

## AGGRESSIVE INTERACTIONS OF FIRECROWNS (*SEPHANOIDES* SPP.; TROCHILIDAE) DURING THE BREEDING SEASON ON ROBINSON CRUSOE ISLAND, CHILE

Coral Wolf<sup>1,2</sup> & Erin Hagen<sup>3,4</sup>

<sup>1</sup>University of Michigan, School of Natural Resources and Environment, Dana Building,  
440 Church Street, Ann Arbor, MI, 48109-1041, USA.

<sup>2</sup>Current address: University of California, Santa Cruz, Ecology & Evolutionary Biology, 100  
Shaffer Road, Santa Cruz, CA 95060, USA. *E-mail:* cawolf@ucsc.edu

<sup>3</sup>University of Washington, College of Forest Resources, Box 352100, Seattle, WA 98195,  
USA.

<sup>4</sup>Current address: Island Conservation, 100 Shaffer Road, Santa Cruz, CA 95060, USA.

**Resumen.** – Interacciones agresivas de picaflores durante la época reproductora en la Isla Robinson Crusoe, Chile. – El Picaflor de Juan Fernández (*Sephanoides fernandensis*) es críticamente amenazado, se encuentra en una sola isla en el mundo, Robinson Crusoe. No se han investigado cuantitativamente las amenazas de su población, pero podrían estar relacionadas con la auto-introducción reciente del Picaflor chico (*Sephanoides sephaniodes*), un competidor potencial. Se examinó la influencia del Picaflor chico sobre el acceso y la disponibilidad de alimentación del Picaflor de Juan Fernández, a través de la comparación de los tiempos invertidos en la interferencia de la competencia, la frecuencia de las interacciones entre especies, y la frecuencia de las interacciones agresivas durante la temporada de nidificación de los picaflores. Se realizaron observaciones focales de ambas especies de picaflor y se registraron todas las interacciones, las especies de los individuos involucrados, y si el ave focal era el agresor o la víctima. Ambas especies de picaflores invirtieron < 2% de su tiempo en persecuciones. Al contrario de las observaciones de investigaciones anteriores, la mayoría de las persecuciones observadas en este estudio eran entre congéneres. No se encontró evidencia que los machos Picaflores de Juan Fernández estuvieran afectados negativamente por el Picaflor chico durante la temporada de nidificación; aunque nuestros resultados sugieren que la competencia por interferencia puede influir negativamente a las hembras de Picaflores de Juan Fernández. Estas hembras fueron más frecuentemente las víctimas, tanto en las interacciones intraespecíficas como en las interespecíficas con el Picaflor chico, lo que sugiere que las hembras podrían estar marginadas del hábitat de alimentación de alta calidad. En resumen, no encontramos una fuerte evidencia de la influencia negativa del Picaflor chico sobre el acceso y la disponibilidad de alimentación del Picaflor de Juan Fernández durante la temporada de nidificación.

**Abstract.** – The critically endangered Juan Fernández Firecrown hummingbird (*Sephanoides fernandensis*) is restricted to only one island in the world, Robinson Crusoe. Reasons for its endangerment have not been quantitatively explored but may be linked to the recently self-introduced Green-backed Firecrown (*Sephanoides sephaniodes*), a potential competitor. We examined the Green-backed Firecrown's influence on the Juan Fernández Firecrown's food availability and access by comparing time budgets for interference competition, frequency of interspecies interactions, and frequency of aggressive interactions during the hummingbirds' breeding season. We performed focal observations of both firecrown species and recorded all interactions, the bird species involved, and whether the focal bird was the aggressor or victim. Both hummingbird species spent < 2% of their time in chases. Contrary to observa-

tions by past researchers, most chases were between conspecifics. We found no evidence that male Juan Fernández Firecrowns were negatively affected by Green-backed Firecrowns during the breeding season, although our results suggest that interference competition may negatively influence female Juan Fernández Firecrowns. These females were more often the victims in both conspecific and interspecific interactions with Green-backed Firecrowns, suggesting that they may be marginalized from high quality foraging habitat. Overall, we did not find strong evidence for the Green-backed Firecrowns' negative influence on Juan Fernández Firecrowns' food availability or access during the breeding season. *Accepted 16 January 2013.*

**Key words:** Green-backed Firecrowns, Juan Fernández Firecrowns, *Sephanooides*, aggression, hummingbirds, interspecific interactions, Robinson Crusoe Island.

## INTRODUCTION

Species introductions have been recognized as a major cause of endangerment and extinction worldwide, and island populations are especially susceptible (e.g., see Reaser *et al.* 2007). Researchers (Case 1996) have found a strong correlation between number of avian introductions to islands and the number of subsequent native extinctions. This growing geographic overlap between conspecific species – through range-expansions and introductions – may result in new competitive interactions for resources (MacArthur 1972) given their shared evolutionary history and oftentimes more similar survival requirements (Grant 1968, Moulton 1985, Jones 1996). Although some foraging ecology studies show introduced, congeneric bird species have no detectable negative effects on co-occurring native bird species (Garrett *et al.* 2007), others predict these congeners will bear a cost (Buchanan *et al.* 2007). Island endemics, in particular, may be at a competitive disadvantage when interacting with congeneric species due to their geographic isolation and a prior absence of competitor species (Manne *et al.* 1999).

Like other Pacific islands, Robinson Crusoe Island (47.9 km<sup>2</sup>), Chile, has experienced a series of species introductions, including both potential competitors and predators of native biota (Wester 1991). As multiple introduced species, including humans, have altered

the native ecosystems, the endemic Juan Fernández Firecrowns (*Sephanooides fernandensis*) – endemic to this island and formerly to Alejandro Selkirk Island – has become critically endangered (IUCN 2011). However, lacking quantitative data, it is unclear whether the Juan Fernández Firecrowns decline is due to predation by introduced mammals (Brooke 1987), habitat loss and food shortages resulting from overharvesting and plant invasions, or interactions with the Green-backed Firecrowns (*Sephanooides sephanooides*), a self-introduced continental species first recorded on Robinson Crusoe Island in 1830 (Colwell 1989, Roy *et al.* 1999).

The Juan Fernández Firecrowns and the Green-backed Firecrowns, the only hummingbirds on Robinson Crusoe Island, are sister species evolutionarily separated 0.5–1 million years ago (Roy *et al.* 1998). Estimates indicate the Juan Fernández Firecrowns population was on the order of 10,000 individuals into the latter half of the 20<sup>th</sup> century (see Brooke 1987). Current estimates vary, but suggest the endemic firecrowns population is stabilizing after a ten-fold reduction from historic population levels; the Green-backed Firecrowns population is estimated to be twice that of the endemic (Hahn *et al.* 2005, Lopez-Calleja & Estades 2006).

The Juan Fernández Firecrowns is highly sexually dimorphic. The males have a brick-red plumage and are more than 50% larger than the turquoise-crowned, green females

(Colwell 1989). Both sexes of the Green-backed Firecrown have a plumage similar to the Juan Fernández female but are differentiated by their duller overall plumage, crown coloration, and an identifying white spot behind the eye. In flight, male and female Green-backed Firecrowns can be distinguished only by their different crown coloration.

Previous studies (Brooke 1987, Colwell 1989) describe interspecific competition between the firecrowns where male Juan Fernández Firecrowns (10.9 g) dominate, and female Juan Fernández Firecrowns (7.0 g) regularly hold a competitive advantage over Green-backed Firecrowns (males 5.7 g, females 4.7 g) (Colwell 1989). This follows dominance patterns observed in other hummingbird communities where competition is related to body size and sex (Wolf *et al.* 1976, Carpenter *et al.* 1993, Dearborn 1998). Although some hummingbird communities partition resources based on physical accessibility (Snow & Snow 1972, Wolf *et al.* 1976, Chavez-Ramirez & Tan 1993), on Robinson Crusoe both firecrown species have similar bill lengths (measuring approximately 15.5 mm) and visit almost all of the same native food plants (Colwell 1989) (although both sexes of the Juan Fernández Firecrown are known to feed on a subset of the 14 non-native flowering plant species visited by the Green-backed Firecrown [Roy *et al.* 1999]). Previous work has examined firecrown interactions at these shared food plants although studies were descriptive, short-term, and performed in the Austral summer months (Brooke 1987, Colwell 1989, Roy *et al.* 1999). As seasons change, food availability and firecrown distribution fluctuate (Meza 1989), and aggressive interactions may also shift (Ewald & Bransfield 1987, Powers & McKee 1994).

In this study, we examined hummingbird aggressive encounters during the breeding season, a time of year with high energy

requirements and when no previous behavioural investigations have been undertaken. During the breeding season, hummingbirds are found foraging in native and exotic forest types, characterized by four dominant flowering tree species: endemic maderas dura (*Sophora fernandeziana*; Fabaceae), endemic juan bueno (*Rhaphithamnus venustus*; Verbenaceae), introduced eucalyptus (*Eucalyptus globulus*; Myrtaceae), and introduced maqui (*Aristotelia chilensis*; Elaeocarpaceae). Maderas dura and juan bueno (both listed as vulnerable by the IUCN [IUCN 2011]) were historically common forest species and likely chief suppliers of nectar during the Juan Fernández Firecrown breeding season (Meza 1989). However, native tree species that offer nectar to hummingbirds have become increasingly scarce due in part to the expansion of introduced plants such as eucalyptus and maqui (Dirnbock *et al.* 2003). No study to date has quantified absolute or relative nectar abundance throughout the year on Robinson Crusoe Island; however, we presume the hummingbird breeding season coincides with high nectar availability (Hagen 2009).

We quantified the aggressive behaviour between firecrown species by comparing time budgets for interference competition, frequency of interspecies interactions, and frequency of aggressive interactions. Our observations of aggressive encounters indicated the strength and direction of the Green-backed Firecrown's influence on food availability and access for the endangered endemic without directly measuring fitness.

## METHODS

*Study site.* Robinson Crusoe Island is part of the remote Juan Fernández Archipelago (33°40'S, 78°47'W), which is composed of three islands that formed over a volcanic hotspot 4 million years ago (Stuessy *et al.* 1984). The archipelago is internationally

recognized for high rates of endemism, however, introduced species have negatively affected its unique biota (Perry 1984, Allen 1985), significantly reducing populations of native species (Dirnbock *et al.* 2003).

*Behavioural observations.* We observed flowering phenology and hummingbird behaviour on Robinson Crusoe Island from late August through November 2006 and August 2007, in 0.25-ha sites (20–325 m a.s.l.) within 3 drainages. We randomly chose 12 distinct study sites from a larger set of established hummingbird census points (Lopez-Calleja & Estades 2006) that were representative of habitat types, contained flowering plants, and were accessible for bimonthly visits. Sites were characterized by the four dominant flowering species. All are ornithophilous species (i.e., they produce sucrose-abundant nectar and medium to high nectar volume, 2.5 to 8.1  $\mu$ l), except for maqui, which produces a nectar reward comparatively high in sucrose and low in nectar volume (1.5  $\mu$ l) (Stone *et al.* 1988; Bernardello *et al.* 2000, 2004). We visited each site regularly to count flowers on each plant within the site.

Conducting a pilot study, we qualitatively described hummingbird prevalence and established the requisite number of open flowers at a study site necessary for a behavioural observation visit: 50 maderas dura, 2 juan bueno, 200 eucalyptus, or 100 maqui flowers. This was the threshold number of flowers for which regular hummingbird activity was observed in the area, and we therefore expected to observe hummingbird interactions. As a result, eight sites were utilized for behavioural observations during this study.

Within each behaviour observation site, we identified three to four observation locations (clearings) where flowering plant species and/or insect activity could be observed. Changes in food resources were expected to

occur during the study duration given climatic and phenological shifts, ensuring that we were not simply conducting observations at one resource density. We conducted behavioural observations in the morning, between 0.5 and 3 h after sunrise, and afternoon, between 4.5 and 1 h before sunset. During a single site visit, 30-min observation periods were carried out consecutively at three different clearings, randomizing visit order.

A focal observation began when a hummingbird entered the clearing and ended once the individual was no longer visible and could not be re-identified as the same individual. We recorded all bird interactions, noting the species and sex of the focal bird and non-focal bird (e.g., interactor) and whether the focal bird was the aggressor or victim (we characterized “aggressors” as those birds chasing a second bird, the “victim”). A total of 1092 focal observations were made during 157 observations hours, involving 494 (45.3%) Juan Fernández Firecrown males, 307 (28.1%) Juan Fernández Firecrown females, 209 (19.2%) Green-backed Firecrowns, and 82 (7.5%) unidentified firecrowns.

*Data analysis.* To avoid a dependency error, we analyzed differences in behavioural interactions and time budgets for interference competition by excluding multiple observations of focal birds that interacted with a bird of the same species and sex as earlier in the focal observation. We examined the 15.9% of all focal observations with recorded chases ( $n_{2006} = 126$ ,  $n_{2007} = 48$ ) and separated these by hummingbirds’ species and sex, as well as year. Ten of these observations were dropped from further analysis when we could not identify the focal individual’s species. All observations of Green-backed Firecrowns were considered together because we were unable to consistently confirm sex (possible only through identification of crown coloration).

TABLE 1. Total chase events for 2006 and 2007. 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. Starred (\*) numbers denote interspecific interactions. <sup>1</sup>JF = Juan Fernández Firecrown.

Focal	Interactor						Total
	JF male	JF female	JF male & female	Green-backed	Other species	Unknown	
JF <sup>1</sup> 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

To determine the proportion of time fire-crowns spent chasing, time spent in chase was summed for each focal individual and divided by the total time a bird was observed. Only observations with a focal bird visible for at least 15 s ( $n = 428$ ) were included in this analysis. A total of 54 chases were observed in this subset of focal observations. These resulting proportions of total time spent in chase were compared between firecrown species and sex combinations (ANOVA; SPSS 15.0).

To compare the frequency of inter- and intraspecific aggression, we conducted two  $2 \times 2 \chi^2$  analyses (Fisher's Exact Test; SAS 9.1.3). Chases were aggregated by aggressor, independent of which species was the focal individual, and distinguished based on the interacting individuals' species. This allowed us to compare the incidence of inter- and intraspecific interactions between the species (sex pooled) as well as between male and female Juan Fernández Firecrowns. For all  $\chi^2$  analyses, we did not include chase observations with non-hummingbird or multiple interactors or those with uncertainty regarding which individual was the aggressor.

We examined the direction of interaction (e.g., whether the focal was the aggressor or victim) by performing an additional  $\chi^2$  analysis (Pearson's Test; SAS 9.1.3). We treated the focal bird species-sex combination as the fixed variable. The Green-backed Firecrown could not be included in this analysis because

of the small number of observed interactions as either aggressor or victim.

An alpha level of 0.05 was used for all tests (SAS or SPSS).

## RESULTS

Firecrowns spent an average of 1.68% (SD = 7.54) of their time in chases. The proportion of time spent in a chase did not differ between species or sexes ( $F_{1,425} = 0.01$ ,  $P = 0.986$ ).

Of the chases considered in  $\chi^2$  analyses, intraspecific interactions were more common than interspecific firecrown interactions (65.2% vs 7.3%); however, species identification of the non-focal bird was not always possible (20.8%, Table 1). Juan Fernández Firecrowns were also observed interacting with two non-hummingbird species (6.7%), the Austral Thrush (*Turdus falcklandii magellanicus*) and the Juan Fernández Tit-Tyrant (*Anairetes fernandezianus*).

Juan Fernández Firecrowns initiated more conspecific chases than did Green-backed Firecrowns (Table 2; Fisher's exact test,  $P = 0.012$ ). Removing Green-backed Firecrowns from the  $\chi^2$  analysis revealed that conspecifics were the important competitor for the Juan Fernández Firecrowns, regardless of sex (Fisher's exact test,  $P = 1.00$ ).

Focal Juan Fernández females were more often the victims in interactions with Juan Fernández males (Table 3, Pearson's  $\chi^2 = 6.4$ ,

TABLE 2. Relationship between species/sex and incidence of intraspecific and interspecific interactions independent of focal individual. Frequencies and row percentages are reported. <sup>1</sup>JF = Juan Fernández.

Aggressor	Intraspecific interactions		Interspecific interactions		Total
	n	%	n	%	N
JF <sup>1</sup> male	64	92.8	5	7.2	69
JF female	21	95.5	1	4.5	22
Green-backed	16	72.7	6	27.3	22
Total	101		12		113

$P = 0.012$ ,  $n = 31$ ). In contrast, analysis of focal male interactions did not demonstrate an effect of interactor identity or chase direction (Table 3; Pearson's  $\chi^2 = 0.01$ ,  $P = 0.942$ ,  $n = 49$ ).

## DISCUSSION

Our quantitative comparison of aggressive behaviour between and within firecrown species contrasts with some results of previous behavioural studies. Our calculated chase time budget was very similar to Brooke's (Brooke 1987) study of three Juan Fernández males that spent "1–2% of their time defending food flowers." However, our results quantifying the type and direction of chases diverge from earlier studies' results. Our findings provide strong evidence that interspecific interactions do not consistently comprise the majority of interactions year-round and begin to challenge the interspecific dominance hierarchy presented consistently by past observers.

We found the majority of Juan Fernández Firecrown chase interactions were conspecific, providing little evidence that interspecific interactions (even non-hummingbird) are a significant cost to the Juan Fernández Firecrown during the breeding season. This contrasts with prior findings of extensive interspecific interactions during the non-breeding season, representing 40.5–97.2% of observed encounters (Brooke 1987, Roy *et al.*

1999). These marked differences may be the result of seasonal variation in flowering phenology, as foraging patterns and competitive interactions change with shifts in food availability (Pimm *et al.* 1985, Temeles *et al.* 2004).

Rates of aggression are expected to be lowest during food scarcity or over-abundance (Grant *et al.* 2002). In contrast, aggression is expected to peak with intermediate levels of food abundance (Grant *et al.* 2002). Given flower loads on trees, eucalyptus and maderas dura appeared to be at their annual height of flowering during our study, suggesting food abundance. However, the quantity or rate of aggression (1.68%) was equal between our study and past studies, not supporting the hypothesis of food over-abundance. It will be important to build a base of data that details nectar abundance throughout the year to examine in conjunction with behavioural data.

Importantly, our detection of a relatively greater proportion of intraspecific interactions may be more likely associated with seasonally-specific territorial and breeding behaviour. Breeding behaviour likely resulted in a greater number of Juan Fernández male-female chase events than observed in other seasons. 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.

Due to a small number of observed interspecific interactions, we were unable to con-

TABLE 3. Summary of Juan Fernández (JF) female and male conspecific interactions for 2006 and 2007. Frequency of chase types and percentage of total are presented when the focal and interacting individuals were Juan Fernández Firecrowns.

Interactor	Focal JF female			Focal JF male		
	Aggressor	Victim	Total	Aggressor	Victim	Total
	% (n)	% (n)	% (n)	% (n)	% (n)	% (n)
JF male	6.5 (2)	61.3 (19)	67.7 (21)	36.7 (19)	12.2 (5)	49.0 (24)
JF female	16.1 (5)	16.1 (5)	32.3 (10)	40.8 (20)	10.2 (5)	51.0 (25)
Total	22.6 (7)	77.4 (24)	N = 31	77.6 (38)	22.4 (11)	N = 49

clude whether or not the Juan Fernández Firecrown dominates over the Green-backed Firecrown; however, we did find trends. In previous works, the Green-backed Firecrown was found being consistently subordinate to both sexes of Juan Fernández Firecrowns (Brooke 1987), with only one published case of an ambiguous chase direction between them (Roy *et al.* 1999). In contrast, we observed the Juan Fernández female as subordinate in five out of six chases with Green-backed Firecrowns. These differences in observed and published dominance hierarchies likely reflect shifts in aggression and dominance related to seasonal changes in food resource availability and breeding behaviours.

Observed Juan Fernández males appear just as likely to chase both conspecific males and females, although the latter are more often victims of chases than males (Table 3). We interpret these results as a possible effect of our observation clearings being located in food-rich areas – locations where males are more likely to maintain territories and thus be observed as our focal bird. We could expect these resident males to be dominant and more often the aggressor in an interaction with an intruding hummingbird.

It is unclear whether the Juan Fernández females face large energetic costs as a result of their position in the dominance hierarchy. Due to their body size, females may be able to

use food resource patches of insufficient quality for larger males, thereby avoiding aggressive encounters and securing access to food (Carpenter *et al.* 1993). However, reproductive energetic expenditures, such as egg development and incubation, nest building, and chick rearing, may in fact result in females bearing the greatest energy costs during the breeding season (Martín 1995). The costs of these activities are difficult to extrapolate without energy budget measurements, which future work should address.

According to population estimates, the Green-backed Firecrown outnumbers the Juan Fernández Firecrown 2:1 on Robinson Crusoe Island. However, in our focal observations Juan Fernández Firecrowns outnumbered Green-backed Firecrown focal birds 4:1, indicating that we did not observe a cross section of the population. We simply did not observe many Green-backed Firecrowns at our clearings, and our data, although not a direct measure of resource removal, suggest that there was no measurable amount of interspecific exploitation competition. Future work should detail food availability, territoriality, and possibly quantify resource removal in an experiment investigating exploitation competition.

Our results suggest that the Green-backed Firecrown is not out-competing the Juan Fernández Firecrown for available food resources during the breeding season; how-

ever, the Juan Fernández female may be affected by aggressive interactions and incurring relatively high energy costs. This scenario presents an opportunity to further our understanding of the potential competitive impacts of non-native species on endemic island species, and provides results to inform conservation actions in ecosystems increasingly at risk from now commonplace species introductions.

#### ACKNOWLEDGMENTS

We are very grateful to Bobbi Low, Kathy Welch, and Johannes Foufopolous for help in preparing this manuscript. We are ever indebted to our friends and co-workers, Christian López, Daniela Bernal, Paola Gonzalez, Scheila Recabarren, Sara de Rodt, David de Rodt, and the park guards of the Juan Fernández National Park. Finally, an enormous thank you to Mari Lopez, Peter Hodum, and James Ha. Field work was supported by the Juan Fernández Islands Conservancy, American Bird Conservancy, Hummingbird Society, and the University of Michigan's International Institute and School of Natural Resources & Environment.

#### REFERENCES

- Allen, D. 1985. Threatened protected natural areas of the world. *Environ. Conserv.* 12: 76.
- Bernardello, G., R. Aguilar, & G. J. Anderson. 2004. The reproductive biology of *Sophora fernandeziana* (Leguminosae), a vulnerable endemic species from Isla Robinson Crusoe. *Am. J. Bot.* 91: 198–206.
- Bernardello, G., L. Galetto, & G. J. Anderson. 2000. Floral nectary structure and nectar chemical composition of some species from Robinson Crusoe Island (Chile). *Can. J. Bot.* 78: 862–872.
- Buchanan, J. B., R. J. Gutierrez, R. G. Anthony, T. Cullinan, L. V. Diller, E. D. Forsman, & A. B. Franklin. 2007. A synopsis of suggested approaches to address potential competitive interactions between Barred Owls (*Strix varia*) and Spotted Owls (*S. occidentalis*). *Biol. Invasions* 9: 679–691.
- Brooke, M. d. L. 1987. The birds of Juan Fernández Islands, Chile. In International Council for Bird Preservation (ICBP). Study Report, Volume 16. Cambridge, UK.
- Carpenter, F. L., M. A. Hixon, E. J. Temeles, R. W. Russell, & D. C. Paton. 1993. Exploitative compensation by subordinate age-sex classes of migrant Rufous Hummingbirds. *Behav. Ecol. Sociobiol.* 33: 305–312.
- Case, T. J. 1996. Global patterns in the establishment and distribution of exotic birds. *Biol. Conserv.* 78: 69–96.
- Chavez-Ramirez, F., & S. S. Tan. 1993. Habitat separation and arthropod resource use in three Lesser Antillean hummingbirds. *Condor* 95: 455–458.
- Colwell, R. K. 1989. Hummingbirds of the Juan Fernández Islands: natural history, evolution and population status. *Ibis* 131: 548–566.
- Dearborn, D. C. 1998. Interspecific territoriality by a Rufous-tailed Hummingbird (*Amazilia tzacatl*): effects of intruder size and resource value. *Biotropica* 30: 306–313.
- Dirnbock, T., J. Greimler, P. Lopez, & T. F. Stuessy. 2003. Predicting future threats to the native vegetation of Robinson Crusoe Island, Juan Fernandez Archipelago, Chile. *Conserv. Biol.* 17: 1650–1659.
- Ewald, P. W., & R. J. Bransfield. 1987. Territory quality and territorial behavior in two sympatric species of hummingbirds. *Behav. Ecol. Sociobiol.* 20: 285–293.
- Garrett, L. J. H., C. G. Jones, A. Cristinacce, & D. J. Bell. 2007. Competition or co-existence of reintroduced, critically endangered Mauritius fodies and invasive Madagascar fodies in lowland Mauritius? *Biol. Conserv.* 140: 19–28.
- Grant, P. R. 1968. Bill size, body size, and ecological adaptations of bird species to competitive situations on islands. *Syst. Zool.* 17: 319–333.
- Grant, J. W. A., I. L. Girard, C. Breau, & L. K. Weir. 2002. Influence of food abundance on competitive aggression in juvenile convict cichlids. *Anim. Behav.* 63: 323–330.

- Hagen, E. 2009. Castaways on Robinson Crusoe Island: influences of introduced species on an endemic hummingbird. Univ. of Washington, Seattle, Washington, USA.
- Hahn, I., U. Romer, & R. P. Schlatter. 2005. Distribution, habitat use, and abundance patterns of landbird communities on the Juan Fernández Islands, Chile. *Ornitol. Neotrop.* 16: 371–385.
- IUCN. 2011. The IUCN Red List of threatened species. *In* Version 2011.2. Downloaded on 10 November 2011 from <http://www.iucnredlist.org>.
- Jones, C. G. 1996. Bird introductions to Mauritius: status and relationships with native birds. Pp. 113–123 *in* Holmes, J. S., & J. R. Simons (eds). *The introduction and naturalisation of birds*. HMSO, London, UK.
- Lopez-Calleja, M. V., & C. F. Estades. 2006. Proyecto estimación de la abundancia del Picaflor de Juan Fernández (*Sephanooides fernandensis*). Univ. Católica de Chile and Univ. de Chile, Santiago, Chile.
- MacArthur, R. H. 1972. *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York, New York, USA.
- Manne, L. L., T. M. Brooks, & S. L. Pimm. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399: 258–261.
- Martin, T. E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65: 101–127.
- Meza, J. 1989. Informe anual del Proyecto Conservación del Picaflor de Juan Fernández *Sephanooides fernandensis*, Invierno 1988 – Otoño 1989. Corporación Nacional Forestal, Viña del Mar, Chile.
- Moulton, M. P. 1985. Morphological similarity and coexistence of congeners: an experimental test with introduced Hawaiian birds. *Oikos* 44: 301–305.
- Perry, R. 1984. Juan Fernández Islands: a unique botanical heritage. *Environ. Conserv.* 11: 72–76.
- Pimm, S. L., M. L. Rosenzweig, & W. Mitchell. 1985. Competition and food selection: field tests of a theory. *Ecology* 66: 798–807.
- Powers, D. R., & T. McKee. 1994. The effect of food availability on time and energy expenditures of territorial and nonterritorial hummingbirds. *Condor* 96: 1064–1075.
- Reaser, J. K., L. A. Meyerson, Q. Cronk, M. De Poorter, L. G. Eldrege, E. Green, M. Kairo, P. Latasi, R. N. Mack, J. Mauremootoo, D. O'Dowd, W. Orapa, S. Sastroutomo, A. Saunders, C. Shine, S. Thrainsson, & L. Vaiutu. 2007. Ecological and socioeconomic impacts of invasive alien species in island ecosystems. *Environ. Conserv.* 34: 98–111.
- Roy, M. S., J. C. Torres-Mura, & F. Hertel. 1998. Evolution and history of hummingbirds (Aves : Trochilidae) from the Juan Fernández Islands, Chile. *Ibis* 140: 265–273.
- Roy, M. S., J. C. Torres-Mura, F. Hertel, M. Lemus, & R. Sponer. 1999. Conservation of the Juan Fernández firecrown and its island habitat. *Oryx* 33: 223–232.
- Snow, B. K., & D. W. Snow. 1972. Feeding niches of hummingbirds in a Trinidad valley. *J. Anim. Ecol.* 41: 471–485.
- Stone, F. T., P. Roberts, K. Gunstone, A. Chisholm, & M. Woolfe. 1988. Final report: Sink-K-Tam “88,” an Oxford University expedition to study hummingbirds in Chile. Oxford Univ., Oxford, UK.
- Stuessy, T. F., K. A. Foland, J. F. Sutter, & M. Silva. 1984. Botanical and geological significance of Potassium-Argon dates from the Juan Fernández Islands. *Science* 225: 49–51.
- Temeles, E. J., A. B. Muir, E. B. Slutsky, & M. N. Vitousek. 2004. Effect of food reductions on territorial behavior of Purple-throated Caribs. *Condor* 106: 691–695.
- Wester, L. 1991. Invasions and extinctions on Masatierra (Juan Fernández Islands): a review of early historical evidence. *J. Hist. Geogr.* 17: 18–34.
- Wolf, L. L., F. G. Stiles, & F. R. Hainsworth. 1976. Ecological organization of a tropical, highland hummingbird community. *J. Anim. Ecol.* 45: 349–379.

