

INTERACTIONS BETWEEN SYMPATRIC HUMMINGBIRDS ON THE JUAN
FERNANDEZ ISLANDS: FORAGING BEHAVIOR AND COMPETITION

by

Coral Ann Wolf

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Thesis Committee:
Professor Bobbi Low, Chair
Assistant Professor Johannes Foufopoulos

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Abstract

The critically endangered Juan Fernández firecrown (*Sephanoides fernandensis*) is restricted to only one island in the world, Isla Robinsonson Crusoe, Juan Fernández Archipelago, Chile. The presence of exotic taxa, in the form of competitors or food resources, frequently have significant effects on the foraging strategies employed by local endemics. We examine here (1) the foraging behavior of the endemic, Juan Fernández firecrown in comparison to the recently arrived continental hummingbird competitor, the green-backed firecrown (*Sephanoides sephaniodes*) in native and non-native habitats, and (2) potential impacts of the green-backed firecrown on food availability and food access for the endemic.

Juan Fernández females spent a significantly greater proportion of their time foraging for arthropods than Juan Fernández males, or green-backed firecrowns. Hummingbirds in native Juan Bueno (*Rhaphithamnus venustus*) habitat spent a significantly greater proportion of their time foraging for arthropods than in any other habitat type, suggesting native habitat is a significantly better source of arthropod resources. Females spent a larger proportion of their time foraging, particularly arthropod foraging. This is likely due to incubation and nestling requirements as well as arthropod availability within native habitat.

Hummingbirds spent on average 1.68% of their time in chases; the majority of chases were between conspecifics. In Juan Fernández conspecific interactions, the Juan Fernández female was significantly more often the victim. Additionally, in the few observed interspecies interactions between green-backed firecrowns and female Juan Fernández firecrowns, the female was more often the victim. Male Juan Fernández individuals appear not to be significantly affected by green-backed firecrown presence during the breeding season. Our results, however, suggest that Juan Fernández females may be marginalized from rich foraging habitat by both male Juan Fernández and green-backed firecrown individuals. Conservation action should focus on the female Juan Fernández firecrown, the limiting sex on population growth, and the most severely impacted by non-native plant and competitor presence.

Chapter 1

FORAGING BEHAVIOR OF SYMPATRIC HUMMINGBIRD SPECIES ON THE JUAN FERNANDEZ ARCHIPELAGO

Abstract

The critically endangered Juan Fernández firecrown (*Sephanoides fernandensis*) is restricted to only one island in the world, Isla Robinson Crusoe, Chile. Island native forest area is now two thirds of what it was historically. An increase in non-native taxa has correlated with the decline of native species. The presence of exotic taxa, in the form of competitors or food resources, frequently have significant effects on the foraging strategies employed by local endemics. We examine here the foraging behavior of the endemic, Juan Fernández firecrown in comparison to the recently self-introduced hummingbird competitor, the green-backed firecrown (*Sephanoides sephaniodes*), in native and non-native habitats during the breeding season. Green-backed firecrown nectar foraging behavior in native Juan Bueno and eucalyptus forests, was significantly greater than Juan Fernández males or females. Female Juan Fernández firecrowns spent a significantly greater proportion of time nectar foraging in maqui habitat than in native or eucalyptus forest. Juan Fernández females spent a significantly greater proportion of their time arthropod foraging than Juan Fernández males, or green-backed firecrowns. Hummingbirds in native Juan Bueno habitat spent a significantly greater proportion of their time arthropod foraging than in any other habitat type, suggesting that arthropods are significantly more abundant. Overall, evidence suggests that Juan Fernández males are able to maintain territories in high quality habitat, spending generally a small proportion of their time budget foraging. Juan Fernández females may be marginalized by both conspecific male presence in high quality nectar habitat and by green-backed firecrown competition within lower quality habitats. Females are spending a larger proportion of their time foraging, particularly arthropod foraging. This is likely due to incubation and nestling requirements as well as arthropod availability within native habitat. Conservation efforts should focus on protecting the Juan Fernández female, including the restoration of native Juan Bueno-dominated forest. Females rely heavily on native forests for nesting as well as arthropod foraging habitat.

Introduction

Small populations are more vulnerable to extinction than larger populations (Mac Arthur and Wilson 1967; Pimm et al. 1988; Tracy and George 1992; Lawton and Newton 1994). This is particularly true on islands, where the majority (90%) of recent bird extinctions have occurred (Johnson and Stattersfield 1990; Manne 1999). Forest birds inhabiting islands in the Pacific Ocean appear to be particularly at risk (Johnson and Stattersfield 1990). In addition, losses of island bird species have been disproportionately biased towards endemic taxa (Chase 1996).

The critically endangered Juan Fernández firecrown (*Sephanoides fernandensis*) is a hummingbird restricted to a single small island, Isla Robinson Crusoe (93 km²) (Roy et al. 1999). Like other Pacific islands, Isla Robinson Crusoe has suffered from a host of alterations following its discovery in 1574. Introduced animal and plant species (both potential competitors and predators of native flora and fauna), habitat degradation (e.g. deforestation), and decline in native species have all led to a highly altered landscape and a 33% decrease in native forest (Dirnbock et al. 2003). Based on finite habitat availability and the Juan Fernández firecrown population's decline in the past century, it is urgent to examine possible contributors relevant to the conservation of the species. In addition, protection of the Juan Fernández firecrown population is critical due to its ecological importance as a pollinator in directly maintaining native flora on an island that's listed as one of the most endangered locations in the world (IUCN 1996).

One factor that makes endemic island birds particularly prone to extinction is habitat loss (Tracy and George 1992; Lawton and Newton 1994; Manne 1999). Introduced taxa, both plant and animal, can have significant ecological effects on island communities (Chase 1996). Island species, having evolved close connections with conspecifics may be significantly affected by perturbations to their ecosystem. The Juan Fernández archipelago in Chile has experienced various introductions of exotic plants and animals over the past 500 years. Coinciding with the resulting habitat changes has been the decline of the Juan Fernández firecrown population, the only endemic oceanic island hummingbird in the world.

Because we lack quantitative data, it is unclear whether the Juan Fernández firecrown decline is due to predation (Brooke 1987), habitat loss, food shortages, or competitive interactions with the continental green-backed firecrown (*Sephanoides sephaniodes*) (Colwell 1989; Roy et al. 1999). Previous discussion of impacts on the Juan Fernández population have highlighted seasonal nectar fluctuations as one of the "key factors" affecting Juan Fernández distribution and population numbers (Roy et al. 1999). The presence of exotic taxa, in the form of competitors or food resources, frequently have significant effects on the foraging strategies employed by local endemics (Pimm et al. 1985). We examine here the foraging behavior of the endemic, Juan Fernández firecrown in comparison to the recently self-introduced hummingbird competitor, the green-backed firecrown. In particular, the purpose of this report is to determine the amount of nectar and arthropod feeding employed by both species in native and non-native habitats during the breeding season.

Understanding the foraging behavior of both species of hummingbirds will provide a basis for understanding and comparing foraging habitat utilization, resource use, and time budgets of two closely related species. Determining hummingbird foraging habitat use patterns will begin to shed light on the potential impacts of these novel environments. In

addition, a comparison with the Juan Fernández firecrown's closest relative and a recent inhabitant to the islands, the green-backed firecrown, will create a clear comparison of how two hummingbird species are distributed across the various habitats.

Study Site: Juan Fernández Archipelago

The remote Juan Fernández Archipelago, located 677 km west of the central coast of Chile (33° 40' S, 78° 47' W), is composed of three islands that formed over a volcanic hotspot about 4 million years ago (Stuessy et al. 1984). Isla Robinson Crusoe is the largest of the three islands and reaches a maximum altitude of 915 meters; annual rainfall averages 900 mm (Wester 1991).

The islands have an extremely high rate of endemism: 69% of the native vascular plant species and 19% of the plant genera are found nowhere else on earth (Wester 1991; Bourne et al. 1992). There are few native animal species: a single mammal (Juan Fernández fur seal), as well as seven terrestrial birds (three endemic species and three endemic subspecies) (Hahn et al. 2005; Bernardello et al. 2006) and six sea bird species breed on the islands.

Owing to its high rates of endemism, the Juan Fernández archipelago was designated a Chilean National Park in 1935 and an UNESCO International Biosphere Reserve in 1977. In 1984, the archipelago was listed as one of the 11 most threatened sites in the world by the IUCN in response to introduced species' pressures on native biota (Perry 1984; Allen 1985).

The influx of introduced plants and animals began with the arrival of humans in 1574. In the century following the islands' discovery, people introduced goats, pigs, cattle, and dogs. Cats and rats arrived on the islands shortly after, in 1709 (Wester 1991). Current feral populations of non-native mammals include goats, rabbits, rats, and coatis (*Nasua nasua*, Procyonidae). Cattle and dogs also inhabit the islands. Although there have been no recorded extinctions of vertebrate species and relatively few recorded plant extinctions, the impacts to the native habitat have been extensive and we predict significant future losses to native biota. Based on environmental factors, 50-80% of the native montane forest has the potential to be invaded (Dirnbock et al. 2003).

The causes of decline are primarily due to direct habitat destruction and the introduction of both plant and animal predators. Native population declines also correlate with an increase in exotic flora. As a result of limited rabbit and goat population control measures by the national park, (Chilean Corporación Nacional Forestal [CONAF]), on Robinson Crusoe, grazing has had observable effects on the native vegetation's ability to regenerate. Other immediate impacts to the island include, native seed predation by introduced rats, seed dispersal by non native birds, and avian adult and nest predation by cats, coatis, austral thrushes, and rats (Cuevas and Van Leersum 2001). The Argentine ant, an extremely invasive arthropod, has also been recently found on all three islands and is an expected threat to native plants and arthropods (Ingram et al. 2006).

Exotic plants have had similarly detrimental impacts on the island ecosystem. Between 1916 and 2000 the bramble, *Rubus ulmifolius* (Rosaceae), and maqui, *Aristotelia chilensis* (Eleocarpaceae), area coverage has increased from 6.5% to 14% and 0% to 7% respectively (Dirnbock et al. 2003). These plant pests, which have been shown to have the greatest impact on the native vegetation structure, invade and shade out native seedlings (Roy et al. 1998). Evidence also suggests that maqui-dominated forests support a less diverse, less abundant arthropod population (E. H. personal observation). The transition to non-native

habitat on the islands translates not only to a change in nectar quantity and quality, but additional alterations can be seen in availability of arthropods. Total habitat loss is a concern; native forest area has decreased by a third since historic times (Dirnbock et al. 2003), and 53% of the island has now been characterized as bare or moderately eroded (Bourne et al. 1992). It is clear that the vegetation structure and composition have experienced severe degradation over the last four centuries since the islands' discovery.

Seventy-five percent of the endemic flora of the Juan Fernández is now endangered (Cuevas and Van Leersum 2001). A number of these plants rely on mutualistic pollination relationships with hummingbirds; an estimated 9% of the extant flora is pollinated by hummingbirds (Bernardello et al. 2000; Anderson et al. 2001). With the endemic Juan Fernández firecrown listed as endangered and a variety of native flora and fauna species listed as threatened, the fragile ecosystem is in obvious peril.

Hummingbird Ecology on the Juan Fernández Islands

The endemic Juan Fernández firecrown is estimated to have arrived on the Juan Fernández Islands less than 1 million years ago (Roy et al. 1998). The species once inhabited the two largest islands: Isla Robinson Crusoe and Isla Alejandro Selkirk. The population, now restricted to Robinson Crusoe, was last recorded on Selkirk in 1908 (Brooke 1987). The green-backed firecrown a continental inhabitant and sister species of the Juan Fernández firecrown, first arrived on Robinson Crusoe in the early 19th century (Brooke 1987; Colwell 1989; Roy et al. 1999), on Isla Alejandro Selkirk in 1981 (Bourne et al. 1992), and is the only other hummingbird species on the archipelago.

Qualitative historical accounts for the 19th century describe the Juan Fernández firecrown population as extremely abundant and rudimentary estimates for the 20th century ranged up to ten thousand individuals (see Brooke 1987). In recent decades, the population has declined dramatically with estimates as low as 250 individuals in the 1970's and 80's (Brooke 1987; Colwell 1989). As the endemic firecrown population has declined, the green-backed firecrown population approached 6000 individuals (Brooke 1987; Colwell 1989). A current accurate population estimate is difficult to report due to differences in population-estimating methodology between researchers (CONAF is the only annually-consistent census), and because the hummingbirds move seasonally. However, reports suggest that the Juan Fernández firecrown population is not as low as it once was; furthermore, estimates demonstrate the firecrown populations may be stabilizing, with anywhere between 691 and 2900 endemic hummingbirds and 1012 and 4500 green-backed firecrowns reported for censuses conducted between 2005 and 2007 (Hahn et al. 2005; Lopez-Calleja 2005; CONAF 2005-2006). Current population estimates place the Juan Fernández firecrown population at approximately one half that of the green-backed population.

These two hummingbirds are the only species (out of a total of 340) to inhabit an oceanic island. The Juan Fernández firecrown plumage is highly sexually dimorphic. The males have a 'brick-red' coloration, while the females have a shiny turquoise-green plumage. In the family Trochilidae, the Juan Fernández firecrown may be the most dimorphic in body size; the females weigh about 7g and males weigh close to 11g (Stone et al. 1988; Colwell 1989).

Both sexes of the green-backed have plumage similar to the Juan Fernández female, but are differentiated by their duller overall plumage, different crown coloration, and an

identifying white spot below the eye. The green-backed firecrown is smaller: average weights of green-backed firecrown females are 4.7g and males are 5.7g (Colwell 1989).

Although body size differs significantly between the species and sexes, the bill (exposed culmen) length does not, measuring about 15 mm for both sexes of Juan Fernández firecrown as well as the green-backed firecrown (Colwell 1989). Thus, the nectar resources are not partitioned between species or sexes based on physical accessibility as it is in some other hummingbird communities (Snow and Snow 1972; Wolf et al. 1976; Chavez-Ramirez and Tan 1993). There are 12 known native hummingbird-visited plants species on the island (Bernardello et al. 2001) all with recorded visits from both species and sexes. Furthermore, there are 15 species of introduced nectar-producing plants, all of which are utilized by the green-backed firecrown. In contrast, only 8 of these have recorded visits by the male and 11 have recorded visits by the female endemic firecrown (Roy et al. 1999).

Hummingbirds are found foraging primarily in four habitats, (which we have characterized by dominant tree species), during the breeding season: native forest containing the endangered native flowering tree, madera dura (*Sophora fernandeziana*; Leguminosae); native forest with juan bueno (*Rhaphithamnus venustus*; Verbenaceae) as the most common nectar source; eucalyptus forest containing (*Eucalyptus globulus*) pine (*Pinus* spp.) and cypress (*Cupressus* spp.); and maqui- (*Aristotelia chilensis*) dominated habitat, where once-native forest is now heavily dominated by maqui.

Of the native trees, juan bueno is the “most visited” bird-pollinated endemic species (Bernardello et al. 2001). Its long flowering period (potentially flowering to some extent all year round) peaks in flower density during October through December, providing a large number of tubular flowers with sucrose-abundant nectar (2.5 $\mu\ell$) (Bernardello et al. 2000), making it a reliable food source. Unlike some other nectar resources in native forest, juan bueno trees are rather dispersed. Madera dura, in comparison, only supports flowers from August through November, however the number of flowers per tree greatly exceeds juan bueno and trees are clumped, although with a very limited distribution (Bernadello et al. 2004). Like juan bueno, madera dura flowers have high nectar volume (8 $\mu\ell$) and sucrose concentration (Bernadello et al. 2004). Madera dura, therefore, has a high resource return but a shorter temporal availability than the juan bueno that reliably provides nectar all year round.

Two introduced trees, eucalyptus and maqui, are also visited by the hummingbirds during the breeding season. Eucalyptus, which is bird-visited in its native environment, likely provides a sufficient volume and concentration of nectar to sustain the island hummingbirds (Hingston et al. 2004). The eucalyptus plantations are an extremely clumped resource with a high density of flowers on the trees from May through September. Throughout the rest of the year, the flowering is characterized as scarce (Meza 1989). In contrast, maqui is an arthropod-visited tree in its native environment, providing high concentration but low volume nectar (E. H. personal observations). The small quantity of nectar may make feeding more energetically profitable for the smaller green-backed than the Juan Fernández firecrown, (as has been hypothesized for other invasive, low-volume nectar producers; Colwell 1989). Maqui flowering occurs primarily in September and October (C. W. and E. H. personal observation). These trees have consumed a great deal of native forest habitat (Dirnbock et al. 2003) and are ubiquitous over large areas of the island. Eucalyptus and madera dura, although clumped, do not have extensive ranges across the island.

Hummingbirds are dependent on a diet that includes both a rich energy source (nectar) and a protein source (arthropods) for muscle maintenance. Nectar makes up nearly 80% of non-reproductive green-backed firecrowns' diets (Lopez-Calleja et al. 2003). Experimental studies have demonstrated that green-backed firecrowns rely on nitrogen found naturally in arthropods to maintain body mass (Wolf et al. 1976; Lopez-Calleja et al. 2003). As few as 150 fruit flies were sufficient to maintain non-reproductive firecrowns' weights (Lopez-Calleja et al. 2003). When nectar availability is high, hummingbirds generally spend a small proportion of their time budget arthropod foraging (Stiles 1995). Some species have been shown to behave normally for 10 days without feeding on any arthropods (Brice 1992).

When nectar availability is low, hummingbirds may be able to increase their arthropod foraging efforts to meet energy requirements (Wolf 1970; Hainsworth 1977; Montgomerie and Redsell 1980). During seasons when flowers became relatively rare, several species in Costa Rica increased their arthropod foraging to more than 70% of their total foraging time (Wolf 1970). López-Calleja et al. (2003) found that when nectar availability was low, green-backed firecrowns supplemented their diet by consuming more arthropods. However, total energy obtained from the arthropod diet was not sufficient to maintain body mass over the 10-day experimental period.

Hummingbirds alter their consumption of nectar and arthropods based on environmental availability, physiological constraints, and energy requirements. As a result, foraging time budgets are expected to reflect, at least partially, the nectar and arthropod availability within a habitat. Wolf and Hainsworth (1971) found male hummingbirds in high value territories spent less of their total time foraging than in low value territories, consistent with optimal foraging theory (Krebs and Davies 1981).

Female hummingbirds may include a much larger proportion of arthropods in their diet during the breeding season. This is likely due to the high-energy demands for female reproduction. In particular, nestlings have high energy development needs, and overnight incubation requires a long-lasting energy resource to maintain temperature (Montgomerie and Redsell 1980; Remsen et al. 1986; Lopez-Calleja et al. 2003).

Native juan bueno forest is currently the best-known arthropod foraging habitat; it supports a significantly more diverse and a more abundant arthropod population than non-native forest dominated by maqui (where a greater number of non-native arthropods were found; E. H. personal observation). This trend also holds for those arthropods that fall within the size range that may be consumed by the firecrowns (≤ 4 mm).

Both hummingbird species' nesting periods begin in early August and continue through November (C. W. and E. H. personal observation). The green-backed firecrown likely has an extended breeding season that continues through the summer months. Active nests have been observed as late as February (E. H. personal observation). Timing of nesting coincides with the flowering of the native juan bueno and madera dura and non-native eucalyptus and maqui. It is apparent that the hummingbirds move between habitats on a daily as well as annual basis (Colwell 1989), depending on the flowering phenology of native and introduced plants.

Possible threats to the Juan Fernández firecrown population include food limitations, competition with the green-backed firecrown, predation (by introduced rats, coatis, and cats), and other habitat limitations (e.g. nesting habitat). A dearth of detailed, long-term studies of the species makes it difficult to identify factors contributing to the population decline and impedes development of a strategic recovery plan.

Objectives

Here we limit the scope of this report to examining possible food limitations during the breeding season, specifically analyzing nectar and arthropod foraging behavior in native and non-native habitats. We focus on nectar and arthropod availability because of the correlation between changes in island flora (Dirnbock et al. 2003) and the steep decline in the Juan Fernández firecrown population. A comparison of foraging behavior between two species with different evolutionary histories and population growth/decline patterns will provide an interesting backdrop for understanding habitat and resource. We examined foraging behavior during the breeding season, because it is a time of year when energy requirements for males and females are high.

We understand little about the effects of introduced nectar and arthropod resource presence on firecrown foraging behavior. Based on bill length, a recent evolutionary divergence, and foraging data from prior studies (Brooke 1987; Colwell 1989; Roy et al. 1999; Bernardello et al. 2001), it is clear that these sympatric species have overlapping ecological niches. Here we compare firecrown foraging behavior between and within species and sex by various habitats. These data will provide insight as to how the endemic and continental species of hummingbirds utilize both native and non-native habitats in acquiring arthropod and nectar resources during the breeding season. We chose to collect foraging data during the breeding season because it is a time of year when energy requirements for males and females are high and food resources are limiting. This research is part of a larger project, examining a broad range of possible agents of firecrown decline that include nesting phenology, interspecies competition, and food availability.

The positive correlation between Juan Fernández firecrown decline and the recent increase in non-native nectar and arthropod resources and increase in green-backed firecrown population lead to a number of hypotheses. Here we examine the possibility that interspecies presence creates (1) foraging behavior overlap between the Juan Fernández firecrown and green-backed firecrown, and (2) habitat use overlap in native forests (inferring possible exploitation competition). Additionally, one might hypothesize that (3) non-native habitat use by the green-backed firecrown confers a foraging advantage over the Juan Fernández firecrown. To test these predictions, we quantified nectar and arthropod foraging behavior at foraging sites over the length of the breeding season.

Materials & Methods

We observed flowering phenology and hummingbird foraging behavior on Robinson Crusoe Island from 28 August 2006 through 9 November 2006. Twelve work sites were established within the town limits of San Juan Bautista (population estimate: ~600) as well as within the national park boundaries, at altitudes ranging between 20 and 325 meters.

We determined flowering phenology monitoring sites by selecting habitat areas based on a list of criteria. Preferred site locations were those that were previously used as biannual hummingbird census points, contained flowering plants, and were accessible for bimonthly visits. Of all available locations, twelve, 28.6 m radius sites (~.25 hectare) were randomly selected and established. We characterized five sites as eucalyptus dominant, one as invasive maqui, and six as native forest. The native sites were further subdivided into four juan bueno-dominant and two madera dura-dominant sites. Sites were visited once every two

weeks for the length of the Juan Fernández firecrown breeding season. During these bimonthly visits, flowers on each plant within the site were counted.

Behavioral observations were conducted on a subset of the flowering phenology sites. Behavioral observation sites were selected among the phenology sites if they met a minimum number of flowers threshold. This threshold was determined based on pilot study work, which provided a qualitative description of hummingbird activity prevalence. Depending on the sites' dominant flowering tree species, we identified a requisite number of open flowers necessary for a behavioral observation visit: 200 eucalyptus, 2 juan bueno, 50 madera dura, or 100 maqui flowers. As a result, of the twelve flowering phenology locations, six were utilized for behavioral observations at some point during the breeding season: three native, one native with madera dura, one maqui-dominant, and one eucalyptus.

Within each behavior observation site, we identified three to four observation locations, termed *claros*. *Claros* were openings within the forest understory or on hillside overlooks where flowering species of plants and/or arthropod activity could be observed. Observation "boundaries" were predetermined so that when an individual bird had left the *claro* it would no longer be observed. *Claro* size varied between 70 m² and 640 m² ($M=295$ m²) depending on the effect of natural tree density, with eucalyptus sites having the largest size *claros*. *Claro* visit order was randomized within the site.

We visited *claros* to conduct behavioral observations both in the morning and afternoon. Morning observations were conducted between 30 minutes and 3 hours after sunrise, and afternoon observations were conducted between 4.5 hours and 1 hour before sunset. Within a single site visit, periods of 30-minute observations would be conducted consecutively at three different *claros*.

Behavioral observations began with a count of visible flowers within the *claro*, a rank of insect abundance (low, moderate, and high), weather measures (recording cloud cover and precipitation, as well as temperature, wind speed, and humidity using a Kestrel weather meter), and a scan for a count of visible hummingbirds. Foraging observations involved an observer and recorder when possible, or a single observer with a tape recorder. A stopwatch was used to record behavioral changes to the second. A total count of all hummingbirds observed within the *claro* was kept. Focal observations were performed on both hummingbird species.

A focal observation began when an individual entered the *claro* and ended once the individual was no longer visible and could not be re-identified as the same bird. Species and sex of focal individuals were recorded whenever identification was possible (unidentifiable individuals were not included in certain analyses). Behaviors of interest for the focal bird were basic movements, (flying, perching, hovering, and hopping) foraging activities (nectar feeding while perching, nectar feeding while hovering, arthropod feeding while hovering, arthropod feeding while perched, and sallying), and inter-bird interactions (generally defined as a chase). For the purpose of our analysis here, we use only the foraging categories:

- 1) *Nectar/Arthropod Perching*. Time the bird spent with feet holding onto branches and feeding from flowers or gleaning arthropods from the flora. Wings could be beating or still.
- 2) *Nectar/Arthropod Hovering*. Time the bird spent feeding from flowers without feet holding onto plant. Most arthropod hovering would consist of a great deal of swooping and maneuvering, feeding on a swarm of small flying arthropods anywhere between treetop- and ground-level.

- 3) *Sallying*. Time the bird spent flying out to capture an arthropod and return to the same perch. This was recorded as an instantaneous behavior that lasted for one second. The amount of time spent sallying (relatively small) was combined with all arthropod hovering behavior for the purpose of analysis.

An additional category of *Not Visible* was also used for times when the bird was hard to see. The number of seconds the bird was not visible was then subtracted from the total focal time to get the total seconds of observation, which was the value used for further analyses.

Foraging bouts per focal observation period were totaled, such that the amount of time spent in each behavior was calculated for every focal individual. Additionally, we calculated the total time for which each focal individual was visible. This allowed calculations of foraging time budgets that could then be compared between individuals.

In comparison with studies of other hummingbird species, we utilized stricter definitions of nectar foraging activity (Wolf and F. R. Hainsworth 1971). We calculated time budget proportions after removing “time not visible.” We expect past researchers’ inclusion of “time not visible” in focal observation totals (Wolf and F. R. Hainsworth 1971; Hainsworth 1977; Stiles 1995) distorted the estimation of behavior proportions.

Hummingbirds were not marked; thus a single individual could have been involved in multiple recorded chases within the same day or over the breeding season. As a result, it is difficult to verify that the assumption of true independence is met.

Results

A total of 124.5 hours of behavioral observations were conducted during the 2006 breeding season. During these observations, 817 individual focal individuals were observed: 301 (36.8%) Juan Fernández males, 279 (34.1%) Juan Fernández females, 162 (19.8%) green-backed firecrowns, and 75 (9.2%) unknown hummingbirds. Foraging behavior was observed in 522 (63.9%) of the focal observations. Although it was occasionally possible to identify the sex of green-backed firecrown individuals, the majority of green-backed observations were of an unknown sex, thus male and females were pooled for the purpose of analysis. Observations were unevenly spread across the four different habitat types, because of varying number of sites per habitat type and varying levels of hummingbird activity. We conducted 110 thirty-minute observations in the 3 native juan bueno habitat sites, compared to 42 to 44 observation periods in each of the other 3 habitat types. Distribution of focal observations across habitat types was as follows: 383 (46.9%) in native with juan bueno forest, 174 (21.3%) native with madera dura, 79 (9.7%) in maqui, and 181 (22.2%) in eucalyptus habitat.

Habitat Distribution and Use

Focal observations were distinguished based on species and sex for Juan Fernández firecrowns. Table 1 summarizes the distribution of habitat types for each species and sex of focal hummingbird (where species was identified). Presence of species/sex is not independent of habitat type, (Pearson χ^2 : (df=6, N=740) = 248.46, $p < .001$). Male Juan Fernández firecrowns were observed more often in eucalyptus habitat than would be expected. Although territorial behavior by Juan Fernández males was observed in all habitat types, male presence was much more common in eucalyptus and madera dura forest. These

habitats had territories that appeared to be maintained by males over the length of the breeding season. Where as a single male would be observed in the native or maqui habitats, multiple males could be seen simultaneously in the eucalyptus and madera dura habitat. Green-backed firecrowns were observed in eucalyptus and madera dura habitat significantly less often than expected. When habitat types were aggregated into native and non-native, we found presence of a hummingbird in relation to its species and sex was also dependent upon habitat category, (Table 2; Pearson χ^2 (2, N=740) = 92.95, $p < .001$). Juan Fernández females used native habitat significantly more than expected.

Table 1. Summary of Hummingbird Species and Sex by Habitat Type. Presence in a habitat type is dependent on hummingbird species (Pearson χ^2 = 248.46; $p < .001$). For each bird group, the first column gives number of focal individuals and the second column gives the corresponding percentage of total sample for that group.

Habitat	Focal Species/Sex						Total	
	JF Male		JF Female		Green-backed			
Native with Juan Bueno	62	20.7%	160	57.6%	110	67.9%	332	44.9%
Native with Madera Dura	83	27.7%	78	28.1%	6	3.7%	167	22.6%
Eucalyptus	132	44.0%	31	11.2%	7	4.3%	170	23.0%
Maqui	23	7.7%	9	3.2%	39	24.1%	71	9.6%
Total	300	40.5%	278	37.6%	162	21.9%	740	

Table 2. Summary of Hummingbird Species and Sex by Habitat Category. Presence in a habitat category is dependent on hummingbird species (Pearson χ^2 = 92.95; $p < .001$). For each bird group, the first column gives number of focal individuals and the second column gives the corresponding percentage of total sample for that group.

Habitat	Focal Species/Sex						Total	
	JF Male		JF Female		Green-backed			
Native	145	48.3%	238	85.6%	116	71.6%	499	67.4%
Non-native	155	51.7%	40	14.4%	46	28.4%	241	32.6%
Total	300	40.5%	278	37.6%	162	21.9%	740	

Foraging Behavior

For the purpose of time budget summaries, only focal observations that lasted at least 15 seconds were included in the analysis. This was done to allow for more behaviors to be observed in a single focal. Limiting focal observations to those exceeding the minimum period of observation time reduced the focal sample size to 428 (Table 3). Median time of observation was 43 seconds (Range: 15 – 565 sec.) for this subset of observations versus 18

seconds for the total observation sample. The median number of behaviors recorded was 10 (Range: 1 – 90 behaviors) for this subset of observations versus 5 observations for the total observation sample. Nonetheless, three focal individuals had only a single behavior recorded for the length of the observation and sixteen focal individuals had only two behaviors recorded. Times spent foraging were analyzed as two dependent variables: (1) proportion of total focal time spent nectar foraging (e.g. nectar feeding while perched or hovering), and (2) proportion of total focal time spent arthropod foraging (e.g. arthropod feeding while perched (gleaning), hovering, or during a sally). For all the following analyses, these dependent variables were transformed by taking the arcsine of the square root of the proportion so that the proportions were more normally distributed.

Table 3. Proportion of Total Observation Time* Spent for All Hummingbirds in Foraging Behaviors by Period of Day and Habitat Type. There was a significant difference in proportion of total observation time hummingbirds spent arthropod foraging in the morning versus the afternoon ($F(1, 428) = 4.695, p=.031$). There was no significant difference in nectar foraging behavior between periods of day ($F(1, 420) = .060, p=.981$).

Time	Habitat Type	Time Arthropod Foraging	Time Nectar Foraging	Total # of Birds Observed in Habitat	
		%	%	N	%
AM**	Native with Juan Bueno	0.31	0.15	98	0.46
	Native with Madera Dura	0.13	0.09	60	0.28
	Maqui	0.10	0.21	18	0.08
	Eucalyptus	0.13	0.02	37	0.17
	Total	0.21	0.11	213	
PM	Native	0.40	0.14	78	0.36
	Native with Madera Dura	0.21	0.09	59	0.27
	Maqui	0.09	0.23	26	0.12
	Eucalyptus	0.17	0.04	52	0.24
	Total	0.25	0.11	215	
Total		0.23	0.11	428	

*Focal observations that lasted at least 15 seconds. Percent of time spent foraging included both focal individuals who did and did not (e.g. 0%) participate in foraging behavior during the focal observation.

**AM denotes observations that were conducted during the first 4 hours following sunrise. PM denotes observations that were conducted within 5 hours of sunset.

Nectar Foraging

To examine the effect of time of day on the proportion of time hummingbirds spent nectar foraging, we conducted a two-way analysis of variance (ANOVA) with the two factors being habitat type and time of day plus their interaction. Proportion of time spent nectar foraging was dependent on habitat type (see below for further analysis). Proportion of time spent nectar foraging was independent of whether data were collected in the morning ($\bar{x} = .177$, $SD = .371$) or afternoon ($\bar{x} = .183$, $SD = .360$; $F(1, 420) = .125$, $p = .724$). No interaction between time of day and habitat type was found, ($F(1, 420) = .060$, $p = .981$). Thus, time of day was not included in subsequent nectar foraging models.

A two-way ANOVA examining proportion of time spent nectar foraging with habitat type, species/sex, and their interaction as the main effects was conducted, and all were found to be significant (Table 4; Table 5; Chart 1). We thus examined the differences between species within each habitat type. Nectar foraging behavior differed significantly between species and was habitat dependent. With relatively large size groups, we assumed normality and Bonferroni post hoc tests were conducted to determine significant differences between variables. P-values are based on the Bonferroni correction for multiple comparisons. There was a significant difference in nectar foraging activity in native with juan bueno and eucalyptus habitat ($F(2, 416) = 6.237$, $p = .002$; $F(2, 416) = 8.032$, $p < .001$ respectively). Comparing species/sex nectar foraging behavior within native and eucalyptus habitats, green-backed firecrews spent a significantly greater proportion of their time nectar foraging than Juan Fernández males or females ($t(416) = 2.58$, $p = .031$; $t(416) = 3.41$, $p = .002$). Differences between species' nectar foraging behavior was not significant in native forest with madera dura or in maqui habitat ($F(2, 416) = .993$, $p = .371$; $F(2, 416) = 2.989$, $p = .051$).

There was a significant difference in nectar foraging activity between habitat types for female Juan Fernández firecrews ($F(3, 416) = 3.358$, $p = .019$). Females spent a significantly greater proportion of time nectar foraging in maqui habitat than in native with juan bueno ($t(416) = 2.90$, $p = .023$) or eucalyptus forest ($t(416) = 3.00$, $p = .017$). Juan Fernández females spent the smallest proportion of time nectar foraging in eucalyptus habitat ($p > .05$).

There was no significant difference in nectar foraging time between habitat types for the Juan Fernández male ($F(3, 416) = 1.473$, $p = .221$) or the green-backed firecrown ($F(3, 416) = 2.418$, $p = .066$). Juan Fernández males followed the same trend as the females, spending the greatest percentage of their time budget nectar foraging in maqui and the least amount of time nectar foraging in eucalyptus forest. Green-backed firecrews spent the greatest proportion of their time nectar foraging in eucalyptus and the smallest proportion in native forest with madera dura.

Table 4. Proportion of Total Observation Time Spent in Foraging Behaviors* by Species/Sex and Habitat Type. Nectar foraging behavior differed significantly between species/sex of hummingbird dependent on habitat type ($F(6,416) = 2.500, p=.022$). There was a significant difference in percent time spent arthropod foraging between species/sex ($F(2,416) = 12.187, p < .001$) and between habitat types ($F(3, 416) = 5.101, p = .002$).

Species/ Sex	Habitat	Nectar Foraging		Arthropod Foraging		Total Birds Observed N
		Time %	Focals #	Time %	Focals #	
Green- backed	Native with Juan Bueno	0.26	16	0.14	19	45
	Native with Madera Dura	0.08	2	0.09	4	5
	Maqui	0.26	12	0.08	13	22
	Eucalyptus	0.60	2	0.00	0	3
	Total	0.26	32	0.11	36	75
JF Male	Native with Juan Bueno	0.09	6	0.23	19	25
	Native with Madera Dura	0.06	10	0.12	29	55
	Maqui	0.10	6	0.10	8	15
	Eucalyptus	0.01	8	0.12	51	75
	Total	0.05	30	0.14	107	170
JF Female	Native with Juan Bueno	0.11	22	0.46	93	106
	Native with Madera Dura	0.11	18	0.22	44	59
	Maqui	0.39	4	0.13	5	7
	Eucalyptus	0.02	2	0.42	11	11
	Total	0.11	46	0.37	153	183
Total	Native with Juan Bueno	0.14	44	0.35	131	176
	Native with Madera Dura	0.09	30	0.17	77	119
	Maqui	0.23	22	0.10	26	44
	Eucalyptus	0.03	12	0.15	62	89
	Total	0.11	108	0.23	296	428

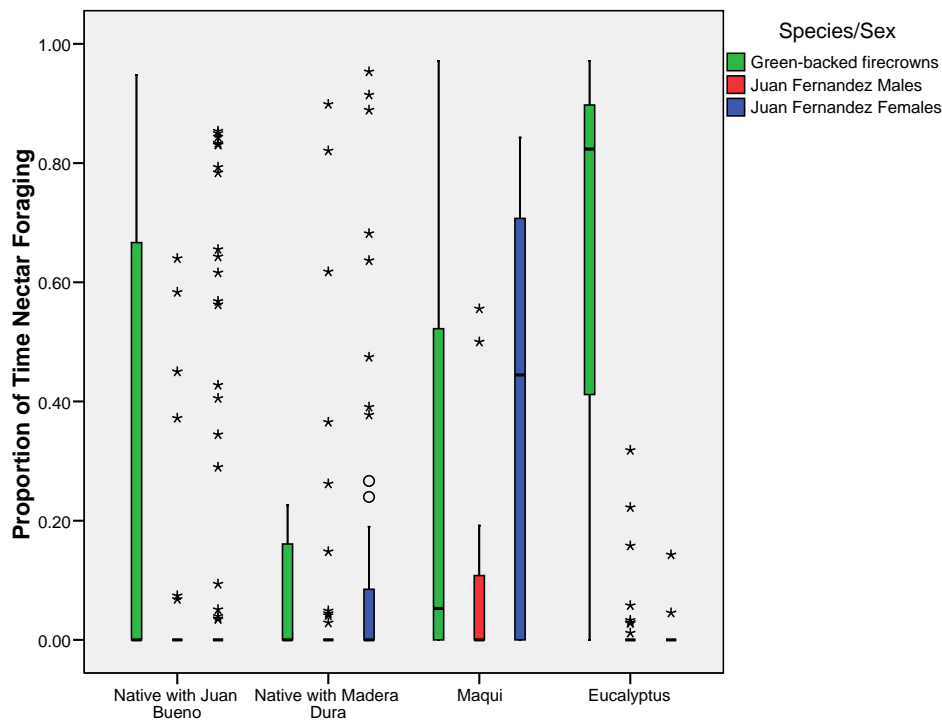
*Only focal observations ≥ 15 seconds. Percent time foraging is an average of both focal individuals that did and did not (e.g. 0%) participate in foraging behavior during the focal observation.

Table 5. Nectar Foraging* ANOVA Results.

Main Effects	df	F	p-Value
Species/Sex	2	10.603	<0.001
Habitat Type	3	3.130	0.026
Species/Sex*Habitat Type	6	2.500	0.022
Error	416		
Total	428		

Chart 1. Time Spent Nectar Foraging by Habitat Type and Species/Sex of Hummingbird. Nectar foraging behavior differed significantly between species/sex of hummingbird dependent on habitat type ($F(6,416) = 2.500, p=.022$).

Time Spent Nectar Foraging by Habitat Type and Species/Sex of Hummingbird



Arthropod Foraging

To examine the effect of time of day on the proportion of time hummingbirds spent arthropod foraging, we conducted a two-way ANOVA with the two factors being habitat type and time of day plus their interaction. Proportion of time spent arthropod foraging was dependent on habitat type (see below for further analysis). The proportion of time spent arthropod foraging was dependent on time of day, such that both species of hummingbirds were significantly more likely to spend time foraging for arthropods in the afternoon ($\bar{x} = .448$, $SD = .417$) than in the morning ($\bar{x} = .368$, $SD = .404$; two-way ANOVA, $F(1, 428) = 4.695$, $p = .031$; Table 3). The interaction effect was non-significant; hummingbirds in all habitats had a similar increase in arthropod foraging in the afternoon ($F(1, 428) = .241$, $p = .868$).

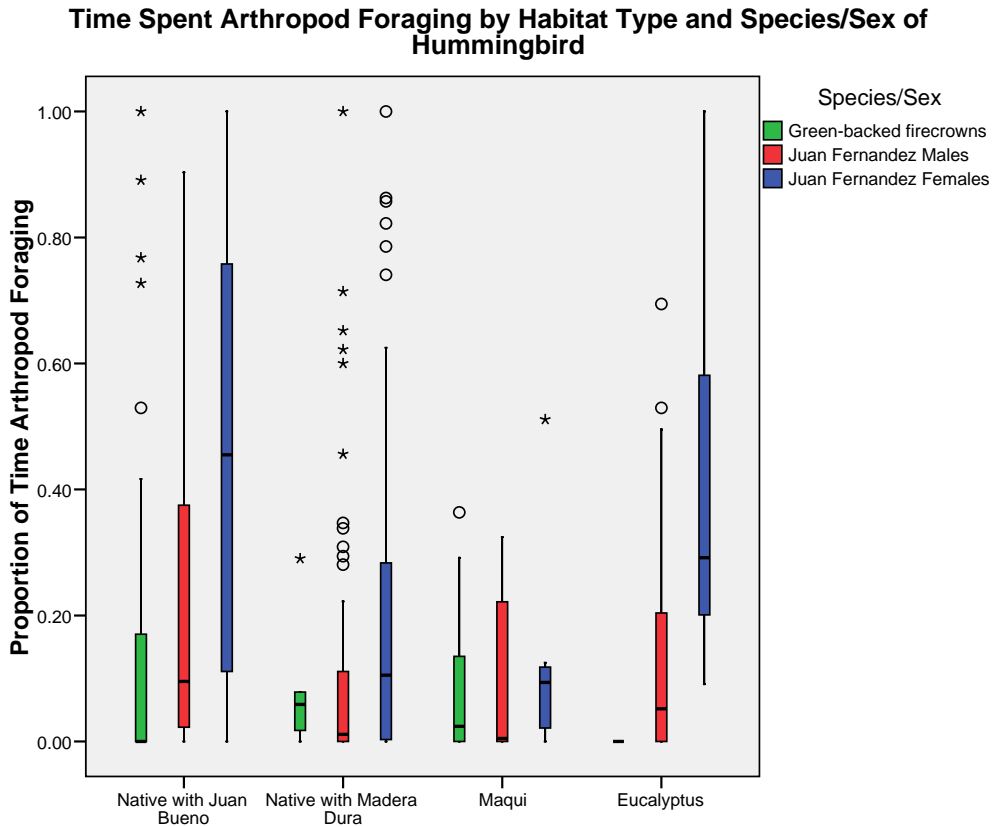
Based on these results, we included time of day as an additional main effect within the ANOVA model along with habitat type, species/sex, and their interaction. Time spent arthropod foraging differed with hummingbird species/sex, ($F(2, 415) = 12.187$, $p < .001$; Table 4; Table 6; Chart 2). Using Bonferroni adjusted α - levels, results indicated that Juan Fernández females spent a significantly greater proportion of their time arthropod foraging ($\bar{x} = .605$, $SD = .445$) than Juan Fernández males ($\bar{x} = .279$, $SD = .306$; $t(415) = 8.50$, $p < .001$), or green-backed firecrowns ($\bar{x} = .223$, $SD = .328$; $t(415) = 7.73$, $p < .001$). A significant difference in proportion of time spent arthropod foraging was also found between habitat types, ($F(3, 415) = 5.101$, $p = .002$). Birds in native habitat with Juan Bueno spent a significantly greater proportion of their time arthropod foraging ($\bar{x} = .558$, $SD = .472$) than in native habitat with Madera Dura ($\bar{x} = .326$, $SD = .363$; $t(415) = 5.43$, $p < .001$), Maqui ($\bar{x} = .225$, $SD = .238$; $t(415) = 4.97$, $p < .001$), or Eucalyptus ($\bar{x} = .315$, $SD = .310$); $t(415) = 5.18$, $p < .001$). No significant interaction was found between habitat type and the species/sex variables, ($F(6, 415) = 1.884$, $p = .082$). The time of day observations were conducted was again significant, ($F(1, 415) = 4.802$, $p = .029$). Birds of all species were more likely to arthropod forage in the afternoon than in the morning.

Table 6. Arthropod Foraging* ANOVA Results.

Main Effects	df	F	p-Value
Species/Sex	2	12.187	0.000
Habitat Type	3	5.101	0.002
Species/Sex*Habitat Type	6	1.884	0.082
Time of Day	1	4.802	0.029
Error	416		
Total	428		

*Dependent variables are transformed proportions of total observed time spent in foraging behavior.

Chart 2. Time Spent Arthropod Foraging by Habitat Type and Species/Sex of Hummingbird. There was a significant difference in percent time spent arthropod foraging between species/sex ($F(2,416) = 12.187, p < .001$) and between habitat types ($F(3, 416) = 5.101, p = .002$).



Discussion

Habitat Distribution and Use

Male Juan Fernández firecrowns inhabit high quality nectar habitats, eucalyptus and native with madera dura, during the breeding season. This is in contrast to Juan Fernández females, which prefer the native habitats. To date, Juan Fernández nests have been found solely in native luma (*Myrceugenia fernandeziana*) trees, particularly in locations not close to invasive plants (Hagen 2005). Although females do make nests within male territories in native madera dura habitat, males have not been observed to aid in any of the nesting activities (Meza 1989; C. W. and E. H. personal observations). Male tolerance of female foraging activity may be greater for females nesting in their territories, but further study is needed. In addition to male Juan Fernández territorial behavior, nesting location requirements and the energetic costs of flying over distances may make it difficult for female Juan Fernández firecrowns to forage extensively in eucalyptus. Although some non-native

habitat does provide superior nectar-feeding opportunities for the Juan Fernández firecrown, the species still depends solely on native habitat for nesting.

Green-backed firecrowns are observed in both native and non-native habitat relatively equally. However, they do not appear extensively in the highest quality habitats (eucalyptus and native with maderas duras). This is not surprising, based on the clear presence of the more aggressive Juan Fernández males, which visibly defend territories in these habitats (Brooke 1987; Stone et al. 1988; Colwell 1989; Roy et al. 1999). In a similar study, Pimm et al. (1985) found the dominant hummingbird's aggressive behavior in a high quality habitat caused the subordinate species to forage in an inferior patch. The strongest predictor of feeding presence in a particular habitat type was the density level of the dominant species; when the dominant hummingbird's population density was moderately high, the subordinate individuals were more likely to use the less productive habitat. In addition, when the dominant hummingbird's population density was higher, a smaller proportion of the dominant species used the high quality habitat as well. These findings are reflective of the habitat utilization trends we see on the Juan Fernández Islands, but in this study we lack benchmarks to determine densities.

High rates of female Juan Fernández firecrown and green-backed firecrown presence in native Juan Bueno habitat supports our hypothesis (2) that native habitat is shared. Green-backed firecrown presence on the island may significantly affect Juan Fernández females, who also demonstrate a preference for native habitat during the breeding season, and whose ecological niche may be being constricted. However, exploitative competition was not measured, thus it is unclear whether native habitat is a limiting resource for foraging or nesting habitat. We observed no chase events between Juan Fernández males and green-backed firecrowns in native habitat (C. W. personal observations). Native habitat use by green-backed firecrowns seems to have little effect on the Juan Fernández males, which prefer to defend clumped, high quality nectar territories in eucalyptus and maderas duras forests.

Our results suggest that counter to our hypothesis (3), both the endemic and continental species of firecrowns benefit from non-native habitat. Observations of green-backed firecrown presence in maqui habitat suggest that green-backed firecrowns' ability to exploit this resource (as a result of its smaller size or a co-evolutionary history on the continent) may confer some advantage. As maqui area coverage expands, the green-backed firecrown will benefit further. In comparison, non-native eucalyptus habitat covers a smaller area but is a significant nectar resource for a number of Juan Fernández male individuals. Juan Fernández males spent the smallest proportion of their time nectar foraging in the eucalyptus habitat, spending relatively lengthy periods of time perching, flying between perches, and calling (e.g. behaviors used to maintain their territory). This is in contrast to the very low number of green-backed firecrown focal individuals recorded in eucalyptus habitat (N=3), where two focal individuals spent the majority of the time nectar foraging before departing. Male Juan Fernández firecrowns, therefore, have a distinct advantage due to their ability to exclude green-backed firecrowns from high quality eucalyptus habitat.

Foraging Time of Day

Unlike other observational studies of hummingbirds, which describe a more intense nectar foraging period in the morning in comparison with the afternoon (Stiles 1995), our data suggest that the proportion of time spent nectar foraging on Isla Robinson Crusoe does

not differ between morning and afternoon. A comparison with daily food availability through direct measurements of nectar production throughout the day would help explain this trend. However, based on nectar foraging observations, it appears as though nectar production is occurring either bimodally or steadily throughout the day.

Also in contrast with daily activity budgets of arthropod foraging in other hummingbird species, which described constant activity throughout the day (Stiles 1995), hummingbirds on Isla Robinson Crusoe foraged for insects significantly more in the afternoon versus the morning. This significant difference is likely the result of warming throughout the day, which promotes insect activity.

Foraging Behavior

Our focal observations included both territorial and non-territorial individuals. Although this made it difficult to watch a single individual for an extended period of time, observations of all firecrown species and sexes allows for a comparison of foraging behavior between groups – an analysis missing from many hummingbird time budget summaries.

Proportion of time spent nectar foraging tended to differ with species and sex: 5% for the Juan Fernández male, 11% for the Juan Fernández female, and 26% for the green-backed firecrown (although note interactions above). A comparison with time budgets of other hummingbird species, (whose methodology allowed for a small number of individuals or a single sex to be observed for an extended period of time), reveals that the Juan Fernández firecrowns have relatively short nectar foraging bouts (Wolf and F. R. Hainsworth 1971; Wolf et al. 1976). Wolf and Hainsworth's (1971) observations of a territorial male hummingbird species (*Eulampis jugularis*) reported a nectar foraging budget ranging between 5% and 21% of the total time the bird was observed.

Male hummingbirds in high value territories have been observed to spend less of their total time foraging than in low value territories (Wolf and F. R. Hainsworth 1971), consistent with optimal foraging theory (Krebs and Davies 1981). Juan Fernández males spent the smallest proportion of time foraging in the high value, nectar rich territories of eucalyptus (1%) and native with madera dura (6%), in comparison to native with juan bueno (9%) and the maqui (10%) habitats (Table 4). The low percentage of nectar foraging in eucalyptus forest may additionally be the result of difficulty in observing tall, dense, large-canopied eucalyptus trees. It was easiest to miss nectar foraging in this habitat type, despite our best attempts in situating ourselves such that we could observe flowers.

Pyke (1980) found hummingbirds (with the exception of nesting females) to spend a much greater proportion of their time nectar foraging than arthropod foraging. Most of these data were collected on males defending nectar-based territories. However, this is not the trend we see for Juan Fernández males in any of our habitat types. A high proportion of time spent arthropod foraging in comparison to nectar-foraging may be the result of (1) an extremely clumped, abundant, and renewable arthropod supply (Montgomerie and Redsell 1980) or (2) nectar limitations (Wolf 1970; Hainsworth 1977; Lopez-Calleja et al. 2003). The Juan Fernández firecrown occasionally sallies for insects, but more commonly conducts continuous hawking flights. This foraging strategy is most appropriate when insect densities are high. Conclusions are impossible, however, without a direct measure of nectar and arthropod availability.

Female Juan Fernández firecrowns also spent a greater proportion of their time arthropod foraging than nectar foraging overall. The proportion of time Juan Fernández

females spent foraging for arthropods was significantly greater than Juan Fernández males or green-backed firecrews independent of habitat type. Intersex comparisons of other hummingbird species yield similar results (Hainsworth 1977; Stiles 1995): when feeding young, females “spent 3 to 4 times more time seeking arthropods than did males” (Stiles 1995). In comparison, the Juan Fernández females spent on average 37% of her time foraging for arthropods -- 2 to 4 times more time than their male counterparts depending on habitat type. Time budgets for arthropod foraging in other breeding female hummingbirds have ranged: a maximum of 6.7% for *Colibri coruscans* during the first week of caring for recently fledged young (Hainsworth 1977); 55% for *Selasphorus platycercus* while nesting (Montgomerie and Redsell 1980). Montgomerie and Redsell (1980) reported the nesting hummingbird female subsisting for a period of a couple days solely on arthropods, although these observations would benefit from further verification (Stiles 1995). The greater intensity of observed arthropod foraging by breeding female hummingbirds is at least partially the result of the protein requirements of producing eggs and rearing nestlings (Hainsworth 1977; Stiles 1995). Observations need to be conducted during other seasons to determine if the females increase their arthropod consumption during the season or rather rely heavily on an arthropod energy source all year round.

Juan Fernández females spent more time foraging for nectar than Juan Fernández males in all habitat types; all interactions were non-significant. In addition, the Juan Fernández female spent a greater proportion of time arthropod foraging on average (37%) than nectar foraging (11%). Only in maqui habitat did Juan Fernández females spend a greater proportion of time nectar foraging than arthropod foraging. These trends are not representative of other hummingbirds (e.g. Hainsworth 1977; Stiles 1995).

Green-backed firecrews’ nectar and arthropod foraging behavior significantly differed from that of the Juan Fernández firecrown. Green-backed firecrews spent relatively little time arthropod foraging, significantly less than Juan Fernández females. In native and eucalyptus habitats, the green-backed firecrews spent a significantly greater percentage of time nectar foraging. Interpreting nectar foraging results by the green-backed firecrown should be done with caution, as very little nectar foraging activity was observed in the eucalyptus or native with maderia dura habitats. More observations need to be conducted to determine actual green-backed firecrown time budgets in these habitats. As shown in the habitat analysis, it is important to note the obvious absence of the green-backed firecrown from these high quality habitat types.

It is unclear why the Juan Fernández firecrown spent more time arthropod foraging overall than nectar foraging. Unavoidable biases in observing both arthropod and nectar foraging do occur (Stiles 1995). Flowers are conspicuous however, and biases are most likely to overestimate the amount of nectar foraging. For taxa that feed on flying insects, the actual time spent insect foraging is often underestimated because the recorded time refers to only the moment of sallying and does not include search time in contrast to the Juan Fernández firecrown’s continuous hawking flights. This foraging strategy is possible as a result of potentially high insect densities and few insectivorous island inhabitants; it results in a higher proportion of arthropod foraging activity than is often seen in hummingbirds that primarily rely on sallying for volant insect feeding. We observed the smallest amount of arthropod feeding in maqui habitat, likely due to low arthropod abundance (E. H. personal communication). We made every effort to observe at nectar- and arthropod-rich locations within our chosen sites – preference was for running water, forest gaps, and plentiful flowers.

Although some sites were naturally drier or wetter overall than others, we do not expect that this significantly impacted the quantity of arthropod foraging observed across habitat types.

Our results were inconclusive as to whether a significant amount of foraging overlap exists between Juan Fernández firecrowns and green-backed firecrowns. In support of our hypothesis (1), native juan bueno forest was the preferred arthropod foraging habitat for all three groups of birds. Nectar foraging habitat preferences were unclear; preferences for a nectar foraging habitat type are confounded by the dominance hierarchy between groups.

Conclusions

By altering food choices, hummingbirds may optimize energy efficiency during all seasons (Wolf and F. R. Hainsworth 1971). Foraging strategies may be updated as food availability and levels of competition change. Green-backed firecrowns have been shown to alter their foraging strategies depending on temperature (cost of thermoregulation) and costs of feeding (Fernandez 2002).

The diets of the sympatric Juan Fernández firecrowns and green-backed firecrowns appear to differ during the breeding season, not based on morphological differences but rather as a result of habitat partitioning possibly due to a strong dominance hierarchy. Differential patterns in nectar foraging may not be caused by birds' preferences for different habitats but rather interspecific competition (Wolf et al. 1975; Feinsinger and Colwell 1978).

It is unclear whether available foraging habitat significantly limits the Juan Fernández population at this point in time. Available nesting and foraging habitats are a critical limitation for the female Juan Fernández firecrown, which relies on native habitat significantly for both. Females, of course, are the limiting sex in terms of population growth. Invasive maqui does not appear to be providing sufficient nectar or insect foraging habitat. In contrast, the non-native eucalyptus plantation does appear to have filled the nectar niche (at least partially) that the rare, endangered maderá dura forest no longer fills. Eucalyptus plantation habitat, however, is limited to areas surrounding the town of San Juan Batista.

Juan Fernández females rely heavily on native habitat during the breeding season, not only for nesting habitat but also foraging habitat. As native forest becomes more and more dominated by the invasive maqui, it is important to account for not only changes in nectar composition within the forest but also impacts to the native arthropod community. Although nectar needs for the Juan Fernández firecrown may be met in the eucalyptus forest as well as native habitat, arthropod availability within eucalyptus habitat is yet to be fully understood.

For nesting females, food limitations do not appear to be a significant issue; nests we visited in 2006 had a relatively high success rate (71.8%) in comparison with female green-backed nests (32.2%) (unpublished data). The Juan Fernández female is clearly the most severely impacted by the presence of green-backed firecrowns; habitat currently preferred by females is now being shared. Females appear to have a limited number of visits to eucalyptus habitat; Juan Fernández male presence as well as lengthy traveling distance from native nesting habitat may prevent extensive nectar foraging by the Juan Fernández female.

Future work should examine how foraging behavior both changes over the length of the breeding season as well as throughout the year. As flowering species come into nectar

production and the abundance and diversity of arthropods changes, we expect so do resource limitations for the Juan Fernández firecrown.

It is still unclear as to whether the removal of the invasive maqui will prevent extinction of the endemic Juan Fernández firecrown. It is apparent that for the Juan Fernández firecrown, like many endangered species, multiple threats may be acting in combination (Gurevitch and Padilla 2004). With multiple exotic species effects, both plant predators and competitors causing declines in native forest habitat, it is important for the national park to address both impact types.

Chapter 2

HUMMINGBIRD COMPETITIVE INTERACTIONS IN NATIVE AND INVADED HABITATS ON THE JUAN FERNANDEZ ISLANDS

Abstract

The critically endangered Juan Fernández firecrown (*Sephanoides fernandensis*) is restricted to only one island in the world, Isla Robinson Crusoe. We examine here the potential impacts of a recently self-introduced hummingbird competitor, the green-backed firecrown (*Sephanoides sephaniodes*), on food availability and access on the endangered Juan Fernández firecrown. In particular, our purpose was to determine the extent of interspecific and intraspecific competition occurring in this novel environment during the hummingbirds' breeding season. Focal observations were performed for both hummingbird species. All inter-bird interactions were recorded, including the interacting species and whether the focal was the aggressor or victim. A total of 174 chases were observed. Hummingbirds spent on average 1.68% of their time in chases, and proportion of time spent chasing did not differ significantly between species. Most chases were between conspecifics. In Juan Fernández conspecific interactions, the Juan Fernández female was more often the victim. Additionally, in the few observed interspecies interactions between green-backed firecrowns and Juan Fernández females, the female was more often the victim. Male Juan Fernández individuals appear not to be significantly affected by green-backed firecrown presence during the breeding season. Our results, however, suggest that Juan Fernández females may be marginalized from rich foraging habitat by both male Juan Fernandez and green-backed individuals. Overall, interspecies interference competition during the breeding season is not significantly impacting the Juan Fernández firecrown, although it may in other seasons.

Introduction

Interactions between the characteristics of a species and the characteristics of its environment are necessary in understanding a species' susceptibility to extinction (Tracy and George 1992). Endemic island birds become endangered due to a variety of factors. Small populations are more vulnerable to extinction than larger populations (Mac Arthur and Wilson 1967; Pimm et al. 1988; Tracy and George 1992; Lawton and Newton 1994). This is particularly true on islands, where the majority (90%) of recent bird extinctions have occurred (Johnson and Stattersfield 1990; Manne 1999). Forest birds inhabiting islands in the Pacific Ocean appear to be particularly at risk (Johnson and Stattersfield 1990). In addition, losses of island bird species have been disproportionately biased towards endemic taxa (Chase 1996). Environmental factors such as alterations to native habitat structure can considerably affect specialized species. Introductions of non-native species are a significant threat to native ecosystems and may pose a more severe threat to island environments (Johnson and Stattersfield 1990). Chase (1996) found a strong correlation between number of avian introductions to islands and the number of subsequent native extinctions. Although this does not clarify cause and effect, the relationship between endemic population declines and non-native establishment exists. Additionally, species characteristics such as competitive dominance can similarly impact a species' probability of extinction (Tracy and George 1992). When non-native species affect both habitat and competitive interactions, the outcome may be severe for an endemic island population.

The critically endangered Juan Fernández firecrown (*Sephanoides fernandensis*) is a hummingbird restricted to a single island, Isla Robinson Crusoe (93 km²) (Roy et al. 1999). Like other Pacific islands, Isla Robinson Crusoe has suffered from a host of introductions following its discovery in 1574. Introduced animal and plant species (both potential competitors and predators of native flora and fauna), habitat degradation (e.g. deforestation), and decline in native species have all led to a highly altered landscape and a 33% decrease in native forest area (Dirnbock et al. 2003). Based on finite habitat availability and the Juan Fernández firecrown population's decline in the past century, it is urgent to examine possible contributors relevant to the conservation of the species. In addition, protection of the Juan Fernández firecrown population is critical due to its ecological importance as a pollinator in directly maintaining native flora on an island listed as one of the most endangered locations in the world (IUCN 1996).

The presence of exotic taxa may have a significant effect on the foraging strategies employed by local endemics. We examine here the potential impacts of a recently self-introduced hummingbird competitor, the green-backed firecrown (*Sephanoides sephaniodes*), on food availability and access on the endangered Juan Fernández firecrown. In particular, our purpose is to determine the extent of interspecific and intraspecific competition occurring in this novel environment during the hummingbirds' breeding season. Although determining a clear cause-effect relationship between green-backed firecrown presence and Juan Fernández firecrown decline is not within the scope of this report, we address the extent and type of competition interactions between hummingbirds during the breeding season. By understanding interspecies competitive interactions, we will identify how resource access is partitioned between species, ultimately affecting reproductive success and recruitment. Additionally, the impact of relatively recent interspecies competitive interactions on endemic

island bird extinctions is difficult to differentiate from anthropogenic changes, principally habitat destruction and introduced predators (Case 1996).

Because we lack quantitative data, it is unclear whether the Juan Fernández firecrown decline is due to predation (Brooke 1987), habitat loss, food shortages, or interactions with the continental green-backed firecrown (Colwell 1989; Roy et al. 1999). Examining the competitive interactions between the Juan Fernández firecrown and the green-backed firecrown in relation to inter- and intraspecies competition in foraging habitat, we can improve our understanding of a potentially significant population limiting factor.

Study Site: Juan Fernández Archipelago

The remote Juan Fernández Archipelago, located 677 km west of the central coast of Chile (33° 40' S, 78° 47' W), is composed of three islands that formed over a volcanic hotspot about 4 million years ago (Stuessy et al. 1984). Isla Robinson Crusoe is the largest of the three islands and reaches a maximum altitude of 915 meters; annual rainfall averages 900 mm (Wester 1991).

The islands have an extremely high rate of endemism: 69% of the native vascular plant species and 19% of the plant genera are found nowhere else on earth (Wester 1991; Bourne et al. 1992). There are few native animal species: a single mammal (Juan Fernández fur seal), as well as seven terrestrial birds (three endemic species and three endemic subspecies) (Hahn et al. 2005; Bernardello et al. 2006) and six sea bird species breed on the islands.

Owing to its high rates of endemism, the Juan Fernández archipelago was designated a Chilean National Park in 1935 and an UNESCO International Biosphere Reserve in 1977. In 1984, the archipelago was listed as one of the 11 most threatened sites in the world by the IUCN in response to introduced species' pressures on native biota (Perry 1984; Allen 1985).

The influx of introduced plants and animals began with the arrival of humans in 1574. Current feral populations of non-native mammals include goats, rabbits, rats, cats, and coatis (*Nasua nasua*, Procyonidae). Although there have been no recorded extinctions of vertebrate species and relatively few recorded plant extinctions, the impacts to the native habitat have been extensive and we predict significant future losses to native biota. Based on environmental factors, 50-80% of the native montane forest has the potential to be invaded (Dirnbock et al. 2003).

The causes of native plant species decline are primarily due to direct habitat destruction and the introduction of both plant and animal predators. Native population declines also correlate with an increase in exotic flora. Grazing by goats, rabbits, and cattle has had observable effects on the native vegetation's ability to regenerate. Exotic plants have had similarly detrimental impacts on the island ecosystem. Between 1916 and 2000 the bramble, *Rubus ulmifolius* (Rosaceae), and maqui, *Aristotelia chilensis* (Eleocarpaceae), area coverage has increased from 6.5% to 14% and 0% to 7% respectively (Dirnbock et al. 2003). These plant pests, which have been shown to have the greatest impact on the native vegetation structure, invade and shade out native seedlings (Roy et al. 1998). Total habitat loss is a concern; native forest area has decreased by a third since historic times (Dirnbock et al. 2003), and 53% of the island has now been characterized as bare or moderately eroded (Bourne et al. 1992). It is clear that the vegetation structure and composition have experienced severe degradation over the last four centuries since the islands' discovery.

Seventy-five percent of the endemic flora of the Juan Fernández is now endangered (Cuevas and Van Leersum 2001). A number of these plants rely on mutualistic pollination relationships with hummingbirds with an estimated 9% of the extant flora pollinated by hummingbirds (Bernardello et al. 2000; Anderson 2001). With the endemic Juan Fernández firecrown listed as endangered and a variety of native flora and fauna species listed as threatened, the fragile ecosystem is in obvious peril.

Hummingbird Ecology on the Juan Fernández Islands

The endemic Juan Fernández firecrown is estimated to have arrived on the Juan Fernández Islands less than 1 million years ago (Roy et al. 1998). The species once inhabited the two largest islands: Isla Robinson Crusoe and Isla Alejandro Selkirk. The population, now restricted to Robinson Crusoe, was last recorded on Selkirk in 1908 (Brooke 1987). The green-backed firecrown, a continental inhabitant and sister species of the Juan Fernández firecrown, first arrived on Robinson Crusoe in the early 19th century (Brooke 1987; Colwell 1989; Roy et al. 1999), on Isla Alejandro Selkirk in 1981 (Bourne et al. 1992), and is the only other hummingbird species on the archipelago.

Qualitative historical accounts for the 19th century describe the Juan Fernández firecrown population as extremely abundant and rudimentary estimates for the 20th century ranged up to ten thousand individuals (see Brooke 1987). In recent decades, the population has declined dramatically with estimates as low as 250 individuals in the 1970's and 80's (Brooke 1987; Colwell 1989). As the endemic firecrown population has declined, the green-backed firecrown population approached 6000 individuals (Brooke 1987; Colwell 1989). A current accurate population estimate is difficult to report due to differences in population-estimating methodology between researchers (CONAF is the only annually-consistent census). However, reports suggest that the Juan Fernández firecrown population is not as low as it once was; furthermore, estimates demonstrate the firecrown populations may be stabilizing, with anywhere between 691 and 2900 endemic hummingbirds and 1012 and 4500 green-backed firecrowns reported for censuses conducted between 2005 and 2007 (Hahn et al. 2005; CONAF 2005-2006; Lopez-Calleja and Estades 2006). Current population estimates place the Juan Fernández firecrown population at approximately one half that of the green-backed population.

These two hummingbirds are the only species (out of a total of 340) to inhabit an oceanic island. The Juan Fernández firecrown plumage is highly sexually dimorphic. The males have a 'brick-red' coloration, while the females have a shiny turquoise-green plumage. In the family Trochilidae, the Juan Fernández firecrown may be the most dimorphic in body size; the females weigh about 7g and males weigh close to 11g (Stone et al. 1988; Colwell 1989).

Both sexes of the green-backed have plumage similar to the Juan Fernández female, but are differentiated by their duller overall plumage, different crown coloration, and an identifying white spot below the eye. The green-backed firecrown is smaller: average weights of green-backed firecrown females are 4.7g and males are 5.7g (Colwell 1989).

Although body size differs significantly between the species and sexes, the bill (exposed culmen) length does not, measuring about 15 mm for both sexes of Juan Fernández firecrown as well as the green-backed firecrown (Colwell 1989). Thus, the nectar resources are not partitioned between species or sexes based on physical accessibility as it is in some other hummingbird communities (Snow and Snow 1972; Wolf et al. 1976; Chavez-Ramirez

and Tan 1993). There are 12 known native hummingbird-visited plants species on the island (Bernardello et al. 2001), all with recorded visits from both species and sexes. Furthermore, there are 15 species of introduced nectar-producing plants, all of which are utilized by the green-backed firecrown. In contrast, only 8 of these have recorded visits by the male and 11 have recorded visits by the female endemic firecrown (Roy et al. 1999).

Hummingbirds are found foraging primarily in four habitats of the island (which we have characterized by dominant tree species) during the breeding season: native forest containing the endangered native flowering tree, madera dura (*Sophora fernandeziana*; Leguminosae); native forest with juan bueno (*Rhaphithamnus venustus*; Verbenaceae); eucalyptus forest containing (*Eucalyptus globulus*) pine (*Pinus* spp.) and cypress (*Cupressus* spp.); and maqui- (*Aristotelia chilensis*) dominated habitat, where once-native forest is now heavily dominated by maqui.

Of the native trees, juan bueno is the “most visited” bird-pollinated endemic species (Bernardello et al. 2001). Its long flowering period (potentially flowering to some extent all year round) peaks in flower density during October through December, providing a large number of flowers with sucrose-abundant nectar ($2.5 \mu\text{l}$) (Bernardello et al. 2000), making it a reliable food source. Unlike some other nectar resources in native forest, juan bueno trees are rather dispersed. Madera dura, in comparison, only supports flowers from August through November, however the number of flowers per tree greatly exceeds juan bueno and trees are clumped, although with a very limited distribution (Bernadello et al. 2004). Like juan bueno, madera dura flowers have high nectar volume ($8 \mu\text{l}$) and sucrose concentration (Bernadello et al. 2004). Madera dura, therefore, has a high resource return but a shorter temporal availability than the juan bueno that reliably provides nectar all year round.

Two introduced trees, eucalyptus and maqui, are also visited by the hummingbirds. Eucalyptus, which is bird-visited in its native environment (Hingston et al. 2004), likely provides a sufficient volume and concentration of nectar to sustain the island hummingbirds. The eucalyptus plantations are an extremely clumped resource with a high density of flowers on the trees from May through September. Throughout the rest of the year, the flowering is characterized as scarce (Meza 1989). In contrast, maqui is an insect-visited tree in its native environment, providing high concentration but low volume nectar (E. H. personal observation). Maqui flowering occurs primarily in September and October (C. W. and E. H. personal observation). These trees have consumed a great deal of native forest habitat (Dirnbock et al. 2003) and are ubiquitous over large areas of the island. Eucalyptus and madera dura, although clumped, do not have extensive ranges across the island.

Both hummingbird species’ nesting periods begin in early August and continue through November (C. W. and E. H. personal observation). The green-backed firecrown likely has an extended breeding season that continues through the summer months. Active nests have been observed as late as February (C. W. and E. H. personal observation). Timing of nesting coincides with the flowering of the native juan bueno and madera dura as well as the non-native eucalyptus and maqui. It is apparent that the hummingbirds move between habitats on a daily as well as annual basis (Colwell 1989), depending on the flowering phenology of native and introduced plants.

Possible threats to the Juan Fernández firecrown population include food limitation, interspecies interference or exploitation competition, predation (by introduced rats, coatis, and cats), and other habitat limitations (e.g. nesting habitat). A dearth of detailed, long-term

studies of the species makes it difficult to identify factors contributing to the population decline and impedes development of a strategic recovery plan.

Objectives

We limited the scope of this report to an analysis of interspecies competition in foraging habitat. Understanding the competitive relationship between the two species is particularly critical given that these two taxa have similar ecological requirements. This research is hence part of a larger project, examining a broad range of possible agents of firecrown decline that include nesting phenology, foraging behavior, and food availability.

We understand little about the effects of competition on resource partitioning in this island ecosystem. Examining the degree of interference and exploitation competition employed by the two species of hummingbirds will shed light on the effects of cohabitation on access to nectar resources and time budgets of defending food. Here we examine aggressive behavior during the breeding season and discuss the potential role of interspecific competition in Juan Fernández firecrown population dynamics. We compare firecrown aggressive encounters between and within species and sex within four habitat types. These data will provide insight as to how green-backed firecrown presence limits food accessibility of the Juan Fernández firecrown. We recorded foraging and aggressive interactions during the breeding season, a time of year when energy requirements for males and females are high and food resources are limiting.

The correlation between Juan Fernández firecrown decline and the recent presence of the green-backed firecrown leads to the following non-exclusive hypotheses: (1) the green-backed firecrown has a competitive foraging advantage over the Juan Fernández firecrown through exploitation (2) the green-backed firecrown has a competitive foraging advantage through interference. To test these two predictions, we recorded hummingbird presence and competitive interactions at foraging sites.

Materials & Methods

We observed flowering phenology and hummingbird behavior on Robinson Crusoe Island from 28 August 2006 through 9 November 2006, and 4 August through 24 August 2007. Twelve work sites were established within the town limits of San Juan Bautista (population estimate: ~600) as well as within the national park boundaries, at altitudes ranging between 20 and 325 meters.

We determined flowering phenology monitoring sites (established in 2006) by selecting habitat areas based on a list of criteria. Preferred site locations were those that were previously used as biannual hummingbird census points, contained flowering plants, and were accessible for bimonthly visits. Of all available locations, twelve, 28.6 m radius sites (~.25 hectare) were randomly selected. We characterized five sites as eucalyptus dominant, one as invasive maqui, and six as native forest. The native sites were further subdivided into four juan bueno-dominant and two madera dura-dominant. Sites were visited once every two weeks for the length of the Juan Fernández firecrown breeding season. During these bimonthly visits, flowers on each plant within the site were counted.

Behavioral observation were conducted on a subset of the flowering phenology sites. Behavioral observation sites were selected among the phenology sites if they met a minimum number of flowers threshold. This threshold was determined based on pilot study work,

which provided a qualitative description of hummingbird activity prevalence. Depending on the sites' dominant flowering tree species, we identified a requisite number of open flowers necessary for a behavioral observation visit: 200 eucalyptus, 2 juan bueno, 50 maderas dura, or 100 maqui flowers. As a result, of the 12 flowering phenology locations, eight were utilized for behavioral observations at some point during one of the two breeding seasons.

Within each behavior observation site, we identified three to four observation locations, termed *claros*. *Claros* were openings within the forest under story or hillside overlooks where flowering species of plants and/or insect activity could be observed. Observation "boundaries" were predetermined so that when an individual bird had left the *claro* it would no longer be observed. *Claro* size varied between 70 m² and 640 m² ($M=295$ m²) depending on the effect of natural tree density, with eucalyptus sites having the largest size *claros*. *Claro* visit order was randomized within the site.

We visited *claros* to conduct behavioral observations both in the morning and afternoon. Morning observations were conducted between 30 minutes and 3 hours after sunrise, and afternoon observations were conducted between 4.5 hours and 1 hour before sunset. Within a single site visit, periods of 30-minute observations would be conducted consecutively at three different *claros*.

Foraging observations involved an observer and recorder when possible or a single observer with a tape recorder. A stopwatch was used to record behavioral changes to the second. Focal observations were performed for both hummingbird species. A focal observation began when an individual entered the *claro* and ended once the individual was no longer visible and could not be re-identified as the same bird. Species and sex of focals were recorded whenever identification was possible (unidentifiable individuals were not included in certain analyses). All instances of bird interactions, including the interacting species and whether the focal was the aggressor or victim, were recorded. A total count of all hummingbirds observed within the *claro* was also kept.

Chases were totaled by focal hummingbirds' species and sex to document whether behavioral interactions differed between taxa or among habitat types. Time spent in observable chase events was also summed along with the total time a bird was visible. These data were analyzed to determine the extent of inter- and intraspecies interactions in the different habitat types, providing both a time budget for interference competition as well as a summaries of habitat use patterns and chase activity.

Hummingbirds were not marked; thus a single individual could have been involved in multiple recorded chases within the same day or over the breeding season. As a result, it is difficult to verify that the assumption of true independence is met (Rosenzweig and Mitchell 1985). To avoid a dependency error, multiple chases were removed from analysis if the focal bird went out of view but returned and was assumed to be the same individual. However, a second chase interaction by a focal was included if the focal bird interacted with a different species or sex than in the original chase.

Results

A total of 157 hours of behavioral observations were conducted during the 2006 and 2007 breeding seasons. During these observations, 1,092 focal individuals were observed: 494 (45.3%) Juan Fernández male, 307 (28.1%) Juan Fernández female, 209 (19.2%) Green-backed firecrests, and 82 (7.5%) unknown.

Of the 1,092 focal hummingbirds, 174 (15.9%) were observed in chase events. Chases occurred in all four habitat types. The total number of focals observed in a habitat type over the two seasons was reflective of the number of chases observed in that habitat type (Table 7; Pearson χ^2 (3, N = 1266) = .325, p = .955).

Table 7. Comparison Between Proportion of Focal observations and Chase Events by Habitat Type. There was no significant difference in proportion of focal individuals and chase events by habitat type (Pearson χ^2 (3, N = 1266) = .325, p = .955). Table entries are frequencies and column percentages of total focal observations and total number of those focals who participated in at least one chase event over the 2006 breeding season.

Habitat Type	Focals		Chases	
	#	%	#	%
Native with Juan Bueno	433	39.7%	67	38.5%
Native with Madera dura	294	26.9%	48	27.6%
Eucalyptus	287	26.3%	45	25.9%
Maqui	78	7.1%	14	8.0%
Total	1092		174	

Between August 28th and November 9th of 2006, we observed 126 chases. Between August 4th and August 24th of 2007 we observed an additional 48 chases for a total of 174 chase events (Table 8). As a result of the small number of observed chases, it was impossible to conduct a simple comparison of chase events between years to determine if data could be combined. Instead, a chi-square analysis was performed to examine whether the frequency of Juan Fernández male (Fisher's exact test, p = .597) and female (Fisher's exact test, p = .493) interspecies interactions differed between years. Because hummingbird interspecies interactions did not differ between 2006 and 2007 field season, chases were pooled across years. During 10 chase events, the focal individual's species was not identified; these were dropped from further analysis.

Table 8. Relationship Between Year and Focal Juan Fernández Firecrown's Interactor species. There was no significant difference between Juan Fernández firecrowns' and green-backed firecrowns' number of conspecific interactions between years. For an interspecies comparison between years, Juan Fernández male and female interactor columns were combined to create 2 x 2 tables. Juan Fernández male: Fisher's exact test, $p=.597$; Juan Fernández female: Fisher's exact test, $p=.493$

There was a significant difference between number of Juan Fernández firecrown male and female conspecific interactions between years. For an intraspecies comparison between years, a 2 x 3 design was used. Juan Fernández male: Fisher's exact test, $p=.004$; Juan Fernández female: Fisher's exact test, $p=.534$

Table entries are frequencies of interaction type per year.

Focal	Interactor			Total	
	JF Male	JF Female	Green-backed		
JF Male	2006	8	19	1	28
	2007	17	6	2	25
JF Female	2006	18	13	3	34
	2007	4	1	1	6
					93

To determine proportion of time hummingbirds spent chasing, only focal observations in which the bird was visible for at least 15 seconds were included in the analysis (N=428). Total chase time for each focal observation was summed and divided by the total time for which the bird was observed. Hummingbirds spent on average 1.68% of their time in chases. The proportion of time spent in a chase did not differ significantly between species (Table 9; $F(1, 425) = .014, p=.986$).

Table 9. Comparison of Proportion of Mean Time Spent Chasing. There was no significant difference between species and sexes of mean time spent chasing as a percent of total visible observation ($F(1, 425) = .014, p=.986$).

Species/Sex	Mean	Std. Dev.	Chase Events (N)	Focal Observations (N)
SS	1.74%	8.85%	6	75
SF Male	1.60%	5.56%	23	170
SF Female	1.72%	8.53%	25	183
Total	1.68%	7.54%	54	428

Of the 164 observed chases, 14.0% were interspecies interactions (Table 10). Thus, the majority of interactions (65.2%) occurred between conspecific individuals; species of the hummingbird interactor was not determined for 20.7% (34) of the cases. The majority of Juan Fernández chases (93.3%) occurred with another hummingbird; however, Juan Fernández hummingbirds were also observed interacting with the austral thrush (*Turdus falcklandii magellanicus*) and the Juan Fernández tit-tyrant, (*Anairetes fernandezianus*). Of these 11 non-hummingbird chases, two involved the chasing of an austral thrush. In the nine chases involving the Juan Fernández tit-tyrant, chase direction was mixed; instances occurred where male and female Juan Fernández firecrews were a victim or an aggressor.

Table 10. Total Chase Events for 2006 and 2007. Of 164 chase events, 23 (14.0%) were interspecies. Frequencies are summarized by focal bird's species and sex and interactor's species. Ten chases where focal bird was unidentified were not included in table. Shaded cells denote interspecific interactions.

Focal	Interactor					Unknown	TOTAL
	JF Male	JF Female	JF Male & Female	Green-backed	Other Species		
JF Male	25	24	5	3	8	18	83
JF Female	23	14	0	4	3	9	53
Green-backed	3	2	0	16	0	7	28
							164

Interspecies aggression is obviously a potential limitation on Juan Fernández firecrown's access to food and energy requirements. Thus, chases were aggregated independent of which species was the focal individual, and distinguished based on interacting individuals' species and sex. Table 11 summarizes conspecific interactions between species (Fisher's exact test, $p=.012$). Juan Fernández firecrews chased conspecifics significantly more than green-backed firecrews chased conspecifics. During the few interspecies interactions, the (non-significant) trend was for the green-backed firecrown to be the victim when interacting with the Juan Fernández male (5 of 6 chases) and the aggressor (5 of 6 chases) when interacting with the Juan Fernández female. Table 12 summarizes intraspecies interactions between sexes for the Juan Fernández firecrown. Removing green-backed firecrews from the chi-square analysis and summarizing conspecific interactions of the Juan Fernández males and females reveals that indeed conspecifics are the important competitor for the Juan Fernández firecrews, regardless of sex (Fisher's exact test, $p=1.000$).

Table 11. Relationship Between Species and Incidence of Conspecific Interaction. A greater proportion of Juan Fernández instigated chases were directed at conspecifics than green-backed firecrown instigated chases (Fisher's exact test, $p=.0119$). Frequencies and row percentages are reported.

Aggressor	Conspecific Interactions		Heterospecific Interactions		Total
JF	85	93.41%	6	6.59%	91
Green-backed	16	72.73%	6	27.27%	22
Total	101		12		113

Table 12. Incidence of conspecific and heterospecific interactions for Juan Fernández males and females. Juan Fernández sex did not affect the proportion of interactions directed at conspecifics versus heterospecifics (Fisher's exact test, $p=1.000$). Frequencies and row percentages are reported.

Agressor	Conspecific Interactions		Heterospecific Interactions		Total
JF Male	64	92.75%	5	7.25%	69
JF Female	21	95.45%	1	4.55%	22
Total	85		6		91

Additional chi-square analyses were performed to examine direction of interaction, with the focal bird species (and sex) as the fixed variable. Chases in which direction of chase was undetermined were removed for analysis. Analysis focused on species and direction of the interaction (e.g. whether the focal was the aggressor or victim), controlling for the species and sex of the focal bird. The green-backed firecrown could not be included in the analysis because of the small number of observed interactions as either aggressor or victim. Focal females were significantly more often the victims in interactions with Juan Fernández males (Table 13, Pearson $\chi^2(1, N = 31) = 6.35, p=.012, n=31$). In contrast, focal males did not demonstrate a significant effect of interactor or chase direction (Table 14; Pearson $\chi^2(1, N = 49) = .01, p=.942$).

Table 13. Summary of Juan Fernández female conspecific interactions for 2006 and 2007. Juan Fernández females were more often the victim in conspecific interactions, (Pearson χ^2 (1, N = 31) = 6.349, $p=.0117$). Table summarizes frequency of chase types and percentage of total when the focal individual was a Juan Fernández female.

JF Female: Interactor and Chase Type						
Interactor	Chase Type				Total	
	Aggressor		Victim			
JF Male	2	6.5%	19	61.3%	21	67.7%
JF Female	5	16.1%	5	16.1%	10	32.3%
Total	7	0.229	24	0.774	31	

Table 14. Summary of Juan Fernández Male Conspecific Interactions for 2006 and 2007. Juan Fernández males acted equally as the victim or aggressor in interactions independent of sex of interactor, (Pearson χ^2 (1, N = 49) = .0052, $p=.942$). Table summarizes frequency of chase types and percentage of total when the focal individual was a Juan Fernández male.

JF Male: Interactor and Chase Type						
Interactor	Chase Type				Total	
	Aggressor		Victim			
JF Male	19	36.7%	5	12.2%	24	49.0%
JF Female	20	40.8%	5	10.2%	25	51.0%
Total	38	0.776	11	0.224	49	

Although we found no significant difference in interspecies interactions for Juan Fernández males or females across the 2006 and 2007 field seasons, it is important to note that Juan Fernández male intraspecies chase behavior did differ significantly between years (above; Table 8). Juan Fernández focal males were more likely to be observed interacting with a conspecific female in 2006 and interacting with a conspecific male in 2007 (Fisher's exact test, $p=.004$). In addition, we observed a higher than expected number of Juan Fernández male focal chases during the 2007 season; the total number of male chases is almost equivalent to the 2006 season, while the number of hours spent observing in 2006 was much smaller. In contrast, the Juan Fernández focal females trend of interacting with slightly more Juan Fernández males than females remained the same between years (Fisher's exact test, $p=.534$).

Further, "year" is confounded with monthly variation, so it is unclear why this difference between field seasons exists. All observations coincided with some stage of observed Juan Fernández breeding activity. However, it is probable that there are seasonal differences in chase behavior specific to various stages of the breeding season. Unfortunately, our sample size is not large enough to examine temporal changes in aggression over the season.

Discussion

Interference competition

The Juan Fernández female is the victim of chases significantly more often than the male. Surprisingly, Juan Fernández focal males' chase behavior did not differ significantly between males and females. Rather, observed Juan Fernández male focals appear just as likely to chase Juan Fernández males or females (Table 13). We interpret these conflicting analyses as an effect of our *claro* locations being located in food rich areas – locations where males are more likely to maintain territories. Thus, we were more likely to observe a territorial male Juan Fernández as our focal. We could expect these resident males to be dominant and more often the aggressor in an interaction with an intruding Juan Fernández male.

Chases targeting females may have involved mating attempts or territorial aggression by a Juan Fernández male. Notably, in five chase observations, the focal Juan Fernández male was involved in a chase with another Juan Fernández male, both chasing a Juan Fernández female (Table 9). These aggressive encounters were likely the result of territorial behavior particular to the breeding season. The confounding factor of breeding season activity may have caused us to observe a greater number of Juan Fernández male-female chase events than during other seasons. Nonetheless, this hierarchy of male dominance is supported by past qualitative research conducted during other seasons and consistent with body size data (Brooke 1987; Stone et al. 1988; Colwell 1989; Roy et al. 1998; Roy et al. 1999).

Past behavioral studies have focused on Juan Fernández male territoriality, with strong evidence supporting their place at the top of the dominance hierarchy (Brooke 1987; Colwell 1989). Roy (1999) described an instance of a female Juan Fernández being chased by and chasing green-backed firecrews. The female left after a couple hours, “leaving the green-backed firecrews to the resource.” There are potential energy costs to the Juan Fernández female as a result of her position in the hierarchy -- inconsistently dominating over the green-backed firecrews while Juan Fernández males only occasionally tolerated female presence and foraging within their territories. Additionally, nectar foraging options are limited by nesting location habitat during the breeding season; Juan Fernández females benefit from foraging on nectar and insects close to their nests. They also have the additional energy costs of egg development, constructing nests, incubating eggs, and feeding chicks. As a result, females, (the limiting sex on reproductive rates), may be enduring the greatest energy costs during the breeding season; furthermore, they likely are not foraging in the richest habitat.

The direction of interspecies aggression is not as conclusive; prior work has been largely anecdotal or limited in time and habitat types. Reports by past observers suggest that female Juan Fernández firecrews are dominant over green-backed firecrews, with male green-backed firecrews able to oust female green-backed firecrews (Brooke 1987; Stone et al. 1988; Colwell 1989; Roy et al. 1998; Roy et al. 1999). In all of the 79 “encounters” recorded by Brooke (1987), the Juan Fernández male or female was identified as “dominant” to the green-backed. Similarly, Stone's (1988) observations (2 Sept. -- 5 Oct. 1988) of chase events in eucalyptus suggested size influenced direction: “. . . larger *S. fernandensis*, of either sex, would chase off smaller *S. sephaniodes* of either sex, but typically not return to forage from the flowers made available by the challenge.” In this study, we were unable to

conclude whether Juan Fernández firecrown dominance over green-backed firecrowns is significantly different than would be expected. Interestingly, where past work has characterized a “consistent” hierarchy, we observed instances where the opposite was true, and a Juan Fernández male or female was a victim in a chase with a green-backed firecrown. Of the six Juan Fernández female-green-backed chase events, the Juan Fernández female was the victim five times, (above).

Prior qualitative research described extensive interspecies interactions between the two hummingbird species (Brooke 1987; Roy et al. 1998; Roy et al. 1999). We found the majority of Juan Fernández firecrown chase interactions during the breeding season occur with conspecifics and the endemic Juan Fernández tit-tyrant. We found little evidence that interspecies interactions are a significant cost to the Juan Fernández firecrown during this time of year.

Our findings differ from prior work; this dissimilarity may be the result of a change in quantity of interspecies interactions over the past decade. In 1999, the difference in population sizes of the green-backed firecrown versus the Juan Fernández firecrown was estimated to be approximately 20:1 (Roy et al. 1999). In contrast, the current population is estimated to be 2:1. It is possible that in the past, interspecies interactions may have been significantly greater than they are today, solely as a result of a change in population ratio. Care should be taken with this assumption though, as the past and current population estimates are controversial.

Alternatively, seasonal variation in flowering phenology may affect the amount of interspecies interactions. Previously collected foraging and aggressive observational research was conducted in December-January (Brooke 1987) and during the “summer months” (Roy et al. 1999). Brooke’s (1987) research, recording town-based chase events in eucalyptus and bramble habitat, found 40.5% of interactions to be interspecies in comparison to our 14.0% (which includes non-hummingbird chase interactions, an activity that apparently was not observed by other researchers). Roy et al. (1999) reported a single intra-specific male-to-male conflict and 97.2% interspecies interactions, a significantly larger proportion than was observed in this study.

Independent of the proportion of interspecies interactions, the consequences of green-backed firecrown presence on the Juan Fernández firecrown population are arguably minimal. It is clear that the Juan Fernández male is able to maintain control over available nectar resources. Moreover, the Juan Fernández firecrowns do not exploit a smaller variety of nectar resources due to exclusion by the green-backed (Brooke 1987). In contrast, it appears that the green-backed firecrown is relegated to the nectar-poor habitats. The Juan Fernández firecrown’s ability to dominate food resources, however, does not mean there are no energy costs. Nectar resources in all four habitat-types are economically defensible, because the number of intruders does not appear to be so great that defense costs are prohibitively high. Equivalent to our calculated chase time budget, Brooke’s study of three Juan Fernández males found male firecrowns spending “1-2% of their time defending food flowers from other hummingbirds.” It is difficult to determine if this is ever a significant energetic cost, since the energetic expenditure is likely determined by the season as well as the nectar resource the male is guarding. Analysis of interspecies interactions during other seasons is needed for further comparison, as well as analysis of energetic costs for the female Juan Fernández during the breeding season.

The general lack of interspecies interactions during the breeding season may be the result of the distribution of food resources and/or the quantity of food resources. If food is either extremely scarce or extremely plentiful, competitive interactions may be limited (Pimm et al. 1985; Grant et al. 2002). Interestingly, one study found dominant male hummingbirds to continue to interact aggressively with conspecifics but largely ignore frequent inter-specific intruders when food was unlimited (Powers and McKee 1994). In the native forest habitat dominated by maderas dura, Juan Fernández males maintain territories with a high number of conspecific encounters and no observed chases of the smaller green-backed firecrown, which were rarely observed. Clumped trees characterize this habitat with hundreds of flowers per tree producing high quality, high volume nectar (E. H. personal observation). Green-backed firecrowns were largely absent from this resource rich habitat apparently independent of interspecies conflict.

Surprisingly, there were two interactions between the Juan Fernández firecrown and the austral thrush as well as nine interactions with the Juan Fernández tit-tyrant. The Juan Fernández tit-tyrant is endemic to the islands and the population is considered abundant (Lopez-Calleja and Estades 2006), as they are observed frequently. The austral thrush is thought to have had a more recent arrival on the island (Hahn et al. 2005) and acts as a disperser of the invasive maqui fruits. Neither bird is a competitor for nectar resources with the Juan Fernández firecrown.

Exploitation competition

Green-backed firecrowns benefit in mainland-plant dominated habitats where they may be better at extracting non-native resources (Hahn et al. 2005). In addition, the smaller green-backed firecrown may not be as reliant on high quality, high quantity nectar resources as the larger, dominant, endemic. The continental hummingbird, in turn, maintains the non-native plant populations through pollination (Hahn et al. 2005).

No measurable amount of interspecies competition by exploitation occurred at our *claros* during the breeding season. Although we did not have a single measure to quantify resource removal, we can compare the population proportion estimates between the Juan Fernández firecrown and the green-backed firecrown (1:2 respectively) to the proportion of birds observed as focals during our observation periods (4:1 respectively). Observation *claros* were located where food availability was expected to be highest, however the green-backed firecrowns are surprisingly absent.

The assumption behind exploitation competition is that individuals are free to go where they will do best (Krebs and Davies 1981). However, Juan Fernández males' ability to exclude females and green-backed firecrowns from high quality, clumped nectar resources make this assumption difficult to meet. Most exploitation competition occurs between females and/or males of the smaller species (Wolf et al. 1976). Additionally, exploitation competition is more likely to occur in habitats where nectar volume and production is low. Thus, interspecies exploitation competition may be occurring in lower quantity nectar habitat where Juan Fernández female and green-backed firecrown activity overlaps (i.e. native forest or maqui-dominated habitat) (C. W. unpublished data). Based on these observations, the green-backed firecrown is not out-competing the Juan Fernández male firecrown through exploitation; however, the exploitative advantage the green-backed firecrown has over the female Juan Fernández firecrown is still unclear.

Conclusion

We found no evidence that the green-backed firecrown is directly or indirectly out-competing the Juan Fernández firecrown for nectar resources during the breeding season. It is unclear what advantage green-backed firecrowns have over the endemic female in its ability to exploit non-native nectar or insect resources. What *is* clear is that the endemic Juan Fernández firecrown is now sharing a limited food supply with a relatively recent island immigrant. We suspect that the green-backed firecrown benefits from an evolution with continental food resources and predators; this may give greenbacks an advantage not measured here. The continental species possesses life history traits that make it well-adapted to the quickly changing island environment.

Future research needs to examine interspecies relationships during other seasons, particularly seasons when food resources may be scarce. Although we expected the breeding season to be resource-limited, due to the cold climate and energetic costs of mate attraction for the males and nesting for the females, other seasons may prove to be either food-limited and or more energetically costly for the hummingbirds. As more observations are collected, other patterns may emerge. Our results support the conclusion that the green-backed firecrown is not out-competing the Juan Fernández firecrown for available food resources during the breeding season; however, the Juan Fernández female may be incurring energy and food availability costs to a greater degree than the Juan Fernández male.

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