; Amico & Aizen 2005, Vergara & Armesto 2009).

In North American temperate forests, mass consumption of arthropods by birds often follows spring outbreaks (Holmes & Schultz 1988, Jaksic & Feinsinger 1991). During these insect outbreaks, Lepidoptera and Hymenoptera larvae are heavily consumed by numerous bird species (Jaksic & Feinsinger 1991). Insect outbreaks seem to be less determinant of feeding behaviors in southern temperate forests as they are less frequently reported; however, they are not absent. Infrequently, outbreaks of *Ormiscodes amphi-*

mone (Lepidopterae) have been reported for winter-deciduous, sub-Antarctic *Nothofagus pumilio* forests (Paritsis et al. 2009), although their impact on bird diet is unknown. The two species of evergreen *Nothofagu*s trees that occur in forests of Chiloé Island, *N. nitida* and *N. dombeyi*, have overlapping distributions with at least two other species of *Ormiscodes*, *O. cinnamomea* and *O. joiceyi* (Angulo et al. 2004). Considering the omnivore *X. pyrope*, Lepidoptera occurred in 33% of its droppings, and one of us (JLC-D) observed feeding on *Ormiscodes* caterpillars in Chiloé Island. Moreover, we found evidence of significant consumption of Lepidoptera by two other bird species classified as omnivores, the Austral Thrush (*Turdus falcklandii*) and *E. albiceps*, and by one insectivorous bird species, *A. spinicauda*. In this context, we suggest that both omnivores and insectivores could play important roles in controlling moth population outbreaks in Austral forests. Although bird predation on *Ormiscodes* and other herbivorous larvae does not occur regularly (Paritsis et al. 2012), experimental studies that have excluded birds from Patagonian *Nothofagus* forests have shown increased damage by insect herbivores (Mazía et al. 2009), suggesting that birds could reduce or control insect outbreaks.

Finally, temperate rain forests, especially in northern Chiloé Island, have been extensively cleared and fragmented throughout the 20th century (Willson et al. 1994, Echeverría et al. 2007). More recently, native forests in the study area have increasingly been replaced by exotic eucalyptus plantations (Armesto et al. 2009). Recent studies in California have revealed that arthropod abundances and diversity were negatively affected by the presence of large eucalyptus plantations in rural landscapes (Fork et al. 2015), affecting resource supplies for avian communities feeding on arthropods. Preliminary data from our study area show that arthropod diversity decreases along the habitat gradient from forest remnants to secondary shrublands, and to anthropogenic pastures (JLC-D unpubl. data). Such changes in arthropod assemblages, associated with land cover change, can be detrimental to bird communities in rural landscapes. Consequently, further studies of temporal variation in arthropod presence in bird diets, as well as the impacts of bird exclusion from forested landscapes, are needed to assess the impacts of the loss of native forest cover and its substitution by eucalyptus plantation on rural bird populations and communities.

ACKNOWLEDGMENTS

We thank S. Abades for assistance with data analysis. A. Ugarte kindly helped with arthropod identification. The study was supported by Iniciativa Científica Milenio (ICM), grants P05-002, and CONICYT grant PFB-23, both to the Institute of Ecology and Biodiversity (IEB), and by a Fondecyt grant 3130672 and PUCV-DI 039364/2016 to JLC. This research complies with current laws of Chile under permit nos. 299 and 4842, respectively, by Servicio Agrícola y Ganadero. We greatly appreciate the comments made by the editor and two anonymous reviewers that substantially im-proved the manuscript. This is a contribution to the Research Programs of Senda Darwin Biological Station and the Chilean Long-Term Socio-Ecological Research Network (LTSER-Chile) supported by the IEB.

REFERENCES

Ainley, DG, LB Spear, SG Allen & CA Ribic (1996) Temporal and spatial patterns in the diet of the Common Murre in California waters. *The Condor* 98: 691–705.

Angulo, AO, C Lemaire & TS Olivares (2004) Catálogo crítico e ilustrado de las especies de la familia Saturniidae en Chile (Lepidoptera: Saturniidae). *Gayana* 68: 20–42.

Amico, GC & MA Aizen (2005) Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién?. *Ecología Austral* 15: 89–100.

Aravena, JC, MR Carmona, CA Pérez & JJ Armesto (2002) Changes in tree species richness, stand structures and soil properties in a successional chronosequence in northern Chiloé Island, Chile. *Revista Chilena de Historia Natural* 75: 339–360.

Arias, ET, BJ Richardson & M Elgueta (2008) The canopy beetle faunas of Gondwanan element trees in Chilean temperate rain forest. *Journal of Biogeography* 35: 914–925.

Armesto, JJ, R Rozzi, P Miranda & C Sabag (1987) Plant/frugivore interactions in South American temperate forests. *Revista Chilena de Historia Natural* 60: 321–336.

Armesto, JJ, M Carmona, JL Celis-Diez, I Díaz, A Gaxiola, AC Gutiérrez, M Núñez-Avila, C Pérez, R Rozzi & C Smith-Ramírez (2009) Old-growth temperate rainforests of South America: conservation, plant–animal interactions, and baseline biogeochemical processes. Pp 367–390 *in* Wirth, C, M Heimann & G Gleixner (eds). *Ecosystem functioning of old-growth forest*. Springer Verlag, Heidelberg, Germany.

Borror, DJ, CA Triplehorn & NF Johnson (1989) *An introduction to the study of insects*. 6th ed. Saunders College Publishing, Philadelphia, Pennsylvania, USA.

Bravo, SP, VR Cueto & GC Amico (2015) Do animal-plant interactions influence the spatial distribution of *Aristotelia chilensis* shrubs in temperate forests of southern South America? *Plant Ecology* 216: 383–394.

Brillouin, L (1965) *Science and information theory*. Academic Press, New York, New York, USA.

Brown, CE, CB Anderson, S Ippi, MF Sherriffs, R Charlin, S McGehee & R Rozzi (2007) The autoecology of the Fío-fío (*Elaenia albiceps* Lafresnaye & D'Orbigny) in subantartic forest of the Cape Horn Biosphere Reserve, Chile. *Anales del Instituto de la Patagonia (Chile)* 35: 29–40.

Carlisle, JD & RL Holberton (2006) Relative efficiency of fecal versus regurgitated samples for assessing diet and the deleterious effects of a tartar emetic on migratory birds. *Journal of Field Ornithology* 77: 126–135.

Carmona, MR, JC Aravena, MA Bustamante-Sánchez, JL Celis-Diez, A Charrier, I Díaz, J Díaz-Forestier, MF Díaz, A Gaxiola, AG Gutiérrez, C Hernández-Pellicer, S Ippi, R Jaña-Prado, P Jara-Arancio, J Jimenez, D Manuschevich, P Necochea, M Nuñez-Avila, C Papic, C Pérez, F Pérez, S Reid, L Rojas, B Salgado, C Smith-Ramírez, A Troncoso, RA Vásquez, MF Willson, R Rozzi & JJ Armesto (2010) Estación Biológica Senda Darwin: investigación ecológica de largo plazo en la interfase ciencia-sociedad. *Revista Chilena de Historia Natural* 83: 113–142.

Chalcoff, VR, MA Aizen & C Ezcurra (2012) Erosion of a pollination mutualism along and environment gradient in a south Andean treelet, *Embothrium coccineum* (Proteaceae). *Oikos* 121: 471–480.

Correa, A, JJ Armesto, RP Schlatter, R Rozzi & JC Torres-Mura (1991) La dieta del Chucao (*Scelorchilus rubecola*), un passeriforme terrícola endémico del bosque templado húmedo de Sudamérica austral. *Revista Chilena de Historia Natural* 63: 197–202.

Díaz, IA, JJ Armesto, S Reid, KE Sieving & MF Willson (2005) Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biological Conservation* 123: 91–101.

Díaz, IA, K Sieving, M Peña-Foxon & JJ Armesto (2012) A field experiment links forest structure and biodiversity: epiphytes enhance canopy invertebrates in Chilean forests. *Ecosphere* 3: 10.1890/ES11-00168.1.

Echeverría, C, AC Newton, A Lara, JM Rey Benayas & DA Coomes (2007) Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. *Global Ecology and Biogeography* 16: 426–439.

Escobar, MAH & MA Vukasovic (2001) Depredación del Jilguero (*Carduelis barbata*) sobre larvas de *Phoracantha* sp. (Coleoptera: Cerambicidae). *Boletín Chileno de Ornitología* 8: 21–23.

Estades, CF (2001) Consumo de semillas de pino (*Pinus radiata*) por Rayaditos (*Aphrastura spinicauda*). *Boletín Chileno de Ornitología* 8: 30–31.

Fork, S, A Woolfolk, A Akhavan, E Van Dyke, S Murphy, B Candiloro, T Newberry, S Schreiban, J Salisburry & K Wasson (2015) Biodiversity effects and rates of spread of nonnative eucalypt woodlands in central California. *Ecological Applications* 25: 2306–2319.

Garlick, NW, GN Newberry & JW Rivers (2014) An assessment of nestling diet composition in the Violet-green Swallow (*Tachycineta thalassina*). *Northwest Science* 88: 49–54.

Gaxiola A, JL Celis-Diez, R Rozzi & J Gutiérrez (2014) Estudios socio-ecológicos de largo plazo en los sitios fundadores de la red RSELP-Chile: desafíos y oportunidades para el futuro. *Bosque* 35: 421–428.

Grigera, D (1976) Ecología alimentaria de cuatro especies de Fringillidae frecuentes en la zona del Nahuel Huapi. *Physis sección C* 35: 279–292.

Grigera, D (1982) Ecología alimentaria de algunas passeriformes insectívoras frecuentes en los alrededores de S. C. de Bariloche. *Ecología* 7: 67–84.

Guinan, DM & SG Sealy (1987) Diet of House Wens (*Troglodytes aedon*) and the abundance of the invertebrate preys in the dune-ridge forest, Delta Marsh, Manitoba. *Canadian Journal of Zoology* 65: 1587–1596.

Koh, LP (2008) Birds defend oil palms from herbivorous insects. *Ecological Applications* 18: 821–825.

Holmes, RT & JC Schultz (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology* 66: 720–728.

Hurtubia, J (1973) Trophic diversity measurement in sympatric predatory species. *Ecology* 54: 885–890.

Jaksic, FM & P Feinsinger (1991) Bird assemblages in temperate forest of North and South America: a comparison of diversity, dynamics, guild structure, and resourse use. *Revista Chilena de Historia Natural* 64: 491–510.

Karp, DS & GC Daily (2014) Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95: 1065–1074.

Lopez de Casenave, J (2001) *Estructura gremial y organización de un ensamble de aves del desierto del Monte.* Tesis doctoral, Univ. de Buenos Aires, Buenos Aires, Argentina.

MacArthur, R (1954) On the relative abundance of species. *The American Naturalist* 94: 25–36.

Mattson, WJ (1977) *The role of arthropods in forest ecosystems*. Springer-Verlag, New York, New York, USA.

Mazía, CN, EJ Chaneton, T Kitzberger & LA Garibaldi (2009) Variable strength of top-down effects in *Nothofagus* forests: bird predation and insect herbivory during an ENSO event. *Austral Ecology* 34: 359–367.

McGehee, S (2007) Consumption of leñadura (*Maytenus magellanica*) seeds by three primarily insectivorous bird species. *Anales del Institutode la Patagonia (Chile)* 35: 71–73.

Mengelkoch, JM, GJ Niemi & RR Regal (2004) Diet of the nestling Tree Swallow. *The Condor* 106: 423–429.

Michel, NL, TW Sherry & WP Carson (2014) The omnivorous collared peccary negates an insectivore-generated trophic cascade in Costa Rican wet tropical forest understorey. *Journal of Tropical Ecology* 30: 1–11.

Milesi, FA, L Marone, J Lopez de Casenave, VR Cueto & ET Mezquida (2002) Gremios de manejo como indicadores de las condiciones del ambiente: un estudio de caso con aves y perturbaciones del hábitat en el Monte central, Argentina. *Ecología Austral* 12: 149–161.

Ojeda, VS & ML Chazarreta (2006) Provisioning of Magellanic Woodpecker (*Campephilus magellanicus*) nestling with vertebrate prey. *The Wilson Journal of Ornithology* 118: 251–254.

Orellana, JL, C Smith-Ramírez, JR Rau, S Sade, A Gantz & CE Valdivia (2014) Phenological synchrony between the Austral Thrush *Turdus falcklandii* (Passeriformes: Turdidae) and its food resources within forests and prairies in southern Chile. *Revista Chilena de Historia Natural* 87: 11, doi:10.1186/s40693-014-0011-5

Paritsis, J, TT Veblen & T Kitzberger (2009) Biodiversity effects and rates of spread of nonnative eucalypt woodlands in central California. *Canadian Journal of Forest Research* 39: 1617–1629.

Paritsis, J, C Quintero, T Kitzberger & TT Veblen (2012) Mortality of the outbreak defoliator *Ormiscodes amphimone* (Lepidoptera: Saturniidae) caused by natural enemies in northwestern Patagonia Argentina. *Revista Chilena de Historia Natural* 85: 113–122.

Peña, LE (2006) *Introducción a los insectos de Chile*. 7º ed. Editorial Universitaria, Santiago, Chile.

Pielou, EC (1975) *Ecological diversity.* John Wiley & Sons, New York, New York, USA.

Powell, LL, NJ Cordeiro & JA Stratford (2015) Ecology and conservation of avian insectivores of the rainforest understory: a pantropical perspective. *Biological Conservation* 188: 1–10.

Ralph, CP, SE Nagata & CJ Ralph (1985) Analysis of droppings to describe diets of small birds. *Journal of Field Ornithology* 56: 165–174.

Ralph, CJ, GR Geupel, P Pyle, TE Martin, DF DeSante & B Milá (1996) *Manual de métodos de campo para el monitoreo de aves terrestres.* General Technical Report PSW-GTR-159. U.S. Department of Agriculture, Forest Service, Albany, California, USA.

Root, RB (1967) The niche exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs* 37: 317–350.

Rozzi, R, JJ Armesto, A Correa, JC Torres-Mura & M Sallaberry (1996a) Avifauna de bosques primarios templados en islas deshabitadas del archipiélago de Chiloé, Chile. *Revista Chilena de Historia Natural* 69: 125–139.

Rozzi, R, D Martínez, MF Willson & C Sabag (1996b) Avifauna de los bosques templados de Sudamérica. Pp 135–152 *in* Armesto, JJ, C Villagrán & MT Kalin (eds). *Ecología de los bosques nativos de Chile*. Editorial Universitaria, Santiago, Chile.

Saunders, DA, RJ Hobbs & CR Margules (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18–32.

Sekercioglu, CH, PR Ehrlich, GC Daily, D Aygen, D Goehring & RF Sandi (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences (USA)* 99: 263–267.

Sekercioglu, CH, GC Daily & PR Ehrlich (2004) Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences (USA)* 101: 18042–18047.

Simberloff, D & T Dayan (1991) The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* 22: 115–143.

Smith-Ramirez, C & JJ Armesto (1998) Nectarivoría y polinización por aves en *Embothrium coccineum* (Proteaceae) en el bosque templado del sur de Chile. *Revista Chilena de Historia Natural* 71: 51–63.

Tomasevic, JA (2004) Consumo de semillas de pino (*Pinus radiata*) por Jilgueros (*Carduelis barbata*) en la zona de Constitución, Centro-Sur de Chile. *Boletín Chileno de Ornitología* 10: 18–19.

Turner, AK (2004) Family Hirundinidae (swallows and martins). Pp 602–685 *in* del Hoyo, J, A Elliott & DA Christie (eds). *Handbook of the birds of the world*. *Volume 9: Cotingas to pipits and wagtails.* Lynx Edicions, Barcelona, Spain.

Willson, MF, TL de Santo, C Sabag & JJ Armesto (1994) Avian communities of fragmented south-temperate rainforests in Chile. *Conservation Biology* 8: 508–520.