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Quantity component of the effectiveness of seed dispersal by birds in the temperate rainforest of Chiloé, Chile

Componente cuantitativo de la efectividad de dispersión de semillas por aves en el bosque templado de Chiloé, Chile

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SUMMARY

The quantity component of the disperser effectiveness of resident birds during the autumn-winter period has not yet been detailed in temperate rainforests of South America. In this study, the potentially frugivorous bird species in the temperate rainforests of southern Chile during the Austral autumn-winter were identified, and the quantity component of the disperser effectiveness of the birds (number of visits and number of seeds dispersed per hour) were evaluated for the tree species *Luma apiculata* and *Aextoxicon punctatum*. During the peak fruiting period of the both *L. apiculata* and *A. punctatum* 10 and 14, respectively, individuals of each species were monitored for a total of 10 days. Results show that four bird species consumed *L. apiculata* fruits. The birds *Turdus falcklandii* were the main fruit consumers (72 % of the visits), with a mean rate of 2.2 visits per hour and 49.2 seeds dispersed per hour. The frugivorous species visiting *A. punctatum* were *T. falcklandii* (97 % of the visits) and *Columba araucana* (3 %). In *A. punctatum, T. falcklandii* consumed 65 fruits in 35 visits, with a mean rate of 1.8 visits per hour and 3.4 seeds dispersed per hour. In conclusion, *T. falcklandii* would be the most effective seed disperser bird for autumn-winter fruiting trees in the Chiloé rainforest of our study site, at least with regard to the quantitative component of disperser effectiveness.

Key words: seed disperser, frugivorous bird, endozoochory, fleshy fruit, South America rainforest.

RESUMEN

El componente cuantitativo de la efectividad de la dispersión de semillas en aves residentes en los bosques lluviosos de Sudamérica durante el período de otoño e invierno no ha sido descrito con detalle. En este estudio se identificaron las potenciales especies de aves frugívoras de los bosques templados del sur de Chile durante el otoño austral y se evaluó el componente cuantitativo de la efectividad de las aves como dispersantes de semillas (número de visitas y número de semillas dispersadas por hora) en las especies arbóreas *Luma apiculata* y *Aextoxicon punctatum*. Durante el periodo de máxima fructificación de los árboles *L. apiculata* y *A. punctatum* fueron monitoreados 10 y 14 individuos, respectivamente, por un período de 10 días. Los resultados mostraron que cuatro especies de aves consumieron los frutos de *L. apiculata*. El ave *Turdus falcklandii* fue el principal consumidor de frutos (72 % de las visitas), con una tasa de 2,2 visitas por hora y 49,2 semillas dispersadas por hora. Los frugívoros que visitaron *A. punctatum* fueron *T. falcklandii* (97 % de las visitas) y *Columba araucana* (3 %). Aquí, *T. falcklandii* consumió 65 frutos en 35 visitas, con una tasa de 1,8 visitas por hora y 3,4 semillas dispersadas por hora. Se concluye que *T. falcklandii* sería la más efectiva ave dispersante de semillas de los árboles que fructifican en otoño e invierno en los bosques templados del sur de Chile, al menos con respecto al componente cuantitativo de la efectividad del dispersante.

Palabras clave: dispersante de semillas, ave frugívora, endozoocoría, fruto carnoso, bosque lluvioso de Sud América.

INTRODUCTION

Approximately 70 % of the woody plant species in the temperate rainforests of Chiloé Archipelago, in southern Chile, produce fleshy fruits (Armesto and Rozzi 1989). This frequency is greater than those recorded for the temperate forests of North America and is comparable to that found in Neotropical forests (Howe and Smallwood 1982, Willson *et al*. 1996a, Aizen and Ezcurra 1998). Birds are the main fruit consumers in Chiloé; up to 90 % of all bird species on the island include fleshy fruits in their diet to some extent (Sabag 1993), mammals and lizards are also important frugivores (Armesto *et al.* 1987, Willson *et al*. 1996b, Aizen *et al.* 2002, Amico *et al.* 2009). Additionally, investigations into seed germination show that birds in Chiloé act as legitimate seed dispersers, scattering viable propagules (Figueroa and Castro 2002). There is evidence that shows that frugivorous bird assemblages in the Chiloé Archipelago had important consequences on the post-glacial colonization (Villagrán *et al*. 1986), forest structure and succession (Hernández 1995, Garcia *et al*. 2010), germination traits (Figueroa 2003), seed dormancy (Figueroa and Armesto 2001), and are actively associated to flowering and fruiting patterns (Smith-Ramírez and Armesto 1994, Smith-Ramírez *et al*. 1998).

Most woody plant species in Chiloé produce their fruits during the austral summer, between November and March (Smith-Ramírez and Armesto 1994). During this period, the most abundant frugivorous birds are the migratory species *Elaenia albiceps* D' Orbigny and Lafresnaye (Tyrannidae). There are previous studies which show that, at least in the temperate rainforests of Chiloé and Argentina, *E. albiceps* is the most important seed dispersal agent in terms of abundance, distribution, and number of visits to fleshy-fruiting plants (Sabag 1993, Hernández 1995, Rozzi *et al*. 1996, Amico and Aizen 2005). Nevertheless, *E. albiceps* migrates to the rainforests of Southern Amazonia during the austral autumn (Araya and Millie 1986), and there is little knowledge on fruit consumers and seed dispersers of fleshy fruits produced during the austral autumn and winter, between May and September (Correa *et al*. 1990, Rozzi *et al*. 1996). From 44 bird species recorded in the temperate rainforests of Chiloé, only three resident species are considered habitual fleshy-fruit consumers (Rozzi *et al*. 1996). There are reports that show that the resident species *Turdus falcklandii* Quoy and Gaimard (Turdinae) may be important frugivores in the secondary rainforests of Chiloé (Willson *et al*. 1996a) and the Coastal Range (Díaz 2005). Also mentioned as frugivores, but to a lesser extent, are *Curaeus curaeus* (Molina) (Icterinae), *Columba araucana* Lesson (Columbidae) and *Scelorchilus rubecula* Kittlitz (Rhinocryptidae) (Correa *et al*. 1990, Rozzi *et al*. 1996). However, disperser effectiveness (*sensu* Schupp 1993) of resident birds during the austral autumn-winter period has not yet been detailed. Disperser effectiveness is the number of new adult plants produced as a result of the activity of one disperser relative to the other dispersers or to nondispersed seeds (Schupp 1993, Calviño-Cancela and Martín-Herrero 2009). The effectiveness of seed dispersers depends both on the interaction event frequency and on the net effect per event (quantity and quality of dispersal *sensu*, Schupp 1993). However, studies in the rainforests of Chiloé on disperser effectiveness during the austral autumn-winter are scarce (Hernández 1995, Figueroa and Castro 2002) despite the importance of these concepts for seed dispersal ecology (Schupp 1993, Godinez-Alvarez *et al.* 2002, Calviño-Cancela and Martín-Herrero 2009). It is hypothesized that during the austral autumn-winter the guild of seed disperser birds is depleted.

Although effectiveness remains largely uninvestigated due to the complexity of its measurement, we aimed to determine the quantitative components of disperser effectiveness for the trees *Aextoxicon punctatum* R. *et* P. (Aextoxicaceae) and *Luma apiculata* (DC.) Burret (Myrtaceae). In Chiloé, both tree species have their maximum fruit crop during the austral autumn and winter (Smith-Ramírez and Armesto 1994).

The main objectives of this investigation are: (1) To identify the potentially frugivorous bird species of two autumnal fruiting trees in the Chiloé rainforest (*Aextoxicon punctatum* and *Luma apiculata*) and the abundance of these birds; (2) to determine the quantitative components of disperser effectiveness of the frugivorous birds in both tree species (number of visits and number of seeds dispersed per hour).

METHODS

Study area and species. The study area was located in the Biological Station "Senda Darwin" (41º 50' S, 73º 38' W), 18 km north-east of Ancud, in Isla Grande, Chiloé, Chile. The landscape is slightly uneven with low slopes and altitudes between 0 and 100 meters above sea level. Soils are thin, of glacial origin and are frequently not well drained. The weather in Northern Chiloé is rainy (annual mean of 2,100 mm) with a strong oceanic influence, which contributes to mild temperatures, with a maximum mean of 16 °C (January) and minimum mean temperatures of 5 °C (July), approximately. The typical vegetation in the area is comprised by a mosaic of antropogenic prairies and patches of primary and successional forests. Primary forests are mainly dominated by *Nothofagus nitida* (Phil) Krasser (Fagaceae), *Drimys winteri* J. R. *et* G. Forster (Winteraceae), *Podocarpus nubigena* Lindl (Podocarpaceae) and several species of Myrtaceae of the genera *Amomyrtus* and *Myrceugenia*. Successional areas are dominated by shrubs such as *Baccharis spp*., *Berberis spp*., and several species of isolated trees, mainly *Drimys winteri*, *Embothrium coccineum* and *Luma apiculata*. To achieve the objectives of the research, we selected the trees *Luma apiculata* and *Aextoxicon punctatum* (table 1) because they produce an abundant crop of fleshy fruits, whereas the production of other tree species is low and sporadic during austral autumn and winter in the study sites.

The two tree species were not selected in the same sites as they do not share habitat. Mainly, *L. apiculata* individuals were selected on the edges of secondary woody vegetation patches, close to water courses where the species is abundant in Biological Station "Senda Darwin". On the other hand, *A. punctatum* trees were selected only in a small patch of remnant forest close to the city of

Table 1. The two tree species studied in the temperate rainforest of southern Chile. Their taxonomic assignment, life form, forest habitat, flowering period, fruiting period and fruit and seed characteristics are indicated.

Dos especies de árboles estudiados en el bosque del sur de Chile. Se indica su filiación taxonómica, forma de vida, hábitat del bosque, periodo de floración, período de fructificación y características de los frutos y semillas.

Characteristics	*Luma apiculata*	*Aextoxicon punctatum*
Family	Myrtaceae	Aextoxicaceae
Life form	Tree	Tree
Forest habitat	Edge	Interior
Flowering period	Autumn	Summer
Fruiting period	Winter	Autumn
Fruit type	Berry	Drupe
Fruit color	Black	Black
Fruit mass (mg)	300	300
Seed mass (mg)	10	260
Seed per fruit	4-7	1

Ancud (Quempillén). This patch was located at less than 50 m from the coastline, adjacent to highway Ruta 5 and close to the Northern of Puente Pudeto (41° 53' S; 73° 50' W). This *A. punctatum* fragment has an estimated area of 18 ha, and is the only patch > 10 ha in the study area. The edges of the patch have recently been colonized by exotic shrubs, particularly *Ulex europaeus* L. (Papilionaceae) and *Cytisus scoparius* L. (Papilionaceae).

Identification and abundance of birds. Potentially frugivorous birds were recorded and identified by direct observation with binoculars along a 2 km long transect, running through the riparian vegetation of Biological Station "Senda Darwin", which presented *L. apiculata* adult established inside the remnant forest of *A. punctatum* ("olivillo"). Over 10 days, transects were repeated between April and May. Transects were performed by walking very slowly and stopping irregularly in order to observe and identify the potentially frugivorous birds. Each transect was performed over a period of at least three hours, approximately.

We considered a bird species as potentially frugivores when its mouth gape was at least as large as the mean fruit diameter of *L. apiculata* and *A. punctatum* (Armesto *et al*. 1987). In this study, there were no narrow mouthed birds consuming fruits, although they may eventually be seed dispersers (see Armesto *et al*. 1987, Correa *et al*. 1990, Rozzi *et al*. 1996, and Díaz 2005 for more details on frugivorous bird species). There are other potentially frugivorous vertebrates identified in secondary forests of Chiloé, for example the marsupial *Dromiciops gliroides* (Microbiotheria: Microbiotheriidae) (Amico *et al*. 2009), which will not be studied in this opportunity.

Quantitative component of disperser effectiveness. Fruit consumption by birds was observed during visits to 10 isolated trees of *L. apiculata* with abundant fruit crops in an area of 2 km^2 in "Senda Darwin". The order of the field observations of the trees was always the same. Consumption on *L. apiculata* was recorded over 13 consecutive days in May and the observations were performed between 08:00 and 16:00 h, with a total of 24 hours.

To record fruit consumption on 14 *A. punctatum* trees, over 10 days between April and May, direct observations were performed. During this period, *A. punctatum* trees present their maximum crop of ripe fruits. Completing a total of 20 hours on *A. punctatum*, observations were made on clear days between 08:00 and 10:00 h, when birds have their highest activity levels in Chiloé (Sabag 1993).

In both tree species, we recorded the number of birds visiting each *L. apiculata* and *A. punctatum* trees per hour, and the number of fruits ingested per hour. To estimate how seeds are dispersed per hour, the number of birds visiting per hour was multiplied by the number of fruits ingested per visit. To obtain the number of *L. apiculata* seeds dispersed per hour it was considered that each fruit contained four seeds (table 1). The *A. punctatum* fruits contain one seed.

We assumed that the frugivorous birds are legitimate seed dispersers during austral winter because there is indirect evidence to indicate this (Correa *et al*. 1990, Hernández 1995, Willson *et al*. 1996c, Figueroa and Castro 2002). Specifically, studies in *L. apiculata* have demonstrated that seeds are not digested by frugivorous birds, and its seeds require that the fruit pulp be digested previously in order to germinate (Figueroa and Castro 2001). Evidence also shows that *A. punctatum* seeds are not digested and germination is not ceased by frugivorous birds: seeds obtained from fruits germinated to the same extent as those seeds ingested by birds[1].

RESULTS

Identification and abundance of birds. Four bird species were recorded as potential *L. apiculata* fruit consumers (table 2). *Turdus falcklandii* was significantly the most abundant (118 individuals), followed by *Phytotoma rara* Molina (Phytotomidae), *Colaptes pitius* Molina (Picidae) and *Curaeus curaeus* Molina with 26, 5, and 2 individuals, respectively (χ^2 = 99.1; P < 0.001). The frugivores found in the "olivillo" forest patch were *T. falcklandii* (1,760 individuals) and *C. araucana* (300 individuals) (table 2). Here, *T. falcklandii* was significantly more abundant than *C. araucana* (χ^2 = 590.1; P < 0.001).

Quantitative component of disperser effectiveness. Turdus falcklandii was the main potential frugivore visiting *L. apiculata* trees, constituting 72 % of the feeding visits recorded (n = 53) at a rate of 2.2 feeding visits per hour

[1] M Salvande: data not published.

Table 2. Identification and abundance of potentially frugivorous birds in the secondary forests and "olivillo" forests of Chiloé, Chile. Birds were recorded between April and May (Austral autumn). Mean of observations ± 1 S.D. is indicated.

Identificación y abundancia de aves potencialmente frugívoras en bosque secundarios y bosques de "olivillo" de Chiloé. Las aves fueron registradas entre abril y mayo (otoño austral). Se indica la media de las observaciones ± 1 D.E.

Forest type	Birds	Abundance (number of individuals)	Percentage	Birds observed per hour
Secondary forest	*Turdus falcklandii*	118	78	4.9 ± 4.9
	Phytotoma rara	26	17	1.1 ± 1.6
	Colaptes pitius	5	4	0.2 ± 0.6
	Curaeus curaeus	2	1	0.1 ± 0.4
"Olivillo" forest	*Turdus falcklandii*	1,760	85	88 ± 62
	Columba araucana	300	15	15 ± 22

(table 3). *Phytotoma rara* constituted 24 % of the feeding visits (n = 18), with a rate of nearly one feeding visit per hour. *Colaptes pitius* and *C. curaeus* were occasional *L. apiculata* fruit consumers, with < 0.1 feeding visit per hour (table 3). Rate of feeding visits of *T. falcklandii* was significantly higher than that of the other birds ($\chi^2 = 44.1$; $P < 0.001$).

In *L. apiculata, T. falcklandii* consumed about 73 % of the total number of ingested fruits, with a mean rate of 5.6 fruits ingested per visit. *Phytotoma rara* presented a similar mean rate of 5.4 fruits ingested per visit (table 3). *Colaptes pitius* presented rates significantly lower of three fruits per visit, and six fruits were consumed in the only feeding visit observed for *C. curaeus* ($\chi^2 = 89.1$; $P < 0.001$).

For *A. punctatum* trees, we recorded a total of 37 feeding visits, 97 % of them (n = 36) by *Turdus falcklandii* individuals, and only one visit by *C. araucana*. We observed 1.8 feeding visits per hour by *T. falcklandii,* whereas *C. araucana* carried out only 0.05 feeding visits per hour (table 2). *Turdus falcklandii* individuals were observed consuming 65 *A. punctatum* fruits in 35 feeding visits, which corresponds to 1.9 fruits ingested per visit. For the only *C. araucana* feeding visit, we recorded a consumption of eight fruits (table 3).

For the quantitative component of disperser effectiveness, in this study *T. falcklandii* presented the greatest effectiveness for both plants. The bird species *T. falcklandii* dispersed 49.2 seeds per hour for *L. apiculata* and 3.4 seeds per hour for *A. punctatum*. *Phytotoma rara* dispersed 17.2 *L. apiculata* seeds per hour. *Colaptes Pitius* and *C. curaeus* presented the significantly lowest effectiveness for *L. apiculata* ($\chi^2 = 1106$; $P < 0.001$), and *C. araucana* had the significantly lowest effectiveness for *A. punctatum* ($\chi^2 = 34.7$; $P < 0.001$) (table 3).

DISCUSSION

The main frugivorous birds observed during the summer months in the temperate rainforests of southern Chile are the migratory *E. albiceps* and the resident *T. falcklandii* (Sabag 1993, Hernández 1995). This study shows that during Austral autumn-winter *T. falcklandii* becomes the most important frugivore. *Turdus falcklandii* was the most abundant bird species throughout the study

Table 3. Quantitative components of disperser effectiveness during autumn and winter in Chiloé forests. Number of bird visits per hour, number of fruits ingested per bird visit, and number of seeds dispersed per hour. Mean of observations ± 1 S.D. is indicated. * Denotes observation of one single individual.

Componentes cuantitativos de la efectividad de los dispersantes durante el otoño e invierno en los bosques de Chiloé. Número de visitas de aves por hora, número de frutos ingeridos por visita de aves y número de semillas dispersadas por hora. Se indica la media de las observaciones ± 1 D.E. *Señala la observación de un solo individuo.

Tree species	Frugivorous bird	Hours of observation	Bird visits per hour	Fruits ingested per visit	Seed dispersed per hour
Luma apiculata	*Turdus falcklandii*	24	2.2 ± 1.7	5.6 ± 3.6	49.2 ± 21.2
	Phytotoma rara		0.8 ± 1.0	5.4 ± 2.9	17.2 ± 15.6
	Colaptes pitius		0.08 ± 0.3	3.0 ± 0	1.0 ± 1.2
	*Curaeus curaeus**		0.04	6	0.24
Aextoxicon punctatum	*Turdus falcklandii*	20	1.8 ± 2.3	1.9 ± 1.2	3.4 ± 3.5
	*Columba araucana**		0.05	8	0.45

period, as has been recorded in other different temperate rainforests in southern Chile during autumn and winter months (Sabag 1993, Hernández 1995).

Although this study does not prove that *T. falcklandii* is a legitimate disperser for the tree species studied, the evidence[2] sustains that this species may well be a disperser of viable seeds of both *L. apiculata* and *A. punctatum* (Figueroa and Castro 2003). Seed germination of both *L. apiculata* and *A. punctatum* obtained from bird feces collected at random in the field, during the autumn, is similar to the seed germination obtained in fruits recently collected on the mother plants (Figueroa and Castro 2003). According to our results of bird abundance, there is a high probability that the feces collected at random in the field during autumn belong to *T. falcklandii*. However, the hypothesis should be corroborated in later studies.

These results confirm that temperate rainforests of South America have low diversity of frugivorous birds (Sabag 1993, Hernández 1995, Amico and Aizen 2005), which contrasts with the observations carried out in other temperate regions around the world (Stepanian 1982, Debussche and Isenman 1989, Stanley and Lill 2002, Jordano *et al*. 2007). This is most likely due to their isolation from other South America forests since the Pliocene (Hinojosa and Villagrán 1997).

Specifically, the "olivillo" forest studied has the lowest diversity of frugivorous birds. Nearly all of the feeding visits on *A. punctatum* trees were of *T. falcklandii* and < 5 % were *C. araucana*. In addition, *T. falcklandii* is also the main visitor of *L. apiculata*, with 65 % of feeding visits. Nevertheless, other three bird species are responsible for the remaining *L. apiculata* fruit consumption.

In the study period, *T. falcklandii* was sighted 18 times more frequently in the "olivillo" patch than in the secondary forest where *L. apiculata* was common. However, *T. falcklandii* has similar rates of feeding visits to both tree species (2.2 and 1.8 bird visits per hours in *L. apiculata* and *A. punctatum,* respectively). Regarding the dispersed seeds per hour (the quantitative component of effectiveness), in this study *T. falcklandii* was less effective on *A. punctatum* fruit (3.4 seeds per hours) than when feeding on *L. apiculata* fruit (49.2 seeds per hours). Also, in this last tree, the quantity of seeds dispersed per hour was significantly greater for *T. falcklandii*, indicating probably higher effectiveness of the quantitative component due to greater abundance in the study site and more seeds per fruit. The remaining bird species dispersed < 30 % of the *L. apiculata* seeds. This greater abundance of *T. falcklandii,* recorded during the study period in Chiloé, may show that the number of visits a disperser makes appears to be a better predictor of the total quantity of seed dispersed than the number of fruits ingested per visit (Schupp 1993).

In addition, a study[3] directly done on the "olivillo" understory shows that > 90 % of the *A. punctatum* propagules were intact in the site and would mean that propagules fall from trees without being consumed by frugivores and/or that animals handle them in a deficient way (Snow and Snow 1988). Studies in different communities also have shown crops that are ignored by endozoochorous dispersers (Snow and Snow 1988, Fuentes 2000). In our study, the proportion of *A. punctatum* fruits dispersed by birds, as well as the number of fruits ingested per visit, is very low when compared to data found for *L. apiculata* and other woody species (Stanley and Lill 2002, Obeso and Fernández-Calvo 2002). Our results seem to suggest that fruit size would be a limiting factor for birds foraging on *A. punctatum* fruits. *L. apiculata* fruits are smaller in size than those of *A. punctatum* (table 1). Therefore, in the temperate rainforests of southern Chile, *L. apiculata* could be a less discriminatory source of ripe fruits than *A. punctatum*, because the bird species present in the region generally have beak gapes smaller than *A. punctatum* fruit diameter (Armesto *et al*. 1987). This may also explain why the lowest diversity of frugivorous birds is found in the patch dominated by *A. punctatum* and the low effectiveness of *T. falcklandii* on *A. punctatum* fruits, at least with regard to the quantitative components of disperser effectiveness. In addition, the relative amount of pulp per fruit is lower in *A. punctatum* than in *L. apiculata*. However, we do not have data regarding nutrient content relative to the pulp for both species, which are important variables when considering fruits as food resources for frugivores (Jordano 1995).

In conclusion, in the study site we observed four frugivorous birds during autumn-winter (*T. falcklandii, P. rara, C. pitius* and *C. curaeus*). Similarly, there is evidence that *T. falcklandii* is an important seed disperser during autumn-winter in the temperate forests of South America (Amico and Aizen 2005). Regarding quantity component of disperser effectiveness, this study shows that *T. falcklandii* would be the most effective disperser bird in the rainforests of Chiloé. First, fleshy fruits produced during austral autumn and winter were principally ingested and the seeds probably dispersed by *T. falcklandii*. Secondly, *P. rara*, which consumes a great number of *L. apiculata* fruits per visit, is present in lower abundance and disperses a lower number of seeds during this period. Finally, as the measurements were obtained on quantitative components of disperser effectiveness and only in one study site by tree species, additional investigation is recommended to extend the research over qualitative components of effectiveness, and over the spatial and interannual variation of the Chiloé forests.

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[3] M Salvande: data not published.

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