BREEDING ECOLOGY AND MIGRATORY CONNECTIVITY OF PASSERINES IN THE WORLD'S SOUTHERNMOST FORESTS

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In the extensive and remote sub-Antarctic forests of South America, birds are the dominant terrestrial vertebrates. Despite considerable efforts to understand the ecology of birds breeding in these forests, our current knowledge for many species is still incomplete. During three breeding seasons (2014 – 2017), I studied the breeding ecology of the five most abundant open-cup forest-dwelling passerines in the sub-Antarctic forest of Navarino Island, Chile (55°04'S, 67°40'W). There were differences in some of the breeding strategies used by birds breeding on Navarino Island versus conspecific populations breeding at lower latitudes. *Milvago chimango* was the main nest predator of open-cup nesting forest passerines, and the main cause of nest failure. In addition, I found that species built their nests in sites with higher density and taller understory; however, these two factors decreased their nest survival. This mismatch could be due to a change in depredation risk on Navarino Island, and thus, passerines breeding there may be in an ecological trap. In addition, using light-level geolocators, I determined that the migratory connectivity of *Elaenia albiceps* is weak as a result of the large spatial spread of individuals on the wintering ground, and that the distances among individuals on the breeding grounds are not maintained in the wintering grounds. My study opens further questions about the mechanisms driving differences in breeding strategies among populations. In addition, further research is needed to assess hypotheses that could explain the mismatch between nest-site selection and nest survival and to understand what drives elaenias' movements, not only during winter but throughout their annual cycle.

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CHAPTER 1

GENERAL INTRODUCTION

In southwestern South America, in the remote sub-Antarctic forests, birds are the dominant terrestrial vertebrate (Rozzi et al. 2014). These extensive lands of evergreen forests represent one of the world's most pristine ecoregions (Mittermeier et al. 2003), characterized by their unique biodiversity and high rates of endemism (Rozzi et al. 2012). Since 2000, considerable mist-netting and bird banding efforts have been carried out to understand the ecology of birds inhabiting these forests (summarized by Rozzi and Jiménez 2014a). Despite these efforts, our current knowledge of the complete annual cycle for many species breeding in these forests is still incomplete.

Twenty-eight bird species breed or forage in these forests (Ippi et al. 2009, Rozzi et al. 2014). However, only eight passerines account for more than 95% of all mist-netting captures recorded between 2000 and 2010 (Rozzi et al. 2014). Among these, *Phrygilus patagonicus, Anairetes parulus, Turdus falcklandii, Elaenia albiceps chilensis,* and *Zonotrichia capensis* (Fig. 1.1) are open cup nesters found in a variety of forest habitats. In general, these five species have large breeding ranges that include the sub-Antarctic forests as their southern limit and extend northward in the South American temperate forests biome and beyond. Particularly in Chile, the breeding range of *P. patagonicus* extends to La Serena (30˚S), of *A. parulus* to the Strait of Magellan (53˚S), of *T. falcklandii* to Chañaral (27˚S), of *E. albiceps chilensis* to Copiapó (27˚S), and that of *Z. capensis* to Aysén (45˚S) (Rozzi 2010). Of these five species, three of them are year-round residents (*P. patagonicus, A. parulus* and *T. falcklandii*) whereas two are migratory (*E. albiceps chilensis* and *Z. capensis*) (Rozzi et al. 2014).

Our knowledge about the basic biology of these species is very limited (Sandvig et al 2020). This lack of information hinders conservation, as we have little ability to predict the impact of invasive terrestrial predators, understand carry-over effects between wintering and breeding seasons, and predict the impact of climate change. In this dissertation, I report my research on multiple aspects of these birds' breeding biology, ecology, and migration. These studies have the potential to not only inform conservation efforts, but also to examine basic ecological hypotheses that have infrequently been explored in South American avifauna.

1.1 Breeding Biology

Birds vary greatly in various aspects of breeding biology, including where they place their nests, the number of eggs they lay, the number of broods per season, their breeding phenology, and the substrate and height of their nests. This variation likely suggests that, as a response to ecological processes (e.g., predation, competition birds adopt varied strategies), birds adopt varied strategies to maximize breeding success and ultimately, fitness. Moreover, large-scale geographical patterns of these characteristics indicate that these strategies vary across the American continent in systematic ways.

For example, special interest has been placed on patterns of variation in clutch size (Lack 1947, Cardillo 2002, Jetz et al. 2008, Rose and Lyon 2013). Specifically, birds breeding at higher latitudes tend to lay larger clutches than those breeding at lower latitudes (Lack 1968). At a global scale, clutch size of birds nesting in temperate regions in the southern hemisphere are smaller than phylogenetically related species breeding in temperate regions in the northern hemisphere (reviewed by Martin 1996). However, studies on clutch size variation within South America found no latitudinal gradient: clutch sizes in tropical latitudes are the same as those in temperate latitudes of southern Chile and Argentina (Johnson 1967, Yom-Tov et al. 1994). Elucidating the factors that drive these patterns has fascinated biologists for decades (Moreau 1944, Lack 1947, Stearns 1976, Ricklefs 1980) and at this time there is no consensus. Among the hypotheses proposed to explain differences in clutch size between northern and southern hemisphere (and lack of pattern within South America) are resource availability (Ashmole 1963, Ricklefs 1980), high predation pressure in the tropics (Woinarski 1985, Yom-Tov 1987), long days at high latitudes (Lack 1947), and high adult mortality for northern hemisphere breeding birds driven by harsh climatic conditions during winter (Yom-Tov et al. 1994). Most of the studies trying to understand this pattern have been conducted across multiple species, and not within species (e.g., Cardillo 2002, Jetz et al. 2008). Although this approach offers large sample sizes to detect patterns, it adds confounding variables, because selection pressure can happen at much smaller scales (e.g., populations). Therefore, intraspecific comparisons are helpful to understand this pattern. Passerines breeding on Navarino Island have a large latitudinal range, which makes them an ideal model for studying variations in clutch size within a species.

Another critical aspect of bird reproductive biology is nesting success. Several studies have determined diverse factors that can affect nest success, including at least five: (i) female arrival date, (ii) female energetic condition upon arrival (e.g., amount of fat; Moore et al. 2005), (iii) age and breeding experience (Ollason and Dunnet 1978), (iv) nest predation (Walankiewicz 2002), and (v) nest-site selection (Li and Martin 1991). Among these factors, nest-site selection and predation have been highlighted as specially important factors (Holway 1991). The nest location may represent a trade-off among factors that determine nest fate, and ultimately, reproductive output. According to this paradigm, birds should select nesting habitat with a low likelihood of predation (Walankiewicz 2002) for eggs and chicks, but also for adults.

1.2 Migration

Bird migration is the annual movement between breeding and wintering grounds, which can encompass flying thousands of kilometers (Newton 2008). Although this is an impressive natural phenomenon that captures both scientific and public interest, many aspects of migration including migratory pathways, timing, and tradeoffs in life history traits are still not fully understood for most species. The study of bird migration in the world shows a large bias toward the northern hemisphere, particularly North America and Europe (Greenberg and Marra 2005). The geography of North America is very different from that of South America. For instance, in South America there is no geographical barrier requiring birds to undertake extensive non-stop flights like the Gulf of Mexico in North America. Furthermore, the continent gets narrower toward the south providing less available habitat and land area, among other characteristics (Faaborg et al. 2010, see also Rozzi and Jiménez, 2014). Consequently, knowledge acquired in northern hemisphere species does not necessarily apply to southern hemisphere species.

Every year, dozens of species migrate between South American temperate latitudes and tropical latitudes in what is known as the Neotropical migration system (Jahn et al. 2020). This is the world’s third largest migration system after the Paleartic-African and Neartic-Neotropical migration systems, and the most extensive migration system in the southern hemisphere (Chesser 1994). Despite its importance, our understanding of this system remains patchy, and only during the last 20 years has there been a growing interest in the ecology of Neotropical migrants (Jahn et al. 2020).

Chesser (1994) provided the first overview of the Neotropical migration system. More than 50% percent of the passerine (songbird) migrants in South America belong to the Tyrannidae family, which contrasts with North American migrants in which the predominant family is Parulidae (Chesser 2005). In addition, the Tyrannidae accounts for 33.2% of all austral migrants (Chesser 1994). Joseph (1996, 1997) proposed a pattern of austral migrant passerine distribution in South America based on daily mean temperatures (DMT). According to Joseph (1996), there is a distributional limit running north-west to south-east through Peru and Bolivia into Brazil overlapping with the 20°C isotherm (Fig. 1.2). This division results in two distinct groups: the first group consists of birds that breed in temperate regions and winter in warm humid lowland tropical zones, north and east of this divide (South American Temperate-Tropical, SATT); birds in the second group breed in cool regions and spend winter in temperate zones, south and west of the division (South American Cool-Temperate, SACT) (Joseph 1996, 1997). This two-group pattern is only a generalization of the South America system; reality is more complex than this. An indication of these complexities is that there are species that are hard to place in either one of these groups, such as the case of the White-crested Elaenia (*E. albiceps*), hereafter 'elaenias' (Joseph 1996, Chesser 2005).

*Elaenia albiceps*is is the longest-distance migrant flycatcher in South America (Chesser 2005). This 16-g flycatcher migrates every year between its wintering grounds in lowland forests in Brazil and temperate forests of southern Chile and Argentina (Jiménez et al. 2016, Bravo et al. 2017). Elaenias therefore cross the distinctive isotherm barrier described above (Joseph 1996, 1997; Chesser 2005). Of particular interest are elaenias breeding in the southernmost forest of the world (Silander 2000), on Navarino Island (56°S), which marks the southern limit of their distribution (Hayes et al. 1994, Rozzi and Jiménez 2014a). These individuals not only belong to the longest distance migratory breeding population of this species, but are also the only long-distance passerine migrant species breeding on Navarino Island (Rozzi and Jiménez 2014b). In summer, elaenias become one of the most abundant birds on Navarino Island (Ippi et al. 2009). This species has high site fidelity (i.e., returns to the same breeding territory every year) and is among the longest living passerines in the region with the maximum recorded longevity of 8.15 years (Brown et al. 2007, Rozzi and Jiménez 2014b). On Navarino Island, this species is most commonly found in shrubland, which differs from elaenias that breed at lower latitudes such as that on Chiloe Island, where they prefer forest edges (Ippi et al. 2009).

The migratory movement of elaenias between their breeding and wintering sites creates a link called ‘migratory connectivity’ (Webster et al. 2002). Migratory connectivity ranges from weak or diffuse (when individuals of different wintering sites migrate to the same breeding site, or vice versa) to strong connectivity (when individuals overwintering in the same area migrate to breed together in the same site) (Webster and Marra 2005). Migratory connectivity is different from the concept of ‘connectivity’ used in landscape ecology in that the former implies large scale movement of individuals across seasons, whereas the latter usually means regional movement of individuals between patches within the same season (Taylor et al. 1993, Tischendorf and Fahrig 2000).

Population dynamics of elaenias on their breeding grounds of Navarino Island can be affected by events happening during migration or on their wintering sites in Brazil (Dolman and Sutherland 1995, Marra et al. 1998, Newton 2008, López Calderón et al. 2019). For example, the habitat quality and climate during winter have been associated with the physical condition of migratory songbirds and their spring departure date (Bearhop et al. 2004), physical condition and arrival date to the breeding grounds (Marra et al. 1998, Gill et al. 2001), and their reproductive success (Marra et al. 1998, Norris et al. 2004, Rockwell et al. 2012). Therefore, for *E. albiceps,* there could be an important relationship between conditions experienced during winter and their later reproductive success, but to fully understand this relationship we need to elucidate the degree of their migratory connectivity.

1.3 Study Area

The Cape Horn Biosphere Reserve (CHBR) consists of an extensive archipelago located within the Magellanic sub-Antarctic ecoregion (Rozzi et al. 2012; Fig. 1.3). This large and remote wilderness area extends from 47 – 56°S, lacks industrial and urban development, and does not have terrestrial connectivity to other landmasses (Rozzi et al 2006). In addition, more than 70% of its native vegetation cover is still conserved, and human population density is very low (0.14 inhabitants/km^2) (Rozzi et al 2006). The Magellanic sub-Antarctic ecoregion is encompassed within the South American temperate forest biome (Fig. 1.4), which is the largest existing temperate forest in the southern hemisphere (Rozzi et al. 2012). Therefore, the southernmost forests of the world located within the CHBR (Silander 2000) serve as an important conservation area for sub-Antarctic biodiversity, including birds.

In the terrestrial transition zone of the CHBR is Navarino Island, Chile (55°04’S, 67°40’W; Fig. 1.4). On the northern coast of this Island is located Omora Ethnobotanical Park (54°56’ – 54°59’S, 67°38’ – 67°42’W), a public-private protected area created in 2000 to facilitate long-term interdisciplinary research, education, and biocultural conservation (Rozzi et al 2006; Fig.

1.4). Omora park extends from the Beagle Channel towards the interior of the island, encompassing 1069 ha and 920 m in elevational range (Rozzi et al. 2010, Rozzi and Jiménez 2014a). This altitudinal gradient allows for the presence of different types of forest in Omora Park, from evergreen forest at sea level to deciduous forest at the tree line (Rozzi et al. 2006; Fig. 1.5). Evergreen forests are dominated by *Nothofagus betuloides*, and deciduous forests are dominated by *N. pumilio* and *N. antarctica* (Rozzi et al. 2006). At mid elevation there are mixed evergreen-deciduous forests dominated by *N. betuloides* and *N. pumilio* (Rozzi et al. 2006; Fig 1.5). The climate of Omora Park is oceanic, with little temperature and precipitation fluctuation from season to season (Rozzi and Jiménez 2014a). Average monthly temperatures range from 1.9 – 10.8°C and monthly precipitation from 15 – 55 mm (Rozzi and Jiménez 2014a).

1.4 Chapter Descriptions

Following this general introduction (Chapter 1), in Chapter 2, I describe and compare the breeding strategies (i.e., nest dimensions, nest height from the ground, egg laying rhythm, clutch size, length of the developmental periods, breeding phenology, and diversity of nesting substrate) of five passerine birds that inhabit sub-Antarctic forests on Navarino Island. Additionally, for *T. falcklandii*, I compare its breeding strategies to another population breeding at lower latitude (39°S) in Araucania Region, Chile. I show that, on Navarino Island, *E. albiceps* starts laying eggs about 2 months later than most species. Additionally, *T. falcklandii* breeding on Navarino Island nest closer to the ground and have larger clutch sizes than those breeding in Araucania Region. This chapter has been published in Revista Chilena de Historia Natural (Jara et al. 2019).

Birds can maximize their reproductive success through careful selection of nest-sites.

Nest predation has been identified as one of the major factors influencing nest-site selection (Martin 1987, 1993; Reidy and Thompson 2018). In Chapter 3, I identify the main nest predators of forest-dwelling passerines on Navarino Island. Furthermore, I examine two hypotheses by which nest placement reduces predation, and thus, increases reproductive success. The `total-foliage' hypothesis predicts that nests concealed in vegetation should have higher survival. The `predator proximity' hypothesis, originally proposed in my study, states that nests placed farther from predators would have higher survival. I test the importance of habitat characteristics on nest-site selection, and determine how habitat characteristics and temporal variables influence daily nest survival rate. I identify the native raptor *Milvago chimango* as the main nest predator and contrary to my expectation, the introduced mammal *Neovison vison* has currently little impact on forest nest survival. I also found support for both the total-foliage and the predator proximity hypotheses. Moreover, I identify a potential disconnect between birds assessing the risk of predation (and selecting the appropriate nest-site) and the actual risk of predation, resulting in birds selecting riskier sites for nesting. In this chapter, I discuss the potential explanations and implications of this apparent disconnection. This chapter has been published in PeerJ (Jara et al. 2020).

For migratory birds, breeding success can also be affected by carry-over effects of events happening in the wintering ground (Dolman and Sutherland 1995, Marra et al. 1998, Newton 2008, López Calderón et al. 2019). The strength of carry-over effects can be shaped by the degree of connectivity between the breeding and the wintering ground (i.e., migratory connectivity) (Myers et al. 1987, Webster et al. 2002, Marra et al. 2006). In Chapter 4, I investigate the migratory connectivity of *E. albiceps*, one of the two migratory forest passerines that breeds on Navarino Island, and the longest-distance migrant flycatcher within South America (Chesser 2005, Jiménez et al. 2016). Using light-level geolocators, I tracked annual movement of 15 individuals breeding on Navarino Island, Chile (54° S). I combined this data with movement data of another 15 individuals of *E. albiceps* breeding in Esquel (42° S), also located within the temperate rainforests of South America. I showed that during winter there was extensive temporal and spatial overlap of individuals from both breeding sites, resulting in weak migratory connectivity.

Finally, in Chapter 5, I synthesize the main findings of these studies and discuss the possible ecological implications for passerines breeding in the southernmost forest of the world. Furthermore, I suggest future studies on the ecology and migratory movement of these species to better understand the factors affecting their population dynamics.

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1.6 Tables and Figures

Figure 1.1: Study species (a) *Phrygilus patagonicus*, (b) *Anairetes parulus*, (c) *Turdus falcklandii*, (d) *Elaenia albiceps chilensis*, and (e) *Zonotrichia capensis*. Photos by Omar Barroso

Figure 1.2: Map of South America showing the distributional division of migrant passerines during winter. This division is based on the winter location of an arc-shaped zone. Birds in group 1 breed in temperate regions and winter in warm humid lowland tropical zones, north and east of this division (South American Temperate-Tropical, SATT); birds in group 2 breed in cool regions and spend winter in temperate zones, south and west of the division (South American Cool-Temperate, SACT). Map reproduced from Joseph (1996).

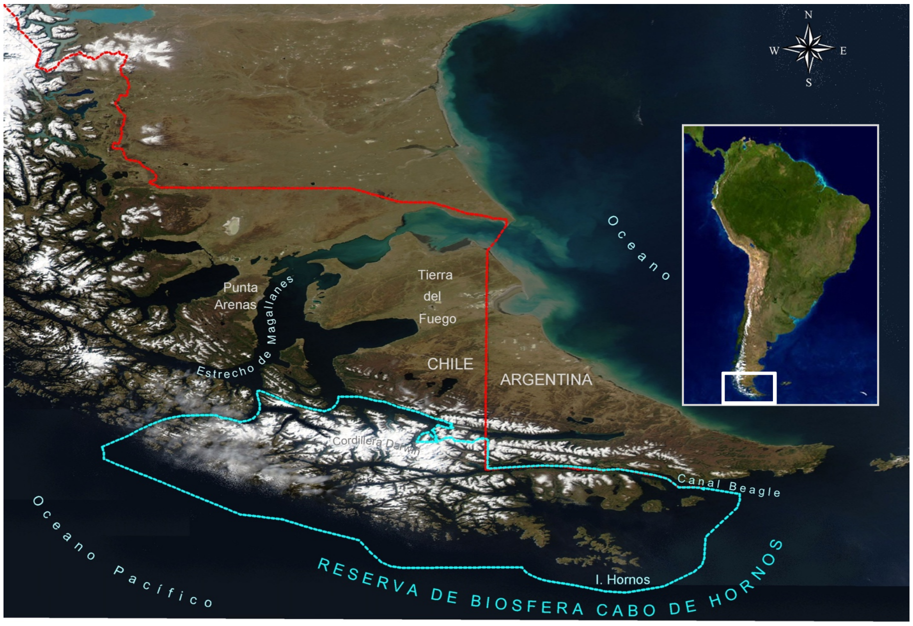

Figure 1.3: Cape Horne Biosphere Reserve (CHBR) (56°S). This reserve includes the archipelago south of Tierra del Fuego Island, in southern South America, and hosts the southernmost-forested ecosystem in the world. Map reproduced from Rozzi et al. (2006).

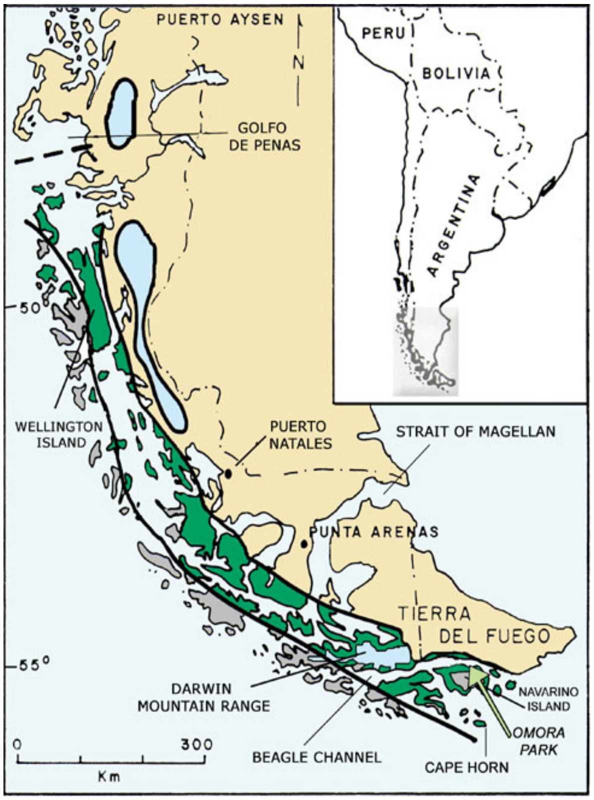

Figure 1.4: Location of Navarino Island and Omora Park and the southern end of South America. Dark green shows the sub-Antarctic Magellanic evergreen rainforest ecoregion, one of the world's most pristine ecoregions (Mittermeier et al. 2003). Map reproduced from Rozzi et al (2006).

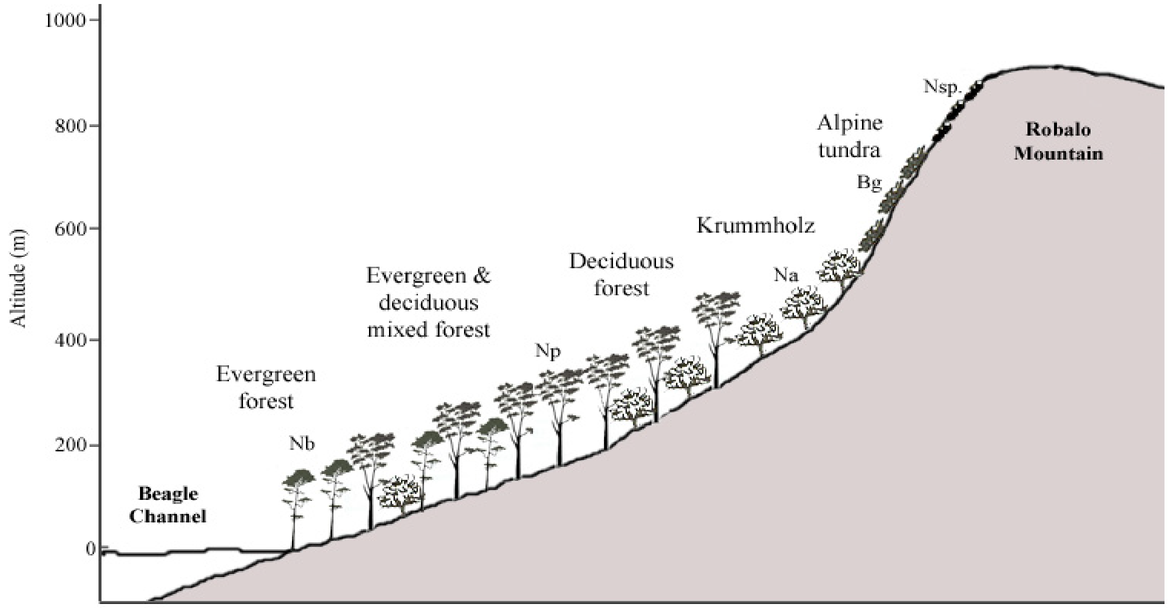

Figure 1.5: Altitudinal gradient of forests in Omora Park, Navarino Island, Chile (54°56′ – 54°59′S, 67°38′ – 67°42′W). Starting at sea level forests are: evergreen dominated by *Nothofagus betuloides* (Nb), mixed evergreen-deciduous dominated by *N. betuloides* and *N. pumilio* (Np), and deciduous dominated by *N. pumilio* and *N. antarctica* (Na). Above the tree line the habitat is dominated by cushion plants (e.g. *Bolax gummifera*, Bg) at lower levels, and by lichens (*Neuropogon sp*., Nsp) at higher levels. Figure reproduced from Rozzi et al. (2006).

CHAPTER 2

BREEDING STRATEGIES OF OPEN-CUP-NESTING BIRDS IN SUB-ANTARCTIC FORESTS OF NAVARINO ISLAND, CHILE*

2.1 Abstract

There is limited knowledge about the breeding strategies of birds inhabiting in South American temperate forests. This is particularly true for open-cup forest passerines breeding at high latitudes (> 42°). To better understand the ecology of these species, in this study we described and compared the breeding strategies (i.e., nest dimensions, nest height from the ground, egg laying rhythm, clutch size, length of the developmental periods, breeding phenology, and diversity of nesting substrate) of five passerine birds that inhabit sub-Antarctic ecosystems. During three breeding seasons (2014–2017), we monitored 103 nests of the five most abundant open-cup forest-dwelling passerines (*Phrygilus patagonicus, Anairetes parulus, Turdus falcklandii, Elaenia albiceps,* and *Zonotrichia capensis*) on Navarino Island (55°S), Cape Horn Biosphere Reserve (CHBR), southern Chile. Additionally, we compared the breeding strategies of *T. falcklandii* to another population breeding at lower latitude (39°S). Most of the species started laying eggs the last week of September; only *E. albiceps* started two months later. During the breeding season of 2016-2017 both *E. albiceps* and *Z. capensis* started laying eggs earlier than the previous year. *Anairetes parulus* and *Z. capensis* were the most specialized in terms of nesting substrate. *Turdus falcklandii* had larger clutch sizes and nested closer to the

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ground on Navarino Island compared to the northern population, which might put this and other ground nesting species of this island at a higher risk of predation by the recently introduced American mink (*Neovison vison*). Our five study species breed exclusively in open-cups (not in cavities) in sub-Antarctic forests, and some of them built their nests closer to the ground compared to populations breeding at lower latitudes. This may be associated with the lack of terrestrial predators on Navarino Island. Our study opens further questions about the mechanisms driving differences in breeding strategies among populations.

Keywords: Anairetes parulus, Elaenia albiceps, Latitude, Nesting, Phrygilus patagonicus, Turdus falcklandii, Zonotrichia capensis

2.2 Introduction

Despite important advances in understanding avian life history traits for many biomes, current knowledge about the breeding strategies of forest birds from southwestern South America (35°-56°S) is still very limited. Existing information for many species is based on the few studies that have been conducted in the northern section of this biome (35–42°S) (Lazo and Anabalón 1992, Rozzi et al. 1996, Estades 1999, Escobar et al. 2004, Marín 2015) and/or mostly on cavity nesters (Ippi et al. 2012, Quilodrán et al. 2012, Altamirano et al. 2015, Botero-Delgadillo et al. 2015). In this work we investigate bird reproduction of open-cup nesters at high latitudes, to provide the foundation for future hypotheses testing about breeding strategies that might affect fitness.

The southernmost forested archipelagoes of the sub-Antarctic Magellanic ecoregion are embedded in the Cape Horn Biosphere Reserve (CHBR) (Rozzi et al. 2006). Navarino Island (55°S) is the main island in this protected area, and its forests provide breeding and/or foraging habitat for approximately 24–28 species of birds (Ippi et al. 2009, Rozzi 2010). In these forests, the lack of herpetofauna and limited number of terrestrial mammals makes birds the dominant terrestrial vertebrates (Rozzi and Jiménez 2014a). The most common open-cup nesting species are the Patagonian Sierra-Finch (*Phrygilus patagonicus),* Tufted Tit-Tyrant (*Anairetes parulus*)*,* Austral Thrush (*Turdus falcklandii*)*,* White-crested Elaenia (*Elaenia albiceps),* and Rufous-collared Sparrow (*Zonotrichia capensis*) (Rozzi and Jiménez 2014a). Despite being locally abundant, little is known about the ecology and breeding strategies of these passerines inhabiting sub-Antarctic forests.

In Chile, these five species have extensive breeding ranges from Cape Horn (56ºS) to the following northernmost latitudinal limits: *P. patagonicus* to 35°S, *A. parulus* to 25°S, *T. falcklandii* to 27°S, *E. albiceps* to 29°S, and *Z. capensis* to 33°S, (Medrano et al. 2018). Passerines breeding in sub-Antarctic forests are exposed to different abiotic and biotic conditions, which could result in different breeding strategies from those breeding at lower latitudes of South American temperate forests (35–42°S). For example, mean temperature during the breeding season (September–February) does not exceed 8°C in the sub-Antarctic forests, whereas in northern sections mean temperature can reach up to 18°C (Explorador Climático 2017). In addition, at latitudes higher than 47°S, the forest understory is much sparser and open, and lacks the dense growth of native and abundant bamboo species of *Chusquea* spp., which characterizes the understory of temperate forests north of 45ºS (Matthei 1997). The different environmental conditions may affect the breeding strategies of these species, expressed as different breeding phenologies and different resource specializations from those reported in northern habitats (Ibarra and Martin 2015). Furthermore, studying the breeding phenology of these species could aid the understanding of how these species could respond to global and local changes in the long-term.

In addition, until the recent introduction of the American mink (*Neovison vison*) (Rozzi and Sherriffs 2003), most forested islands south of Tierra del Fuego lacked mammalian predators (Anderson et al. 2006). Therefore, forest avifauna has evolved free of this predation pressure, leaving diurnal and nocturnal raptors as the top predators in this ecosystem. This creates an opportunity to investigate how birds have responded to the lack of ground predation pressure as compared to northern mainland populations where they evolved with a myriad of predators (Zúñiga et al. 2008, Altamirano et al. 2013).

Here, we studied the breeding strategies of *P. patagonicus, A. parulus, T. falcklandii, E. albiceps,* and *Z. capensis* in the sub-Antarctic forests on Navarino Island, investigating three general goals, and two questions focused on *T. falklandii*. (1) We characterized and compared the breeding strategies of the five species by describing their (a) nest dimensions, (b) nest height from the ground, (c) egg laying rhythm, (d) clutch size, and (e) length of the developmental periods. (2) We characterized their breeding phenology, including inter-annual variations by recording egg-laying dates of species and conducting comparisons between two breeding seasons. Given that *E. albiceps* arrives at the breeding ground considerably later (Rozzi and Jiménez 2014a), we predicted it to start laying eggs later in the season compared to the other species. (3) We characterized the breeding habitat by quantifying breadth of nesting substrate. We expected to find differences given that anecdotal information available for these species has described some as habitat generalists, while others as more habitat specialists (Escobar et al. 2004, Ibarra and Martin 2015). (4) We tested if *T. falcklandii* places its nests closer to the ground on Navarino Island as compared to mainland populations. Given the absence of native mammal predators on Navarino Island (Rozzi and Jiménez 2014a), we predicted that *T. falcklandii* would place their nests closer to the ground compared to mainland populations. Finally, (5) we tested for differences in clutch size between Navarino Island and mainland populations of *T. falcklandii.* Following the pattern of larger clutch size towards higher latitudes (Lack 1968, Cardillo 2002, Jetz et al. 2008), we expected larger clutch sizes for *T. falcklandii* breeding on Navarino Island than farther north.

2.3 Methods

2.3.1 Study Area

We conducted our study on the northern coast of Navarino Island (55°S; Fig. 2.1). There, the forests are composed of a mixture of evergreen and deciduous species, and an understory of low shrubs, herbs, and diverse mosses (Rozzi et al. 2014). The elevational gradient in this area is characterized by sharp slopes, with the tree line at about 600 m.a.s.l. (Rozzi et al. 2006). The climate of the region is oceanic, with mild summers and winters, and with average temperatures of 10.8°C and 1.9°C, respectively. The annual rainfall of 467 mm is equally distributed throughout the year (Rozzi et al. 2014).

2.3.2 Data Collection

Our study included three breeding seasons between 2014 and 2017. During the first breeding season (2014 – 2015), we made exploratory observations from the end of November until early January. During the second (2015 – 2016) and third (2016 – 2017) seasons we included the whole breeding period, conducting observations from early October through mid-

February and January, respectively. We located active nests (i.e., having at least one egg or nestling) in the forest based on the observation of breeding or nesting behavior of adults (i.e., we followed adults to their nest, wherever the nests were placed). We also used a thermal imaging device (FLIR One, 2014 © FLIR® Systems, Inc.) to scan the vegetation where we thought there could be a nest based on adult behavior. After a nest was located, we deployed a camera trap (Bushnell Trophy Cam: Bushnell Corp., Overland Park, KS, USA) in front of it at varying distances depending on the habitat around the nest, but setting it at least 1 m away. We set cameras to take three pictures per detection with one minute delay. When a nest was located during the laying period, we delayed the deployment of the camera trap until the second half of the incubation period to avoid nest abandonment.

We typically checked nests every other day. During each nest visit, we first looked around to verify that no potential predators were nearby (particularly raptors perched) that could see our activity and could later prey on the nest. If a potential predator was present, we did not approach the nest at that time. After nest failure or fledging, we measured the nest (i.e., cup diameter, cup depth, nest diameter, and nest depth), height from the ground (measured to the rim of the nest), and recorded the substrate species (i.e., the plant species where the nest was located). For ground nests, we considered the substrate as the plant species that provided the most concealment within 30 cm of the nest (Martin et al. 1997). We determined nesting stage (i.e., laying, incubating, or nestling) and the duration of these stages based on the data from visits and pictures from the camera trap. For example, when a change in stage occurred between visits, we used pictures from the camera trap to determine when this change happened, based on adult behavior (i.e., a change from adult sitting on nest to adult bringing food to the nest indicated that eggs have hatched). For cases in which nests were located after the day the first egg was laid, we estimated this date by subtracting the average incubation and nestling period length (both determined for our region), and clutch size (assuming one egg was laid per day) (Martin et al. 1997). We estimated egg-laying rhythm as (# days between first and last egg laid)/(# of eggs laid), and report the minimum # of days required per egg. During the laying period, 90% of the visits occurred between 9:30 am and 2:30 pm, and nests were visited only once per day.

2.3.3 Statistical Analyses

We report nest dimensions (mean ± standard error [SE]) for all the species including nest diameter, nest depth, cup diameter, and cup depth. We also estimated a ratio (nest diameter/depth) for every species to describe the shape of the nest. In addition, we report the mean and SE for nest height from the ground, clutch size, and length of developmental periods.

We compared mean egg-laying date among species as a function of breeding season, species, and their interactions, using the non-parametric two-way ANOVA Scheirer-Ray-Hare (H) test. For *post hoc* pairwise comparisons we used a Nemenyi test with a Chi-squared approach (Pohlert 2014). We compared the distribution of egg-laying dates between breeding seasons for each species using a two-sample Kolmogorov-Smirnov (D) test. We plotted the distribution of egg-laying date over time for each breeding season using the beanplot (Kampstra 2008). Our statistical comparison did not include the first season (2014-2015) because our data did not represent a full breeding season. We considered $p < 0.05$ as significant for all statistical tests.

As an indicator of the degree of nesting-habitat specialization, for each species we quantified the breadth of nesting substrate with the standardized Levins' niche breadth index B_s (Levins 1968). The equation is $B = \frac{1}{\sum p_i^2}$, where B is Levins' measure of substrate breadth and p_i is the proportion of nests found on substrate i for a particular species. We standardized B as $B_{S=}\frac{B-1}{n-1}$, where n is the total number of substrates used by the species of interest (Colwell and Futuyma 1971). This index ranges from 0 to 1, with 1 indicating the broadest niche in terms of substrate used by a species. All analyses were performed with the R programing software (version 3.4.1) (R Developement Core Team 2018).

2.3.4 Comparison to Other Populations of *T. falcklandii*

We compared the breeding strategies of *T. falcklandii* that breeds on Navarino Island to those breeding in La Araucanía Region (39°S), Chile (Fig. 2.1). The study site in La Araucanía Region is also within the temperate forests of southern South America. Unlike Navarino Island, this region is inhabited by several ground predators of bird nests including carnivores and reptiles (Lazo and Anabalón 1992, Zapata et al. 2005, Zúñiga et al. 2008, Altamirano et al. 2013, Menezes and Marini 2017). As part of a different study in La Araucanía Region, nests of *T. falcklandii* were located by adult behavior (i.e., individuals exhibiting breeding behavior were followed). Data on these particular nests have not been published, but for more details on the methodology see (Altamirano et al. 2017). Using a Wilcoxon test (W) with continuity correction we compared the nest height from the ground and clutch size between *T. falcklandii* from Navarino Island and La Araucanía populations.

2.4 Results

On Navarino Island, we found 103 nests during the three seasons (*P. patagonicus* n = 17, *A. parulus* n = 16*, T. falcklandii* n = 8*, E. albiceps* n = 28, and *Z. capensis* n = 34). Most nests were found during the last two seasons (2015–2016 = 51, 2016–2017 = 42). Additional information on sample size per species by breeding season can be found in APPENDIX 2.1. All nests were open cups (Table 2.1). Regarding dimensions and the shape of the nests, two species built flat nests in which the diameter/depth ratio was 2 (*T. falcklandii*) or > 2 (*Z. capensis*). In contrast, the other three species built rounded nests in which the diameter/depth ratio were 1.2 for *A. parulus*, 1.6 for *P. patagonicus* and 1.5 for *E. albiceps* (Table 2.1). Additional information on nest building behavior is found in APPENDIX 2.2.

One species, *Z. capensis*, built its nest most often on the ground, or very close (< 5 cm) to it (Table 2.1). Two other species, *T. falcklandii* and *P. patagonicus*, built their nests occasionally on the ground, and on average at heights less than one meter above the ground. Only the two smallest species did not build nests on the ground and placed them on average above a meter off the ground, reaching branches as high as up to 8 m (*A. parulus*) or 3.5 m (*E. albiceps*) above the ground.

For the nests for which we were able to monitor the laying period, we estimated that the egg-laying rhythm for *P. patagonicus* was at least 1.1 days/egg (n = 2), for *A. parulus* was at least 2.25 days/egg (n = 1), for *E. albiceps* was at least 1.5 days/egg (n = 2), and for *Z. capensis* was 1 day/egg (n = 2). Clutch size was three eggs for three species (*A. parulus, T. falcklandii*, and *Z. capensis*), between three and four eggs for *P. patagonicus* and two eggs for *E. albiceps* (Table 2.2). Length of development periods (i.e., incubation and nestling) are shown in Table 2.2. When combining incubation and nestling periods, *A. parulus* had the longest developmental period (up to 32 days) and *Z. capensis* the shortest (22 days), assuming incubation starts when the last egg was laid. However, this might not necessarily be the case for every individual/species as we recorded one case of delayed incubation in *Z. capensis* (see APPENDIX 2.2).

Most species started laying eggs in September (Fig. 2.2). However, egg-laying date varied significantly among species ($H_4 = 43.0$, $p < 0.001$). *Elaenia albiceps* started breeding later (last week of November) than all other species ($p < 0.002$) except *P. patagonicus* ($p = 0.344$). Interestingly, we found annual differences in egg-laying date between the last two breeding seasons ($H_1 = 5.3$, $p = 0.022$), but no significant interaction between seasons and species was found ($H_4 = 1.7$, $p = 0.791$). Specifically, *E. albiceps* ($D = 0.8$, $p = 0.035$) and *Z. capensis* ($D = 0.7$, $p = 0.001$) started breeding earlier in the 2016–2017 season than in the previous season (Fig. 2.2). For the other species, we did not find statistical support for annual differences.

A total of 15 different substrates were used for nesting (Fig. 2.3). Of the five species studied here, *A. parulus* (standardized Levins' index $B_s = 0.31$) and *Z. capensis* ($B_s = 0.38$) were the most specialized in terms of nesting substrate, with the former preferring *Berberis microphylla* (Magellan Barberry) and the latter forbs and grasses (Fig. 2.3). By contrast, the most generalist species were *T. falcklandii* ($B_s = 0.87$) and *E. albiceps* ($B_s = 0.71$), which used up to six and eight different substrates, respectively, without selecting a particular one (Fig. 2.3).

In La Araucanía Region we found 12 nests of *T. falcklandii.* In contrast to the nests found on Navarino Island (all open-cup), all these nests were in non-excavated tree cavities (Table 2.1). Mean nest height from the ground was ten times higher for the population breeding in La Araucanía Region (mean = 389 cm) compared to Navarino Island (37 cm, n = 8; $W = 94$, $p < 0.001$; Fig. 2.4a; Table 2.1). Clutch size on Navarino Island (3.2 ± 0.2 eggs, n = 5) was larger than in La Araucanía Region (2.4 ± 0.2 eggs, n = 9; $W = 8$, $p = 0.034$; Fig. 2.4b).

2.5 Discussion

We report the first data on the breeding biology of the five most abundant open-cup forest-dwelling birds in their breeding grounds at the southernmost forests of the world. Although most of these species are facultative cavity nesters in other localities (Ojeda and Trejo 2002, Altamirano et al. 2017), we found they exclusively built open cup nests on Navarino Island. It is noteworthy that we found differences in nesting strategies of *T. falcklandii* breeding at different latitudes.

In general, the relative nest abundances for each species parallels their frequency of capture in the study area during the breeding season (Rozzi and Jiménez 2014b). The main exception is *P. patagonicus*, which was the most frequently captured bird (Rozzi and Jiménez 2014b), but represented only 17% of the nests we found. A possible explanation for this difference could be due to the difficulties in locating nests for this species. One cue we used to find nests was observing birds flushing from a nest. Unlike the other species, *P. patagonicus* did not flush from nests, even when we were less than 1 m away.

The observed nest characteristics for each species in our study generally agreed with those described in other locations (Housse 1945, Goodall et al. 1957, Johnson 1967, De la Peña 2006). However, farther north, four of our species have also been described nesting in cavities (Ojeda and Trejo 2002, Altamirano et al. 2017). Specifically, *T. falcklandii* has been described as a facultative cavity nester (10.1 – 90.0% of nests in tree cavities), *P. patagonicus* as a marginal cavity nester (1 – 10% of nests in cavities), and both *E. albiceps* and *Z. capensis* as incidental cavity nesters (< 1% of nests in cavities) (Ojeda and Trejo 2002, Altamirano et al. 2017). We did not find any active cavity nests for these species. This finding could be a response to the relatively low number of potential predators in the study area, as it is traditionally accepted that cavities confer protection from predators (Lack 1954, Nilsson 1986).

The fastest egg laying rhythm was for *Z. capensis* that laid daily, and the slowest was *A. parulus*, which separated eggs by more than two days. Only two previous studies reported this breeding trait, both referring to *Z. capensis*, indicating the same daily laying rhythm that we report here (Mason 1985, Mezquida 2003). If a nest was located after the first egg had been laid, then egg laying rhythm was taken into consideration when we estimated nest initiation date. In general, when this information is not available, authors assume one egg is laid per day (as we did in this study) (Martin et al. 1997, Mezquida 2003, Auer et al. 2007). However, as our records suggest, this does not necessarily apply to every passerine species. Given that some species, such as *A. parulus* and *E. albiceps*, might lay less than one egg per day, this assumption may bias estimation of egg laying date towards later in the season.

The present study is the first that reports developmental periods (i.e., incubation and nestling periods) for *P. patagonicus*, which lasted approximately one month from the start of incubation until chicks fledged (Table 2.2). Duration of these periods for *T. falcklandii* and *Z. capensis* were similar to those that have been described previously (Housse 1945, Mason 1985, Mezquida 2003, Fernández and Duré Ruiz 2007, Willson et al. 2014). The only records for *A. parulus* are from Housse (1945) who reports, without specifying the region, that incubation lasts 12 days and nestling 13 days. For this species, we observed longer developmental periods on Navarino Island (incubation = 15.5 days [n = 2], nestling = 16.1 [n=4]). Based on only one observation in an unknown location, Housse (1945) also described the incubation and nestling period of *E. albiceps* as 12 and 13 days, respectively. On Navarino Island we observed somewhat longer developmental periods for this species (incubation = 14.5 days [n = 3], nestling =16.1 days [n = 6]). Our observations agree with the developmental periods of *E. albiceps* on Chiloé Island, Chile, where incubation lasts 14 – 15 days and nestling 14 – 17 days (Willson et al. 2014).

As predicted, we found that *E. albiceps* breeds later compared to most of the other species. This is the only long-distance forest migratory species that breeds on Navarino Island (Chesser 2005, Jiménez et al. 2016) and is the last to arrive on the breeding ground (in October). The other migratory species, *Z. capensis*, arrives in August from central Chile (Rozzi and Jiménez 2014b). The same pattern occurs in central Chile, where *E. albiceps* breeds later than other sympatric species (Estades 1999); it arrives in September but it starts breeding in November, with its peak of breeding activity in December (Escobar et al. 2004). Interestingly, over 3500 km south on Navarino Island, *E. albiceps* also starts breeding in November, with its peak of breeding activity also in December, even though it arrives to the island in mid-October, a month later than the northern population. Therefore, on Navarino Island *E. albiceps* starts breeding considerably sooner (one month) after arrival compared to lower latitude populations. This raises evolutionary questions about adaptive behaviors for a small bird worth studying along the latitudinal breeding range.

Both *E. albiceps* and *Z. capensis* started breeding earlier during the last breeding season. Coincidently, spring temperatures during the 2016–2017 breeding season were higher than the previous season. In September, the mean temperature in 2015 was 1.83°C (SE = 0.51) and in 2016 it was 5.33°C (SE = 0.34) (Explorador Climático 2017). Given our limited data, we were not able to test whether there is an effect of spring temperature on egg-laying date. However, we urge scientists to implement a long-term monitoring program on the breeding phenology of these species on Navarino Island to assess whether climate change may be affecting local species. Contrastingly to these two species, we did not find annual differences in laying dates for the resident species; nevertheless, this result should be taken with caution given the limited sample size. In addition, there seems to be only one brood per species per season (Fig 2.2).

As predicted, species differed in substrate used for nesting, but overall, they were generalists. The substrates used by the five species on Navarino Island coincided with reports from other locations (Housse 1945, Goodall et al. 1957, Mezquida 2003); however, no previous study has reported a substrate diversity index. We found that *E. albiceps* had one of the highest diversity indexes, suggesting that this species may be more adaptable to potential changes in its environment. Noteworthy, *E. albiceps* uses exotic pine plantations as a substrate for nesting in central Chile (Escobar et al. 2004). In contrast, a less substrate-generalist species such as *A. parulus*, might not be able to respond to the rapid landscape changes that are currently taking place on Navarino Island.

As predicted, and possibly associated with the lack of terrestrial predators on Navarino Island (Rozzi and Sherriffs 2003), we found that two of the five birds in our study area were primarily ground nesters, and the other three placed nests on average less than 1.5 m from the ground. Interestingly, *E. albiceps* and *T. falcklandii* on Navarino Island nested closer to the ground than populations farther north. In our study area, *E. albiceps* nested between 0.4 m and 3.6 m from the ground, with 50% of them under 1 m. This only partially corresponds to what has been described for this species in a study conducted in central Chile (35°S), where this species nested between 0.5 and 15 m above the ground (Escobar et al. 2004). Additionally, Housse (1945) described three nests for this species, all at least 2 m above the ground. *Turdus falcklandii* also nested very close to the ground (median = 10 cm) on Navarino Island, which differs from what we found in La Araucanía Region (median = 319 cm) and with previous studies that have reported this species building its nests at least a few meters from the ground. In our study area, the average canopy height was about 15 m, but we did not find nests near that height for either *E. albiceps* or *T. falcklandii*, even though these birds often feed in the canopy. Unlike the forest community in La Araucanía Region, which includes ground predators such as wild cats and foxes (Zúñiga et al. 2008, Altamirano et al. 2013), on Navarino Island birds evolved in the absence of ground mammalian predators. It could be that by placing their nests closer to the ground in this island, birds avoid nest depredation by native raptors (Marzluff 1988, Peluc et al. 2008). Today, this behavior could, however, put Navarino birds at a higher risk of predation by recently introduced ground predators, particularly the American mink (*N. vison*) (Rozzi and Sherriffs 2003, Schüttler et al. 2009). Similar naivety to mink predation given the lack of coevolution was suggested for small rodents on this island (Crego et al. 2018). However, because previous reports (Housse 1945, Goodall et al. 1957), as well as our analysis, are based on a limited sample size, these comparisons should be taken with caution. Furthermore, placing nests closer to the ground could be a response to different biotic and abiotic factors, such as understory structure, temperature, and/or wind speed.

We found no major differences when comparing clutch sizes for the five passerines from Navarino Island to the descriptions available in the literature (Germain 1860, Bullock 1929, Millie 1938, Housse 1945, Goodall et al. 1957, Barros 1958, Johnson 1967, Woods 1975, Mason

1985, De la Peña 1988, Lazo and Anabalón 1992, Estades 1999, Mezquida 2003, Auer et al. 2007, Fernández and Duré Ruiz 2007, Barron et al. 2010, Hayes 2014, Marín 2015). However, when we made this comparison based on our data the difference in clutch size was clear. As predicted, the clutch size for *T. falcklandii* on Navarino Island (3 – 4 eggs) was statistically higher than La Araucanía Region (2 – 3 eggs). This corresponds with the frequently described pattern of larger clutch size at higher latitudes (Lack 1954, Cardillo 2002, Jetz et al. 2008, Rose and Lyon 2013). It also corresponds with the pattern of larger clutch size for species nesting on islands compared to continents (Covas 2012). Finally, it could also be that a larger clutch size of *T. falcklandii* on Navarino Island is an interaction between latitude and island habitat (Covas 2012).Conclusions

This study represents the first extensive description of breeding strategies for the five most abundant forest passerine species of the sub-Antarctic forests. All of them breed exclusively in open-cups (not in cavities), and some of them built their nests closer to the ground compared to populations breeding at lower latitudes. This may be associated with the lack of terrestrial predators on Navarino Island. Our results suggest that populations of bird species with extensive breeding ranges exhibit changes along latitudinal gradients in terms of nest placement and other aspects of their breeding biology. This study opens further questions regarding the mechanisms driving differences in breeding strategies among populations.

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2.7 Documentation

2.7.1 Declarations

- Ethics approval and consent to participate: Not applicable
- Consent for publication: Not applicable
- Availability of data and material: The datasets supporting the conclusions of this article are included within the article (and its appendices).
- Competing interests: The authors declare that they have no competing interests

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2.7.3 Authors' Contributions

RFJ conducted the research, edited and analyzed the data, and wrote the draft manuscript. RFJ and RDC conceived the idea, while RR and JEJ provided considerable resources for the research, and contributed substantially to the paper. RDC, FJA, TAA, and JTI contributed with data collection and made significant contributions editing the manuscript. All authors read and approved the final manuscript.

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2.9 Tables and Figures

Table 2.1: Nest height from ground, and nest and cavity dimensions (cm) of five forest-nesting bird species.

Nest Dimensions*	Height from Ground	Nest Diameter	Nest Depth	Nest Diam/Depth Ratio	Cup Diameter	Cup Depth
P. patagonicus (n = 17)	74.5 ± 10.5 (0-140; 90)	12.7 ± 0.6	7.8 ± 0.6	1.6	7.5 ± 0.4	6.0 ± 1.6
T. falcklandii (n = 8)	36.5 ± 19.9 (0-133; 10)	16.6 ± 1.2	8.4 ± 2.5	2.0	9.0 ± 1.2	5.0 ± 0.7
A. parulus (n = 16)	130.1± 45.5 (43-800; 78)	8.4 ± 0.3	6.9 ± 0.4	1.2	4.1 ± 0.3	3.7 ± 0.4
E. albiceps (n = 28)	121.0 ± 14.1 (40-355; 99)	10.2 ± 0.4	6.9 ± 0.5	1.5	5.4 ± 0.2	3.4 ± 0.2
Z. capensis (n = 34)	3.7 ± 2.2 (0-55; 0)	14.0 ± 1.0	5.9 ± 0.6	2.4	6.6 ± 0.4	4.0 ± 0.3
Cavity Dimensions†	**Height from Ground**	**Entrance Diameter**	**Entrance Height**	**Interior Depth**	**Interior Height**	**DCH‡**
T. falcklandii (n = 12)	388.6 ± 78.3 (81-1120; 319)	13.2 ± 2.3	3.9 ± 34	34.2 ± 2.4	22.0 ± 4.4	56.1 ± 4.1

Data are expressed as means ± 1 standard error (SE). In addition, for height from the ground, we report range and median in parenthesis. *Measurements of nests found on Navarino Island. † Measurements of the cavities used for nesting by *T. falcklandii* in La Araucanía Region. ‡ DCH = Diameter of the trunk at the cavity height.

Table 2.2: Clutch size and duration of incubation and nestling periods

	Clutch Size	Incubation (Days)	Nestling (Days)
P. patagonicus	3.5 ± 0.3 (11)	13.4 ± 1.0 (5)	15.5 ± 0.9 (5)
A. parulus	3.0 ± 0.2 (7)	15.5 ± 2.5 (2)	16.1 ± 0.4 (4)
*T. falcklandii**	3.2 ± 0.2 (5)	-	16.5 ± 0.5 (2)
E. albiceps	2.2 ± 0.1 (18)	14.5 ± 0.9 (3)	16.1 ± 0.4 (6)
Z. capensis	3.0 ± 0.1 (23)	11.3 ± 0.3 (2)	12.3 ± 0.2 (6)

Data are expressed as means ± 1 SE with sample size in parenthesis. * We were not able to determine the exact incubation period because all the nests found were either in the incubation or nestling period.

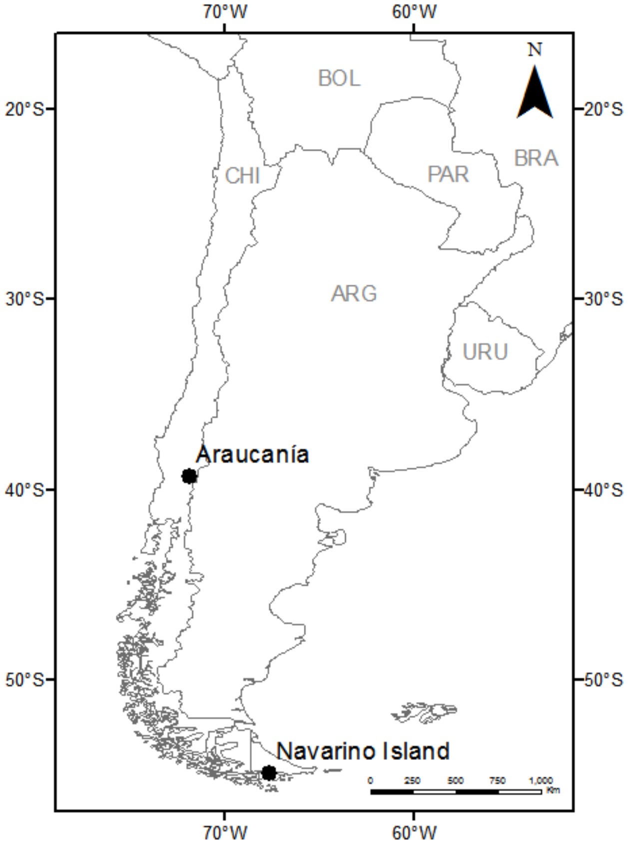

Figure 2.1: Map showing the study sites. Navarino Island was the main study area, and we also present data from La Araucanía Region for *Turdus falcklandii*.

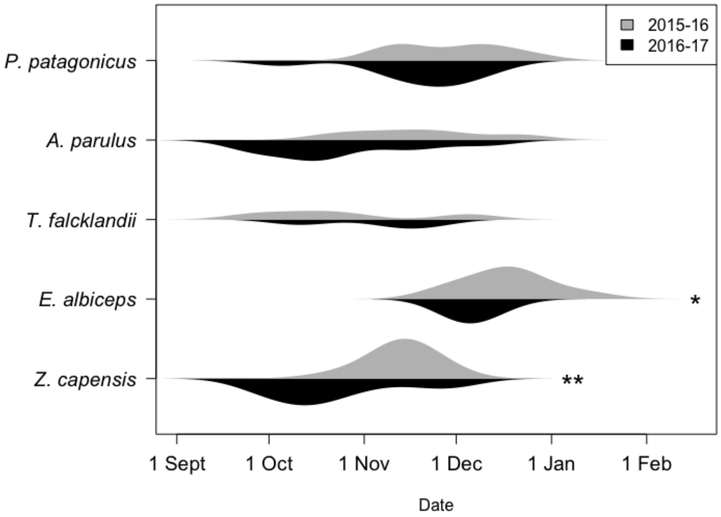

Figure 2.2: Egg-laying date for five open-cup forest-nesting birds that breed on Navarino Island, southern Chile. Sample sizes per season are as follow: *P. patagonicus* 2015–16 = 7 and 2016–17 = 9, *A. parulus* 2015–16 = 5 and 2016–17 = 9, *T. falcklandii* 2015–16 = 4 and 2016–17 = 3, *E. albiceps* 2015–16 = 15 and 2016–17 = 5, and *Z. capensis* 2015-16 = 17 and 2016-17 = 15. ** = $0.001 < P < 0.01$, * = $0.01 < P < 0.05$ for the difference between seasons assessed with a two-sample Kolmogorov-Smirnov test.

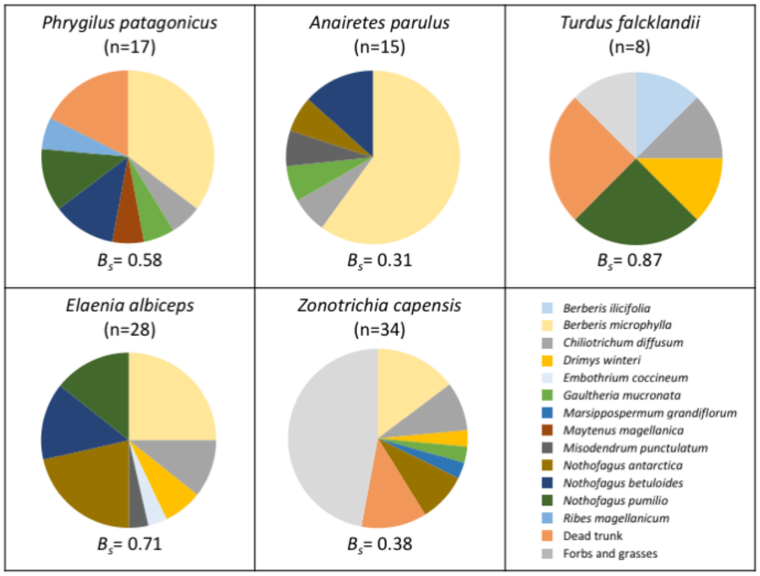

Figure 2.3: Substrates used for nesting by five open-cup forest-nesting passerines that breed on Navarino Island (55°S), Cape Horn Biosphere Reserve, Chile. Sample sizes are in parentheses. B_s represents the standardized Levins' niche breadth index.

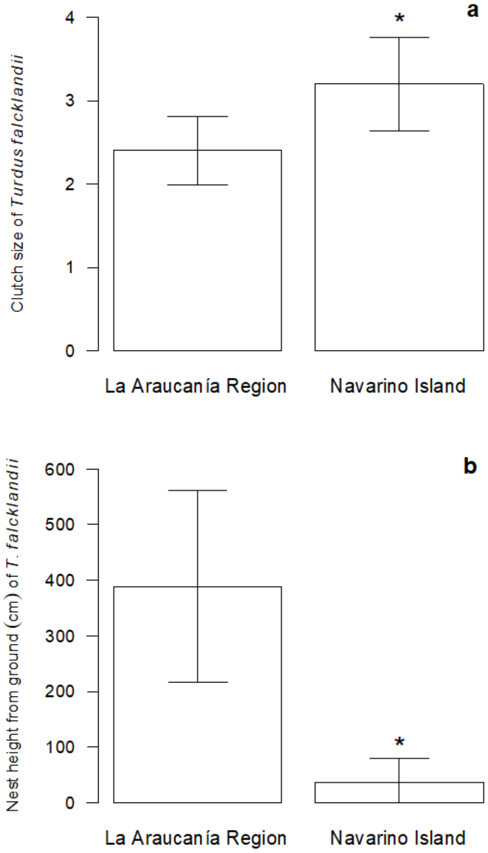

Figure 2.4: Comparison of nesting strategies of *Turdus falcklandii* between different populations. (a) Nest height (cm from the ground) for La Araucanía Region (*n* = 12) and Navarino Island (*n* = 8)

breeding populations. (b) Clutch size for La Araucanía Region (*n* = 9) and Navarino Island (*n* = 5). Bar heights represent mean value, and vertical bars represent 95% Confidence Interval. * represents statistical difference compared to La Araucanía Region.

2.10 Appendices

Appendix 2-A.1: Number of nests by breeding season for five open-cup forest-nesting birds that breed on Navarino Island, southern Chile.

Species	Total	Breeding Season		
		2014-15	2015-16	2016-17
P. patagonicus	17	1	7	9
A. parulus	16	1	6	9
T. falcklandii[*]	8	0	5	3
E. albiceps	28	8	15	5
Z. capensis	34	0	18	16
Total	103	10	51	42

Appendix 2-A.2: Observations of Previously Unknown Breeding Strategies for *Zonotrichia capensis*, *Elaenia albiceps*, and *Anairetes parulus*

2-A.2.1 Delayed Incubation - *Zonotrichia capensis*

We observed an individual of *Zonotrichia capensis* that laid the last of three eggs on November 3, 2015. When we monitored the nest on November 5, the parents were not around when we approached it (uncommon behavior for this species in our study site) and the eggs were cold (temperature a few degrees above 0˚ C, measured with the thermal camera). We suspected the nest had been abandoned (at that point we had not installed the camera trap yet). However, when we monitored the nest on November 7 there was an adult sitting on the nest, thus the incubation process had started. Therefore, after the last egg was laid, the start of incubation was delayed at least two days. Coincidently, on October 31 (the first egg was found the morning of Nov 1) a snow storm that lasted about a week hit the area. Particularly, the night of November 3 (when the last egg was laid) accumulated at least 4 inches of snow on the ground. The minimum T˚ that day was -0.6˚ C and maximum 10.5˚ C. On November 5 the nest was surrounded by snow (but not covered as it was built under vegetation). By November 7 the storm had passed and the temperature increased (min = 3.5˚ C and max = 12˚ C). Thus, it could be that what we observed was that even though the clutch was complete, the start of incubation was delayed, likely until the snow storm had passed.

2-A.2.2 Nest Building Behavior - *Elaenia albiceps*

- *A roof for the nest*

On November 28, 2014, we found a nest of *Elaenia albiceps* were the female was incubating two eggs. The nest was placed on a branch of *Nothofagus antarctica*, close to the ground (55 cm) and not very concealed. The tree was partially dead and the nest located in the dead portion of it. After looking closely, we noticed that exactly above the nest, at about 10 – 15 cm from it, there was a group of twigs that, due to its location, it was serving the purpose of overhead concealment (it provided 70% concealment, estimated from 1 m above de nest looking down). It was interesting to note that most of the twigs had a similar length (between 15 –20 cm) and were well organized, parallel to each other (as parallel as it can be considering these were natural twigs), forming what looked to us to be a roof. The twigs were all dead and located under a bigger branch and on top of smaller ones (Picture 1). Because of how well organized it was, it did not look like the twigs arrived there naturally (i.e. as the effect of wind, or falling directly from the tree). This looked more like a structure that may have been have been built by some organism, maybe by the parent/s, to protect the nest. However, because we did not witness this process, this is merely speculation.

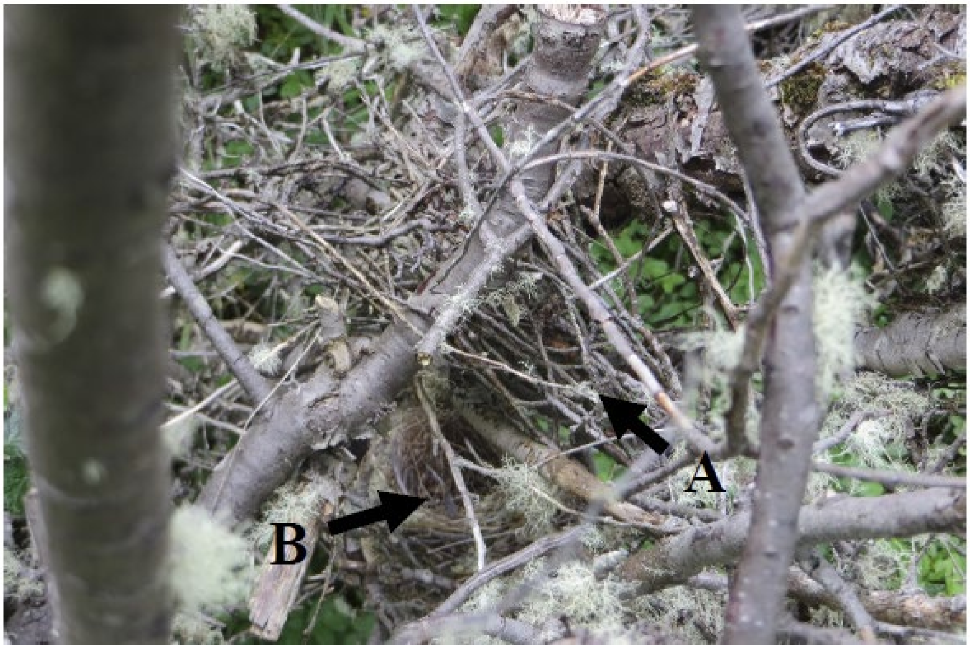

Figure A.1: Right in the center of the picture are the twigs (A), underneath a bigger branch. Below this structure, at about 10-15 cm, was the nest (B). This is the structure that provided most of the overhead concealment for this nest.

- *Removal of nesting material*

The following year, on November 29, and as part of another study, we deployed a camera trap in front of the same nest described above (i.e. it was an old nest then). Due to the weathering of winter and exposure to wind, the nest was partially damaged, but still held its shape (the roof was gone though). Soon after we installed the camera, an individual of *E. albiceps* visited the nest. For the following two days, it visited at least 20 times, taking material from the nest and transporting it away in its bill. It repeated the process until it completely removed the old nest. The time of the year that this happened overlaps with the time when individuals of this species are actively building their nests. Thus, it is likely that the material was utilized to build another nest.

- *Building a nest inside another nest*

As part of the same study where we deployed camera traps in front of old nests, we detected some unusual activity. We were monitoring an old nest of *Turdus falcklandii* (based on the shape, nest material, and size, as we never saw this nest while it was active). On November 29, after four days of having deployed the camera, we observed an individual of *E. albiceps* visiting the nest. It stood on the edge of the nest, then sat and moved around inside. For the following 22 days, it continued to visit the nest sporadically (every 2-5 days) repeating the behavior described above, sometimes spending up to seven minutes inside the nest. The morning of December 21 it brought material to the nest. It continued to bring material, such as lichens and dry grass, for the following three days. During this period, it actively worked on shaping the nest. December 24, after spending the whole morning in the nest, was the last day that the Elaenia spent significant time on it. Unfortunately, because of the angle of the camera, we could not see the content of the nest to see if it had laid eggs. On December 25, an Austral Blackbird (*Curaeus curaeus*) visited the nest. The following day as well as on December 28, a native raptor, Chimango Caracara (*Milvago chimango*), also visited the nest. The pictures did not show whether these birds ate any content of the nest or not (the camera was set to trigger three pictures per detection with a delay of one minute), but after this event the Elaenia did not spend time in the nest, and it only visited briefly twice a few days later (although we do not know if it was the same individual).

- *Nest building behavior* – Anairetes parulus*: The translocated nest*

On December 10, 2015, we located a nest of *Anairetes parulus* that was being built. It was placed on a *Gaultheria mucronata*, but mostly concealed by *Chiliotrichum diffusum*. At the time we located it, it had most of the external structure in place, exhibiting a clear cup shape. There was no internal lining yet. We decided not to disturb the building process and the bird, and came back to visit the nest four days later. To our surprise, the cup was not there anymore, and only a few grasses were left in the spot where the nest had previously been placed. As we were documenting this, a pair of *A. parulus* approached us aggressively with alarm calls (common behavior for this species when an intruder is near their nest). We decided to hide and visually follow the parents. A few minutes later we saw one of them carrying material to a shrub. After they left to collect more material we approached the site and located the nest. It was almost finished and it was located only 3 m from the place we originally found a nest four days previous.

Many explanations or scenarios can be speculated here. Our field experience working with this species tells us that they are very territorial, exhibiting aggressive behavior against any intruder (either of the same or of a different species). Also, based on our observations, their territory is larger than 3 m^2. Finally, we have also observed that when one of the individuals of the pair disappears, the other continues to defend the territory for weeks after. Thus, is it likely that both nests were built by the same pair and maybe they reused the material from the first nest to build the second one. An alternative explanation is that both members of the couple disappeared and the territory was occupied by a new couple who started building their nest immediately.

CHAPTER 3

NEST-SITE SELECTION AND BREEDING SUCCESS OF PASSERINES IN THE WORLD'S SOUTHERNMOST FORESTS[*]

3.1 Abstract

Birds can maximize their reproductive success through careful selection of nest-sites. The 'total-foliage' hypothesis predicts that nests concealed in vegetation should have higher survival. We propose an additional hypothesis, the 'predator proximity' hypothesis, which states that nests placed farther from predators would have higher survival. We examined these hypotheses in the world's southernmost forests of Navarino Island, in the Cape Horn Biosphere reserve, Chile (55°S). This island has been free of mammalian ground predators until recently, and forest passerines have been subject to depredation only by diurnal and nocturnal raptors. During three breeding seasons (2014 – 2017), we monitored 104 nests for the five most abundant open-cup forest-dwelling passerines (*Elaenia albiceps*, *Zonotrichia capensis*, *Phrygilus patagonicus*, *Turdus falcklandii*, and *Anairetes parulus*). We identified nest predators using camera traps and assessed whether habitat characteristics affected nest-site selection and survival. Nest predation was the main cause of nest failure (71% of failed nests). *Milvago chimango* was the most common predator, depredating 13 (87%) of the 15 nests where we could identify a predator. By contrast the recently introduced mammal *Neovison vison*, the only ground predator, depredated one nest (7%). Species selected nest-sites with more understory cover and taller understory, which according to the total-foliage hypothesis would provide

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more concealment against both avian and mammal predators. However, these variables negatively influenced nest survival. The apparent disconnect between selecting nest-sites to avoid predation and the actual risk of predation could be due to recent changes in the predator assemblage driven by an increased abundance of native *M. chimango* associated with urban development, and/or the introduction of exotic mammalian ground predators to this island. These predator assemblage changes could have resulted in an ecological trap. Further research will be needed to assess hypotheses that could explain this mismatch between nest-site selection and nest survival.

Keywords: Anairetes parulus, Elaenia albiceps, Exotic species, Nesting, Phrygilus patagonicus, raptors, Turdus falcklandii, Zonotrichia capensis, Predation, Navarino, Island.

3.2 Introduction

Where do birds place their nests? This question has intrigued ornithologists since the early days of the discipline (Birkhead et al. 2014, Lovette and Fitzpatrick 2016). For open-cup nesters, early studies pointed to food availability as the most important factor for nest-site selection, but predation has been increasingly considered as another major factor (Martin 1987, 1993; Reidy and Thompson 2018). Predation can directly affect survival of eggs, juveniles, and adults, and has been identified as the main cause of nest failure in passerines (Nice 1957, Ricklefs 1969, Liebezeit and George 2002, Bellamy et al. 2018, Reidy and Thompson 2018). According to these studies, we predict that birds will select those habitat characteristics that reduce predation risk and thus increase the probabilities of nest survival (Jaenike and Holt 1991, Fontaine and Martin 2006).

Several hypotheses have been proposed to explain the mechanisms by which nest placement reduces predation. One of these, the ‘total-foliage’ hypothesis, predicts that nests located in sites with more surrounding foliage would have higher concealment, as well as more interference with the transmission of odors and sounds that could be detected by a predator. Thus, a larger amount of foliage reduces predation risk (Martin and Roper 1988, Martin 1993). In the present study we introduce another, but not mutually exclusive hypothesis, which we call the ‘predator proximity’ hypothesis. This hypothesis assesses types of predators according to their mode of attack, particularly aerial versus terrestrial. This hypothesis assumes that passerine birds select nest sites that avoid discovery and attack by the major type of predators in their ecosystem, and it predicts that: (i) when predation is dominated by aerial predators, birds will place nests near the ground and (ii), in contrast, when predation is dominated by ground predators, birds will place nests at greater height from the ground (Jara et al. 2019). Another factor that we consider in this hypothesis is canopy cover. Some aerial predators search for prey while perched in the canopy. Hence in habitats dominated by aerial predators that exhibit sit and wait behavior, we predict that passerine birds will place nests in sites where there is less canopy cover and/or where the canopy is taller (both factors, will effectively put raptors farther away from nests placed in the understory).

High-latitude forests offer ideal natural laboratories because they have a simpler structure compared to tropical forests (i.e., the canopy is dominated by a few species belonging to only one genus, and the understory has low abundance and richness of shrub species; Rozzi et al. 2008). Consequently, sub-Antarctic forests of South America provide unique opportunities to test the total-foliage and predator proximity hypotheses and collect evidence to understand the mechanisms that explain nest-site selection and nest survival. Navarino Island (55°S), located in the Cape Horn Biosphere Reserve, hosts the world's southernmost forests (Rozzi et al. 2012) and serves as the breeding ground to 28 bird species (Ippi et al. 2009, Rozzi 2010). Here, passerines are the most diverse and abundant group of terrestrial vertebrates, due to the absence of herpetofauna and the limited number of native terrestrial mammals (Dardanelli et al. 2014). Hence, nest-site selection takes place in the context of a simple assemblage of vertebrate predators, which until the end of the twentieth century included only diurnal and nocturnal raptors (e.g., *Accipiter chilensis*, *Caracara plancus*, *Glacidium nana*, *Falco sparverius*, *Milvago chimango*, and *Strix rufipes*; Ippi et al. 2009, Schüttler et al. 2009). Among the most common open-cup passerines breeding in these forests are the White-crested Elaenia (*Elaenia albiceps*), Rufous-collared Sparrow (*Zonotrichia capensis*), Patagonian Sierra-Finch (*Phrygilus patagonicus*), Austral Thrush (*Turdus falcklandii*), and Tufted Tit-Tyrant (*Anairetes parulus*) (Rozzi and Jiménez 2014). Although abundant across their range (Medrano et al. 2018), little is known about these species regarding their nesting habits and nest survival.

In other systems birds prefer to nest in sites with lower risk of depredation by avian predators (Sergio et al. 2003, Roos and Pärt 2004, Latif et al. 2012). On Navarino Island, bird nesting strategies also may be aimed at reducing the risk of depredation by raptors, the top native predators in this ecosystem. Preliminary evidence suggests that, for example, *T. falcklandii* on Navarino Island breeds closer to the ground than mainland populations (Jara et al. 2019) where the predator assemblage includes several terrestrial species such as wild cats and foxes (Zúñiga et al. 2008, Altamirano et al. 2013). However, the simple predator-prey system on Navarino Island, dominated almost exclusively by raptors, was disrupted two decades ago with the introduction of the American mink (*Neovison vison*) (Rozzi and Sherriffs

2003), and the rapid increase of feral domestic cats (*Felis catus*) and dogs (*Canis lupus familiaris*) (Rozzi et al. 2006b). These three exotic predators actively prey on passerine birds on Navarino Island (Schüttler et al. 2008, 2018), and worldwide (Ferreras and Macdonald 1999, Bartoszewicz and Zalewski 2003, Doherty et al. 2016). Hence, the arrival of these mammals presented a new predation pressure for birds nesting on Navarino Island and may represent an ecological trap for birds that evolved in the absence of terrestrial predators. The increasing abundance of these novel predators during the first two decades of the 21st century coincides with the rapid disappearance from the island of the Magellanic tapaculo (*Scytalopus magellanicus*), a small passerine with poor flying capacity that inhabits the understory of South American temperate forests (Rozzi et al. 1996). This bird was detected in the Omora Ethnobotanical Park until 2003 (Ippi et al. 2009), but not in recent surveys of the area (Rozzi and Jiménez 2014, R.D. Crego, 2015, pers. comm.).

According to the total-foliage hypothesis, to reduce the risk of predation, passerines should nest in sites that provide more nest concealment (Table 3.1). According to the predator proximity hypothesis, passerines should select nest-sites that avoid the presence of predators, thus reducing the risk of predation. Based on these hypotheses, we predicted that on Navarino Island birds place nests in sites with denser and taller understory, and would avoid placing nests close to the canopy (exposing them to perched raptors), or too close to the ground (exposing them to recently introduced ground predators) (Table 3.1). We also predicted that survival rates would be lower in nests located at these extremes of the vertical axis of the forest structure. To test these hypotheses, we collected data on forest-dwelling passerines in the world's southernmost forests with two general goals: i) to test the importance of habitat characteristics on nest-site selection, and ii) to determine how habitat characteristics and temporal variables influence daily nest survival rate (DSR). We examined habitat variables that are relevant for nest survival according to the total-foliage and predator proximity hypotheses (Table 3.2).

3.3 Materials and Methods

3.3.1 Study Site

The study site is located on the northern coast of Navarino Island (54°S), within the Cape Horn Biosphere Reserve, at the southern end of South America. Its forests encompass a mixture of only six tree species, and are dominated by the broadleaf evergreen species *Nothofagus betuloides* (Rozzi et al. 2008). The understory has low abundance and diversity of shrub species, but is covered by s diverse and dense carpet of bryophytes (Rozzi et al. 2008). The regional climate is oceanic, resulting in a mean rainfall of 467 mm homogeneously distributed throughout the year, and in low annual temperature range, with a mean temperature of 10.8°C during warmest month in summer of and 1.9°C in the coldest month in winter (Rozzi et al. 2014). We surveyed for nests along 28 km throughout the northern shore forests; however, most of our efforts were concentrated within the more accessible and protected forests in the Omora Ethnobotanical Park (54°56’S, 67°39’W) (Rozzi et al. 2006a).

3.3.2 Nest Searching and Monitoring

We searched for nests during three breeding seasons: 2014 – 2015 (November – January), 2015 – 2016 (October – February) and 2016 – 2017 (October – January). We located active nests (under construction or containing at least one egg or young) by observing and following adults exhibiting signs of breeding or nesting behavior (carrying nest material, defending territory via alarm call, or carrying food or fecal sacs in their bills). In cases where we suspected the nest was in a well-delineated small area, but we were unable to see it, we scanned the vegetation with a thermal imaging camera (FLIR One, 2014 © FLIR® Systems, Inc.) to help locate the nest. We monitored active nests until young fledged or the nest failed, using both camera traps (Bushnell Trophy Cam: Bushnell Corp., Overland Park, KS, USA) and nest visitation. We deployed a camera trap between 1 – 3 m from the nest, depending on the surrounding vegetation. We set cameras to take three consecutive pictures per trigger (to increase chances of detecting the predator) and set a minute delay between triggers. We did not deploy cameras during the laying and early incubation period to prevent nest abandonment (Pietz and Granfors 2000). Approximately 10% of nests did not have cameras deployed at any stage. We typically visited nests every other day, unless we suspected a possible change of nest developmental stage (i.e., laying, incubation, nestling), in which case we visited them every day. During our nest visits, we verified that no predators were in the vicinity to observe our movements and later prey on the nest. Otherwise, we did not approach the nest at that time. We considered a nest successful if: i) the nest was empty and there were fledglings near it, ii) the camera detected them fledging in the absence of predators, and/or iii) the nest was empty and there was fecal matter on the rim of the nest or underneath it. We considered a nest to have failed if: i) there were dead nestlings on or around it, ii) it was empty (either intact or destroyed) before the earliest possible date of fledging, or iii) the eggs never hatched and there was no adult activity (i.e., abandoned during incubation).

3.3.3 Nest Site Characteristics

After nesting ended, we characterized the nest site following a modified BBIRD protocol (Martin et al. 1997). We measured habitat features that might influence the presence of predators and their ability to find nests, including potential perching substrates for raptors, and features that contribute to nest concealment. Within a 5-m radius plot, centered on the nest, we recorded nest height from ground (cm) (hereafter nest height, measured to the rim of the nest), mean nest coverage (%) (hereafter, concealment, estimated as the mean nest coverage measured from 1 m above the nest and from each cardinal direction), canopy cover (%), canopy height (m), understory cover (%), and understory height (cm). We also visually estimated a ground predator (i.e., American mink, rodents, dogs, and cats) accessibility index for every nest. This index ranged from 0 – 2 with 0 indicating nests that were difficult for a ground predator to access (i.e., nest placed high in a tree without easily accessible branches from the ground), 1 indicating nests that could be accessible from the ground (i.e., nest above ground level but of easy access for a ground predator through climbable branches), and 2 indicating nests that were placed on the ground and could have been easily accessed by potential ground predators.

We assessed nest site selection by measuring the same habitat characteristics (except those specifically related to the nest) using a paired-random plot for each nest. Each random plot was located at a random direction and random distance between 25 – 70 m from the nest. We chose this distance to maximize the chances the plot was within the home range of the breeding pair. However, because there is no information of home range sizes for these species, these distances are based on personal observations during the study. Before we measured habitat characteristics at the random-paired plot, we verified that active nests of these species were not present at the plot.

3.3.4 Statistical Analyses

3.3.4.1 Nest-Site Selection

We used logistic regression to investigate whether habitat characteristics influenced nest-site selection. We developed separate candidate models for each species to assess the probability that a plot contained a nest as a function of canopy cover, canopy height, understory cover, and understory height (Table 3.1). The response variable was either 1 or 0, indicating presence or absence of a nest, respectively. We ran these four univariate models, as well as all possible combinations of variables, excluding interactions, and estimated their Akaike information criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002). We selected the top model as the one having the lowest AIC_c, and evaluated parameter importance by determining whether or not their 95% confidence interval (CI) included zero (Tabachnick and Fidell 2001). Before fitting the models, we checked for outliers with Cook's distance (D), and for correlation among covariates ($r > 0.75$). For *T. falcklandii* there was one outlier for understory height (Cook's D > 1). Replacing this value with the mean of the variable produced similar results as the original value. Furthermore, this variable did not have a meaningful effect on the response variable (see Results). Therefore, we conducted the analysis with this outlier in the data. We used χ^2 tests to determine goodness of fit of the final models, accepting the model if $p > 0.05$. We calculated the odds ratio to determine the effect of significant habitat predictor variables on the likelihood of a plot containing a nest.

3.3.4.2 Nest Survival

We used the logistic exposure method (Shaffer 2004) to investigate temporal and habitat variables that influenced daily nest survival rate (DSR) by species (Table 3.2). We evaluated alternative models using a two-stage process. First, we evaluated temporal variables: nest age (days since first egg was laid; linear vs quadratic effects), nest stage (egg [laying and incubation] vs nestling), and day of year (linear vs quadratic effects). We used the best model from this first stage (the one with lowest AIC_c) as the starting model and evaluated habitat variables in the second stage: concealment, canopy cover, canopy height, understory height, understory density, nest height (linear vs quadratic effects), and ground predator accessibility index. From the second stage, we selected the model with lowest AIC_c as the final model for each species. We evaluated the importance of each parameter in the final model by determining whether their 95% CI included zero (Tabachnick and Fidell 2001). For both stages, we built candidate models using all possible combinations of variables, excluding interactions. Finally, we assessed the goodness of fit of the final models with χ^2 tests, accepting the model if $p > 0.05$. We estimated overall nest survival with the final DSR model for every species, holding continuous variables at their standardized mean value ($\overline{x} = 0$). For models with categorical variables, we estimated a separate DSR for each level of the variable(s). To estimate total survival, we raised DSR to an exponent equal to the average number of risk days (i.e., either per nesting stage or whole nesting cycle) per species. We used duration of incubation and nestling periods determined for these species in the same study area (Jara et al. 2019). Because the duration of incubation of *T. falcklandii* is still unknown, we used 13 days as it is the average incubation of *T. migratorius* (Ehrlich et al. 1988).

For the two species with largest number of nests (*E. albiceps* n = 27 and *Z. capensis* n = 35) we used generalized linear mixed models (R package lme4 v1.1.18.1; Bates et al. 2015), using breeding season as a random factor to control for annual differences. For the other three species (*P. patagonicus* n = 16*, T. falcklandii* n = 7, and *A. parulus* n = 14), sample size was insufficient for mixed model convergence. Therefore, we used generalized linear models (R Developement Core Team 2018) and excluded breeding season from the analysis, which was correlated with ground predator index for these three species. Furthermore, in a prior analysis we determined that breeding season did not have a meaningful effect on DSR for any of these three species. We checked for outliers with Cook's distance, correlation among continuous variables ($r > 0.75$), and correlation among categorical variables (assessed with a χ^2 test $p < 0.05$). For *T. falcklandii* there was one outlier for concealment (Cook's D > 1) that did not affect model results. Therefore, we conducted all the analyses with this outlier in the data. The only significant correlation among covariates was between canopy height and understory height ($r = -0.97$) for *T. falcklandii*. We included understory height in the candidate models because it would be easier to measure in the field for future studies. For *Z. capensis,* we only evaluated explanatory variables for nests that were on the ground because all three nests above the ground were successful (there was quasi-complete separation of data points). We replaced missing values with the mean of the variable (Acock 2005). Across species and variables, 2.6% of exposure periods — the time between nest visits — had missing values. All continuous variables were standardized to a mean of zero with one unit of standard deviation for analysis (Schielzeth 2010).

Before we fit nest survival models for each species, we evaluated the potential for a researcher effect on DSR based on camera deployment and nest visitation. Deploying a camera and/or visiting a nest could negatively affect DSR because parents could abandon their nests due to the disturbance. To evaluate the effect of camera presence, we incorporated an indicator variable where 1 = nests with a camera for that exposure period, and 0 = nests without a camera for that exposure period. To evaluate the effect of visits on DSR we created a continuous variable of cumulative number of visits. For this, we assumed that the effect of visiting a nest was delayed (it occurred after we left the nest) and it was higher the more times we visited a nest. If either camera or visit effect were significant, we kept the variable(s) in the final model. All analyses were performed in R 3.5.1 (R Developement Core Team 2018).

3.4 Results

3.4.1 Nest-Site Selection

We located 104 nests for the five species during three breeding seasons (*E. albiceps* n = 28, *Z. capensis* n = 35*, P. patagonicus* n = 17*, T. falcklandii* n = 8, and *A. parulus* n = 16). Nest-site habitat characteristics varied both within and among species (APPENDIX 3.1). Understory cover positively influenced nest-site selection in three of the five species (*Z. capensis*, *P. patagonicus,* and *A. parulus*) (Fig. 3.1 and Table 3.3). The odds of a plot containing a nest of any of these three species increased by a factor of 1.03 with every 1% increase in understory cover. Conversely, this parameter negatively influenced nest-site selection for *E. albiceps*; however, its 95% CI overlapped zero (Table 3.3). Understory height positively influenced nest-site selection of *P. patagonicus* (Fig. 3.1 and Table 3.3). Finally, there was a weak effect of understory height and canopy height on nest-site selection of *A. parulus* (Table 3.3). The models provided a good fit for the data (APPENDIX 3.2). For *T. falcklandii*, the best model was the null model (Table 3.3), indicating that none of the habitat characteristics that we measured showed strong effects on nest location. For a complete list of competing nest-site selection models, see APPENDIX 3.3.

3.4.2 Nest Survival

Of the 98 nests monitored that had a known fate, 52% of them failed (n = 51). The success rate per species was: *E. albiceps* 33% (n = 18), *Z. capensis* 44% (n = 34), *P. patagonicus* 63% (n = 16), *T. falcklandii* 43% (n = 7), and *A. parulus* 71% (n = 14). Of the 51 failed nests, 71% (n = 36) were due to predation. However, we were unable to identify the predator for 58% (n = 21) of the predation events (either the nest did not have a camera, or the camera failed to capture the event). We only identified three predators in the system: *M. chimango*, *N. vison* and *Glaucidium nana*, which accounted for 13 (87%), 1 (7%), and 1 (7%) of the depredated nests where we were able to identify the predator, respectively. *Milvago chimango* mostly depredated nestlings, whereas the latter two depredated eggs. Most predation events (69%) occurred during the nestling stage. Nest abandonment accounted for the remaining failed nests (n = 15). *Elaenia albiceps* and *T. falcklandii* had the highest abandonment rate, 26% (n = 7) and 29% (n = 2), respectively. In contrast, *P. patagonicus* and *A. parulus* abandoned 0% and 7% (n = 1) of their nests, respectively. *Zonotrichia capensis* abandoned 15% (n = 5) of its nests. Most abandonments (80%, n = 12) occurred during the incubation stage.

There was no evidence that researcher visitation affected DSR for any species. Thus, we examined the influence of temporal and habitat variables without considering the effect of our visits. *Zonotrichia capensis* was the only species where camera presence affected DSR; DSR increased by 22% when a camera was present ($\hat{\beta}$=1.97; 95% CI = 0.20 - 3.61; Fig. 3.2). Thus, for this species only, we proceeded with model selection by including a camera effect. Overall nesting success, based on DSR, was highest for *P. patagonicus* (87.0%) and *A. parulus* (99.9%), although the latter had a large amount of uncertainty around the mean estimate (Fig. 3.3).

For the DSR best-supported model of *E. albiceps*, we found that there was a positive, non-linear effect of nest age, as well as a negative effect of canopy cover and understory height (Fig. 3.4). For *Z. capensis*, in addition to the camera effect, DSR was strongly influenced by nest age (Fig. 3.2). DSR followed a similar pattern in the presence or absence of a camera, although survival was higher when a camera was present (Fig. 3.2A). Nestlings had a higher probability of surviving than eggs (Fig. 3.2). Overall nest survival during the egg stage (based on DSR) was 26.8% and 1.4%, in the presence and absence of cameras, respectively. Overall nest survival during the nestling stage was 89.2% and 45.0%, in the presence and absence of cameras, respectively (Fig. 3.3). DSR of *P. patagonicus* declined slightly with increasing nest age, understory cover, and understory height, and it strongly increased with more nest concealment (Fig. 3.5). For *T. falcklandii*, DSR declined with increasing understory cover (Fig. 3.6). Finally, we did not find any strong temporal or habitat effects on DSR for *A. parulus* (APPENDIX 3.4), though estimates showed a weak positive relationship with nest height and understory cover, and a positive quadratic relationship with nest age. The best-supported model for every species were good fits for the data (APPENDIX 3.2). For details on parameter estimates and CIs of the best-fitted nest survival models for each species, see APPENDIX 3.4. For a list of competing nest survival models, see APPENDIX 3.5.

3.5 Discussion

Our study provides new evidence that nest survival is influenced by predation. In addition to supporting previous studies that have found similar effects (Nice 1957, Ricklefs

1969, Liebezeit and George 2002, Bellamy et al. 2018, Reidy and Thompson 2018), we propose a novel hypothesis that combines characteristics of the *habitat* where the nest is built (canopy height, canopy cover, understory height, understory cover – total-foliage hypothesis) and of the *habits* of potential and actual predators (attack mode of aerial vs terrestrial predators – predator proximity hypothesis) that influence (a) nest-site selection and/or (b) nest survival (breeding success). In several cases, our sample sizes are limited, providing DSR estimates with considerable uncertainty. Therefore, our results should be taken as preliminary findings that represent baseline data for most of these species and, as a whole, provide support for both nest placement hypotheses.

3.5.1 Nest-Site Selection

We found percentage of understory cover was the most important habitat variable explaining nest-site selection, as it affected three of the five species. *Zonotrichia capensis*, *P. patagonicus* and *A. parulus* significantly preferred nesting sites with greater percentage of understory cover (Fig. 3.1). In addition, *P. patagonicus* preferred to nest in sites with taller understory (Fig. 3.1). These findings are consistent with the total-foliage hypothesis, which assumes that more foliage reduces the risk of depredation because it interferes with visual, auditory, and olfactory cues for avian and mammalian nest predators (Martin and Roper 1988, Martin 1993). Our findings for these three species are also consistent with previous studies on North American passerines, where species placed their nests in higher understory density and/or cover compared to non-nest random plots (Liebezeit and George 2002, Benson et al. 2009, Wynia 2013).

The other two passerine species, *E. albiceps* and *T. falcklandii*, selected nest sites with characteristics that were no different from random-paired plots. There are at least two possible explanations for this lack of effect. First, there is a pattern(s) that we were unable detect, perhaps due to limited sample size. Among the five species studied, *E. albiceps* and *T. falcklandii* exhibit the highest diversity of substrates used for nesting (Jara et al. 2019). In addition, *E. albiceps* and *T. falcklandii* nest at the high and low extremes of the vertical forest profile (Jara et al. 2019). The high heterogeneity of nesting substrate and position in the vertical axis of the forests could make it more complex to detect a pattern. Second, birds could be using an unstructured pattern for nest placement to deter predators from learning to scan for nests. This has been suggested for Hermit Thrush (*Catharus guttatu*; Martin and Roper 1988) and White-tailed Ptarmigan in North America (*Lagopus leucurus*; Wiebe and Martin 1998). This mechanism could also provide an explanation for the lack of significant association between nest-sites and the other two examined habitat variables (canopy height, canopy cover) in the five studied passerine species. More research with larger sample sizes is needed to elucidate this potential explanation for predator avoidance.

3.5.2 Nest Survival

3.5.2.1 Overall Nest Survival

Overall nest survival rates were high for *P. patagonicus* (87.0%) and *A. parulus* (99.9%) (Fig. 3.3). Nest survival rate recorded for *T. falcklandii* (48%) in the remote sub-Antarctic forests on Navarino Island is higher than the 20% that has been recorded for conspecific populations in temperate forests farther north in southwestern Patagonia on Chiloé Island (42°S), Chile (Willson et al. 2014). In contrast, survival rates were low for *E. albiceps* (31.0%) and *Z. capensis* (1.4 – 89.2% depending on camera presence and nest stage; Fig. 3.3). The low rates we found for these two species are similar to the rates found for conspecific populations of *E. albiceps* breeding on Chiloé Island, Chile (27% nest success) (Willson et al. 2014), and of *Z. capensis* breeding on central Monte Desert, Argentina (34°S; 9.4% nest success) (Mezquida and Marone 2001).

On Navarino Island, *T. falcklandii* builds its nests closer to the ground than farther north in the temperate forest biome (Jara et al. 2019). This could be associated with the fact that mammalian ground predators are present in temperate forests, but until recently, were absent on Navarino Island (Jara et al. 2019). Our results thus open the following new questions regarding survival rate: (1) Could the difference in proximity to prevailing predators explain the differences in nest-placement and nest survival in *T. falcklandii* at different latitudes? (2) Can the historical absence of ground mammalian predators and the presence of aerial bird predators on Navarino Island explain the high survival rates of *P. patagonicus* and *A. parulus*? (3) Why do the nest-survival rates of these species differ from the low rates detected for *E. albiceps* and *Z. capensis*?

3.5.2.2 Nest Predators

The main cause of nest failure (71%), regardless of species, was predation. This is consistent with passerines breeding in northern hemisphere forests (Ricklefs 1969, Murphy 1983, Martin 1993, Wilson and Cooper 1998, Duguay et al. 2001, Liebezeit and George 2002, Wesolowski and Tomialojc 2005). On Navarino Island, the native raptor *M. chimango* was the most common predator, accounting for 87% of the depredated nests where we were able to identify the predator, corresponding with previous studies on this island (Ibarra 2007, Schüttler et al. 2009, Maley et al. 2011, Crego 2017). On Chiloé Island, farther north within the south-temperate rainforest, *M. chimango* is also the main predator of passerine nests (Willson et al. 2001).

Milvago chimango is a common raptor in southern South America that inhabits a variety of habitat types, including forests, shrub-lands, steppes, and coastal ecosystems, as well as anthropogenic habitats such as plantations and cities (Rozzi et al. 1996). This opportunistic raptor is a generalist predator that uses a wide variety of foraging techniques. It can fish using a ‘glide-hover' technique, catch fleeing insects while flying through fires, or wade to catch frogs and tadpoles (del Hoyo et al. 1994, Sazima and Olmos 2009). In the forests of Navarino Island, it mostly searches for prey while perched and flying overhead (R.F. Jara and R.D. Crego personal observation 2015). On Navarino Island *M. chimango* also depredates nests irrespective of their height from the ground (Crego 2017). Consequently, it exerts a predation pressure from above (like other raptors) and from below (like ground predators). This suggests that birds on this island may have already developed nesting strategies to avoid ground predation pressure, even before mammalian ground predators were introduced. *Milvago chimango* populations increase with human disturbance, like those generated on Navarino Island during the last couple of decades by the king-crab industry dumping large quantities of shellfish exoskeletons. Thus, it is possible that this raptor’s population has increased on the study site over time, which would represent an ecological trap, because birds on this island evolved under different historical and current predator abundance conditions (Chalfoun and Schmidt 2012). We therefore recommend monitoring population growth and subsequent impact of *M. chimango* on nesting passerines in the Cape Horn Biosphere Reserve.

The only ground mammalian predator we identified was *N. vison*, which depredated 7%

of nests with a known predator. This semi-aquatic mustelid was introduced to Navarino Island at the end of the 20th century (Rozzi and Sherriffs 2003) and is known for its negative impacts on native birds on Navarino Island (Schüttler et al. 2008, 2009, Maley et al. 2011), and worldwide (Ferreras and Macdonald 1999, Nordström and Korpimäki 2004, Bonesi and Palazon 2007, Brzeziński et al. 2012). However, and contrary to our expectations, its nest depredation rate on passerines was very low. A possible explanation could be a mismatch between the periods of *N. vison's* peak activity in the forest (summer) (Crego 2017) and the onset of passerine nesting season (Spring) (Jara et al. 2019). Alternatively, because we were unable to identify the predator in 58% of the events, we may have underestimated the effect of this mustelid — and other potential predators such as feral cats and dogs — on nest survival, as birds are part of *N. vison* and cat diets (Schüttler et al. 2008, 2018). Contrary to previous findings on artificial nests (Willson et al. 2001, Maley et al. 2011), we found no evidence of nest predation by rodents or House Wrens (*Troglodytes aedon*). This may be because in our study of natural nests, parents can actively deter rodents and/or House Wrens (Jara et al. *in prep*).

3.5.2.3 Habitat and Temporal Effects on Nest Survival: Support for Nest Placement Hypotheses

Nest-site selection was positively influenced by higher percentage of understory cover (*Z. capensis, P. patagonicus,* and *A. parulus*) and taller understory (*P. patagonicus*) (Table 3.3). However, for *Z. capensis* and *A. parulus*, understory cover and understory height did not affect nest survival. Furthermore, for *P. patagonicus,* these two habitat characteristics had an opposite effect, negatively influencing DSR (Figs. 3.4C, 3.5B, 3.5C, and 3.6A). Thus, it seems that these species may be selecting nest-sites that not only have a neutral effect on nest survival, but actually decrease their survival rates. Given that predation was the main cause of nest failure, it is possible that there is a disconnect between birds assessing the risk of predation (and selecting the appropriate nest-site) and the actual risk of predation. This again might be due to the above-mentioned ecological trap regarding the increased abundance of *M. chimango* due to anthropogenic factors. Furthermore, passerine populations on this island have evolved with a different predator assemblage (i.e., only aerial predators), but this has been disrupted with the introduction of exotic mammalian ground predators to this island, and the rapid increase of feral domestic cats and dogs, less than 20 years ago. This ecological trap would imply a delay in the ability of birds to adapt nesting behavior in response to a new type and/or abundance of predators. Alternatively, the mismatch between nest-site selection and DSR also could be due to methodological problems (e.g., limited sample size, wrong choice of habitat variables, etc.), or ecological-evolutionary reasons (e.g., tradeoffs with other selection pressures such as microclimate and access to food, etc.) (reviewed by Chalfoun and Schmidt 2012). Further research will be needed to assess hypotheses that could explain this mismatch between nest-site selection and nest survival.

For two of the three species in which we found a nest age effect on DSR (*E. albiceps*, *Z. capensis*, and *P. patagonicus*), the pattern was similar (i.e., quadratic effect) even though its magnitude varied considerably (Figs. 3.2A and 3.4A). The low rates of nest failure during the laying and incubation periods suggest marginal effects of nest abandonment and depredation by *M. chimango* and *N. vison* (the only two identified predators during these nest stages) during the first half of the nesting cycle. Daily survival rates were lowest soon after hatching (Figs. 3.2A and 3.4A). This may reflect the sudden increase in cues to predators coming from nestlings (visual, auditory, and olfactory) and parents (visual and auditory, as their nest visitation frequency suddenly rises) (Cresswell 1997, Martin et al. 2000, Grant et al. 2005), which increases their vulnerability to predation. After reaching its lowest rate after hatching, nest survival increased steadily during the nestling period (Figs. 3.2A, and 3.4A). This pattern, which has previously been observed in passerines (Pietz and Granfors 2000, Grant et al. 2005), could be due to increased parental nest defense as nestlings get closer to fledging (Montgomerie and Weatherhead 1988). This is particularly relevant for these five species on Navarino Island, as they only have one brood per breeding season (Jara et al. 2019), and therefore have a greater incentive to protect their nest as young near fledging. Another non-exclusive explanation includes 'forced-fledging' of nestlings by potential predators (Pietz and Granfors 2000). Nestlings that are close to fledging age may avoid depredation by leaving the nest prematurely when they are at imminent risk. This behavior may decrease depredation-induced nest failures towards the end of the nesting cycle.

Higher nest concealment for *P. patagonicus* increased its nesting success (Fig. 3.5D), which is consistent with the total-foliage hypothesis (Martin and Roper 1988, Martin 1993). According to this hypothesis, predators have a harder time locating nests with higher concealment, because it may be harder to detect them visually, aurally, and/or olfactorily. It has been suggested that *M. chimango* can detect nests visually (Crego 2017), so it seems *P. patagonicus* may be trying to avoid being detected by nest predators in this system. The parental behavior of this passerine may also be an important contributing factor. *Phrygilus patagonicus* sits still on the nest in response to the presence of a predator, unlike what we observed for the other species, which flush considerably sooner and exhibit alarm behaviors

(R.F. Jara, personal observation 2015). In the other species, higher nest concealment may not improve nesting success due to their more agitated parental behavior that, in contrast to *P. patagonicus,* may counteract any concealment advantage.

We found that higher percentage of canopy cover above nests of *E. albiceps* decreased their nest survival (Fig. 3.4B). This is consistent with the predator proximity hypothesis where nests at higher risk of predation (i.e., aerial or ground) should have lower survival. More canopy cover allows for the presence of *M. chimango*, the most common nest predator we were able to identify, because this forest raptor not only nests in the canopy, but also uses branches in the canopy to perch and look for prey (R.F. Jara and R.D. Crego, personal observation 2015).

3.5.2.4 Camera Effect on Nest Survival

We found evidence that for *Z. capensis*, the presence of a camera increased DSR by 22%. This positive camera effect has been reported for other bird species or systems (Thompson III et al. 1999, Buler and Hamilton 2000, Pietz and Granfors 2000, Small 2005, reviewed by Richardson et al. 2009). Cameras may have a deterrent effect on predators, possibly through neophobia towards these devices, which would consequently reduce depredation of these nests. However, this is unlikely to be the case for our study system because *M. chimango* was the main nest predator across all five species, but we only found a camera effect for *Z. capensis*. This suggests *M. chimango* did not exhibit neophobia towards the cameras. Furthermore, this raptor has been described as having low neophobia (Biondi et al. 2010). Alternatively, there could be a bias introduced by delaying the camera deployment until later in the nesting cycle. Nests that failed earlier in the cycle, when the camera was absent, may then positively bias our estimates of DSR for nests with a camera later in the cycle. Finally, and possibly a more likely explanation, this result was an artifact of limited exposure periods without cameras (i.e., 7.7%; n = 83/1077).

3.6 Conclusions

This study provides the first data on nest-site selection and survival of open-cup-nesting passerines in sub-Antarctic forests. We also propose a novel hypothesis that represents a relationship between the habitat and type of predators. Although our study was conducted on a single location, this hypothesis could be tested for nest-site selection and nest survival in other regions. The bird species we studied selected nest-sites with more understory cover and taller understory, which according to the total-foliage hypothesis would provide more concealment against predators. However, more understory cover and taller understory decreased nest survival. There seems to be a disconnect between birds assessing the risk of predation (and selecting the appropriate nest-site) and the actual risk of predation, resulting in birds selecting riskier sites for nesting. This could be attributed to an ecological trap, where birds on this island evolved with a different predator assemblage, which has been disrupted with the introduction of exotic ground mammal predators to this island and/or the increased abundance of native *M. chimango* associated with urban development. Further research with larger sample size will be needed to assess hypotheses that could explain this mismatch between nest-site selection and nest survival.

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3.9 Tables and Figures

Table 3.1: Variables incorporated into candidate models assessing habitat characteristics influencing nest-site selection by five forest passerines on Navarino Island, Chile.

Variable	Hypothesis	Predictions	Rationale
Canopy cover	Predator proximity	Negatively associated with nest presence	More canopy cover allows for the presence of aerial predators, imposing a threat to nesting birds and their nests.
Canopy height	Predator proximity	Positively associated with nest presence	Higher canopy puts perched raptors farther away from birds nesting in the understory, making it harder to detect bird breeding activity.
Understory cover	Total-foliage	Positively associated with nest presence	More understory cover provides more visual nest concealment and interferes with the transmission of odors and sounds coming from the nest that could be detected by a predator.
Understory height	Predator proximity/Total-foliage	Positively associated with nest presence	Taller understory provides more nest concealment against predators, and allows for higher nest placement, which reduces accessibility for ground predators.

Table 3.2: Justification of variables incorporated into candidate models for estimating daily nest survival rate of five forest passerines on Navarino Island, Chile.

Model	Variable	Predictions	Rationale
Null	Intercept only	Nest survival is random	Assumes daily survival rate (DSR) is constant.
Temporal effects	Day of year	Negatively associated with DSR	Late nesters will have lower nest survival because of the overlap with increased depredation pressure in the forest interior (i.e. *N. vison*), due to their breeding dynamics.
	Nest age (linear vs quadratic effects) and nest stage	Negatively associated with DSR	Nest age and stage influence adult behavior around the nest (increased nest visitation for food provisioning), and increased noise and odor from nestlings. These cues could be detected by predators.

Model	Variable	Predictions	Rationale
Habitat effects	Concealment	Positively associated with DSR	Under the ‘total-foliage’ hypothesis, more nest concealment not only protects the nest and its content from predators, but also the adults entering and leaving it.
	Nest height off the ground (linear vs quadratic effects)	Positively associated with DSR	Under the ‘predator proximity’ hypothesis, nests closer to the ground will be more susceptible to ground predators
	Ground predator index	Negatively associated with DSR	Under the ‘predator proximity’ hypothesis, nests with higher index score will be more susceptible to predation.
	Canopy cover, canopy height, understory cover and understory height	Variables associated with nest-site selection will have equivalent effect on DSR.	Rationale of these variables’ effect on DSR is equivalent to that described in nest-site selection (Table 3.1).

Table 3.3: Parameter estimates (95% confidence interval) for the best model explaining nest-site selection by five forest-nesting bird species on Navarino Island, Chile, 2014 – 2017.

Species (n)	**Coefficients in the best model β (95% confidence interval)**		
	Understory cover	**Understory height**	**Canopy height**
Elaenia albiceps (22)	-0.13 (-0.298 – 0.004)		
Zonotrichia capensis (33)	0.03 (0.007 – 0.047)		
Phrygilus patagonicus (17)	0.03 (0.003 – 0.054)	0.02 (0.0003 – 0.0423)	
Turdus falcklandii (8)	a	a	a
Anairetes parulus (16)	0.03 (0.003 – 0.059)	0.02 (-0.0001 – 0.0538)	-0.19 (-0.482 – 0.026)

a. The final model for this species was the null model.

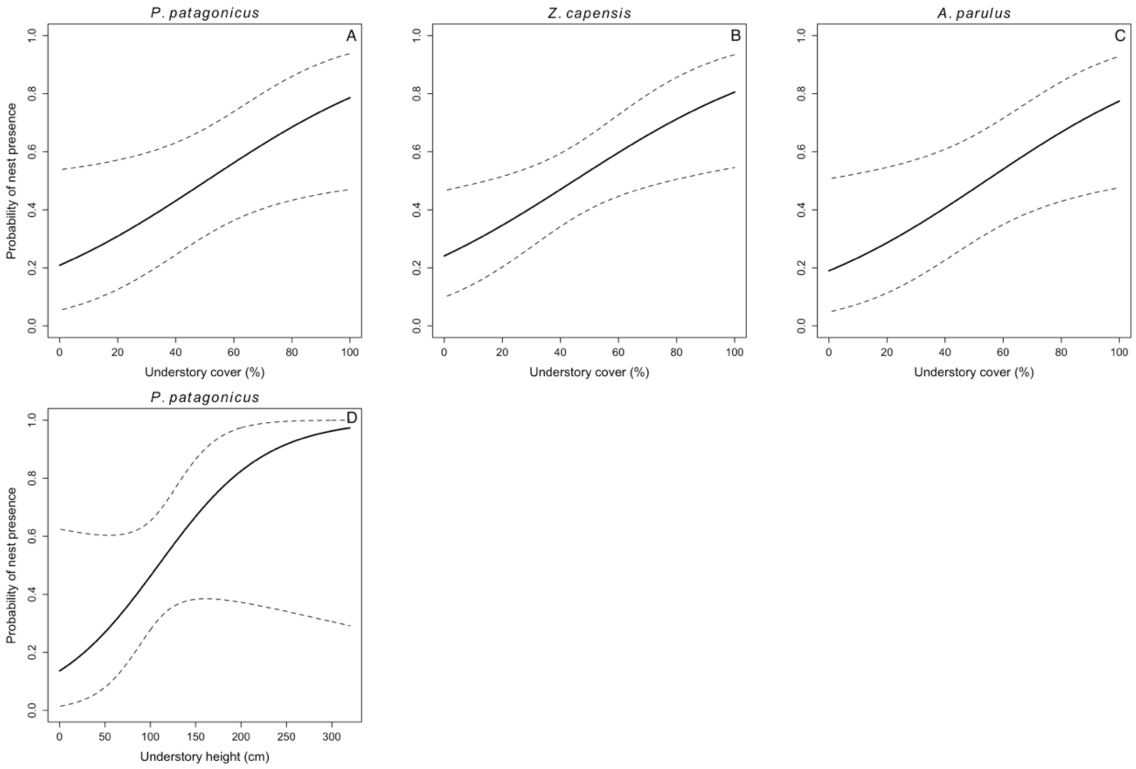

Figure 3.1: Probability of nest presence (and 95% CI) as a function of habitat characteristics for *P. patagonicus* (A and D), *Z. capensis* (B), and *A. parulus* (C) on Navarino Island, Chile, 2014-2017. We only present parameters of the final model for which their CI did not overlap zero.

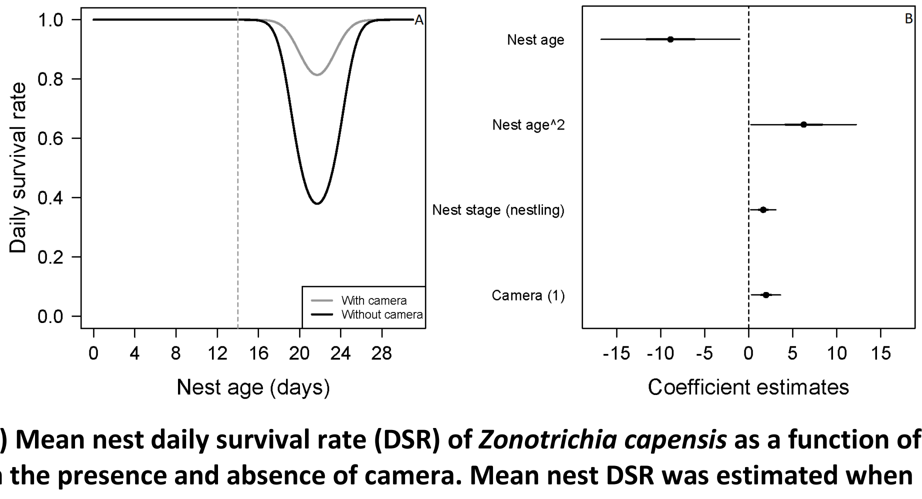

Figure 3.2: (A) Mean nest daily survival rate (DSR) of *Zonotrichia capensis* as a function of nest age and nest age^2, in the presence and absence of camera. Mean nest DSR was estimated when nest stage = nestling (1). Dashed line represents mean hatch day for this species (Jara et al. 2019). (B) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer lines) and 50% credible intervals (thick-inner lines).

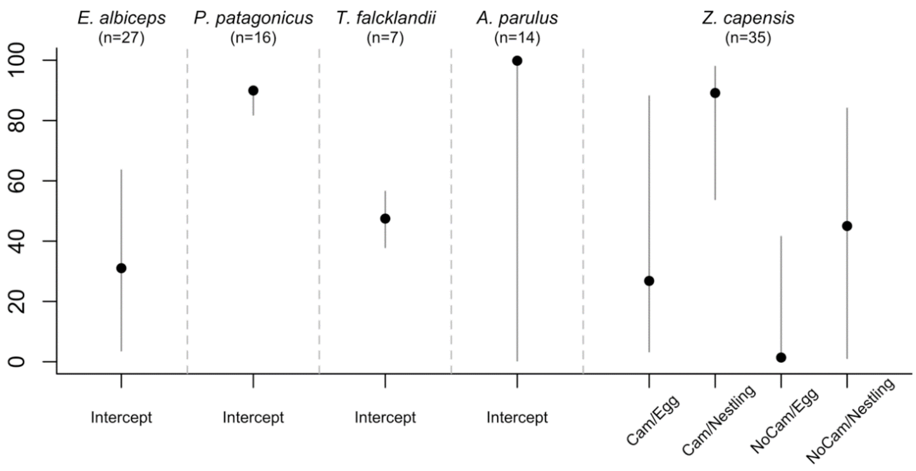

Figure 3.3: Overall nest survival rate by species. Estimated with the final DSR model for each species, holding continuous variables at their standardized mean value ($\bar{x}$ = 0). Therefore, for models in which all variables were continuous, the overall nest survival rate corresponds to the intercept. For *Z. capensis*, there were both continuous and categorical variables in the final model. Thus, we estimated separate survival rates for each level of the categorical variable(s) (i.e., camera presence vs camera absence, and egg vs nestling), while holding the continuous variables at their standardized mean value of 0. Once we obtained a DSR value, we raised it to an exponent representing the average number of days in the nesting cycle for each species.

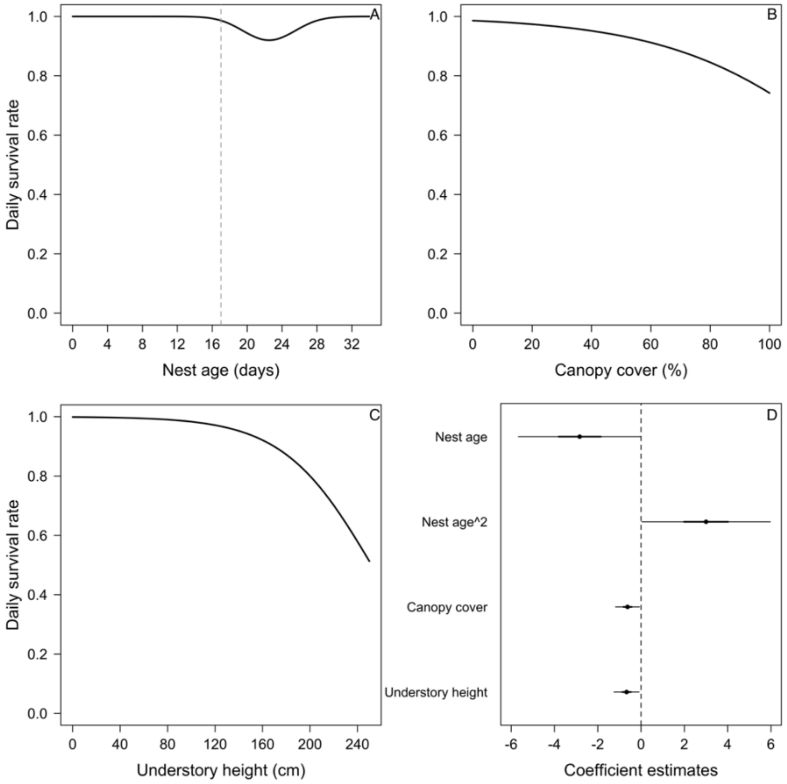

Figure 3.4: Mean nest daily survival rate (DSR) of *Elaenia albiceps* as a function of (A) nest age and nest age^2, (B) canopy cover, and (C) understory height. Mean nest DSR for each variable estimated

holding the other variables at their standardized mean value ($\bar{x}$ = 0). Dashed line in (A) represents the average hatch day for this species (Jara et al. 2019). (D) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer lines) and 50% credible intervals (thick-inner lines).

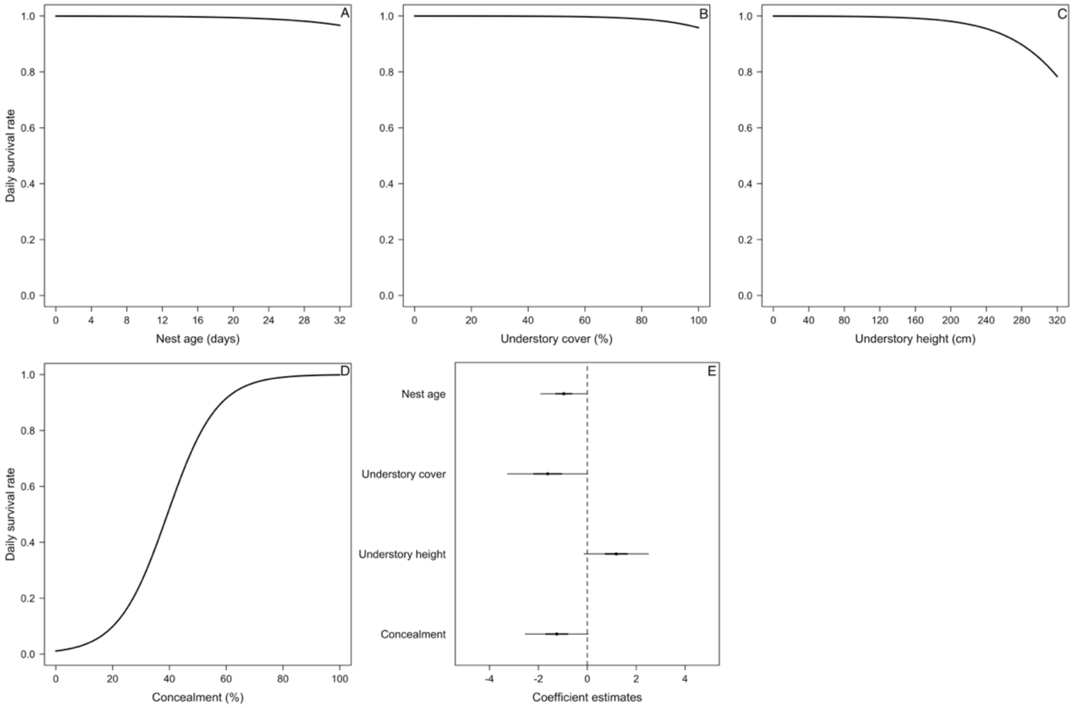

Figure 3.5: Mean nest daily survival rate (DSR) of *Phrygilus patagonicus* as a function of (A) nest age, (B) understory cover, (C) understory height, and (D) concealment. Mean nest DSR for each variable estimated holding the other variables to their standardized mean value ($\bar{x}$ = 0). (E) Coefficient estimates (filled circles) for the best model ± their 95% CI (thin-outer lines) and 50% credible intervals (thick-inner lines).

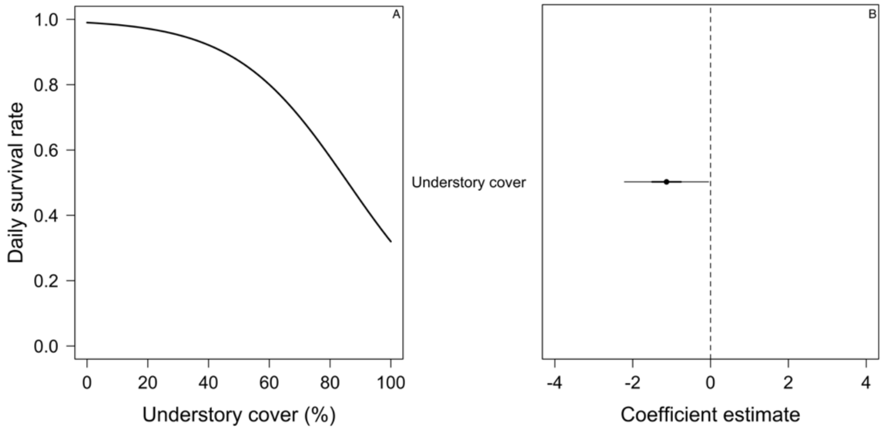

Figure 3.6: Mean nest daily survival rate (DSR) of *Turdus falcklandii* as a function of (A) understory cover. (B) Coefficient estimate (filled circle) for the best model ± its 95% CI (thin-outer lines) and 50% credible interval (thick-inner lines).

3.10 Appendices

Appendix 3-A.1: Mean value ± 2 standard error (SE) of habitat characteristics measured in nest plots of five forest-nesting bird species on Navarino Island, Chile, 2014-2017.

Species (n)	**Canopy Cover (%)**	**Canopy Height (m)**	**Understory Cover (%)**	**Understory Height (cm)**
E. albiceps (22)	37.8 ± 8.9	6.5 ± 1.7	39.4 ± 8.5	122.26 ± 16.9
Z. capensis (33)	26.8 ± 6.8	5.3 ± 1.2	45.0 ± 6.7	100.1 ± 9.9
P. patagonicus (17)	24.6 ± 10.6	10.0 ± 7.8	49.8 ± 12.0	107.6 ± 19.1
T. falcklandii (8)	46.4 ± 17.0	11.1 ± 4.2	30.3 ± 17.0	95.8 ± 20.6
A. parulus (16)	21.8 ± 11.2	4.3 ± 2.4	68.0 ± 13.8	95.8 ± 20.2

Appendix 3-A.2: Goodness of fit of final models of nest-site selection and daily survival rate, for five forest dwelling passerines on Navarino Island, Chile, 2014-2017.

We assessed this with χ^2 tests, accepting the model if $p > 0.05$.

Species	**Nest Site Selection Model**		**Daily Nest Survival Rate Model**	
	χ^2	***p*-value**	**χ^2**	***p*-value**
Elaenia albiceps	4.92	0.766	286.65	0.511
Zonotrichia capensis	8.78	0.361	162.87	1.000
Phrygilus patagonicus	10.95	0.205	0	1.000
Turdus falcklandii	*	*	17.78	1.000
Anairetes parulus	4.73	0.786	0	1.000

[*] The final model for this species is the null model

Appendix 3-A.3: Candidate models describing nest-site selection of five forest dwelling passerines on Navarino Island, Chile, 2014-2017

The habitat variables we tested included canopy cover, canopy height, understory cover, and understory height. Models are ranked by AICc, with the best supported model given in bold (i.e., the model with lowest AICc).

3-A.2.1 *Elaenia albiceps*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Canopy height	2	-28.77	61.7	0.00	0.203
~ Canopy height + understory height	3	-28.11	62.8	1.12	0.116
~ Canopy height + canopy cover	3	-28.25	63.1	1.38	0.101
~ Intercept	1	-30.50	63.1	1.39	0.101
~ Canopy height + canopy cover + understory height	4	-27.30	63.6	1.92	0.078
~ Canopy height + understory cover	3	-28.66	63.8	2.23	0.067
~ Understory height	2	-29.82	63.9	2.24	0.066
~ Canopy height + canopy cover + understory cover	4	-27.51	64.0	2.34	0.063
~ Understory cover	2	-30.36	65.0	3.31	0.039
~ Canopy height + understory height + understory cover	4	-28.11	65.2	3.54	0.035
~ Canopy cover	2	-30.50	65.3	3.58	0.034
~ Canopy height + canopy cover + understory height + understory cover	5	-26.86	65.3	3.60	0.034
~ Canopy cover + understory height	3	-29.76	66.1	4.42	0.022
~ Understory height + understory cover	3	-29.81	66.2	4.52	0.021
~ Canopy cover + understory cover	3	-30.25	67.1	5.38	0.014
~ Canopy cover + understory height + understory cover	4	-29.66	68.3	6.63	0.007

3-A.2.2 *Zonotrichia capensis*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory cover	2	-42.21	88.6	0.00	0.303
~ Understory cover + understory height	3	-41.79	90.0	1.36	0.153
~ Understory cover + canopy height	3	-42.07	90.5	1.93	0.116
~ Understory cover + canopy cover	3	-42.13	90.7	2.05	0.109
~ Understory cover + canopy height + canopy cover	4	-41.65	92.0	3.36	0.056

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory cover + understory height + canopy height	4	-41.71	92.1	3.48	0.053
~ Understory cover + understory height + canopy cover	4	-41.75	92.1	3.54	0.052
~ Understory height	2	-44.24	92.7	4.06	0.040
~ Intercept	1	-45.76	93.6	4.95	0.025
~ Understory cover + understory height + canopy height + canopy cover	5	-41.45	93.9	5.30	0.021
~ Understory height + canopy cover	3	-44.06	94.5	5.90	0.016
~ Understory height + canopy height	3	-44.19	94.8	6.16	0.014
~ Canopy cover	2	-45.36	94.9	6.30	0.013
~ Canopy height + canopy cover	3	-44.42	95.2	6.62	0.011
~ Canopy height	2	-45.59	95.4	6.76	0.010
~ Understory height + canopy height + canopy cover	4	-43.65	96.0	7.35	0.008

3-A.2.3 *Phrygilus patagonicus*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory cover	3	-18.84	44.5	0.00	0.283
~ Understory cover + understory height	2	-20.85	46.1	1.61	0.127
~ Understory cover + canopy height	4	-18.60	46.6	2.11	0.098
~ Understory cover + canopy cover	4	-18.68	46.7	2.25	0.092
~ Understory cover + canopy height + canopy cover	2	-21.41	47.2	2.72	0.073
~ Understory cover + understory height + canopy height	3	-20.23	47.3	2.79	0.070
~ Understory cover + understory height + canopy cover	3	-20.32	47.4	2.97	0.064
~ Understory height	3	-21.08	49.0	4.48	0.030
~ Intercept	5	-18.49	49.1	4.64	0.028
~ Understory cover + understory height + canopy height + canopy cover	4	-19.88	49.1	4.66	0.028
~ Understory height + canopy cover	1	-23.57	49.3	4.78	0.026

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory height + canopy height	3	-21.25	49.3	4.83	0.025
~ Canopy cover	2	-22.56	49.5	5.04	0.023
~ Canopy height + canopy cover	2	-23.01	50.4	5.93	0.015
~ Canopy height	3	-22.25	51.3	6.82	0.009
~ Understory height + canopy height + canopy cover	4	-20.98	51.3	6.86	0.009

3-A.2.4 *Turdus falcklandii*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory cover	1	-11.09	24.5	0.00	0.339
~ Understory cover + understory height	2	-10.67	26.3	1.79	0.139
~ Understory cover + canopy height	2	-10.72	26.4	1.89	0.132
~ Understory cover + canopy cover	2	-11.02	27.0	2.49	0.098
~ Understory cover + canopy height + canopy cover	2	-11.05	27.0	2.56	0.094
~ Understory cover + understory height + canopy height	3	-10.56	29.1	4.64	0.033
~ Understory cover + understory height + canopy cover	3	-10.60	29.2	4.73	0.032
~ Understory height	3	-10.66	29.3	4.85	0.030
~ Intercept	3	-10.66	29.3	4.85	0.030
~ Understory cover + understory height + canopy height + canopy cover	3	-10.70	29.4	4.93	0.029
~ Understory height + canopy cover	3	-11.01	30.0	5.55	0.021
~ Understory height + canopy height	4	-10.32	32.3	7.82	0.007
~ Canopy cover	4	-10.55	32.7	8.27	0.005
~ Canopy height + canopy cover	4	-10.59	32.8	8.34	0.005
~ Canopy height	4	-10.60	32.8	8.36	0.005
~ Understory height + canopy height + canopy cover	5	-10.32	36.6	12.17	0.001

3-A.2.5 *Anairetes parulus*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Understory cover	4	-16.78	43.0	0.00	0.170
~ Understory cover + understory height	2	-19.33	43.1	0.04	0.166
~ Understory cover + canopy height	3	-18.22	43.3	0.27	0.148
~ Understory cover + canopy cover	3	-18.67	44.2	1.15	0.095
~ Understory cover + canopy height + canopy cover	5	-16.02	44.3	1.30	0.089
~ Understory cover + understory height + canopy height	3	-19.10	45.1	2.02	0.062
~ Understory cover + understory height + canopy cover	3	-19.31	45.5	2.45	0.050
~ Understory height	4	-18.01	45.5	2.47	0.049
~ Intercept	4	-18.11	45.7	2.67	0.045
~ Understory cover + understory height + canopy height + canopy cover	1	-22.18	46.5	3.46	0.030
~ Understory height + canopy cover	2	-21.10	46.6	3.57	0.028
~ Understory height + canopy height	2	-21.40	47.2	4.18	0.021
~ Canopy cover	4	-18.97	47.4	4.40	0.019
~ Canopy height + canopy cover	3	-20.86	48.6	5.54	0.011
~ Canopy height	2	-22.16	48.7	5.70	0.010
~ Understory height + canopy height + canopy cover	3	-21.38	49.6	6.59	0.006

Appendix 3-A.4: Best supported models explaining variability in mean nest daily survival rate (DSR) for each of the five forest-nesting bird species on Navarino Island, Chile, 2014-2017.

We report estimate (**β**) and their 95% confidence interval.

Coefficients in the Best Supported Model	*Elaenia albiceps*	*Zonotrichia capensis*	*Phrygilus patagonicus*	*Turdus falcklandii*	*Anairetes parulus*
Nest age	- 2.58 (-7.14 – -0.89)	- 8.90 (-18.68 – -2.62)	-1.25 (-2.75 – -0.10)		-24.94 (-54.35 – 4.48)
Nest age^2	3.66	6.25			23.93

Coefficients in the Best Supported Model	***Elaenia albiceps***	***Zonotrichia capensis***	***Phrygilus patagonicus***	***Turdus falcklandii***	***Anairetes parulus***
	(0.88 – 7.32)	(1.40 – 13.64)			(-3.59 – 51.46)
Nest stage		1.65 (0.23 – 3.17)			
Nest height					6.15 (-4.84 – 16.59)
Canopy cover	- 0.78 (-1.39 – -0.20)				
Understory height	- 0.85 (-1.49 – -0.24)		-0.96 (-2.09 – -0.04)		
Understory cover			-1.62 (-3.77 – -0.28)	-1.13 (-2.68 – -0.26)	1.12 (-0.09 – 2.33)
Concealment	-0.51 (-1.70, 0.13)		1.18 (0.06 – 2.90)		
Camera		1.97 (0.20 – 3.61)			

Appendix 3-A.5: Candidate models describing daily nest survival rate (DSR) of five forest dwelling passerines on Navarino Island, Chile, 2014-2017

In the first stage of model selection, we evaluated temporal parameters. On the second stage, we added habitat parameters to the best-supported model from stage one. On the first stage we tested for nest stage (egg [laying and incubation] vs nestling), day of year (date, linear and quadratic effects), and nest age (linear and quadratic effects). On the second stage, the parameters we tested for included nest coverage (concealment, computed as the mean side [measured at the four cardinal directions] and overhead cover), canopy cover, canopy height, understory cover, understory height, nest height, and ground predator accessibility index (predator index, ranging from 0-2, indicating increasing nest accessibility for a potential ground predator). Models are ranked by AIC$_c$, with the best supported model given in bold (i.e., the model with lowest AIC_c). For each stage of model selection, we present the first 10 candidate models only.

3-A.2.1 *Elaenia albiceps*

Model **All models include season as random effect**	**K**	**LL**	**AIC_c**	**ΔAIC_c**	**Weight**
Stage 1: Temporal variables					
~ Nest age + nest age^2	4	-62.40	132.9	0.00	0.151
~ Intercept	2	-64.88	133.8	0.86	0.098
~ Nest age + nest age^2 + date	5	-62.16	134.5	1.60	0.068
~ Nest age + nest age^2 + nest stage	5	-62.18	134.6	1.62	0.067
~ Date	3	-64.62	135.3	2.38	0.046
~ Nest age + nest age^2 + date + date^2	6	-61.65	135.6	2.65	0.040
~ Nest stage	3	-64.86	135.8	2.87	0.036
~ Nest age	3	-64.86	135.8	2.88	0.036
~ Nest age + nest age^2 + date + nest stage	6	-62.03	136.3	3.41	0.027
~ Date + date^2	4	-64.23	136.6	3.66	0.024
Stage 2: Habitat variables					
~ Nest age + nest age^2 + understory height + canopy cover + concealment	7	-57.79	130.0	0.00	0.046
~ Nest age + nest.age^2 + understory height + canopy cover	6	-59.02	130.3	0.37	0.038
~ Nest age + nest.age^2 + understory height + canopy cover + concealment + canopy height	8	-57.15	130.8	0.83	0.030
~ Nest age + nest.age^2 + understory height + canopy cover + concealment + nest height	8	-57.17	130.8	0.87	0.030
~ Nest age + nest.age^2 + understory height + canopy cover + concealment + nest height + canopy height	9	-56.14	130.9	0.95	0.029
~ Nest age + nest.age^2 + understory height + canopy cover + nest height	7	-58.59	131.6	1.61	0.021

Model All models include season as random effect	K	LL	AIC_c	ΔAIC_c	Weight
~ Nest age + nest age^2 + understory height + canopy cover + concealment + understory cover	8	-57.70	131.9	1.94	0.018
~ Nest age + nest age^2 + understory height + canopy cover + canopy height	7	-58.82	132.0	2.06	0.016
~ Nest age + nest age^2 + understory height + canopy cover + concealment + predator index	9	-56.82	132.3	2.30	0.015

3-A.2.2 *Zonotrichia capensis*

Model All models include season as random effect	K	LL	AIC_c	ΔAIC_c	Weight
Stage 1: Temporal variables					
~ Camera + nest age + nest age^2 + nest stage	6	-55.97	124.2	0.00	0.215
~ Camera + nest age + nest age^2 + nest stage + date	7	-55.71	125.8	1.56	0.098
~ Camera + nest age + nest age^2 + nest stage + date + date^2	8	-55.31	127.1	2.88	0.051
~ Camera + nest age + nest ge^2	5	-58.56	127.3	3.09	0.046
~ Camera + nest age + nest age^2 + date	6	-57.95	128.2	3.97	0.030
~ Camera + nest age + nest stage + date	6	-58.54	129.4	5.14	0.016
~ Camera + nest age + nest age^2 + date + date^2	7	-57.56	129.5	5.28	0.015
~ Camera + nest age + nest stage	5	-59.66	129.5	5.31	0.015
~ Camera + nest age + date	5	-59.79	129.8	5.55	0.013
~ Camera + nest age + nest stage - date + date^2	7	-57.77	129.9	5.70	0.012
Stage 2: Habitat variables					
~ Camera + nest age + nest age^2 + nest stage	6	-55.97	124.2	0.00	0.118
~ Camera + nest age + nest age^2 + nest stage + concealment	7	-55.85	126.1	1.86	0.046

Model All models include season as random effect	K	LL	AIC_c	ΔAIC_c	Weight
~ Camera + nest age + nest age^2 + nest stage + canopy height	7	-55.89	126.2	1.94	0.045
~ Camera + nest age + nest age^2 + nest stage + understory height	7	-55.95	126.3	2.05	0.042
~ Camera + nest age + nest age^2 + nest stage + canopy cover	7	-55.97	126.3	2.09	0.041
~ Camera + nest age + nest age^2 + nest stage + understory cover	7	-55.97	126.3	2.09	0.041
~ Camera + nest age + nest age^2 + nest stage + concealment + canopy height	8	-55.81	128.1	3.89	0.017
~ Camera + nest age + nest age^2 + nest stage + concealment + understory height	8	-55.84	128.2	3.94	0.016
~ Camera + nest age + nest age^2 + nest stage + concealment + understory cover	8	-55.85	128.2	3.97	0.016
~ Camera + nest age + nest age^2 + nest stage + concealment + canopy cover	8	-55.85	128.2	3.97	0.016

3-A.2.3 *Phrygilus patagonicus*

Model	K	LL	AIC_c	ΔAIC_c	Weight
Stage 1: Temporal variables					
~ Nest age	2	-26.78	57.6	0.00	0.075
~ Nest stage	2	-26.92	57.9	0.28	0.065
~ Intercept	1	-27.96	57.9	0.34	0.064
~ Date	2	-27.11	58.3	0.66	0.054
~ Nest age + nest age^2	3	-26.12	58.3	0.72	0.053
~ Date + date^2	3	-26.31	58.7	1.09	0.044
~ Nest age + date	3	-26.54	59.2	1.55	0.035
~ Nest stage + date	3	-26.60	59.3	1.68	0.033
~ Nest age + nest stage	3	-26.71	59.5	1.90	0.029
~ Nest age + date + date^2	4	-25.78	59.7	2.09	0.026
Stage 2: Habitat variables					

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Nest age + concealment - understory cover - understory height	5	-22.53	55.3	0.00	0.034
~ Nest age + concealment + understory cover + understory height + canopy cover + canopy height + nest height	8	-20.03	56.6	1.30	0.018
~ Nest age + concealment + understory cover + understory height + canopy cover + canopy height + nest height + nest height^2	9	-19.16	57.0	1.70	0.015
~ Nest age + concealment + understory cover + understory height + canopy cover	6	-22.39	57.1	1.80	0.014
~ Nest age + concealment + understory cover + understory height + canopy height	6	-22.44	57.2	1.90	0.013
~ Nest age + concealment + understory cover + understory height + nest height	6	-22.53	57.4	2.08	0.012
~ Nest age + concealment + understory cover	4	-24.62	57.4	2.10	0.012
~ Nest age + understory cover + understory height	4	-24.70	57.5	2.27	0.011
~ Nest age	2	-26.78	57.6	2.33	0.011
~ Concealment + understory cover + understory height	4	-24.84	57.8	2.55	0.010

3-A.2.4 *Turdus falcklandii*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
Stage 1: Temporal variables					
~ Nest age + nest age2 + nest stage	4	-7.04	22.7	0.00	0.258
~ Nest stage + stage	3	-8.97	24.3	1.63	0.114
~ Nest age + nest age2	3	-9.01	24.4	1.69	0.111
~ Nest stage	2	-10.36	24.9	2.21	0.085
~ Nest age + nest age2 + nest stage + date	5	-7.03	25.0	2.30	0.081
~ Nest stage + date	3	-9.41	25.2	2.50	0.074
~ Nest age + nest stage + date	4	-8.81	26.2	3.54	0.044
~ Nest age + nest age2 + date	4	-8.87	26.3	3.66	0.041
~ Intercept	1	-12.40	26.9	4.17	0.032

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Date	2	-12.24	28.7	5.98	0.013
Stage 2: Habitat variables					
~ Understory cover	2	-8.89	22.0	0.00	0.060
~ Nest age + nest age2 + nest stage	4	-7.04	22.7	0.72	0.042
~ Understory cover + nest age + nest age2	4	-7.08	22.8	0.80	0.040
~ Understory cover + nest stage	3	-8.45	23.3	1.30	0.031
~ Understory cover + concealment	3	-8.57	23.5	1.54	0.028
~ Nest age + nest age2 + canopy height	4	-7.64	23.9	1.93	0.023
~ Nest stage + canopy height	3	-8.78	23.9	1.97	0.022
~ Understory cover + nest age	3	-8.82	24.0	2.03	0.022
~ Understory cover + canopy height	3	-8.83	24.0	2.07	0.021
~ Understory cover + understory height	3	-8.89	24.1	2.18	0.020

3-A.2.5 *Anairetes parulus*

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
Stage 1: Temporal variables					
~ Nest age + nest age2	3	-12.65	31.4	0.00	0.366
~ Nest age + nest age2 + date + date2	5	-11.16	32.7	1.24	0.197
~ Nest age + nest age2 + date	4	-12.63	33.49	2.06	0.131
~ Nest age + nest age2 + date + date2 + nest stage	6	-10.87	34.23	2.81	0.090
~ Nest age + nest age2 + date + nest stage	5	-12.35	35.05	3.62	0.060
~ Intercept	1	-18.91	39.85	8.42	0.005
~ Nest stage	2	-18.87	41.81	10.38	0.002
~ Date	2	-18.87	41.81	10.39	0.002
~ Nest age	2	-18.91	41.90	10.47	0.002
~ Date + date2	3	-18.05	42.24	10.81	0.002
Stage 2: Habitat variables					
~ Nest age + nest age2 + nest height + understory cover	5	-9.42	29.2	0	0.145

Model	K	LL	AIC$_c$	ΔAIC$_c$	Weight
~ Nest age + nest age2 + nest height + nest height2 + understory cover	6	-8.37	29.2	0.03	0.143
~ Nest age + nest age2 + nest height	4	-11.04	30.3	1.11	0.083
~ Nest age + nest age2 + nest height + nest height2	5	-10.11	30.6	1.37	0.073
~ Nest age + nest age2 + nest height + nest height2 + understory cover + canopy cover	7	-8.29	31.2	2.04	0.052
~ Nest age + nest age2 + understory height + canopy cover	5	-10.51	31.4	2.17	0.049
~ Nest age + nest age2	3	-12.65	31.4	2.23	0.048
~ Nest age + nest age2 + understory cover + canopy cover	5	-10.62	31.6	2.39	0.044
~ Nest age + nest age2 + nest height + canopy cover	5	-10.62	31.6	2.40	0.044
~ Nest age + nest age2 + understory cover + understory height + canopy cover	6	-9.88	32.3	3.06	0.032

CHAPTER 4

WEAK MIGRATORY CONNECTIVITY OF *Elaenia albiceps* REVEALED BY LIGHT-LEVEL GEOLOCATORS

4.1 Abstract

For migratory birds, the degree of migratory connectivity between breeding and wintering grounds can shape the strength of carry-over effects between seasons. When migratory connectivity is strong, events happening on the wintering ground can have strong consequences for population dynamics on the breeding ground. Conversely, when connectivity is weak, events happening in one of the wintering sites can have a weaker but widespread effect on multiple breeding populations. We assessed the migratory connectivity of the White-crested Elaenia (*Elaenia albiceps*), the longest-distance migrant flycatcher within South America. Using light-level geolocators we tracked the annual movements of elaenias breeding in two different sites within the temperate rainforests of South America. We found extensive spatial and temporal overlap of elaenias from the two breeding sites during winter, which generally included at least two separate areas that were used successively while in Brazil. These results indicate weak migratory connectivity for this species. Further research is needed to understand what drives elaenias' movement, not only during winter but throughout their annual cycle. This information is critical to understanding and possibly predicting this species' response to global change.

4.2 Introduction

For migratory birds, events happening on the wintering grounds or during migration can have strong carry-over effects on subsequent breeding success of individual birds (Dolman and

Sutherland 1995, Marra et al. 1998, Newton 2008, López Calderón et al. 2019). If the association is strong enough, carry-over effects can impact the population dynamics of a species, with the strength of carry-over effects being shaped by the degree of connectivity between the breeding and wintering grounds (i.e., migratory connectivity) (Myers et al. 1987, Webster et al. 2002, Marra et al. 2006).

Migratory connectivity exists as a continuum from strong to weak connectivity (Webster et al. 2002), with strong connectivity occurring when most individuals from a breeding population overwinter together in the same region (Webster et al. 2002). For example, Golden-winged Warblers (*Vermivora cyanoptera*) breeding in the Great Lakes region overwinter in Central America, whereas Golden-winged Warblers breeding in the Appalachian Mountains winter in a separate region in northern South America (Kramer et al. 2018). Conversely, weak connectivity may occur when individuals of one breeding population are spread out over many different locations during winter, or when individuals from different breeding populations co-occur in the same wintering site (inter-population mixing) (Finch et al. 2017). For example, Purple Martins (*Progne subis subis*) breeding in far distant and different habitats such as British Columbia, Minnesota, and Texas, co-occur in northern Brazil near the Amazon river during winter (Fraser et al. 2012).

The strength of migratory connectivity has important implications for population dynamics. For example, American Redstarts (*Setophaga ruticilla*) that overwinter in habitat that varies in quality differ by the number of chicks they produce and the time at which they fledge, which can have important implications on productivity and population dynamics (Norris et al. 2004). Thus, under a strong connectivity scenario, local habitat disturbance on the wintering grounds could have strong consequences on population recruitment in a specific breeding area (Webster et al. 2002). In contrast, if individuals of a breeding population use separate wintering sites and co-occur with individuals from other breeding populations (i.e. weak migratory connectivity), the effect of a local habitat disturbance in one of their wintering sites would be a weaker but widespread effect on multiple breeding populations (Finch et al. 2017).

In order to account for these differences, migratory connectivity patterns include two key components: population spread and inter-population mixing (Finch et al. 2017). Population spread describes how much a single breeding population spreads out across the wintering grounds (Finch et al. 2017). This can be assessed through the documentation of geographical distances maintained among individuals on the wintering grounds. Inter-population mixing can be defined as the degree of co-occurrence of individuals from different breeding populations on the wintering grounds (Finch et al. 2017). In general, high population spread may result in high inter-population mixing, (i.e., weak migratory connectivity), and low population spread may result in low inter-population mixing (i.e., strong migratory connectivity). However, inter-population mixing does not always depend upon population spread. For example, breeding populations may have high population spread, yet inter-population mixing may remain low if the wintering grounds are large (Finch et al 2017). Consequently, ‘strong or weak connectivity’, as originally employed by Webster et al (2002), are not always directly related to these two measures. Thus, when assessing migratory connectivity we should estimate and report both components: population spread and inter-population.

Every year, dozens of species migrate within South America as they track seasonally available resources and avoid harsh winters (Somveille et al. 2015, Jahn et al. 2020). Among these, the White-crested Elaenia (*Elaenia albiceps chilensis*; hereafter ‘elaenia’) is the longest-distance migrant flycatcher within South America (Chesser 2005, Jiménez et al. 2016). This small approximately 16-g flycatcher migrates yearly between its wintering grounds in Brazil and its breeding grounds in the temperate forests of southern Chile and Argentina (Jiménez et al. 2016, Bravo et al. 2017). Elaenias breed from Copiapo, Chile (29˚S) (Medrano et al. 2018) to the southernmost forests of the world within the Cape Horn Biosphere Reserve (56˚ S) (Jara et al. 2019). However, their wintering range, which extends from southeast Colombia and eastern Peru, to Paraguay and the Atlantic coast along Brazil (Ridgely and Tudor 2009), is much larger than their breeding range. Using light-level geolocators we assessed the migratory connectivity of elaenias breeding in southern temperate forests. We predicted weak migratory connectivity for this species for two main reasons. First, elaenias have a large area of suitable habitat available to overwinter in northern South America. Second, in South America there are no geographic barriers creating bottlenecks that could force migrating individuals to funnel or overwinter in the same location. Therefore, individuals from different breeding sites would likely spread out in their wintering grounds, rather than using discrete site-specific wintering locations.

4.3 Methods

4.3.1 Study Sites

Migratory connectivity of elaenias was assessed for two breeding sites in South America. The first included adult elaenias from the northern coast of Navarino Island (54° S), within the Cape Horn Biosphere Reserve, Chile (Fig. 1.3). We concentrated our efforts in the more accessible forests of Omora Ethnobotanical Park (54°56’ S, 67°39’ W) and immediately surrounding areas (Fig. 1.4). The forests on Navarino Island are a mixture of deciduous and evergreen species, dominated by *Nothofagus sp*., and the understory is composed of shrubs and new-growth forest (Rozzi et al. 2014). In this region, the proximity to the ocean results in an oceanic climate, characterized by small seasonal changes in temperature (i.e., mild summers and winters) (Rozzi et al. 2014). The second breeding site is located at the "Cañadón Florido" cattle ranch (42° 55' S, 71° 21' W), near Esquel, Province of Chubut, Argentina (hereafter Esquel breeding site) (Bravo et al. 2017). The forests here are dominated by *Maytenus boaria*, *Schinus patagonicus* and *Nothogafus antarctica* (Bravo et al. 2017).

4.3.2 Bird Capture and Geolocator Deployment

On Navarino Island, we captured individuals with mist nets mesh size 30 mm and 12 m long. We also placed a decoy of the species nearby (usually centered to the net and no more than 3 m away; Fig. 4.1), as well as broadcasting conspecific calls and songs. Once captured, we determined age, gender, weight and breeding status based on size of cloacal protuberance or brood patch development. We banded each captured bird with a Chilean Agriculture and Livestock Service (SAG, by its acronyms in Spanish) aluminum band, and three plastic color leg bands to facilitate with future identification without requiring recapture. We deployed 117 light-level geolocators (Intigeo P55B1-7, Migrate Techonology, Ltd, Coton, Cambridge, UK) on breeding/post breeding adults; 57 during the 2014/2015 breeding season and 60 during the 2015/2016 breeding season. We also included recorded data from an additional five geolocators in this study. Three of the five (H795, H796, and H820) were deployed during the 2013/2014 breeding season as an earlier pilot study, and the other two were deployed as part of a long-term migration study during the 2016/2017 and 2017/2018 breeding seasons (BC037 and BJ354, respectively). Both H796 and BJ354 recorded light data for the full annual cycle, with the latter recording data for 2 years (Fig. 4.3). However, to maintain consistent analysis among all samples, we analyzed the data from only the first annual cycle for sample BJ354. Similarly, on Esquel, during the breeding seasons of 2013/2014 and 2014/2015, 45 adult elaenias were fitted with same model of geolocators that we used at Navarino Island in this study (see Bravo et al. 2017 for specific details concerning field methods). Geolocator data from Esquel are publicly archived in Movebank Data Repository (Cueto and Bravo 2017). Geolocator settings deployed in both breeding sites measured light levels every minute and recorded maximum light level every 5 min.

The geolocators were attached as a backpack using leg-loops (Rappole and Tipton 1991). Teflon ribbon or flexible nylon stringing cord, depending on availability, was used to make the leg-loop harness. We applied fast-drying glue to the knot of the Teflon ribbon to close the loop. For the nylon coated stringing cord, we closed the loop by melting the ends of the cord together using heat. We approached the ends of the cords to a woodburning pen, but without touching it. When the ends of the cords started to melt, we strongly connected them and held them in place until they cooled down, forming a continuous loop.

Of the 117 individuals with geolocators from Navarino Island, 57.3% (n = 67) were males and 31.3% (n = 37) were females. We were unable to determine the sex in the remaining individuals (11.1%, n = 13). After processing, we released the individuals in the same capture location, and monitored each bird for a 1 – 3 minutes after release to make sure the geolocator did not interfere with their ability to fly. Including the harness, the average weight of the geolocators was 0.60 g, representing 3.76% ± 0.44 (SD, n = 10) of the bird’s body weight.

During the following breeding season, we visually searched for color-banded individuals in the areas where we captured and marked birds. Once re-sighted, we recaptured and recovered geolocators following the same capture protocol described above. None of the recaptured individuals had signs of abrasions or lesions associated with the geolocator. Banded individuals were considerably less responsive to the decoy and playback, resulting in a relatively low recapture rate low.

Permission to handle our study animals was given by SAG (permit numbers 1058/2014, 300/2015 and 5158/2016). We combined the published raw geolocator data from 15 geolocators deployed and recovered at Cañadón Florido, Esquel, Argentina (Cueto and Bravo 2017) with data from geolocators deployed and recovered on Navarino Island, Chile, and analyzed all data with the same methods described below.

4.3.3 Data Analysis

For all data processing and location estimation, we used custom open-source tools for geolocator-analysis in R (R version 3.5.2) (R Developement Core Team 2018). We annotated twilight events using the "preprocessLight" function in TwGeos package with a threshold light level value of 1. We removed aberrant twilight events manually with the "preprocessLight" function. On average, we removed 5.09% ± 3.01 (SD, n = 15) of the twilight events for Navarino, and 2.18% ± 1.97 (n = 15) for Esquel. We calibrated the geolocators on the birds while on the breeding grounds (i.e., this was the known location). To derive the period that the birds stayed on the breeding grounds, we used the "plot_slopes_by_location" function in the FLightR package.

To estimate locations based on light intensity data, we used a particle filter in FLightR package (Rakhimberdiev et al. 2015, 2017). FlightR uses a hidden Markov chain model to estimate a probability distribution of the bird's location, which produces the most likely migration route based on light-level data. Because elaenias are known to inhabit islands (e.g., Navarino Island), we created a land mask where we allowed birds to fly over oceanic water (up to 1000 km from the coast) but stationary periods can only occur on land. We used the "stationary.migration.summary" function in FlightR (with a 0.3 probability of movement) to estimate stationary periods (stopover, wintering and breeding sites) and to estimate when birds arrived and departed from those sites. We defined a given wintering site as a stationary period that lasted at least 20 days. We chose that cut-off value as there was a natural break in the duration of stationary periods data once analyzed. Results were similar when we used a cut-off value of 30 days, which was the value used in another study investigating migration patterns with another neotropical migrant flycatcher (*Tyrannus savana*; Jahn et al. 2019). We defined fall migration as the period between the date when a bird left the breeding site and the date of the first stationary period that lasted at least 20 days. Similarly, we defined initiation of spring migration as the first day of movement after a stationary period of at least 20 days that was not followed by another stationary period of at least 20 days or more. Termination of spring migration occurred on the day the birds arrived in the area where they were captured the previous year during their breeding period.

To describe population spread on the wintering grounds, we estimated the pairwise distance among individuals. We calculated distances based on the median longitude and latitude of each individual wintering sites using the Alteryx software version 2020.2.3.27789 (Irvine, CA, USA). To visualize the spread of each breeding site and quantify their overlap during their overwintering period, first we estimated the 50% and 75% kernel density utilization distribution (kernel UD) of all the points occurred during the overwintering period of each individual, using the “adehabitatHR” package (De Solla et al. 1999, Calenge 2006, Anderson et al. 2019). Interestingly, we observed two overwintering periods with elaenias from both breeding areas (see Results), which required additional analyses exploring the spread of each breeding site. For the first wintering site, we had data from 15 individuals from each breeding site (Esquel and Navarino), but due to some of the geolocators failing to record data after they left the first wintering site, we had data for the second wintering site from only 12 individuals for Esquel and 7 for Navarino. The amount of overlap of wintering sites between elaenias from different breeding sites was estimated using the “kerneloverlaphr” of the “adehabitatHR package”. Specifically, we used “HR” method, which estimated the proportion of the wintering site used by elaenias from one breeding site that overlapped with the wintering site used by elaenias from the other breeding site.

We quantified the strength of migratory connectivity with the Mantel correlation coefficient (r_M) (Ambrosini et al. 2009). This coefficient is a measure of the correlation between two matrices representing the geographic distances among individuals in both the breeding and wintering grounds. To estimate these distance matrices we combined individuals from both breeding sites. A strong positive correlation between the two matrices results when individuals that breed and also overwinter in close proximity to each other (strong migratory connectivity). Conversely, a weak or negative correlation results when individuals that breed close together overwinter in different locations (weak connectivity) (Ambrosini et al. 2009). Because elaenias from both breeding sites used two overwintering sites sequentially (see Results), we tested the strength of migratory connectivity considering both wintering sites separately.

We also assessed whether there was temporal overlap on the wintering grounds between individuals from both breeding sites by testing for differences in arrival and departure dates for both wintering sites separately using a Wilcoxon Rank Sum test.

4.4 Results

4.4.1 Navarino Island Breeding Site

At Navarino Island, we recovered a total 12 geolocators, six from each of the two breeding seasons (10.5% and 10.3% recovery rate for the first and second season, respectively). All 12 geolocators were recovered < 1 km from the location were we deployed them further supporting previous studies suggesting that adult elaenias have high inter-annual site fidelity (Rozzi and Jiménez 2014). All retrieved geolocators were not recording data upon arriving to Navarino Island, providing incomplete light intensity data for the full annual cycle, thus, we shipped them to Migrate Technology to download each tag's data. Furthermore, two of the geolocators recorded light data that were strongly affected by shading, preventing the use of curve-fitting analysis methods. Thus, we did not include those two geolocators our analysis. Therefore, in the present study we only analyzed data recorded from the remaining ten recovered geolocators, plus data from five geolocators recovered from a pilot study and/or long-term migration study (see methods).

4.4.2 General Migration Patterns of Navarino Island Elaenias

During fall migration, 13 of the 15 tagged elaenias departed Navarino Island following Temperate forests to the north along the Andes, one flew north along the Atlantic coast, and the remaining one did it through Patagonian steppe (Fig 4.3). Then, all of them flew east crossing the Humid Pampas, Espinal, and Low Monte ecoregions in Argentina reaching Bahia Interior and Coastal Forests along the Atlantic (Fig 4.3). The tagged elaenias then migrated north until reaching the Caatinga and Bahia Coastal Forests ecoregion were all of them spent the first part of the winter (i.e., first overwintering site) before continuing their winter migration to central Brazil (i.e., second overwintering site). For the individuals for which we have spring migration data (n=7), most of the tagged elaenias migrated south through Dry and Humid Chaco in Paraguay and Argentina, and then southwest, crossing the Humid pampas, Espinal, and Low monte ecoregions in Argentina (Fig 4.3). From there, the tagged elaenias followed a similar route as shown with fall migration, flying south along the Andes until arriving at Navarino Island (Fig 4.3).

4.4.3 Esquel Breeding Site

A total of 15 of the 45 geolocators deployed at the Esquel breeding site were recovered (Bravo et al. 2017). Most of the publicly available data archived in Movebank include light records of individuals from their breeding season through the initiation of their spring migration (n= 12), but only seven tags recorded light intensity for the complete annual cycle (Cueto and Bravo 2017). A third of the elaenias breeding on Esquel used a similar route towards their wintering sites route than those breeding on Navarino (Bravo et al. 2017). This route involved crossing from the temperate forests of the Andes to Bahia Interior and Coastal Forests through the Humid Pampas, Espinal, and Low Monte ecoregions in Argentina (Bravo et al. 2017). The rest of the individuals used two other fall migration routes, which are described in detail in Bravo et al (2017).

4.4.4 Migratory Connectivity

On average, elaenias from both breeding sites spent ~6.4 months overwintering in Brazil. During that period, they sequentially occupied two distinct overwintering sites (Fig. 4.2). In each of these wintering sites they had 1–3 stationary periods in slightly different locations but within the same general overwintering site. The first overwintering site was located in northeastern Brazil, in the Caatinga dry forest ecoregion. No difference in arrival date at this site was observed between elaenias originating from both breeding sites (March 24 and 25 for Navarino and Esquel breeding sites, respectively; $W = 108.5$, $p = 0.884$; Fig. 4.2). However, individuals from Esquel departed on average from the first overwintering site at a later date than elaenias from Navarino (Jun 6 and May 26 for Esquel and Navarino respectively; $W = 225$, $p < 0.001$; Fig 4.2). The second overwintering site was located in central Brazil, where elaenias from Esquel remained for an average of 110 days and those from Navarino 127 days, with no difference in length of stay regarding breeding site origin ($W = 25.5$, $p = 0.348$). The second overwintering site for most of the elaenias (77%) was Mato Grosso seasonal forest and the tropical savanna of the Cerrado ecoregion (Fig. 4.2). There were no differences in arrival and departure date between Esquel and Navarino Island elaenias associated with the second overwintering site (Arrival $W = 65.5$, $p = 0.051$; departure $W = 37.5$, $p = 0.925$). However, sample size was limited because a high proportion of the geolocators of birds tagged on Navarino Island (87%) were no longer recording data before they arrived at their second overwintering site (Table 4.1).

Mantel tests indicated weak migratory connectivity for both the first ($r_{M\,=}$ -0.017, $P =$ 0.621) and second ($r_M = 0.096$, $P = 0.280$) overwintering sites; the distance between breeding sites did not correspond with the distance between the overwintering sites that the same individuals occupied. Furthermore, while most individuals from both breeding sites generally used the same first and second overwintering sites, there was considerable spread, since they used locations that were on average 591 km apart (maximum distance = 2102 km) within the first overwintering site, and 454 km (maximum distance = 1476 km) within the second overwintering site (Fig. 4.2). Moreover, there was considerable overlap between the overwintering sites, with 47% overlap in the overwintering site used by elaenias from Navarino Island with those from Esquel (or 40% overlap by elaenias from Esquel with those from Navarino Island) (Fig. 4.2). The observed overlap is larger when considering only the first overwintering site in northeastern Brazil, with 85% overlap by elaenias from Esquel with those from Navarino Island (Fig. 4.2).

4.5 Discussion

Overall, we found extensive spatial overlap of elaenias from two of their breeding sites during winter, which included two separate areas used consecutively while in Brazil. The overwintering sites were up to 2102 km of kilometers in overall area, and the amount of overlap between the two sampled breeding populations was as high as 85% (Fig. 4.2) with no spatial correlation relative to breeding site. Additionally, overall timing of arrival and departure from both overwintering sites were similar between elaenias originating from both breeding sites, with the only observed difference was individuals from Esquel departed from their first overwintering site on average 10 days later than those from Navarino Island. Therefore, as predicted based on Webster et al. (2002), these results indicate weak migratory connectivity for elaenias breeding in southern temperate forests.

Our findings for elaenias correspond with those for long-distance migrant land-birds in general. Even though there are varying levels of migratory connectivity in migrant land-birds, weak connectivity appears common for long-distance migrants. For example, Whinchats (*Saxicola rubetra*) from different breeding populations overlapped across a wide overwintering area in western Africa (Burgess et al. 2020). Furthermore, studies investigating migratory connectivity of species that use two trans-continental flyways (the Nearctic-Neotropical and Palearctic-Paleotropical) found that 64% of 28 species showed weak migratory connectivity (Finch et al. 2017).

Weak migratory connectivity of elaenias may allow for increased migration adaption potential. Elaenias using different overwintering sites may be under different selection pressures during winter if they are exposed to different environmental conditions. If so, gene flow during the breeding season between individuals that overwintered in different locations can allow for substantial genetic variability within each breeding site (Webster and Marra 2005). This is of crucial importance when considering the potential effect of wintering habitat loss in Brazil, because more genetic variability within each breeding site may allow for increased adaptation potential associated with migration, such as changing the frequency of individuals migrating to a different wintering ground.

The quality of winter habitat can also have direct consequences on individual fitness via carry-over effects. For example, low quality winter habitat may result in individuals having lower body condition at the end of winter, resulting in a delayed spring migration and late arrival on the breeding grounds (e.g.,Ninni et al. 2004, Norris et al. 2004, Cooper et al. 2011). Late arrival can result in a delay in the initiation of breeding (e.g.,Cristol 1995, Smith and Moore

2005), which can translate to lower reproductive success (Møller 1994, Norris et al. 2004, Gienapp and Bregnballe 2012, Bejarano and Jahn 2018). The three ecoregions that the tagged elaenias occupied most frequently during winter — Caatinga, Mato Grosso, and Cerrado — are currently under increasing pressure due to anthropogenic activities, and extensive areas of native vegetation in all three ecoregions have been cleared to allow for increased agriculture and cattle ranching (Ratter et al. 1997, Alves et al. 2009).

Increasing habitat degradation may have important implications for elaenia's demographic patterns. Elaenia populations breeding at high latitudes, such as at Navarino Island (this study), have a much smaller temporal window of opportunity for breeding than populations further north. On Navarino Island (54° S), elaenias initiate breeding approximately one month after their arrival (Jara et al. 2019), whereas elaenias breeding in forests of central Chile (i.e. 35˚S) start breeding 2 months after their arrival (Escobar et al. 2004). Therefore, later arrival of individuals to Navarino Island could have stronger negative consequences for recruitment for this breeding population compared to breeding populations further north because they will have less time to acquire the energetic reserves necessary for reproduction, and less time to provision their young (Walsberg 1983). Thus, due to the weak migratory connectivity among the studied elaenias, habitat disturbances on their wintering grounds may have consequences that are widespread among breeding populations (see also Finch et al. 2017), but the severity of those consequences may differ among breeding populations.

In conclusion, this study provides the first assessment of migratory connectivity for *E. albiceps*, the longest-distance migrant flycatcher in South America. We showed weak migratory connectivity between their southern breeding sites in South American temperate forests and their overwintering sites in northeastern and central Brazil. Elaenias coming from two different breeding sites had extensive spatial and temporal overlap during winter, which included two separate wintering areas used in succession. We do not understand why elaenias move to a second wintering site. We suggest that they may be tracking resource availability which would drive them from an area of declining resource availability to an area of greater available resources (Stutchbury et al. 2016, Knight et al. 2019). Alternatively, they could be tracking their local climate niche, like Yellow Warblers (*Setophaga petechiai*) do across their annual cycle (Bay et al. 2021). Further research is needed to understand what drives elaenias' movement, not only during winter but throughout their annual cycle. This information is critical to understanding and possibly predicting this species' response to global change.

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4.7 Tables and Figures

Table 4.1.Individual migration schedule of *Elaenia albiceps* breeding in two site within the South American Temperate forests. All durations are expressed in number of days.

Breeding site	ID	Year	Fall migration		Winter								Spring migration	
			Departure date	Arrival date	No. wintering sites[2]	Arrival at 1st site	Departure from 1st site	Days at 1st site	Arrival at 2nd site	Departure from 2nd site	Days at 2nd site	Overall winter duration	Departure date	Arrival date
Esquel	H750	2014	21-Feb	16-Mar	3	16-Mar	11-Jun	87	11-Jun	24-Oct	135	222	24-Oct	
Esquel	H753	2014	22-Feb	4-Apr	2	4-Apr	22-Jun	79	29-Jun	22-Oct	115	201	22-Oct	6-Nov
Esquel	H755	2014	12-Feb	20-Mar	4	20-Mar	27-May	68	10-Jun	27-Sep	109	191	27-Sep	
Esquel	H757	2014	21-Feb	1-May	2	1-May	4-Jun	34	6-Jun	29-Sep	115	151	29-Sep	22-Oct
Esquel	H760	2014	18-Feb	1-Mar	5	1-Mar	13-May	73	13-May	3-Oct	143	216	3-Oct	23-Oct
Esquel	H762	2014	20-Feb	21-Mar	3	21-Mar	5-Jun	76	5-Jun	8-Oct	125	201	8-Oct	
Esquel	H764	2014	2-Mar	2-Apr	3	2-Apr	23-May	51	20-Jun	29-Aug	70	149	29-Aug	
Esquel	H769	2014	27-Feb	14-Mar	2	14-Mar	11-Jun	89	23-Jun	2-Oct	101	202	23-Oct	
Esquel	H773	2014	5-Mar	21-Mar	4	21-Mar	6-Jul	107	6-Jul	15-Oct	101	208	15-Oct	17-Oct
Esquel	H775	2014	21-Feb	11-Mar	3	11-Mar	13-Jun	94	21-Jun	20-Aug	60	162	20-Aug	23-Oct
Esquel	H777	2014	27-Feb	14-Mar	3	14-Mar	31-May	78	1-Jun	5-Oct	126	205	5-Oct	11-Oct
Esquel	H780	2014	21-Feb	16-Mar	4	16-Mar	10-Jun	86	21-Jun	21-Oct	122	219	21-Oct	
Esquel	P859	2015	14-Mar	14-Apr		14-Apr	20-May	36						
Esquel	P868	2015	25-Feb	31-Mar		31-Mar	15-Jun	76						
Esquel	P872	2015	12-Feb	6-Apr		6-Apr	31-May	55						
Average			24-Feb	25-Mar	3	25-Mar	6-Jun	73	14-Jun	2-Oct	110	194	2-Oct	22-Oct
Navarino	h795	2014	8-Feb	8-Mar	2	8-Mar	13-May	66	16-May	6-Oct	143	212	6-Oct	

Breeding site	ID	Year	Fall migration		Winter								Spring migration	
			Departure date	Arrival date	No. wintering sites[2]	Arrival at 1st site	Departure from 1st site	Days at 1st site	Arrival at 2nd site	Departure from 2nd site	Days at 2nd site	Overall winter duration	Departure date	Arrival date
Navarino	h796	2014	21-Feb	11-Mar	3	11-Mar	20-Jun	101	21-Jun	21-Sep	92	194	21-Sep	19-Oct
Navarino	h820	2014	12-Feb	25-Mar	3	25-Mar	29-May	65	1-Jun	21-Sep	112	180	21-Sep	
Navarino	p438	2015	5-Feb	14-Mar		14-Mar	18-May	65						
Navarino	p543	2015	5-Mar	28-Mar		28-Mar	11-Jun	75						
Navarino	p461	2015	11-Feb	5-Apr		5-Apr	25-May	50						
Navarino	p472	2015	28-Jan	6-Mar		6-Mar	3-May	58						
Navarino	p481	2015	27-Jan	22-Feb		22-Feb[3]	18-May	85						
Navarino	p488	2015	12-Mar	16-Apr		16-Apr	20-Jun	65						
Navarino	v859	2016	12-Mar	21-Mar		21-Mar	5-Jun	76						
Navarino	v860	2016	16-Mar	12-Apr		12-Apr								
Navarino	v873	2016	15-Mar	1-Apr		1-Apr	14-May	43	14-May					
Navarino	v876	2016	17-Feb	6-Apr	2	6-Apr	30-Apr	24	1-May	10-Oct	162	187	10-Oct	
Navarino	BC037	2017	5-Mar	25-Mar	2	25-Mar	13-Jun	80	15-Jun	5-Oct	112	194	5-Oct	
Navarino	BJ354	2018	8-Mar	4-Apr	2	4-Apr	29-May	55	31-May	20-Oct	142	199	20-Oct	10-Nov
Average			22-Feb	24-Mar	2	24-Mar	27-May	65	28-May	4-Oct	127	194	4-Oct	30-Oct

[1] For schedule estimation purposes, if an individual used more than one wintering site within the same general area/ecoregion, we grouped these sites to estimate arrival and departure date, as well as length of stay.

[2] If a geolocator stopped recording data before the initiation of spring migration, we do not report number of wintering sites used by that individual.

[3] This individual's first sedentary period (where it stayed 20 days) was located in central-eastern Argentina, in the Humid Pampas ecoregion. This area is along the fall migration route for many other elaenias breeding in either Esquel or Navarino. In addition, it is located over 3,000 km south of the average first wintering site of the other 29 individuals. After stopping at this site, the next long sedentary period was in the Bahia Coastal Forests in Brazil, where the bird spent 20 days, and which is within the wintering sites occupied by the rest of the tagged birds. We therefore treated the sedentary period in Argentina as a fall migration stopover, and consider the second sedentary period in Brazil as the first wintering site for this individual.

Figure 4.1: Decoy (left) used to lure elaenias to the mist net. Photo on the right shows an elaenia (a) responding to the decoy (b)

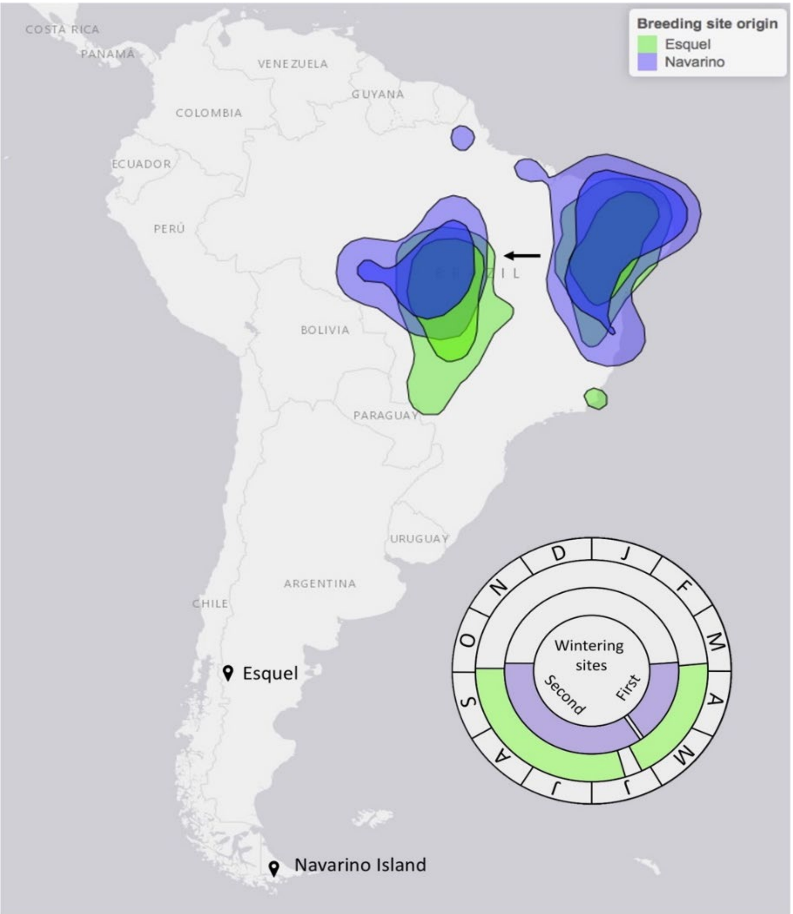
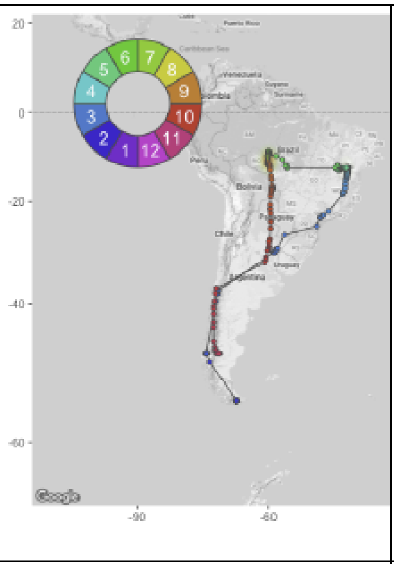
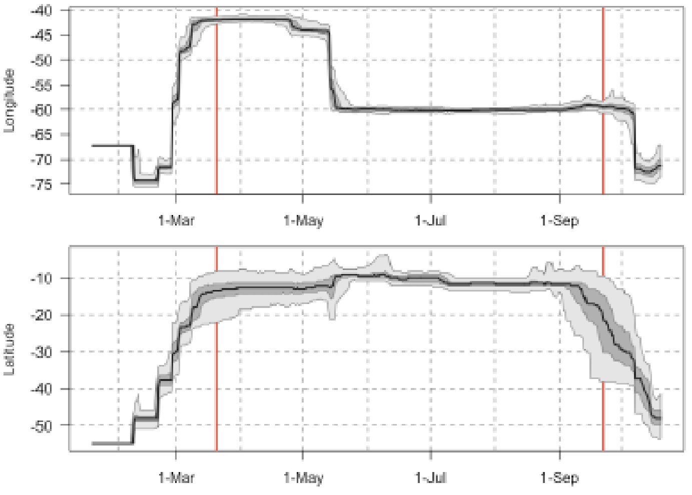
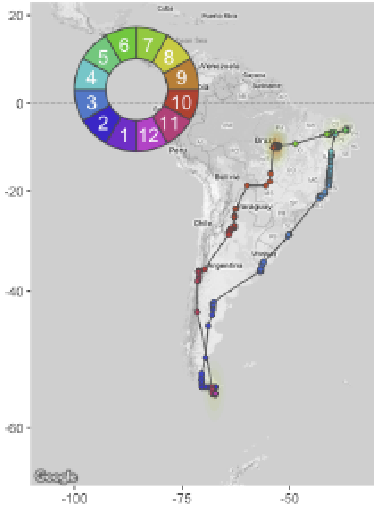
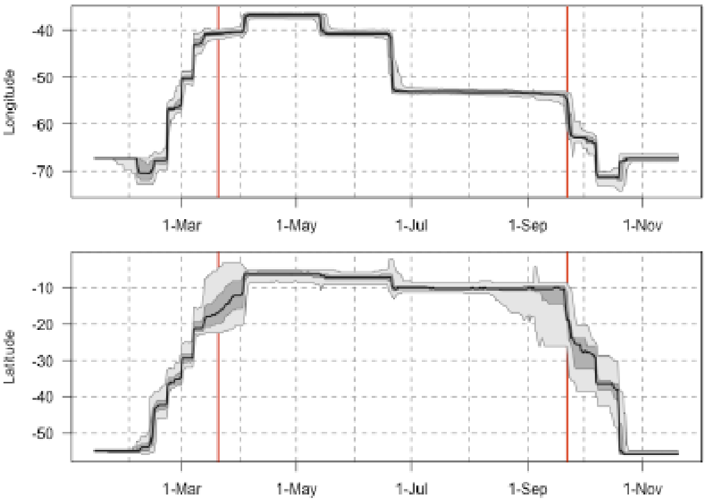
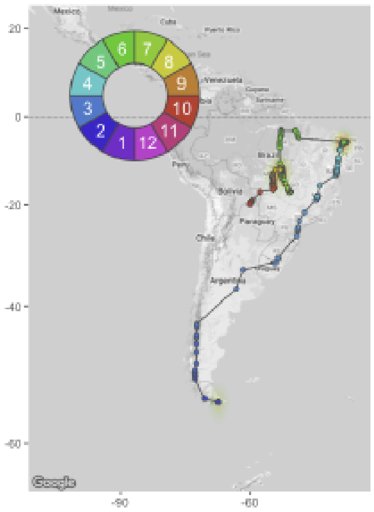
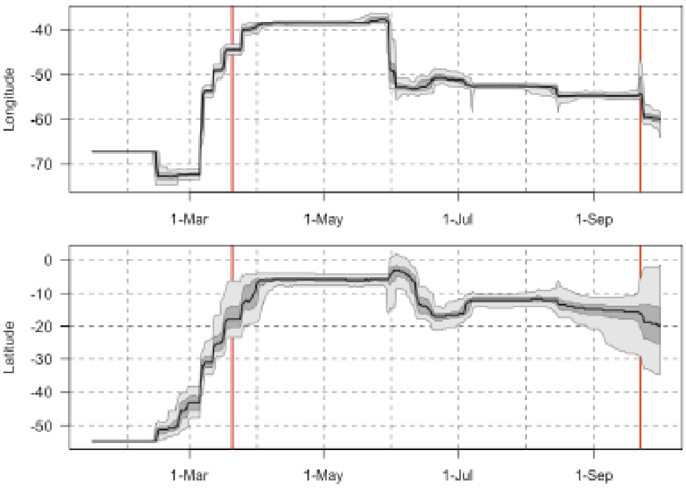
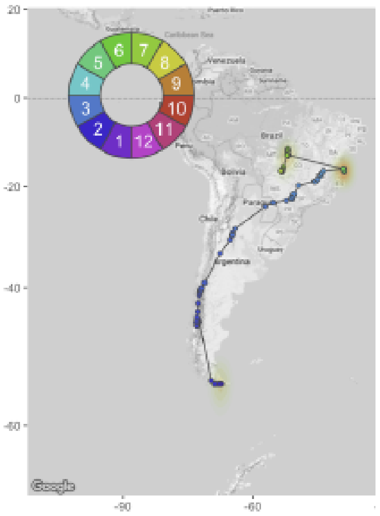
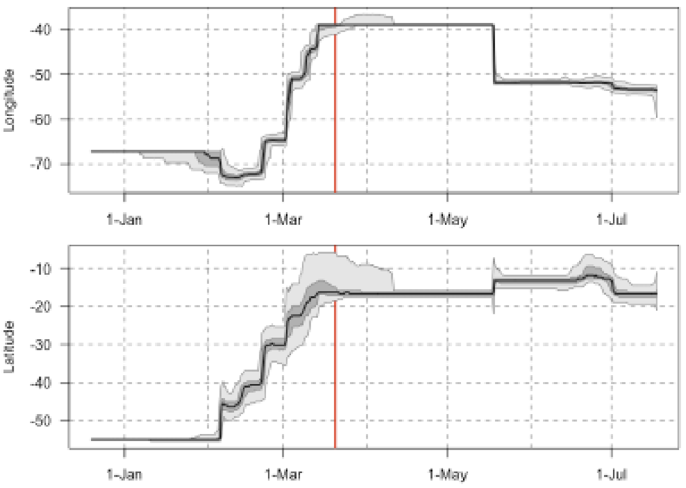
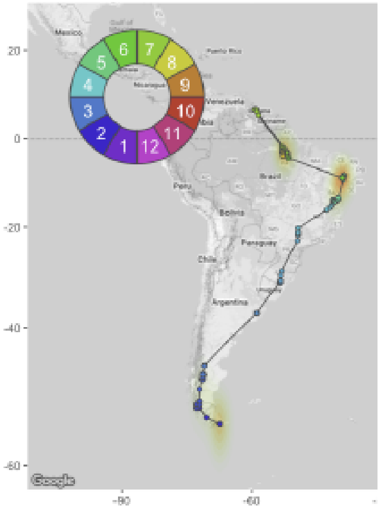
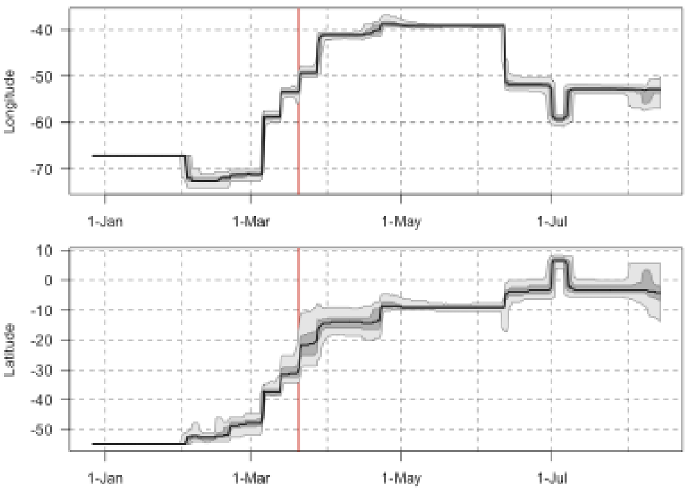
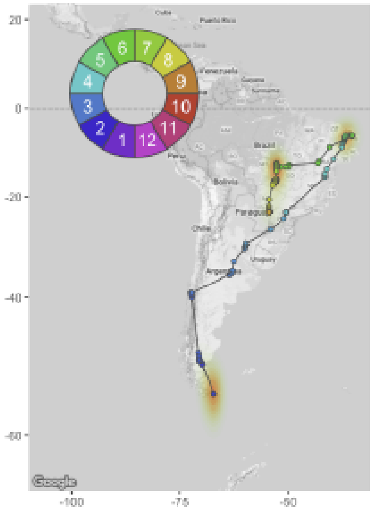
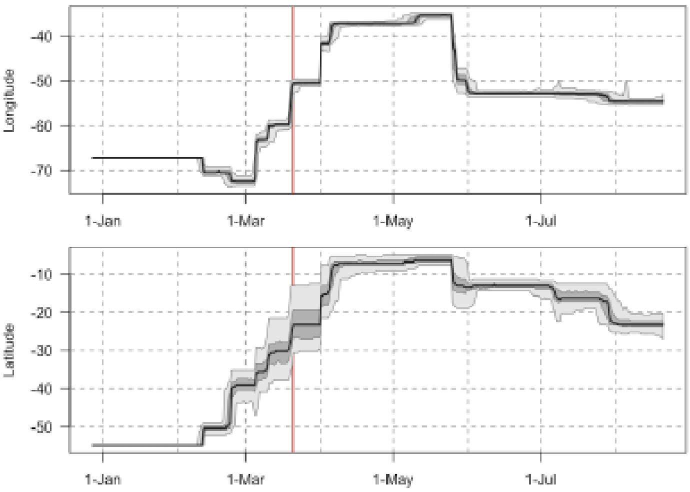


Figure 4.2: Overwintering sites for *Elaenia albiceps* breeding in Esquel and Navarino Island. The polygons depict the 50% (darker shade) and 75% (lighter shade) kernel density utilization distribution of all the points occurred during the overwintering period of each individual.

H795		
H796		
H820		

P438		
P453		
P461		

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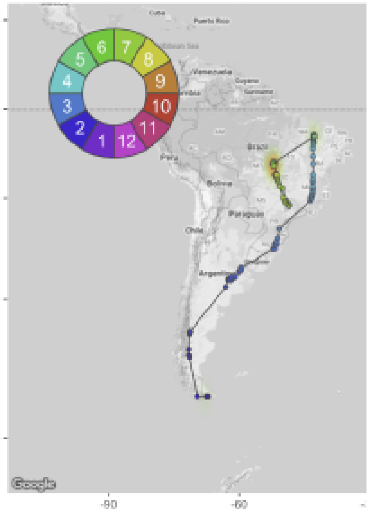

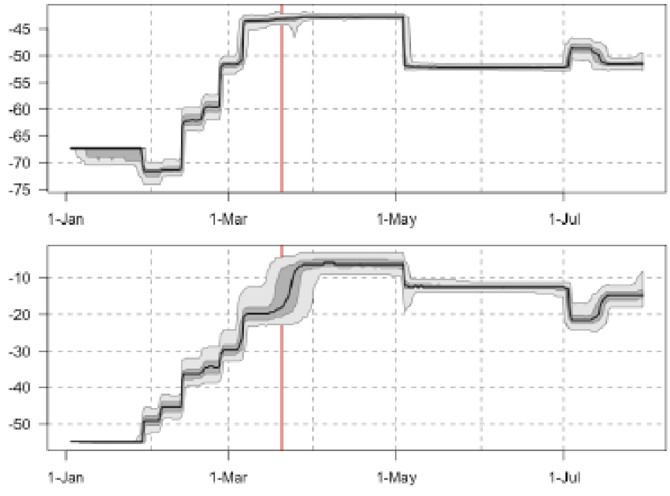

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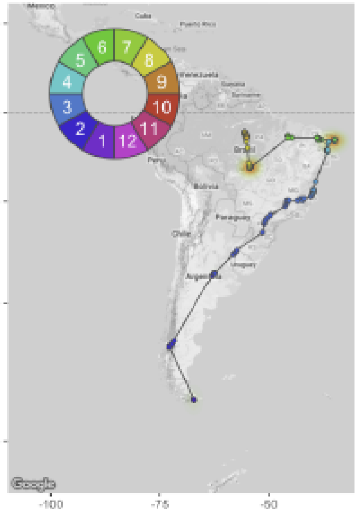

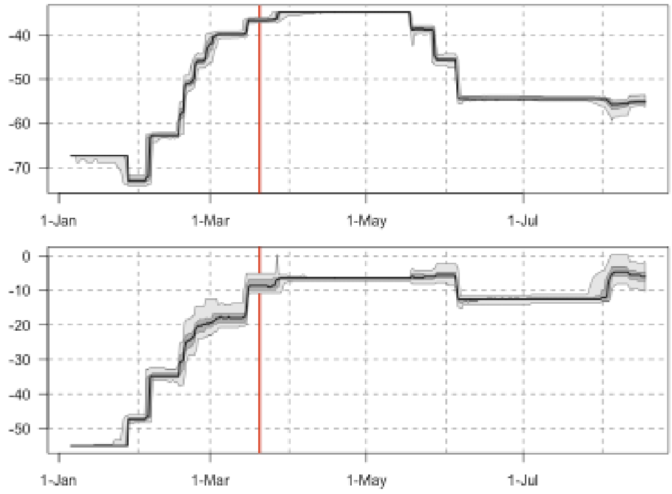

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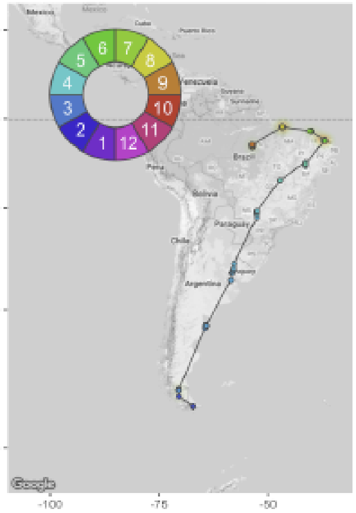
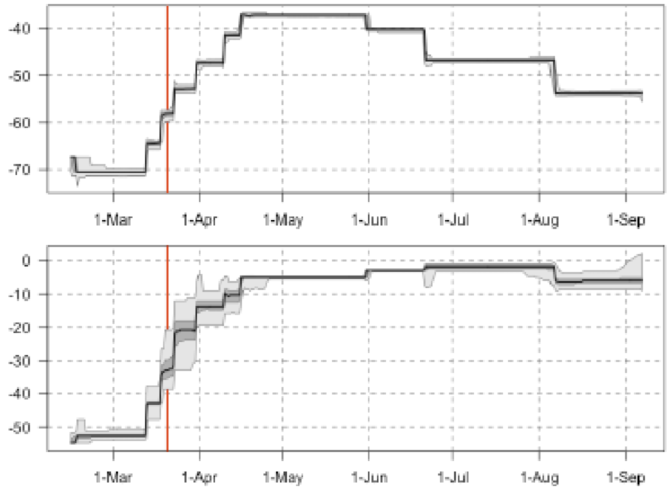
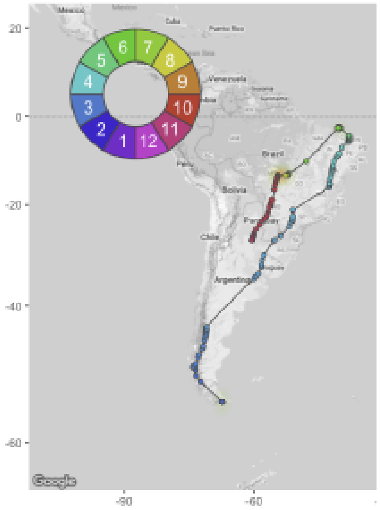
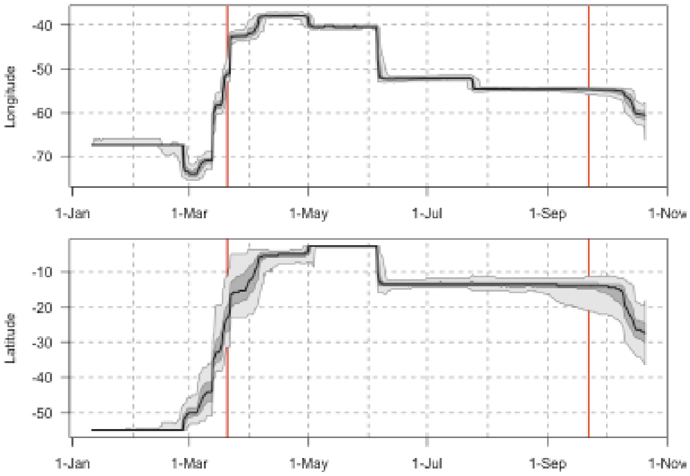
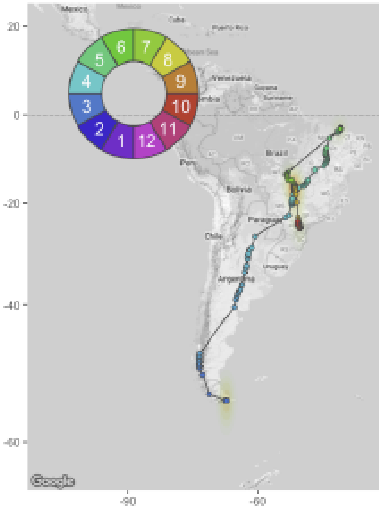
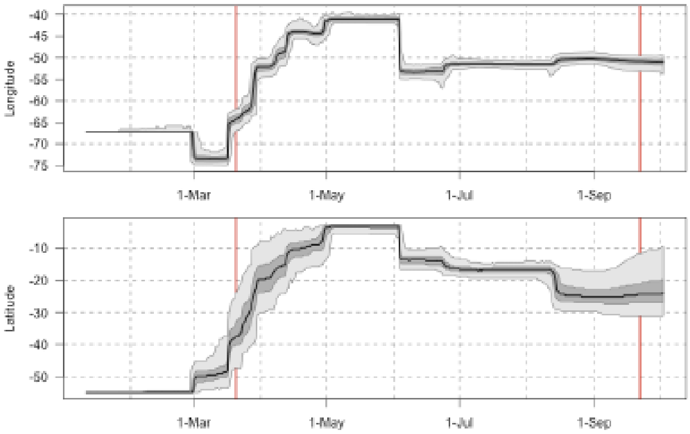
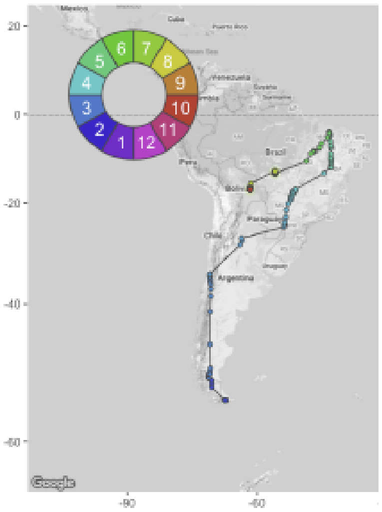
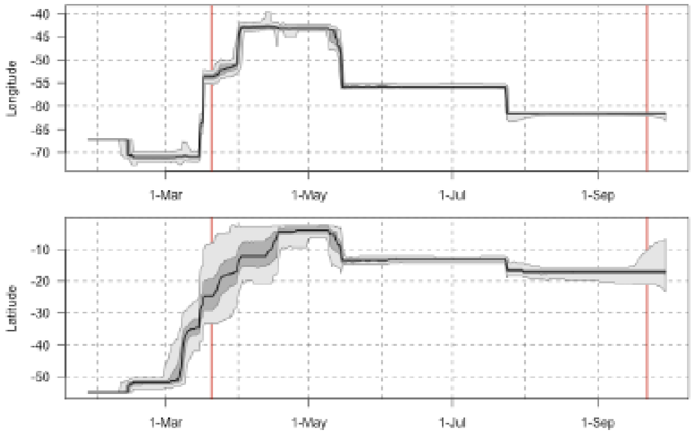




V859		
V860		
V873		

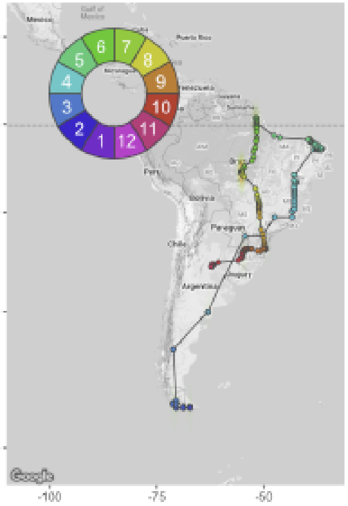
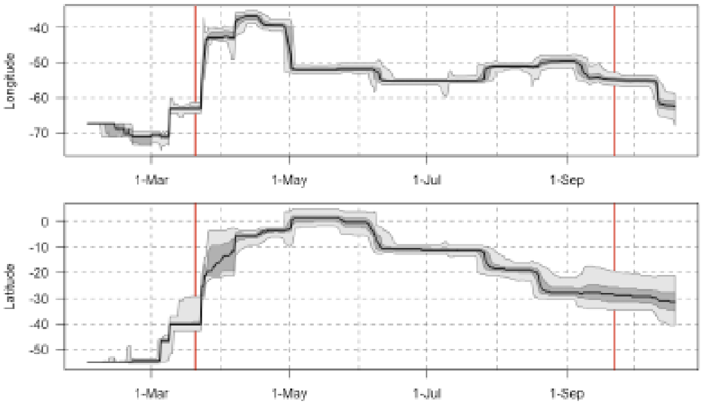
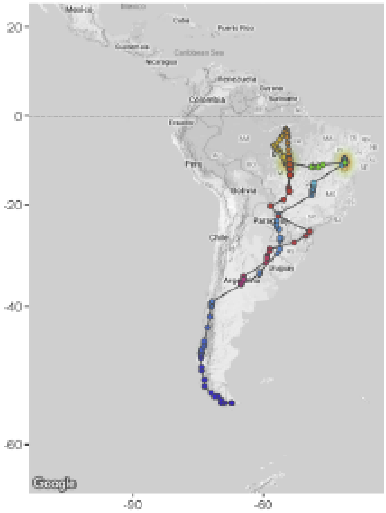
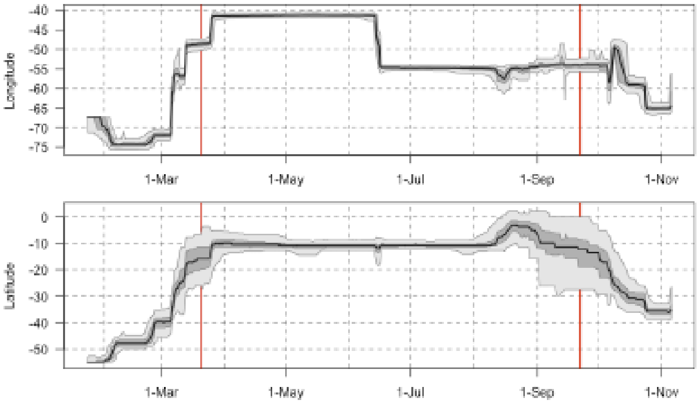
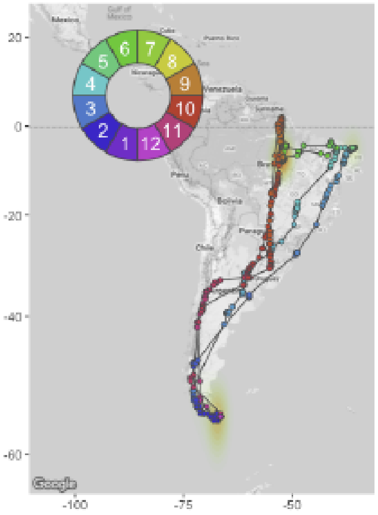
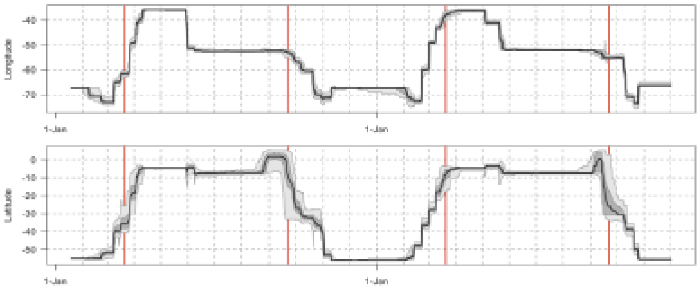
V876		
BC037		
BJ354		

Figure 4.3: Individual movement maps of elaenias breeding on Navarino Island. Dots connected by lines in the left column figures represent the median of estimated locations for each twilights. The colors of these circles vary according to the legend (color-wheel), with different colors representing each month. Shades of orange represent the utilization distribution, with darker orange representing locations where the bird spent more time. Figures on the right column show changes in estimated longitude (top panels) and latitude (bottom panels). The black lines represent the median of the estimated location, dark shade represent the interquartile range and light gray the 95% credible interval. Red vertical lines represent equinoxes (Rakhimberdiev et al. 2017).

CHAPTER 5

GENERAL CONCLUSIONS

5.1 Main Results

During three breeding seasons (2014 – 2017) I studied the ecology of five forest passerines in the sub-Antarctic forest of Navarino Island, Chile (55°04'S, 67°40'W). Specifically, I provided the first extensive data on the breeding biology of *Phrygilus patagonicus, Anairetes parulus, Turdus falcklandii*, *Elaenia albiceps chilensis,* and *Zonotrichia capensis*, the five most abundant open-cup forest-dwelling passerines in the southernmost forests of the world (Rozzi and Jiménez 2014). Additionally, because population dynamics on the breeding ground can be affected by events occurring on their wintering ground, I determined the migratory connectivity of *E. albiceps*, the only long-distance passerine migrant breeding on Navarino Island (Chesser 2005, Jiménez et al. 2016).

In Chapter 2, I found that all five passerines breed exclusively using open-cups nests on Navarino Island, not in cavities as they sometimes do at lower latitudes (Ojeda and Trejo 2002, Altamirano et al. 2015). I described egg-laying rhythm, highlighting that not all species exhibit the pattern of one egg laid per day (Martin et al. 1997, Mezquida 2003, Auer et al. 2007), which is an important consideration for accurately determining breeding phenology in birds. Furthermore, in this study I provided the first report of developmental periods (i.e., incubation and nestling periods) for *P. patagonicus*, which lasted approximately one month from the start of incubation until chicks fledged. I found that *E. albiceps* starts breeding later compared to most of the other species; it arrives in October and starts breeding in November. This is an expected result considering *E. albiceps* is the last of these species to arrive to the island.

Elaenias breeding at lower latitude (35°S) also start breeding in November, however, they start arriving to their breeding ground in September (Escobar et al. 2004). This suggests that elaenias breeding on Navarino Island are further time constrained than other conspecific breeding populations, which could make them more vulnerable to changes in spring arrival timing. I also detected that both *E. albiceps* and *Z. capensis* started breeding earlier during one season, which coincided with warmer spring temperatures. Finally, I showed that clutch size of *T. falcklandii* is larger on Navarino than at lower latitudes (39°S). This result suggests that breeding populations of bird species with extensive breeding ranges exhibit variation along latitudinal gradients in terms of clutch size and other aspects of their breeding biology. This study opens further questions regarding the mechanisms driving differences in breeding strategies among populations.

In Chapter 3, I report that *Milvago chimango* is the main nest predator of open-cup nesting forest passerines, and the main cause of nest failure. In addition, I found that species built their nests in sites with higher density and taller understory; however, these two factors decreased their nest survival. Because birds should select sites that decrease their risk of depredation (Martin 1993a, b), it seems like these species may be selecting the least appropriate nest-site. We propose that the risk of depredation has been changing on Navarino Island, and thus, passerines may be in an ecological trap. First, the introduction of ground mammalian predators (Schüttler et al. 2019) has shifted the predator assemblage that until then was dominated by aerial pressure (i.e. mostly raptors). And second, the abundance of *M. chimango* may be increasing in the study site, due to rapid changes in land cover and easy access to food provided by the proximity to an urban settlement and its associated landfill (R.F.

Jara, personal observation 2015). Although interesting, these results are based on a limited sample size, therefore, they must be taken with caution.

In Chapter 4, I determined that the migratory connectivity of *E. albiceps* is weak. Individuals breeding in two different sites that are >1,000 km apart within the South American temperate forest biome, overlap in both space and time during winter, which included two sites in Brazil used consecutively. As mentioned above, *E. albiceps* breeding on Navarino Island are much more time constrained during their breeding season than those breeding at lower latitudes (Escobar et al. 2004). On Navarino Island, elaenias only have one month from arrival before they start laying eggs, whereas in Central Chile they have 2 months. Because the quality of winter habitat can affect spring migration timing, I hypothesize that elaenias breeding on Navarino should be more vulnerable to habitat disturbance in their wintering sites, as they may not be able to delay their reproduction without compromising their fitness.

5.2 Future Research

This dissertation provided the first information on the breeding biology of the five most abundant open-cup nesting passerines in the southernmost forests of the world. This is just the first step in understanding the full annual cycle of these birds. More research with larger sample sizes is needed to answer further questions about the mechanisms driving differences in breeding strategies among populations, the effect of global change on nesting phenology, population abundance and density of the main nest predator in this system (*Milvago chimango*), and the factors driving movements of *Elaenia albiceps* during the nonbreeding season.

I found that some species placed their nests closer to the ground on Navarino Island

(55°S) than in the Araucania region (39°S). I proposed that one possible explanation for this could be differences in predator assemblage, because on Navarino Island there are fewer potential ground predators, all of which have been introduced. Further research should expand on this by including islands of the Cape Horn Biosphere Reserve that still are completely free of terrestrial predators. This would provide more data to understand whether or not birds are selecting nest-sites based on the risk of depredation, and how this affects their nest survival.

I found that the two migratory species included in this study started breeding earlier one season compared to the previous year, opening further questions regarding the factors driving nesting phenology. Nesting phenology is a major determinant of individual fitness in birds (Nager and van Noordwijk 1995). Breeding too early or too late in the season may result in nesting in adverse weather conditions, missing the peak of food availability, or facing time constrains for re-nesting, among others (Martin 1987, Nager and van Noordwijk 1995, Visser et al. 1998). One determinant of breeding initiation date is spring temperature. Several studies on the impact of climate change on birds have correlated changes in spring temperature with the advancement of breeding initiation date (Dunn and Winkler 1999, Sanz 2003, Townsend et al. 2013), with fitness consequences of breeding earlier in the season varying among species (Wilson and Arcese 2003, Visser et al. 2006, Husby et al. 2009, Townsend et al. 2013). Further research should explore the relationship among spring temperature and food availability, breeding initiation, and nesting success on Navarino Island, such that we can predict the effect of climate change on avian breeding phenology and determine its possible consequences for fitness.

I showed that the main cause of nest failure in these forest breeding passerines was depredation. Furthermore, the main nest predator I identified was the native raptor *M. chimango*. This generalist species is common in southern South America, and is commonly found in anthropogenic habitats such as cities (Rozzi et al. 1996). Given this raptor's importance in the recruitment of these passerines, I recommend to monitor the population of *M. chimango* on Navarino Island. Increased abundance and densities of this raptor in the study area, possibly subsidized by nearby human settlement, could have cascading effects on the population dynamics of forest nesting passerines.

Multiple breeding populations of elaenias made sequential use of two wintering grounds during the nonbreeding season. Reports of migratory songbirds undertaking these movements during the nonbreeding season are increasing (Heckscher et al. 2011, Delmore et al. 2012, Jahn et al. 2013, Lerche-Jørgensen et al. 2017). It is still unclear what drives these movements. One possibility is that birds track resource availability during winter, driving individuals to move from an area of declining resource availability to higher-quality areas (Stutchbury et al. 2016, Knight et al. 2019). Research about why elaenias move during winter is essential, as this knowledge is fundamental for understanding population dynamics of this migratory species, and how these dynamics could be influenced by environmental change (Thorup et al. 2017).

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