

# Frugivory and seed dispersal of *Podocarpus nubigena* in Chiloé, Chile

Frugivoría y dispersión de semillas de *Podocarpus nubigena* en Chiloé, Chile

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## ABSTRACT

We studied seed dispersal of mañío macho (*Podocarpus nubigena* Lindl.) by birds in rainforests of Chiloé. Austral thrushes (*Turdus falcklandii*) were the predominant agent of seed dispersal, carrying about 18% of seeds at least three tree-crowns away from the parent tree. Several other passerines also dispersed some seeds. Chilean pigeons (*Columba araucana*) virtually always dropped seeds below the parent. Although seeds did not germinate in the laboratory, in field experiments, seeds germinated regularly. The density of seedlings and juveniles exceeded 15/m<sup>2</sup> under female mañíos and 1/m<sup>2</sup> under other trees in the forest.

**Key words:** frugivory, seed dispersal, fleshy fruit, Chilean rainforest.

## RESUMEN

Al estudiar la dispersión de semillas por las aves en el bosque lluvioso de Chiloé se ha encontrado que los zorzales (*Turdus falcklandii*) son los principales agentes dispersantes del mañío macho (*Podocarpus nubigena* Lindl.), transportando alrededor del 18% de las semillas al menos a una distancia equivalente a dos copas de árboles de la planta madre. Además del zorzal, otros paseriformes también dispersan algunas semillas. Las torcazas (*Columba araucana*) casi siempre dejan caer las semillas debajo de la planta madre. Aunque no se obtuvo germinación en laboratorio ni en experimentos de campo, las semillas germinaron regularmente en la naturaleza. La densidad de plántulas y de juveniles excede 15/m<sup>2</sup> debajo de los árboles hembras y 1/m<sup>2</sup> debajo de otros árboles dentro del bosque.

**Palabras clave:** Frugivoría, dispersión de semillas, frutos carnosos, bosque lluvioso de Chile.

## INTRODUCTION

The temperate rainforest of southern Chile is characterized by a high diversity of fleshy-fruited trees (Armesto & Rozzi 1989). An important fleshy-fruited canopy species of montane forests between 40° and 42°S and lowland forests south of 42° S is the dioecious gymnosperm "mañío macho" (henceforth "mañío"; *Podocarpus nubigena* Lindl.; Podocarpaceae). Although many species of forest birds eat fruits and disperse the seeds of rainforest plants in southern Chile (Armesto et al. 1987, Sabag 1993), seed-dispersal ecology has not been studied for any species in these forests. The study of seed-dispersal ecology has importance not

only for understanding fundamental species interactions that help determine community organization and function (Willson 1991), but also for practical applications, such as maintaining natural regeneration of species in forests that are increasingly fragmented. Here we document seed dispersal ecology of mañío, providing information on avian frugivores, seed-handling behavior and location of seed deposition, seed predation, seed germination, and seedling distributions.

## STUDY SITE AND METHODS

We use the Chilean common names of the birds in the text, by preference. English

common names and scientific names are given in Table 1.

The study site was located in the northeast part of Isla Grande de Chiloé, just west of Linao. An extensive lowland forest is comprised principally of tepual, a swamp forest in which tepú (*Tepualia stipularis* (H. et A.) Griseb.), a small tree often with creeping stems, is common. Coigües (*Nothofagus dombeyi* (Mirb.) Oerst. were common emergents, and mañío was frequent in the canopy and as juveniles in the understory. Selective logging (especially of coigüe and mañío) had thinned the edge of this forest for a distance of about 100 m. All focal trees for avian observations were located within or near this disturbed edge, where visibility was relatively good. Mañío produces ripe fruits in spring, at a time of the year when few other fruits are available to frugivores. Most vertebrate-dispersed plants produce mature fruits in summer and autumn.

One or two observers watched each group of focal trees for 2-3 hours per morning, recording species of birds foraging in mañíos, seed-handling behavior and fate of seed, and other behavior of frugivores including flight distances and aggression. In all, there were 95 hours of observation in early October 1993, largely before the arrival of the migratory, frugivorous fío-fío, and 93 hours in late October 1994, after the fío-fíos had arrived. Foraging birds were often hidden behind the trunk or in dense foliage, so it was seldom possible to record all seeds handled by the birds. Over 25 mañío trees were included in the observations.

The "fruits" of mañío are unlike those of some other gymnosperms and most vertebrate-dispersed angiosperms, in that the edible portion does not enclose the seeds but rather consists of an aril at the base of the seed. The aril is red, sweet to human taste (about 32% sugar, 1% lipid, 4% protein; analyses by the Palmer Research Center, Palmer, Alaska), and juicy (about 81% water) when ripe. The mature seed is black. The aril is usually about the same size (and often shape) as the seed: the aril averages 8.5 mm in length (SE = 0.7) and 8.2 mm in diameter (SE = 0.9), the seed averages 9.7 mm in length (SE = 0.6) and 7.9 mm in diameter (SE = 0.6) (Figure 1). The shape of

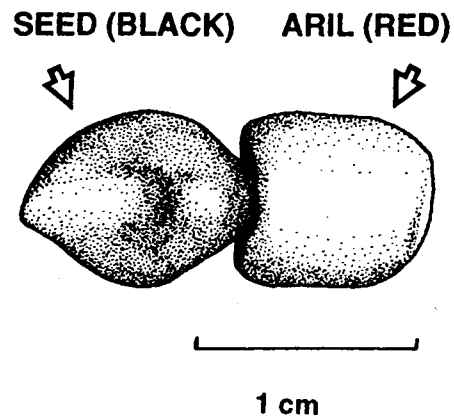


Fig. 1: A mature dispersal unit of *Podocarpus nubigena*, consisting of seed and aril. Drawn approximately 3x actual size.

Unidad de dispersión madura de *Podocarpus nubigena*, consistente en una semilla y un arilo. El dibujo es aproximadamente 3 veces el tamaño real.

TABLE 1

Fruit-eating avian visitors to mañío trees: percent of seeds (of observed fate) handled by each species. + = < 1%

Aves frugívoras que visitaron los árboles de mañío macho: porcentaje de semillas (con destino observado) manipulados por cada especie. + = < 1%

Scientific name	Chilean common name	English common name	Early Oct., 1993 N = 456	Late Oct., 1994 N = 955
<i>Turdus falcklandii</i>	zorzal	austral thrush	91%	60%
<i>Curaeus curaeus</i>	tordo	austral blackbird	6	+
<i>Phrygilus patagonicus</i>	cometocino	Patagonian sierra-finch	3	1
<i>Elaenia albiceps</i>	fío-fío	white-crested elaenia	+	2
<i>Pyrope pyrope</i>	diucón	fire-eyed diucon	-	+
<i>Aphrastura spinicauda</i>	rayadito	thorn-tailed rayadito	-	+
<i>Columba araucana</i>	torcaza	Chilean pigeon	-	36
<i>Enicognathus leptorhynchus</i>	choroy	slender-billed parakeet	-	1

both seed and aril is usually oval or barrel-shaped, and the mature aril does not resemble the illustrations in Rodríguez et al. (1983) or Hoffman (1982). One seed per aril is common, but occasionally two seeds are borne on a single aril, which is generally larger and less symmetrical than usual.

Freshly fallen seeds collected from the forest floor in October 1993 were pre-treated by holding at 4° C for 60 days. They were then placed in a germination chamber at the Facultad de Ciencias, Universidad de Chile, Santiago, for ten months at 20° C with 12 hours of exposure to light each day. Sample sizes were 100 seeds without arils, distributed equally among ten germination dishes, and 100 seeds with attached arils, similarly distributed. In the field 200 seeds with arils and 200 without arils were placed on the ground in the study site, in wire-mesh enclosures in October, 1993. The enclosures were pressed into the ground about 2 cm and held in place with pegs, to prevent ready access by ground-foraging vertebrates. There were 20 seeds/enclosure and 10 enclosures per treatment (with arils or without arils). The enclosures were set out in pairs (one with arillate seeds and one with arilless seeds) along a 100 m transect. Seeds in the enclosures were monitored for germination in January and November, 1994.

Seed predation was examined experimentally in October 1993. Ten seeds without arils and ten arillate seeds were placed on the ground at each of twelve stations and checked the following day for evidence of seed removal or damage. The experiment was repeated nine times during October.

Seedling and juvenile density, as a function of distance from female trees, was surveyed in October 1993. Two 1-m<sup>2</sup> quadrats were haphazardly placed under each tree sampled. Five female individuals of mañío, 13 other kinds of trees (male individuals of mañío, coigües, canelos [*Drimys winteri* J. R. et G. Forster]) adjacent to females, and five trees at least three tree-crowns away from females ("far") were sampled. Differences in average densities of young mañíos at three distances (under female, under adjacent tree, or "far") were tested by Kruskal-Wallis test.

## RESULTS

The zorzal was the most frequently recorded consumer of mañío in both field seasons, and a number of other birds harvested "fruits" (Table 1). Although the fío-fío is a major frugivore in these forests (Sabag 1993), it accounted for only a small proportion of seeds handled in this study.

Zorzales handled seeds and arils in several ways. They often swallowed the entire dispersal unit (seed + aril), regurgitating the seed several minutes later. After swallowing several dispersal units, a zorzal usually sat quietly for several minutes, and then ejected one to several seeds. Occasionally a seed was brought up and reswallowed. Seed ejection was usually accomplished with little overt physical effort, and close observation was needed to see it happen. Alternatively, zorzales frequently held the dispersal unit by the aril and struck it against a branch, often many times, until the seed (usually) fell off or the whole dispersal unit was dropped. Occasionally, however, the seed remained attached and the whole unit was then swallowed. Finally, zorzales sometimes carried dispersal units away in their bills. The relative frequency of swallowing and striking differed between seasons (Table 2). Dispersal units bearing two seeds were uncommon; they appeared to be more difficult to handle than one-seeded units and were often dropped.

Zorzales were commonly very aggressive while foraging on mañío. They chased each other, sometimes vigorously, on most occasions when more than one individual was present. However, on some occasions, several zorzales foraged simultaneously in the same tree, so they cannot be said to be successfully territorial in mañíos. Zorzales also sometimes chased fío-fíos and cometocinos but were not observed to try to displace torcazas or tordos.

Zorzales that foraged in the focal trees often arrived from and departed to considerable distances. We often observed them flying over a large, shrubby field adjacent to the forest, a minimum distance of several hundred meters from the next nearest stands of trees. Furthermore, we found several mañío seeds (and seedlings) in this field, over 100 m from the forest edge.

TABLE 2

Seed-handling behavior of frugivores (those with > 10 observations).  
N = number of seeds. The data are percentages of occurrence, for each bird species

Comportamiento de manipulación de semillas por las aves frugívoras (sólo aquellas especies con más de 10 observaciones).  
N = números de semillas. Los datos son porcentajes de ocurrencia, para cada especie de ave

Species	Year	N (seeds)	Swallow	Strike	Drop	Carry
zorzal	1993	414	19%	64%	3%	14%
	1994	575	61	29	9	1
cometocino	1993	14	–	92	–	8
	1994	12	–	75	8	17
fío-fío	1994	16	6	75	19	–
torcaza	1994	339	–	98	2	–
tordo	1993	27	4	59	30	7

Torcazas were only observed on seven occasions, but they sometimes stayed a long time (almost an hour) in the same tree, foraging almost continually. They customarily plucked the dispersal unit, bit off the seed, which fell to the ground, and then swallowed the aril, but sometimes they picked and dropped the seed before plucking the aril. In either case, they did not serve as effective dispersal agents.

Cometocinos and tordos usually consumed the aril while still in the parent-tree crown, but occasionally dispersal units were carried away (Table 2). The tordo often held a dispersal unit against a branch with its foot and pecked at the aril, or struck off the seed as the zorzales did. Cometocinos usually nibbled small bites from the aril and dropped the seed. Rayaditos usually pecked at the aril in situ but were once observed to carry off the whole dispersal unit. Both fío-fíos and diucones commonly knocked off the seed before swallowing the aril but sometimes carried fruits away from the parent tree.

Choroyes bit off the aril and let the seed fall, during our focal-plant observations. However, on the forest floor we sometimes found accumulations of seeds that had been split neatly open and the embryo extracted. We suspected this to be the work of choroyes (Sabag, pers. obs.).

We estimated that 75% of all seeds were dropped beneath the parent trees in 1994, and that 18% were carried "far" from the parent. The remainder (6%) fell under trees adjacent to the parent (Table 3).

Few seeds disappeared from the experimental seed-predation plots, but slightly more arillate seeds (5%) were taken than seeds without arils (2%); removal of arillate seeds exceeded that of arilless seeds on 7 of 9 days (Sign Test,  $P = .09$ ). No seeds were destroyed in situ, although some appeared to have been chewed slightly. On the other hand, 8% of the arils were chewed, pecked, or consumed.

Experimental germination tests failed completely, both in the germination chamber and in the field. However, it is clear that natural germination occurs regularly, because seedlings and juveniles (up to 1 m tall) are common. Their average density under female mañíos was 15.5 individuals/m<sup>2</sup> ( $n = 10$ , SE = 2.9). In contrast, the density under adjacent trees was only 3.4 individuals/m<sup>2</sup> ( $n = 26$ , SE = 0.5). It was difficult to find sites within the

TABLE 3

Deposition patterns of mañío seeds handled by avian frugivores, 1994 data. Separate entries only when  $n \geq 10$  seeds per bird species, expressed in percentages

Patrones de deposición de las semillas de mañío por las aves frugívoras. Datos de 1994. Entradas separadas sólo cuando  $n \geq 10$  semillas por especie, expresadas en porcentajes

Species	N	Parent tree	Adjacent tree	"Far"
zorzal	353	52%	12%	36%
cometocino	10	60	10	30
fío-fío	12	83	–	17
torcaza	339	100	–	–
All birds	730	75	6	18

study area that were distant from female mañíos: a small sample ( $n = 6$ ) yielded an average density of 1.4 (SE = 2.6), only slightly lower than that under trees adjacent to females. The densities of young mañíos differed significantly at different distances (Kruskal-Wallis  $H = 16.6$ ,  $P < .01$ ).

#### DISCUSSION

The zorzal, a member of a genus well-known as frugivores and seed vectors in North American and Europe (Willson 1986, Snow & Snow 1988), was clearly the predominant agent of seed dispersal in this study. Nevertheless, zorzales probably deposited most of the seeds they handled immediately under the parent tree. Most of the other visitors were rare and/or deposited an even higher proportion of seeds below the parents. High levels of aggression by proprietary zorzales probably contributed to the frequency at which avian foragers retreated to nearby trees to consume mañío "fruits" and also to the broad distribution of seeds and seedlings. Furthermore, zorzales appeared to have difficulty handling two-seeded arils and frequently dropped them; failure of dispersal away from the parent tree may create selection pressure against two-seeded dispersal units. Zorzales sometimes travel some distance to visit fruiting mañíos, commonly cross open fields, and are capable of dispersing seeds from mañíos in perturbed and isolated woodlots as well (Willson et al. 1994). Thus, mañíos growing in fragmented forests may still obtain seed-dispersal services from zorzales.

Although vertebrate-dispersed seeds may be carried very long distances in some cases (Fleming & Heithaus 1981, Willson 1993), few studies assess the seed shadow of wood plants in ways that allow direct comparison with our study. For *Virola surinamensis* in Panama, the proportion of seeds carried more than an estimated three crown-diameters from the parent plant was 65% for three species of large birds (toucans, guan), but <4% for two smaller bird species (trogon, motmot; Howe & Vande Kerckhove 1981), although another study of the same species suggested that very few seeds were carried

away from the parental vicinity (Howe et al. 1985). Other studies also indicate considerable variation in the probability of a seed travelling far from the parent (e.g., Debussche et al. 1985, Dirzo & Domínguez 1986, Holthuijzen et al. 1987, Debussche & Isenmann 1994). Our estimate that zorzales carry about 18% of seed "far" from the parent thus falls within the observed variation for other species in other places, but good comparisons are not possible with present information (Willson 1993).

The importance of mañío arils for zorzales is not known. The crop ripens early in the breeding season (usually October), when most zorzales are nest-building or incubating, but some dispersal units may remain on the tree as late as December. Several observations suggest that mañío provides an important food source at this time. In October, some zorzales fly considerable distances and spend long periods foraging in mañío trees. The level of aggression among zorzales foraging in mañíos in Chiloé was much higher than that of zorzales foraging on *Drimys* fruits in Tierra del Fuego (Willson & Sabag, pers. obs., February 1995). Moreover, the availability of other fruits is very low at this time of year. Incidentally, on two occasions, we also saw zorzales harvesting inner bark of mañío for nest material.

Mañío seed failed to germinate in the laboratory, as reported also by Urrutia (1986). The seeds also did not germinate in our field tests, although natural recruitment is excellent in this forest. It is possible that germination of mañío seeds requires more time or some specific interactions with forest soil that was somehow precluded by our exclosures. In contrast to other trees such as some *Nothofagus* and *Drimys* (which commonly germinate on fallen logs), mañío germinates directly on the forest floor.

Although some seeds were removed from the seed-predation plots, it is not clear that removal constitutes predation in this case. The arils of arillate seeds were often chewed and sometimes destroyed, in situ, and removal may have occurred because the consumer sought the aril. If so, this would constitute dispersal. The attractive properties of the aril may explain the slightly higher removal rates of seeds with arils. The hard

covering of the embryo is resinous and about 2 mm thick, which may deter some would-be predators. Although there was little good evidence of predation in the experiment, seeds that fall naturally to the forest floor usually disappear within about two months. The most likely predators on the forest floor are probably rodents. Reasons for the difference between experimental and natural removal of seeds are not known.

Although zorzales can ingest several arillate seeds at one sitting, they often remove the seed before ingesting the aril. Knocking off the seed commonly required vigorous action (often 30-60 strikes). On the other hand, ingestion of the whole dispersal unit requires internal handling for several minutes and limits the number of arils eaten per unit time, because the seeds then occupy space in the upper digestive tract. We observed that the relative frequency of ingestion vs knocking off the seed varied among birds and/or among trees, suggesting that the costs of aril harvesting may also vary, with possible consequences for both foraging and seed dispersal.

Zorzales are probably more common in this part of Chiloé now, as the forest is increasingly cleared for timber-harvest and agriculture (Willson et al. 1994), than in the time of Darwin over 150 years ago (Willson & Armesto, 1996). This frugivore would probably be less common in primeval forests than in the present landscape of woodlots and fencerows, but it is not clear what (or if) other frugivores might have been the principal aboriginal dispersal agents of *mañfo*.

Comparison of frugivory and seed dispersal with other species of *Podocarpus* in Chile and elsewhere in the southern hemisphere would be interesting. Seed size and color, aril size and color, growth form, and habitat all vary (Salmon 1980, Floyd 1989), as do the potential disperser assemblages. These systems might be suitable for determination of the relative importance of phylogeny vs. regional ecology in the evolution of fruiting characteristics.

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