

Spatial segregation of the endemic versus non-endemic hummingbird on Robinson Crusoe Island, Chile: the effect of competitor abundance but not resources or habitat

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Abstract Competitive pressure from invasive species tends to have a particularly strong impact on remote islands, and knowledge of such phenomena can be crucial to the conservation of endemic biodiversity. Of the two hummingbird species inhabiting Robinson Crusoe Island, Juan Fernández Archipelago, Chile, one (Green-backed Firecrown, *Sephanoides sephaniodes*) has a wide mainland distribution while the other (Juan Fernández Firecrown, *Sephanoides fernandensis*) is endemic and critically endangered. Even though habitat degradation and predation by exotic mammal species are known to pose major threats, little attention has been given to the influence of

interspecific competition for floral nectar resources. In this study, we investigated the existence of interspecific competition by testing for spatial segregation of the two species using point counts dispersed within their suitable habitats. We additionally considered the influence of habitat type and flower abundance, which could also cause spatial segregation between the species. We found a negative association between the point count abundance of the two hummingbirds species, which remained consistent when accounting for the role of habitat type and flower abundance. Together, this could be an indication of interspecific competition in which individuals of *S. fernandensis* may benefit from aggregation by sharing the individual costs of chasing the vastly more abundant *S. sephaniodes*.

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Zusammenfassung

Räumliche Trennung endemischer und nicht-endemischer Kolibris auf der Robinson Crusoe-Insel, Chile: Die Abundanz von Konkurrenten spielt eine Rolle, nicht jedoch die Ressourcenverfügbarkeit oder der Habitattyp

Konkurrenzdruck seitens invasiver Arten hat tendenziell besonders starke Auswirkungen auf abgelegenen Inseln, und dieses Wissen kann entscheidend sein, um endemische Artenvielfalt zu schützen. Eine der zwei Kolibriarten auf der Robinson Crusoe-Insel im Juan Fernández Archipel, Chile, der Chilekolibri (*Sephanoides sephaniodes*), ist auf dem Festland weit verbreitet, während die andere, der Juan-Fernandez-Kolibri (*Sephanoides fernandensis*),

endemisch und vom Aussterben bedroht ist. Obwohl bekannt ist, dass Habitatzerstörung und Prädation durch exotische Säugetierarten Hauptbedrohungen darstellen, ist dem Einfluss interspezifischer Konkurrenz um Blütennektarressourcen bislang nur wenig Beachtung geschenkt worden. In dieser Studie haben wir das Vorhandensein interspezifischer Konkurrenz untersucht, indem wir mit Hilfe von Punktzählungen, die über die geeigneten Habitate hinweg verteilt waren, die räumliche Trennung der beiden Arten erforscht haben. Wir haben außerdem den Einfluss von Habitattyp und Blütenabundanz betrachtet, die ebenfalls zu einer räumlichen Trennung der beiden Arten führen könnten. Wir fanden einen negativen Zusammenhang zwischen den Punktzählungs-Abundanzen der beiden Arten, der auch bestehen blieb, wenn die Rolle von Habitattyp und Blütenabundanz berücksichtigt wurde. Zusammengefasst könnten diese Ergebnisse auf interspezifische Konkurrenz zwischen den Arten hindeuten, wobei Individuen von *S. fernandensis* vom Aggregieren profitieren könnten, da die individuellen Kosten des Verfolgens der weitaus häufigeren *S. sephaniodes* dann geteilt würden.

Introduction

Flower-visiting birds are often heavily dependent on nectar produced by a set of plant species, making their assemblages prone to interspecific competition for limited floral resources. Hence, for specialized nectarivorous birds such as hummingbirds (Fleming and Muchhala 2008), competition has often been invoked to explain segregation patterns that emerge in communities (Kodric-Brown et al. 1984; Brown and Bowers 1985). In multi-species assemblages, species tend to exhibit behavioral adaptations that encompass distinct strategies of competition by exploration or interference. Notably, small-bodied species tend to be more efficient at exploring poorer nectar sources, but they usually lose in direct encounters with aggressive larger-bodied species, which typically defend richer resource patches (Wolf et al. 1976; Feinsinger and Colwell 1978; Kodric-Brown et al. 1984). Ultimately, spatiotemporal segregation in species distribution emerges due to resource partitioning (Maruyama et al. 2014) and differences in competitive efficiency (Fonseca et al. 2015). Indeed, when food resources are not limited, several hummingbird species coexist, as happens, for instance, around artificial feeders (Sonne et al. 2016). Accordingly, competition has also been invoked to explain trait composition within communities, specifically those traits associated with flower exploration, territorial defense and energetic tradeoffs such as bill length, body mass and wing area, respectively (Brown and Bowers 1985; see also

Weinstein et al. 2014). Alternatively, hummingbird species can segregate across distinct habitats and/or according to the distribution of their preferred food plants (Feinsinger and Colwell 1978; Maruyama et al. 2014) instead of segregating in response to competition.

The Juan Fernández Firecrown (*Sephanoides fernandensis*) is a critically endangered hummingbird endemic to the remote Robinson Crusoe Island, Chile, in the Pacific Ocean. While habitat degradation and predation from invasive mammals species have been documented as major threats, little attention has been given to the possible impact of interspecific competition with its closest relative and the only other hummingbird occurring on the island—the Green-backed Firecrown (*Sephanoides sephaniodes*) (Colwell 1989; Wolf and Hagen 2012; Roy et al. 2016a, b).

The island likely represents a recent zone of distributional overlap, where colonization of the congeneric *S. sephaniodes* probably took place recently, i.e. in post-industrial time (Roy et al. 1998). Today, *S. sephaniodes* vastly outnumbers the endemic *S. fernandensis* (Hahn et al. 2006; BirdLife International 2016). Even though the two species tend to vary in utilization of habitat types during the breeding season (Hahn et al. 2011a, b), strong competition between them is expected at other times of the year, as they are found foraging in the same areas and on the same food plants (Colwell 1989; Roy et al. 1999). Despite great differentiation in body mass and wing morphology, the bill morphology is highly similar between the two species, which has been suggested as a remarkable example of convergent evolution (Colwell 1989). Both species strongly defend patches with flowering plants against intruders, and even though *S. fernandensis* is larger, and therefore often competitively superior in direct confrontations (Roy et al. 1999; Wolf and Hagen 2012), the high abundance of *S. sephaniodes* could constitute an indirect competitive pressure through reduced resource availability and/or increased energy and time spent by the endemic *S. fernandensis* to chase away intruders.

Competitive pressure from alien species tends to have a particularly strong impact on remote islands, which often house high concentrations of endemic species (Sax and Gaines 2008). Thus, in insular ecosystems, where active conservation efforts are commonly required to avoid species extinction, greater knowledge regarding the interactions in which the target species is engaged is crucial for developing proper management strategies to conserve the endemic biodiversity, in this case, to preserve a viable population of *S. fernandensis*.

In this context, we investigated the differences in distribution of *S. fernandensis* and *S. sephaniodes* on Robinson Crusoe Island. By conducting point counts placed within the suitable habitat of both species, we tested whether the local abundance of the two species was related. If interspecific

competition matters, then we expected to find that species abundance was inversely proportional to the competitor species abundance, irrespective of the variation in habitat type and food availability. In this sense, by considering possible differences in habitat and resource use between the species, we discuss how this could provide evidence of interspecific competition outside the breeding season.

Methods

Study system and sampling

The study was carried out on Robinson Crusoe Island, located in the Pacific Ocean 667 km from the central Chilean coast. The island, together with the Santa Clara and Alejandro Selkirk islands, forms the volcanic Juan Fernández Archipelago, an oceanic island group never connected to the mainland. Radiometric analyses of the geology of Robinson Crusoe Island have estimated an age of approximately four million years (Stuessy et al. 1984); this isolation has given rise to a distinctive diversity of plants and animals. Terrestrial bird diversity is low, comprising only eight species, but with three being single-island endemic species or subspecies: *Columba livia* f. *domestica*, *Passer domesticus*, *Turdus falcklandii magellanicus*, *Asio flammeus suinda*, *Falco sparverius fernandensis* (endemic), *Anairetes fernandezianus* (endemic), *S. sephaniodes* and the iconic *S. fernandensis* (endemic). The two hummingbird species are the sole members of the genus *Sephanoides*, and now coexist on the island after a recent self-colonization of *S. sephaniodes* (Roy et al. 1998). The species differ considerably in body mass: the male *S. fernandensis* may weigh nearly 11 g and the female 7 g, while an adult male *S. sephaniodes* weighs just 5–7 g (Colwell 1989). While *S. sephaniodes* is listed as a “Least Concern” species, with a wide continental distribution along the Patagonian Andes, *S. fernandensis* is restricted to 11 km² on Robinson Crusoe Island, with its estimated population of less than 1000 individuals declining at an estimated rate of 1–9% per decade (IUCN 2015). As for many oceanic island endemic species, habitat degradation and predation by introduced mammal species now pose a major threat to the endemic hummingbird (Roy et al. 1999), which is now classified globally as “Critically Endangered” (BirdLife International 2016).

Data collection was carried out from 23 February through 1 March 2016—outside the breeding season of both species. Throughout the humid areas of Robinson Crusoe Island where *S. sephaniodes* and *S. fernandensis* occur, we conducted 10-min point counts ($n = 27$ points) (Bibby et al. 2000), with a distance of at least 100 m between locations, covering the most representative habitat types (see

Figure S1). For each point count, we quantified the abundance of both species as the maximum number of individuals simultaneously recorded by sight and vocalizations within a radius of 30 m. We classified the point count locations according to dominant habitat type (i.e. native forest, tree plantation, thicket or urban area). We defined habitat types as follows: native forest was forested habitat where native tree species formed a canopy and few invasive plants were present; tree plantations were areas covered by exotic trees, mostly *Eucalyptus* spp. and *Cupressus* spp., planted for wood exploitation; thicket habitats were areas dominated by invasive mainland shrubs such as *Ugni molinae*, *Rubus ulmifolius* and *Aristotelia chilensis*; and urban areas were those dominated by human buildings and infrastructure in the village. Additionally, we quantified the abundance of the flowering plants most frequently visited by hummingbirds during the study by counting open flowers at all individuals of native (i.e. *Dendroseris litoralis*, *Rhaphithamnus venustus*) and exotic species (i.e. *Lobelia tupa*, *Abutilon* sp.) (Roy et al. 1999; Hahn et al. 2011a) found within a 5-m radius of the center of the point count. *Rubus ulmifolius*, an abundant invasive species, was excluded from abundance measures because it produces little nectar per flower and was only scarcely visited by hummingbirds during the study (personal observation.). *Eucalyptus* spp., which are also important food resources, were not flowering at the time of sampling (pers. obs.). Point count locations where neither hummingbird species was recorded were excluded prior to statistical analyses ($n = 3$). The local abundance of the two species was \ln -transformed to meet statistical assumptions of normality. All raw data are presented in the online supplementary material (Table S1).

Statistical analyses

As neither *S. sephaniodes* nor *S. fernandensis* was assumed a priori to drive the pattern of distribution, we used major axis regression to test for an association between their respective abundance. This statistical method was used because it makes no assumptions about the predictive directions among variables. Because the effects of competition decrease as the total density of birds decreases, we excluded point counts for which the summed abundance of the two hummingbird species was less than or equal to five. Sensitivity analyses were applied to evaluate the influence of different cutoff values (i.e. summed abundance $\leq 4, 5$ and 6). The major axis regression was fitted using the R package ‘lmodel2’ (Legendre 2008). To account for the influence of spatial autocorrelation, we tested the association between the abundance of the two hummingbird species in a spatial correlation framework following Dutilleul’s correction method (Dutilleul et al. 1993). The spatial correlation analyses were conducted in SAM

(Rangel et al. 2010). We then conducted an analysis of covariance (ANCOVA) to test whether the association between the abundance of *S. sephaniodes* and *S. fernandensis* was related to differences in habitat type. Finally, to assess the relationship between floral resource availability and the proportional difference in *S. sephaniodes* and *S. fernandensis* abundance, we tested the association between floral abundance of the most frequently used plant species and the proportion of *S. fernandensis* at each point count location. Because of zero inflation in the floral abundance variable, we were unable to fit a generalized linear model (GLM) on the full dataset due to violation of the assumption of residual normality. Instead, we separated floral abundance into two variables: one binary variable that simply determined whether flowers were observed at a given point count location, and one continuous variable (total number of flowers) containing only point count locations in which flowers were observed. The latter was log-transformed prior to statistical analyses. The association between the presence/absence of flowers and the proportion of *S. fernandensis* was analyzed using a two-tailed Wilcoxon rank-sum test. For locations with flower presence only, the association between the flower abundance and the proportion of *S. fernandensis* was analyzed using a GLM with a logit link function.

Results

We recorded hummingbirds in 24 of the 27 point counts, with a total of 110 individuals recorded, of which 82 were *S. sephaniodes* and 28 were *S. fernandensis* (mean = 4.6 individuals per point count location, SD = 3.4, $n = 24$). Seven (25%) of the observed *S. fernandensis* were females.

We found a negative association between the abundance of *S. sephaniodes* and *S. fernandensis* (major axis regression coefficient; $\beta = -1.18$, $R^2 = 0.75$, $p < 0.001$, $n = 11$; Fig. 1) in point counts with summed abundance ≥ 5 hummingbirds of both species. This result was insensitive to the abundance cutoff values: for point counts having a total number of ≥ 4 hummingbirds ($\beta = -1.32$, $R^2 = 0.64$, $p < 0.001$, $n = 13$) and for point counts having ≥ 6 hummingbirds ($\beta = -1.35$, $R^2 = 0.80$, $p = 0.007$, $n = 6$), a negative association between the abundance of the two species remained. Similarly, the negative association remained after applying Dutilleul's correction method in a spatial correlation analysis: for point counts with summed hummingbird abundance ≥ 5 (Pearson's corrected $F = 24.77$, corrected $p = 0.001$, $n = 11$). The applied ANCOVA showed a nonsignificant role of habitat type on the association between *S. sephaniodes* and *S. fernandensis* for point counts having a total number of hummingbirds ≥ 5 ($F = 1.05$, $p = 0.435$; $n = 11$). Finally, for flower

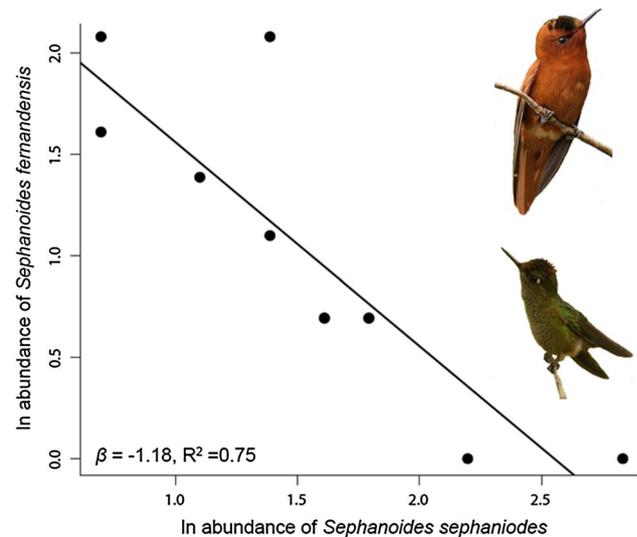


Fig. 1 Scatterplot showing the association between the \ln -transformed abundance of Juan Fernández Firecrown *Sephanoides fernandensis* (upper) and Green-backed Firecrown *S. sephaniodes* (lower) obtained from 10-min point counts within an observation radius of 30 m. Trend line was fitted using major axis regression. Birds photographed by J. Sonne

availability, we found no influence of flower abundance on the observed proportion of *S. fernandensis* (Wilcoxon = 51.5, $p = 0.21$, $n = 24$). Similarly, no association was found between floral abundance and the proportion of *S. fernandensis* (GLM Coefficient = 0.11, $p = 0.81$, $n = 11$).

Discussion

We have shown that the two hummingbird species *S. sephaniodes* and *S. fernandensis* exhibit a pattern of spatial segregation in the post-breeding season, in that individuals of each species tend to aggregate in areas where the congeneric species is less abundant (Fig. 1). As suggested by follow-up analyses, this is not related to differences in either habitat type or flower abundance.

These findings are in accordance with the hypothesis that the high abundance of *S. sephaniodes*, which are competitively inferior in direct confrontations (Colwell 1989; Roy et al. 1999), may constitute a competitive pressure that influences the abundance and distribution of *S. fernandensis*. In addition, it is possible that individuals of *S. fernandensis* could benefit from aggregation with conspecifics in shared resource defense (Davies and Houston 1981), thus driving the observed spatial segregation to some extent. This is expected in a situation where the competitively inferior species greatly outnumbers the superior species, as is the case for *S. fernandensis* and *S. sephaniodes*. By assuming random interactions among individuals, the skewed abundance towards the

competitively inferior species would then result in reduced probability of interspecific confrontations for the competitively superior species. On the other hand, as conspecific individuals tend to aggregate locally, more intraspecific interactions would be expected to occur at a small scale, resulting in the observed trend of *S. fernandensis* males chasing more conspecifics, especially females, than *S. sephaniodes* individuals (Wolf and Hagen 2012). Despite the costs associated with intraspecific competition, the advantages of aggregation with conspecifics may ultimately outweigh these costs, thus resulting in the observed spatial segregation. However, further studies are needed to properly investigate the economic costs of resource defense, and the Juan Fernández hummingbirds offer a remarkable opportunity for such an investigation.

Previous research has indicated that the abundance and distribution of these two hummingbird species during the breeding season is structured according to differences in habitat preference and flower availability (Hahn et al. 2015), which suggest that competition for nesting sites during this period may be mainly intraspecific (Hahn et al. 2011a). Indeed, another study investigating behavioral interactions and territorial defense during the breeding season found intraspecific competition among individuals of *S. fernandensis*, but did not document extensive interspecific competition, which could be related to low resource limitation, as the flowering of most important food plants was peaking (Wolf and Hagen 2012). In contrast, our results suggest that habitat and flower availability do not affect the negative association between the abundance of the two species. This could be related to a greater limitation in floral resources outside the breeding season, forcing the birds to seek resources throughout their range. Alternatively, as these hummingbirds are highly vagile (Roy et al. 1999), it is possible that their abundance is influenced by flower availability at a broader scale (i.e. landscape) than that measured in our study (plots with 5-m radius), therefore not simply reflecting a direct response to competitor abundance. Nevertheless, we found hummingbird abundance of both species to vary extensively within small distances (see Table S1). Moreover, the lack of association between flower abundance and the spatial segregation between the two hummingbird species in our short-term study is unlikely to be related to the small spatial scale at which the flowers were counted, as both species exhibit territorial behavior and defend small patches of resources (Colwell 1989; Wolf and Hagen 2012).

In summary, we show that the two resident hummingbird species of Robinson Crusoe Island exhibit spatial segregation during the non-breeding season, arguably as a consequence of interspecific competition. This evidence contrasts with the situation observed during the breeding season (Wolf and Hagen 2012). Thus, our empirical

findings are in accordance with the hypothesis that competition with the recently self-colonized *S. sephaniodes* is presently limiting the population size of the endemic *S. fernandensis*.

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