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Hummingbirds of the Juan Fernández Islands: natural history, evolution and population status

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Two hummingbird species inhabit the Juan Fernández Islands, nearly 700 km off the Chilean coast in the Pacific Ocean—the endangered endemic Juan Fernández Firecrown *Sephanoides fernándensis* and the continental Green-backed Firecrown *S. sephaniodes*. In terms of body size, the endemic species is the most sexually dimorphic species of hummingbird known; it also displays an extraordinary degree of sexual dichromatism. Both sexes hold feeding territories, within which courtship probably occurs. It is suggested that sexual selection, and selection for gender recognition and the absence of indigenous predators may explain the evolution of sexual dimorphism and dichromatism in the Juan Fernández Firecrown. In spite of a more than twofold difference in body size, the bill lengths of both sexes in both species are nearly identical and closely match the flower tube length of the several species of endemic plants they pollinate.

The endemic Juan Fernández Firecrown has become extinct on one of the two main islands (Isla Alejandro Selkirk) and its population on the other main island (Isla Róbinson Crusoe) has greatly declined in recent decades. In contrast, the population of the Green-backed Firecrown has probably increased on Róbinson Crusoe and the species has recently become established on Alejandro Selkirk. Because historical records show that Green-backed Firecrown survived centuries of potential competition from Juan Fernández Firecrown, massive habitat destruction, plagues of rats, feral cats and dogs and the effects of feral livestock before beginning its recent decline, it is suggested that the introduction earlier in this century of the bramble *Rubus ulmifolius*, the coati *Nasua nasua* and possibly the rabbit *Oryctolagus cuniculus* may have differentially favoured the Green-backed Firecrown at the expense of the Juan Fernández Firecrown.

Names reversed by the Editor in Proof.
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Only nine species of indigenous land birds inhabit the Juan Fernández Islands, lying nearly 700 km off the coast of Chile in deep Pacific waters. Two of the nine are hummingbirds—the Green-backed Firecrown *Sephanoides sephaniodes*, also found along the Chilean coast from the Atacama Desert to Patagonia and Tierra del Fuego, and the remarkable Juan Fernández Firecrown *S. fernándensis*, endemic to the islands. Of the 340 species of hummingbirds known, only these two occupy oceanic islands. As with other ancient inhabitants of remote islands, the evolution of the Juan Fernández Firecrown has clearly been shaped in unusual ways, setting it apart from other species of hummingbirds in both morphology and behaviour.

Unfortunately, this intriguing species may be in serious danger of extinction (Collar 1985, Brooke 1987, Stiles 1987). This paper provides an account of what little is known of *S. fernándensis* and of its evolutionary, ecological and behavioural relations with *S. sephaniodes*, and attempts to place the current population status of these species in a historical context by following changes in their populations over the four centuries since the islands were discovered. Sources of information include recent observations on density, association with food plants and behaviour of these

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birds as well as scattered historical records of naturalists and other visitors to the islands.

The islands

The Juan Fernández Islands consist of Isla Róbinson Crusoe (93 km^2; 33°40′ S, 78°33′ W), 667 km west of the Chilean coast, and Isla Alejandro Selkirk (85 km^2; 33°45′ S, 80°51′ W), lying 160 km west of Róbinson Crusoe. Some smaller islets, the largest of which is Santa Clara (0·5 km^2), lie off Róbinson Crusoe (Medina 1975).

For the first 300 years after its discovery in 1574, Isla Róbinson Crusoe was simply called 'Juan Fernández' (e.g. Rogers 1712, Walter & Robins 1748, Graham 1824, Howell 1829, Vicuña Mackenna 1883, Hemsley 1884). Eventually, Isla Róbinson Crusoe came to be called 'Más a Tierra' (or 'Masatierra'), to distinguish it from the archipelago as a whole and from Isla Alejandro Selkirk, which had long been called 'Más Afuera' (in various spellings) (Sclater 1871). The current official names for the islands, established by the Chilean government in 1966, are derived from the true story of Alexander Selkirk, a Scottish mariner marooned in 1704 on Isla Róbinson Crusoe (Rogers 1712, Steele 1713, Anonymous 1745, Sutcliffe 1843), after whom Defoe is believed to have patterned *Róbinson Crusoe*, which appeared in 1719 (Howell 1829, Ross 1965, Simmons 1982). Some contemporary authors continue to use the names 'Masatierra' and 'Masafuera' (e.g. Sanders *et al.* 1982, Stuessy *et al.* 1984). In this paper, I follow Medina (1975), Gerlach *et al.* (1986), Brooke (1987) and Stiles (1987) in using the official names.

The hummingbirds

Sephanoides fernándensis

The Juan Fernández Firecrown is the most dimorphic in body size (Table 1) of 200 hummingbird species examined in a morphometric study of the family Trochilidae (Colwell, in press): the female weighs 7 g and the male nearly 11 g. In plumage, it is among the most strikingly sexually dichromatic of hummingbirds. The female has a glittering green or turquoise-green back and rump, slaty wings, snow-white underside, each feather of the throat and flanks spangled with a turquoise-bronze discal spot, central rectrices and inner webs of the outer rectrices bluish-green, outer webs of the latter white; but most unusual, for a female of a strongly dichromatic hummingbird, is the iridescent purplish-blue crown.

The body colour of the male, a stunning contrast with the green female and unique among hummingbirds, has been described as 'brick-red' (Johnson & Goodall 1967, Busse 1971, Brooke 1987 and my own field notes), 'rich cinnamon-red' (Salvin & Hartert 1892), 'cinnamon-rufous' (F. G. Stiles *in litt.*), or 'incandescent copper' (W. R. P. Bourne *in litt.*). The wings and tail are very dark, nearly black; the crown is an iridescent coppery-orange—identical in morphology to the crown of the female, but utterly distinct in coloration. The feet of both sexes are extremely large for a hummingbird (as also noted by Stiles 1987), being the largest (absolute size) or third largest (weight-corrected) of 200 species I have measured (Colwell in press). This trait is shared with the Green-backed Firecrown which ranks just behind the Juan Fernández Firecrown for foot size.

The sexes of the Juan Fernández Firecrown differ so greatly that they were described as distinct species (the male as *Trochilus fernandensis* and the female as

Table 1. *Morphometrics of* Sephanoides *hummingbirds of the Juan Fernández Islands and the Chilean mainland**

Species	Locality	Sex	Weight† (g)	Wing-length‡ (mm)	Bill-length§ (mm)
Green-backed Firecrown					
S. sephaniodes	Mainland	F	—	57·5 ± 1·77 (9)	15·6 ± 0·69 (9)
		M	—	62·5 ± 0·81 (11)	14·8 ± 0·40 (11)
	R. Crusoe	F	4·7 ± 0·22 (12)	56·0 ± 1·52 (12)	16·0 ± 0·68 (15)
		M	5·7 ± 0·18 (15)	61·1 ± 0·76 (18)	14·8 ± 0·40 (20)
Juan Fernández Firecrown					
S. fernándensis	R. Crusoe	F	7·0 ± 0·06 (2)	68·8 ± 0·93 (15)	15·5 ± 0·38 (16)
		M	10·9 ± 0·32 (15)	79·4 ± 0·60 (35)	15·4 ± 0·25 (35)
	A. Selkirk¶	M	—	78·0 ± 0·00 (2)	15·5 ± 13·2 (2)

* Figures are sample means ± 1/2 the 95% confidence interval for the mean; sample sizes in parentheses.
† One-way ANOVA yields $F_{3,40} = 556$ for body weight, $P < 0{\cdot}001$, all pairwise comparisons significant at $P < 0{\cdot}001$ by the Tukey-Kramer test (Sokal & Rohlf 1981). All weights from individuals netted on Isla Róbinson Crusoe by the author or by F. G. Stiles (1987 and unpublished raw data). No specimens with weights available in museums visited (AMNH; Calif. Academy; Cornell Museum; FMNH; LSU Museum; Museo Chileno de Ciéncias Naturales; MCZ, Harvard; MVZ, Berkeley; Occidental College; USNM).
‡ One-way ANOVA yields $F_{3,76} = 705$ for wing-chord, $P < 0{\cdot}001$, all pairwise comparisons significant at $P < 0{\cdot}001$ by the Tukey-Kramer test. Measurements from individuals netted on Isla Róbinson Crusoe by the author or by F. G. Stiles (1987 and unpublished raw data); data for mainland only from specimens in AMNH, Cornell Museum, FMNH, Museo Chileno de Ciéncias Naturales and MCZ.
§ Exposed culmen; total culmen 2–3 mm longer. Bill-length barely differs significantly among the four morphs. (A one-way ANOVA yields $F_{3,82} = 5{\cdot}70$, $P = 0{\cdot}002$, with only the 1·2-mm difference between the largest mean, for female Juan Fernández Firecrowns, and the smallest, for male Green-backed Firecrowns, significant by the Tukey–Kramer test.) Source of measurements as in ‡.
¶ No female specimens from Isla Alejandro Selkirk were available in the museums listed †.

T. stokesi) by King (King 1831, Sclater 1871). In his plates, Gould (1861) depicted the adult females as 'males' and females in immature green plumage (no iridescent crown) as 'females' of *stokesi*; likewise, he considered the immature red males (no iridescent crown) as 'females' of *fernándensis*.

The truth was not recorded until 1866, when E. L. Landbeck reported that the two supposed species 'were observed *paired* [his italics], and the red and green young ones found together in the same nest' (Sclater 1866, 1871). Reed (1874) confirmed that the 'red birds' were all male and the 'green birds' all female on the basis of field dissections of specimens he collected in 1872. Later, Reed (1883) reaffirmed Landbeck's observation that the adult difference in plumage is already evident in the nestlings, on the basis of his dissection of 'seventy or eighty' individuals of *S. fernándensis*, although it is not clear that all were nestlings. The only other case of marked sexual dimorphism in nestling hummingbirds of which I am aware is in the Andean Hillstar *Oreotrochilus estella* (Carpenter 1976), in a genus fairly close to *Sephanoides* (R. Zusi *in litt.*).

Until 1869 all specimens of *S. fernándensis* were collected from the more accessible Isla Róbinson Crusoe (Johnson & Goodall 1967). Gould (1870), who studied the first specimens from Isla Alejandro Selkirk (one female and some males), named a new species, *leyboldi*, for the single *female* specimen, on the basis of some

plumage differences from the Róbinson Crusoe specimens known to him. Later, the specific name *leyboldi* was also applied to the males of *S. fernándensis* on Selkirk (e.g. Reed 1874, Dabbene 1929). More critical authorities chose to demote the Selkirk population to a subspecies of *S. fernándensis* (e.g. Hellmayr 1932). Lönnberg (1920) (citing K. Bäckström) and Johnson & Goodall (1967) considered even subspecific status unjustified, pointing out that plumage in the species varies considerably with maturity and season and even varies substantially among mature, sympatric individuals collected on the same day.

On Isla Alejandro Selkirk, the Juan Fernández Firecrown is probably now extinct, although inaccessible parts of this rugged island may still hide a lingering population (Brooke 1987, W. R. P. Bourne *in litt.*). The last reliable sighting on the island was in 1908, by Skottsberg; 9 years later, during an extended visit on his second expedition in 1917, not a single individual was seen (Skottsberg 1928). Johnson & Goodall (1967) claimed that 'when Bäckström and Philippi visited the island in 1917 and 1928 respectively it was reasonably common.' Johnson and Goodall were clearly mistaken about Bäckström on the basis of whose work with the Skottsberg expedition in 1917 the Juan Fernández Firecrown was omitted from the species listed for Alejandro Selkirk (Lönnberg 1920). Likewise, I can find no independent record of a visit to the island by Philippi in 1928. Johnson & Goodall (1967) and Skottsberg (1956) affirm, however, that the species could no longer be found on Alejandro Selkirk by the 1950s. Neither Bourne (1983a, b), on a 10-day visit in June 1983, nor Brooke (1987), during a month's visit in January–February 1986, was able to find a single Juan Fernández Firecrown on Isla Alejandro Selkirk. The species continues to survive only on Isla Róbinson Crusoe.

Sephanoides sephaniodes

The Green-backed Firecrown is a much more typical hummingbird. Females (4·7 g) are more or less uniformly bronze-green above, greyish-buff on the underside, with a speckled throat but no iridescent crown. Adult males are virtually identical, except for size (5·7 g), but they possess a brilliant orange-red iridescent crown. This minor sexual differentiation contrasts sharply with the extreme sex differences in the Juan Fernández Firecrown.

The Green-backed Firecrown on Isla Róbinson Crusoe differs little from the birds from coastal Chile, either in morphology or plumage (Lönnberg 1920, Johnson & Goodall 1967); only wing length (chord) for males differs significantly (Table 1).

The first historical record of the Green-backed Firecrown on Isla Róbinson Crusoe was apparently in 1830 (King 1839, p. 307). The lack of divergence from its mainland counterpart suggests recent colonization of the islands. Alternatively, colonization may have been more ancient and the similarity maintained by continuing gene flow, although regular migration (Lönnberg 1920) across the 600 km of open ocean dominated by the cold Humboldt Current seems unlikely. Molecular genetic studies might resolve this question.

Until very recently the Green-backed Firecrown was known in Juan Fernández Islands only from Isla Róbinson Crusoe. Bourne (1983a, b), however, reported seeing the species on Isla Alejandro Selkirk in introduced *Eucalyptus* trees near the settlement on the island. Fishermen from Róbinson Crusoe, who visit Alejandro Selkirk seasonally, told Bourne that the birds first appeared on Selkirk in 1981. Brooke (1987) confirmed the continuing presence of the species on Alejandro Selkirk, where he saw scattered individuals in various parts of the island. It is not known if these birds represent a breeding population or have wandered to the island from Róbinson Crusoe (or even from the mainland).

The complex history of synonymy for the generic name *Sephanoides* was established by Hellmayr (1932). (The synonyms '*Thaumaste*' and '*Eustephanus*' appear most frequently in the older literature.) The generic name *Sephanoides* was introduced by Gray (1840), as (apparently) a misspelling of the specific name *sephaniodes*, which Lesson & Garnot (1830) introduced for the type, and which Lesson repeated with the same spelling (Lesson 1828, 1831). Peters (1945) and earlier authors (e.g. Bonaparte 1850, Salvin & Hartert 1892, Simon 1921) transferred Gray's generic spelling incorrectly to the specific name, even in their citation of Lesson & Garnot (1830). I have chosen to follow Hellmayr (1932), Johnson & Goodall (1967), De Schauensee (1970), and Howard & Moore (1980) here in using Lesson's original spelling for the species, Gray's spelling for the genus. The same species is referred to by the synonym '*galeritus*' in much of the literature (Ortiz-Crespo 1986, Brooke 1987, Stiles 1987), with arguable historical justification (Barros 1952), but doubtful legitimacy (see Hellmayr 1932, p. 234, footnote 1).

Behaviour

The following account is based on studies on Isla Róbinson Crusoe in 1973 (30 November–4 December), in collaboration with M.-C. King. Finding the Juan Fernández Firecrown exceedingly rare in natural vegetation, we resorted to making detailed behavioural observations on both species of hummingbirds in a very large, heavily flowering *Eucalyptus* tree about 200 m south of El Pangal pier. (*Eucalyptus* was introduced to the island late in the last century.) Close observation of all parts of the tree's crown was feasible from a steep slope just behind it. On 4 consecutive days, we studied two male and two female Juan Fernández Firecrowns feeding in the tree, together with some 40–50 Green-backed Firecrowns (males and females more or less equally represented). These densities and behaviours were typical of hummingbirds in *Eucalyptus* trees elsewhere in the vicinity of El Pangal and the town of San Juan Bautista, based on more cursory observations.

Foraging behaviour and territoriality

Both sexes of the Juan Fernández Firecrown foraged on flowers located deeper in the foliage than do Green-backed Firecrowns—flowers in the crowns of the trees were tended almost exclusively by Green-backed Firecrowns. Stiles (1987) reported that the Juan Fernández Firecrown preferred to forage in shadier places in general, including dense stands of *Albizzia* and heavily shaded *Dendroseris* in gardens in the town.

Like other hummingbird species with especially large feet for their body mass (Colwell in press), both species (but especially the Juan Fernández Firecrown) frequently perched to feed on nectar, sometimes vertically or nearly upside down. When perching vertically to feed, both sexes of the Juan Fernández Firecrown spread their tails against twigs or foliage, presumably to help support the body.

In striking contrast with the great majority of hummingbirds, individuals of both sexes of the Juan Fernández Firecrown defended separate foraging territories, using apparently identical behaviour. They called frequently from perches occupied repeatedly at two or three particular points within the defended area, threatening intruders by facing them in the air hovering in place (or occasionally while perched) with tail spread, 'dipping' rhythmically to flash the iridescent crown. Intruders were often chased aggressively, frequently 100–200 m away from the tree. As with nestling

dichromatism (above), the Andean Hillstar resembles the Juan Fernández Firecrown in the manifestation of territoriality in both sexes (Carpenter 1976).

Male Green-backed Firecrowns also defended foraging territories, but females did not, feeding opportunistically in the interstices of male territories and on the outermost flowers of the tree, which were generally undefended. In our study, a fairly consistent dominance hierarchy was observed, ranked by body size: male Juan Fernández Firecrowns ousted all intruders, female Juan Fernández Firecrowns dominated both sexes of the Green-backed Firecrown and male Green-backed Firecrowns chased the females of their own species. These observations are supported by the studies of both Brooke (1987) and Stiles (1987).

Courtship and breeding

Nesting records for both species are scarce. Millie (in Goodall *et al.* 1957) found three active nests of the Green-backed Firecrown on 25 October 1955; Brooke found one in December 1986 (Brooke 1987). Information on timing of the breeding season of the Juan Fernández Firecrown is equally scanty and inconclusive. Bäckström described active nests in December (Lönnberg 1920) but noted that not many birds were moulting at the time. M. de L. Brooke (*in litt.*) also found some individuals moulting in late December 1985. In March 1987, F. G. Stiles (*in litt.*) found all 15 individuals examined in fresh plumage, with no evidence of recent breeding. Assuming post-nuptial moult, these data suggest that breeding might begin as early as September or October, continuing among some individuals into December. Juveniles of both sexes have been collected in mid-November (Sclater & Salvin 1878, Salvin & Hartert 1892).

We recorded one apparent courtship sequence for the Juan Fernández Firecrown on 2 December 1973. As a female entered the defended area of a male, he flew at her, making the usual territorial defence movements and calls. Instead of retreating, the female flew further into the male's territory, advancing some 50 cm at a time through the air, after each advance pausing to turn around and spread her tail *facing away* from the male, while hovering motionless—in effect, a reversal of the usual threat display. The male followed just behind, spreading his tail and calling. The female alighted on a branch, continuing to face away from the male, about 20–30 cm in front of him, while both spread their tails against the branch. Another episode of halting, tail-spreading flight ensued, then more perching, as before. This pattern was repeated for some 2 minutes, until the female suddenly flew off, for no apparent reason. F. G. Stiles (*in litt.*) observed a similar episode in March 1987 (causing further confusion about the timing of breeding). Although no copulation was seen in either case, the 'reverse threat' display by the female—which had previously been chased by the same male from his territory—and the prolonged interaction are certainly suggestive of courtship.

Colonization, evolution and coevolution

Colonization of the islands

Various authors (from Sclater 1871 and Reed 1883 to Ortiz-Crespo 1986) have suggested that the Juan Fernández Firecrown arose from an ancient colonization by a bird resembling the Green-backed Firecrown. Wallace (1878) expanded Sclater's account at length to illustrate how variation and natural selection may produce rapid changes in novel environments.

Stuessy *et al.* (1984) suggest an age for the Juan Fernández Islands, which were never connected with the mainland, of only about 4 million years, based on potassium–argon dating of basalts. The islands were once thought to be somewhat more ancient, based on the extreme weathering of the volcanic landscape and the high rate (60%) of floral endemism (Skottsberg 1956). If the Stuessy date is correct and the Juan Fernández Firecrown did indeed reach its current remarkable degree of divergence from an ancestral colonist resembling the Green-backed Firecrown, then its rate of post-colonization morphological evolution has been rapid indeed, perhaps on a par with the most divergent of Darwin's finches in the Galápagos (Grant 1986) and with the bizarre endemic flora of the Juan Fernández islands themselves (Skottsberg 1922, 1956, Perry 1984, Sanders *et al.* 1987).

Despite strong distinctions in size and plumage, the two species of *Sephanoides* resemble each other in many details of morphology, although detailed osteological and biochemical studies of the South American lineage of hummingbirds to which they belong (the 'high-Andean' group of related genera—*Oreotrochilus*, *Chalcostigma*, *Metallura* and allies) are needed before reaching the conclusion that the two *Sephanoides* indeed form a monophyletic group (R. Zusi *in litt.*). Thus, the possibility cannot at present be ruled out that the Juan Fernández Firecrown is a relict species, having diverged on the mainland from some other lineage in this group of related genera, achieving more or less its current form before colonizing the islands.

Evolution of dimorphism and dichromatism in the Juan Fernández Firecrown

It is tempting to take the extraordinary sexual differences in the Juan Fernández Firecrown, in themselves, as indicative of the effects of isolation from many of the selective pressures that have moulded—or constrained—mainland hummingbirds. The absence of indigenous predators probably played a role in permitting the evolution of large size and conspicuous coloration and displays in both sexes (Endler 1980). Neither land mammals nor reptiles occur naturally on the islands and the only potential avian predators (American Kestrel *Falco sparverius* on Isla Róbinson Crusoe and Red-backed Buzzard *Buteo polyosoma* on Isla Alejandro Selkirk) are not known to prey on hummingbirds (Lönnberg 1920, Johnson & Goodall 1965) nor to hunt in the dense foliage favoured by Juan Fernández Firecrowns. In fact, W. R. P. Bourne (*in litt.*) reports seeing a male Juan Fernández Firecrown chasing a kestrel.

The absence of predation, however, cannot in itself explain the remarkable evolutionary divergence of the sexes in this species. Sexual selection probably accounts for the size dimorphism and for many aspects of the striking dichromatism as well. Large male size is probably an advantage in male–male (and male–female) territorial combat and may also be favoured by female choice. In females, the advantage of larger size in territorial confrontations must be weighed not only against the increased total costs of physiological maintenance and territorial defence, as for males, but also against the costs of reproduction. The balance for females may thus be struck at a much smaller size than for males if, like all other hummingbirds known, males participate in none of the chores of parenthood.

Selective advantage in territorial encounters may explain why females in this species, like males, are brightly coloured, but cannot explain why female coloration is so completely distinct from that of the male. Because both sexes are fiercely territorial and both use the same behaviours—crown and tail flashing—in territorial signalling, some unambiguous means of turning aside aggression during courtship is required. Thus, it seems a plausible conjecture that selection for gender recognition

may have driven the evolution of the dichromatism in this species, perhaps from an ancestral starting point already moderately dichromatic (e.g. the Green-backed Firecrown), but lacking territoriality and bright coloration in the female. The origin and significance of female territoriality itself, however, remain unanswered questions for this species.

There is currently little evidence for any form of niche partitioning in the Juan Fernández Firecrown in relation to sexual dimorphism. In fact, the strong stabilizing selection on bill length (see below) clearly suggests that both sexes use the same floral resources—the most obvious candidate for resource partitioning among hummingbirds. Even so, males may dominate high-density patches of flowers, while females are left with dispersed flowers.

Evolution of bill morphology

In view of the more than twofold weight range covered by sexes of the two species on Róbinson Crusoe (from the 4·7 g female Green-backed Firecrown to the 10·9 g male Juan Fernández Firecrown), the bills (exposed culmen) of all four morphs are remarkably similar in length (Table 1). In contrast, both body weight and wing-chord—wing-length must scale with the square root of body weight (Colwell in press) to permit hovering flight—differ significantly among all four morphs. In effect, taking the Green-backed Firecrown as a standard, the bills of Juan Fernández Firecrowns show pronounced negative allometry, suggesting strong stabilizing selection for a common bill length of about 15 mm, in spite of greatly differing body sizes.

Coevolution: food plants and pollination

At least 12 species of plants indigenous to the Juan Fernández Islands are primarily or partially dependent on hummingbirds for pollination (Table 2). Of these, the most consistently mentioned in the literature as an indigenous hummingbird food plant on Isla Róbinson Crusoe is the tree called 'juanbueno' *Rhaphithamnus venustus* (Reed 1874 [using the synonym *Citharexylon*], Moseley 1879, Chapin 1936, Murphy 1936). Recent visitors and my own observations confirm continuing use of this plant (Brooke 1987, F. G. Stiles & T. F. Stuessy *in litt.*). Unlike most of the other species in Table 2, which tend to grow in clumps, *Rhaphithamnus* is rather generally dispersed throughout the native forest (F G. Stiles *in litt.*).

Based on extensive direct observations in 1908 and 1916–17 and on pollen samples from hummingbird specimens, Skottsberg (1928) listed all but three of the species in Table 2. The species Skottsberg missed are all rosette trees in endemic genera of Compositae (*Centaurodendron dracaenoides* and two species of *Dendroseris*)—a large plant family with only a few hummingbird-pollinated plants, despite its great ecological and geographical diversity. Skottsberg (1922, 1928) never saw *Centaurodendron* in flower (the flowers were unknown until 1935 (Skottsberg 1938)); he considered all species of *Dendroseris* to be insect-pollinated (Skottsberg 1928). Hummingbird visits to *Dendroseris litoralis* were reported by Brooke (1987) and Stiles (1987) for plants cultivated in a garden on Isla Róbinson Crusoe. T. F. Stuessy (*in litt.*) observed visits to both *D. litoralis* and a garden specimen of *D. macrantha* (the last known individual of the species, now extinct).

It seems quite likely that all four species of Skottsberg's subgenus '*Eudendroseris*', which have quite similar flowers, are (or were) visited by hummingbirds, based on morphology, colour and the recent observations of M. de L. Brooke, F. G. Stiles and T. F. Stuessy. All four of the species, *D. macrantha* (Róbinson Crusoe),

Table 2. *Indigenous plants visited by hummingbirds on the Juan Fernández Islands*

Plant*	Distribution† and flowering	Flower colour	Corolla-depth (mm)‡
Ochagavia elegans (Bromeliaceae)	RC: Oct–Apr	Red-violet	18–20
Phrygilanthus berteroi (Loranthaceae)	RC: Unknown	Bright red	??
Escallonia callcottiae (Saxifragaceae)	RC: Aug-Apr	Carmine-red	14–15
Sophora fernándeziana (Leguminosae)	RC: All year	Yellow	18§
S. masafuerana	AS: All year	Yellow	18§
Eryngium bupleuroides (Umbelliferae)	RC: Jul–Mar	Green	6
Rhaphithamnus venustus (Verbenaceae)	RC & AS: Nov–Jul	Purple	20–25
Cuminia fernándezia (Labiatae)	RC: Nov–Apr	Violet	12
Nicotiana cordifolia (Solanaceae)	AS: Aug–May	Greenish-purple	22–25
Centaurodendron dracaenoides (Compositae)	RC: Mar–Jun	Dark blue	??
Dendroseris litoralis (Compositae)	RC: Nov–Mar	Deep orange	16
D. macrantha	RC: Dec–Mar	Deep orange	16–18

*First nine species from Skottsberg (1928); *Centaurodendron* from Brooke (1987); *Dendroseris* species from Brooke (1987), Stiles (1987) and T. F. Stuessy (*in litt.*).
†RC = endemic to Isla Róbinson Crusoe; AS = endemic to Isla Alejandro Selkirk; RC and AS = endemic to the archipelago.
‡Taken from descriptions or estimated from drawings by Skottsberg (1922, 1928, 1953).
§Estimated from length of floral keel and wing (Skottsberg 1922), assuming the hummingbird would insert its head into the flower as far as possible.

D. marginata (Róbinson Crusoe), *D. litoralis* (Santa Clara, Morro Viñillo and perhaps originally also on Róbinson Crusoe) and *D. macrophylla* (Alejandro Selkirk), bear large bright orange florets in a large head, in contrast with the smaller, creamy-white florets of the other members of the genus (Skottsberg 1922). To take nectar from *D. litoralis* and *D. macrantha*, hummingbirds typically perch on the phyllaries of the flower heads, which appear to have been strongly modified under selection for hummingbird feeding and pollination (T. F. Stuessy *in litt.*, F. G. Stiles *in litt.*). The heads are extraordinarily large and solid for the family, have an unusually pronounced flange on the outer phyllaries and hang downward, which is atypical for a composite (T. F. Stuessy *in litt.*). F. G. Stiles (*in litt.*) suggests that strong winds, which make hovering to feed a difficult task on these islands, may have selected for the large feet and propensity to perch while feeding in *Sephanoides*.

The species (and sexes) of hummingbirds on Róbinson Crusoe clearly do not partition the floral resource by differences in bill-length, in contrast with many other hummingbird assemblages, including other island ones (Feinsinger & Colwell 1978). Either of the firecrowns could feed legitimately on any of the plants in Table 2, as far as floral morphology is concerned. The most probable explanation for the essentially identical bill-length in both sexes of both species and the corresponding limited range of flower depths would seem to be coevolutionary convergence by

birds and plant species alike on some narrow, 'consensus' range of corolla/bill-length. This conjecture is made all the more plausible by the endemism and diversity of the plant taxa in Table 2. All are endemic species, while *Ochagavia*, *Cuminia*, *Centaurodendron* and *Dendroseris* are endemic genera. Nearly all are markedly differentiated from their closest relatives elsewhere and all but *Ochagavia* and *Phrygilanthus* are trees, including *Eryngium bupleuroides*, unlike its mainland congeners (Skottsberg 1956).

Wallace (1878) first suggested that the 'large and showy' flowers on Isla Róbinson Crusoe, in contrast with the drab flowers of the Galápagos flora, are an evolutionary consequence of dependence on hummingbird pollination. Some of the plant species listed in Table 2 belong to families (Bromeliaceae, Labiatae, Verbenaceae) or even genera (*Phrygilanthus*, *Escallonia*, *Nicotiana*) that include hummingbird-pollinated species on the mainland. These species are unlikely to have been successful colonists of the islands without the presence of hummingbirds. Some species in Table 2, however, have few or no mainland allies that are hummingbird-pollinated (*Eryngium bupleuroides*, *Sophora* spp. and the three composites)—strongly suggesting local evolution in response to a long-standing mutualistic relationship with hummingbirds on the islands.

Population densities

Current status

In early December 1973 M.-C. King and I attempted to estimate the density of hummingbirds in a walking survey of accessible parts of Isla Róbinson Crusoe (deforested areas between Salsipuedes and Punta Bacalao around Cumberland Bay and El Pangal and relatively undisturbed upland forest between El Yunque and Portezuelo, along the central ridge). In the wooded highlands, we failed to find any Juan Fernández Firecrowns, but the Green-backed Firecrown was fairly common (two to three pairs per ha), feeding on *Rhaphithamnus venustus*. In the lowlands, the Green-backed Firecrown was common in gardens and both species were actively feeding on flowers of introduced *Eucalyptus* trees, which were at the peak of their flowering season. For the island of Róbinson Crusoe as a whole, we estimated that there could not be more than a few hundred (200–400) individuals of the Juan Fernández Firecrown and perhaps 4000–8000 Green-backed Firecrowns. Because we did not visit all areas of the island, this estimate was based on the assumption that densities in areas not visited approximated densities in the areas we surveyed, for the same kinds of habitat.

Two recent and more systematic studies of the status of the hummingbird populations of Isla Róbinson Crusoe, by Brooke (1987) and Stiles (1987), produced estimates of the current population sizes that are entirely consistent with each other and with our own estimate some 13 years earlier (given the difficulties of estimation). Brooke's estimates, based on 5 weeks' work in December 1985 and January 1986, were 250 individuals for Juan Fernández Firecrown and 6160 Green-backed Firecrowns. Stiles put the Juan Fernández Firecrown at 400 individuals and the Green-backed Firecrown at 'several thousand', based on a 6-day visit in March 1987. Comparing data from these three censuses on the distribution of the two species among habitat types on the island (*Eucalyptus*, gardens, degraded forest and relatively undisturbed forest), the birds clearly move among habitats frequently throughout the course of the year, no doubt in response to flowering patterns in both native and introduced plants.

Thus, although the population of the Juan Fernández Firecrown on Isla Róbinson Crusoe is certainly perilously low and the species is apparently already extinct on Isla Alejandro Selkirk (see above), it seems not to have declined significantly on Isla Róbinson Crusoe in the past fifteen years.

Historical changes in densities

The earliest records of hummingbirds on Isla Róbinson Crusoe appear in the narratives of privateers and explorers (Funnell 1707, Cooke 1712), but most of these records are not sufficiently accurate or detailed to identify the species seen. The most credible early observer was Shelvocke (1726), who reported seeing hummingbirds 'of a fine scarlet, and, as it were, slightly burnished over with gold'—a fair description of the male Juan Fernández Firecrown. King (1831), who collected the first Juan Fernández Firecrowns, provided no information on population densities. Reed (1874, 1883) and Moseley (1879) were the first to provide any details of the natural history and densities of the hummingbirds of Isla Róbinson Crusoe, from which it appears that the scarcity of Juan Fernández Firecrowns and the relative commonness of Green-backed Firecrowns on Róbinson Crusoe are comparatively recent phenomena. Reed (1874) found that the Green-backed Firecrown was 'by no means common' on the island; during a 20-day scientific expedition to the island in 1872, he succeeded in shooting only half a dozen specimens. As for the Juan Fernández Firecrown, it was '. . . very easy to kill up to a hundred of the males in a day. The females seem less numerous, one can scarcely see or hunt ten or twelve in the same period.' Moseley (1879), who visited the island in 1875, wrote: 'The humming-birds were extremely abundant, hovering in every bush. . . [the] endemic humming-bird seemed more abundant than the continental one. Any number of specimens might have been shot.'

In accord with Reed's (1874) comments, specimens collected by the *Challenger* expedition (13–15 November 1875) also show a strong male bias, about 2:1 (Sclater & Salvin 1878), as do the rest of the specimens in the British Museum as of 1892 (Salvin & Hartert 1892). More recently, Busse (1970) and Stiles (1987) also noted a male-biased sex ratio. Stiles pointed out, however, that male Juan Fernández Firecrowns are gregarious and are more conspicuous, aggressive and louder than the females, so that their apparent greater abundance may be at least partly illusory. On the other hand, differential mortality among females (perhaps while nesting) could also explain the male bias, assuming a sex ratio at hatching near 1:1.

In 1916–17 the Juan Fernández Firecrown was 'common in the forests' of Isla Róbinson Crusoe (Lönnberg 1920). By the 1930s, Chapin (1936) found the Green-backed Firecrown in gardens and the Juan Fernández Firecrown in adjacent forest; he mentioned no difficulty in finding either during a 1-day visit. Johnson & Goodall (1967) claimed that the Juan Fernández Firecrown was 'quite abundant, especially in area covered with *Dicksonia* ferns on Róbinson Crusoe', but they gave no date for this observation.

A brief, informal account by Busse (1970) has come to figure prominently in recent status reports (Brooke 1987, Stiles 1987) on the Juan Fernández Firecrown. On the basis of a visit to Isla Róbinson Crusoe during February–March 1970, Busse (1970, 1971) wrote that he found 'both species relatively abundant.' He claimed that there were 'on the order of tens of thousands' of hummingbirds on the island, of which 'approximately 40 percent' (Busse 1970) or 'about half' (Busse 1971) were Juan Fernández Firecrowns—estimates greatly at variance with ours just 3 years later and with more recent ones (Brooke 1987, Stiles 1987).

Busse's approximations were almost certainly far too high. The overestimate may perhaps be explained by the fact that Busse counted and marked birds coming to feeders, rather than making a systematic census of undisturbed birds (Busse 1970, 1971). Moreover, the habitats where Busse worked and the greater aggressiveness and fearlessness of Juan Fernández Firecrowns may have biased the proportions of the two species he saw at feeders. The only other plausible explanation for the discrepancy between Busse's reports and later studies is epidemic disease, sometime between 1970 and 1973, which cannot be completely discounted.

Whatever the cause, the Juan Fernández Firecrown evidently declined from much higher densities and total population size in the nineteenth century and the early part of this century, while Green-backed Firecrown populations have clearly increased over the same period.

Historical alterations of habitat and biota

Habitat destruction

The effects of habitat destruction on Isla Róbinson Crusoe are grossly apparent to any visitor to the island today. The island was probably forested throughout originally (Skottsberg 1953) but lowland forests fell victim to three centuries of wood-cutting for ship repair and firewood (Walter & Robins 1748, Graham 1824, Howell 1829) and later for the construction of settlements on the island (Woodward 1969, Orellana 1975) and for commercial shipment to the mainland (Skottsberg 1922, Ruh 1975). Massive anthropogenic forest fires added to the process of deforestation (Woodward 1969) and subsequent erosion of the loose topsoil of the lowlands. By 1976, some 15% of the island was severely eroded and devoid of vegetation (CONAF/FAO 1976) and the process is continuing (Perry 1984, Sanders *et al.* 1982).

The current level of deforestation, however, differs surprisingly little from the status of the forests on Isla Róbinson Crusoe a hundred years ago, as documented by historical accounts (beginning with Moseley 1879) and photographs taken in 1885 (in Ermel 1889) and early this century (Bürger 1922, photographs from 1900; historic photographs in Orellana 1975). Skottsberg (1954) juxtaposes photographs of Isla Róbinson Crusoe taken in 1952 with those he took in 1908, concluding that the size and shape of forested patches had changed very little. In turn, his photographs differ negligibly from my own of corresponding vistas, taken in 1973, or from those of Perry (1984).

Introduced mammals

Clearly, the profound changes in hummingbird populations on the island since the early part of this century cannot be explained by deforestation alone. In addition, however, the Juan Fernández Islands have been subject, like every other oceanic island, to a continual barrage of exotic animals and plants, introduced either intentionally or accidentally.

Over the past 400 years, a procession of introduced mammals (birds are the only native vertebrates) has exacerbated soil erosion and threatened the native fauna and flora, on both Róbinson Crusoe and Alejandro Selkirk (Skottsberg 1954). The Spanish released goats on both islands soon after the discovery of the archipelago in 1574. On Isla Róbinson Crusoe, not only goats but cats and rats (probably *Rattus*

rattus, although *R. norvegicus* is now also resident (Atkinson 1985)) had become extremely abundant on Isla Róbinson Crusoe by 1704 (Funnell 1707, Rogers 1712, Steele 1713, Howell 1829). Dogs were also released on both islands to control goats and rats (Shelvocke 1726, Walter & Robins 1748) but are no longer present (Skottsberg 1954, Ruh 1975). Rats, however, remained unchecked well into the present century (Walter & Robins, 1748, Miller 1829, Ruh 1975, CONAF/FAO 1976, Atkinson 1985) but have apparently declined recently (Skottsberg 1954, Ruh 1975) and feral cats are no longer numerous (CONAF/FAO 1976, Valenzuela 1978). Indeed, Stuessy reports that only one rat and not a single feral cat or dog was seen in natural vegetation on the island in the course of four lengthy expeditions to the island in the past decade (T. F. Stuessy *in litt.*).

Goats are now uncommon on Róbinson Crusoe (Brooke 1987) but a large population still exists on Isla Alejandro Selkirk, where their effect on the vegetation has been extremely detrimental (Sanders *et al.* 1982) and may have contributed to the extinction of the Juan Fernández Firecrown there through the destruction of nectar plants. On Isla Róbinson Crusoe sheep, cattle, horses, donkeys and pigs became feral during the nineteenth century (Ruh 1975) but today all except cattle have been eliminated. Semi-feral cattle are currently an important cause of further habitat deterioration and erosion on Isla Róbinson Crusoe (Skottsberg 1954, Hernández & Monleon 1975, Sanders *et al.* 1982, Perry 1984) but their management is complicated by local cultural traditions (Hernández & Monleon 1975).

The most recent round of mammalian introductions on Isla Róbinson Crusoe may well have been the most unfortunate of all for the hummingbird populations. According to Guzman Parada (1951), both the European rabbit *Oryctolagus cuniculus* and the South American coati *Nasua nasua* were introduced intentionally in 1935, though Miller & Rottmann (1976) record 1940 as the date the coati was introduced. De Vos *et al.* (1956, citing L. E. Peña *in litt.*) reported that the 'kinkajou' *Potos flavus* was introduced to the 'Isle of Juan Fernández' to control rats but was destroying birds. This report surely refers not to the kinkajou but to the coati.

The rabbits have severely affected elements of the low-elevation flora, including some hummingbird nectar plants (e.g. *Dendroseris litoralis*; F. G. Stiles *in litt.*). The coati, on the other hand, thrives today not only in degraded lowland parts of the island but in the upland forests as well (Kunkel 1968, Muñoz Pizarro 1969, Cuadrado 1971, CONAF/FAO 1976, Valenzuela 1978). Coatis are opportunistic foragers, taking fruit, insects and small vertebrates, including birds (Kaufmann 1962, referring to the congeneric *N. narica*, and *in litt.*). Guzman Parada (1951) claims that the coati is responsible for the decline in the population of black rats and takes domestic fowl and eggs. It seems a reasonable conjecture that coatis would also take hummingbird eggs or nestlings, or an adult found brooding or perching at night (Sanders *et al.* 1982).

Introduced plants

The two most serious intruders among woody plants are the small tree *Aristotelia chilensis* ('maqui', Elaeocarpaceae) and the bramble *Rubus ulmifolius* ('zarzamora', Rosaceae). Although it continues to increase its penetration into native vegetation (Sanders *et al.* 1982), *Aristotelia* was already a severe pest in the last century, allegedly having been intentionally introduced in 1883 (Johow 1893, 1896). The bramble, introduced sometime in the decade before 1927 (Looser 1927), has since come to form dense thickets over wide areas of Isla Róbinson Crusoe, including native woodland (F. G. Stiles *in litt.*).

Likely causes of recent changes in hummingbird densities

Why, then, has the population of the Juan Fernández Firecrown declined to its present perilous level and why has the relative abundance and, almost certainly, the absolute abundance of the Green-backed Firecrown increased? Certainly, deforestation, damage by rabbits, foraging and trampling by livestock, erosion and encroachment by introduced plants not usable by hummingbirds have all taken their toll on both species over the past 200 years or so.

Nonetheless, the Juan Fernández Firecrown seems to have held its own on Isla Róbinson Crusoe until well into this century in the face of widespread deforestation, the introduction and spread of *Aristotelia* and other exotic plants, the 300-year plague of rats and the effects of livestock. To these indirect threats must be added the direct effect of collecting pressure from scientists and especially from merchants of bird skins for private collectors (Vicuña Mackenna 1883) and for tourists (Schmitt 1928).

It is possible that the decline of the Juan Fernández Firecrown in this century has been the result of the steady effects of these pressures. Perhaps key seasonal sources of nectar have declined to the point that they represent a yearly resource bottleneck for the hummingbirds (Brooke 1987, Stiles 1987), although no obvious candidate plants are yet known. On the other hand, two of the most recent exotics, bramble and coatis, appear suspiciously likely to have accelerated the process—by shifting the resource base in favour of the Green-backed Firecrown and focusing predation on the Juan Fernández Firecrown.

Resources: bramble

Both Brooke (1987) and Stiles (1987) report that European bramble is heavily used as a nectar source by Green-backed Firecrowns. Brooke also recorded feeding visits to bramble by Juan Fernández Firecrowns. Stiles, however, points out that the small quantities of nectar produced by the flowers of bramble make foraging on it energetically more profitable for the smaller-bodied Green-backed Firecrown, whereas the cost to the much larger Juan Fernández Firecrown (particularly males) to extract the nectar from a flower of this plant may barely exceed the energy the birds gain by doing so, because of the greater total flight costs for larger hummingbirds. Moreover, unlike the native nectar plants, bramble provides no place to perch while feeding, forcing Juan Fernández Firecrowns to hover. On the other hand, the introduction of *Eucalyptus* late in the last century (Johow 1893, 1896) and other cultivated plants that produce large nectar volumes, such as *Albizzia* and *Abutilon* (Stiles 1987), may well have helped to forestall the decline of the Juan Fernández Firecrown (Brooke 1987, W. R. P. Bourne *in litt.)*.

Competition theory predicts that relative, rather than absolute, carrying capacities may determine the outcome of interspecific competition (MacArthur 1972). In effect, if Green-backed Firecrowns are better suited than Juan Fernández Firecrowns to feed on bramble—even slightly—, any increase in the supply of bramble will lead to an increase in the population of the Green-backed Firecrown. This increase will, in turn, intensify the competitive impact on the Juan Fernández Firecrown (through intruder pressure on its feeding territories) at plants that both species use, such as the native *Rhaphithamnus* or the introduced *Eucalyptus*.

If this conjecture is correct, then elimination or even partial control of bramble could help reverse the decline of the Juan Fernández Firecrown. Oehrens & Garrido (1985) discuss the potential for biological control of bramble in the Juan Fernández

Islands, using a fungus (*Phragmidium violaceum*) that has been successful in greenhouse tests.

Predation: coatis

Although recent reports (Collar 1985, Brooke 1987, Stiles 1987) emphasize other factors, several earlier observers declared the coati a serious threat to the survival of the Juan Fernández Firecrown (Kunkel 1968, Muñoz Pizarro 1969, CONAF/FAO 1976, Valenzuela 1978). In 1976, the coati population was estimated to have reached 2500–5000 (CONAF/FAO 1976), but F. G. Stiles (*in litt.*) reports that the population now may be declining.

The vulnerability of nesting female hummingbirds and their eggs and nestlings to coati predation would appear to be high. Lönnberg (1920) describes nests of Juan Fernández Firecrowns placed on the midrib of a low-growing endemic fern, *Blechnum schotti* (see Skottsberg 1953, plate 58–2), a vulnerable site typical of birds of oceanic islands historically free of terrestrial predators. The nest of the Green-backed Firecrown on Róbinson Crusoe presumably resembles nests of the species on the mainland, as described by Barros (1952) and Johnson & Goodall (1967)—suspended from fern fronds or slender branches in a variety of trees or even under the eaves of buildings. In short, the Green-backed Firecrown is probably more catholic in its choice of nest sites and perhaps uses less accessible sites than the Juan Fernández Firecrown. If the coati is indeed responsible for accelerating the decline of Juan Fernández Firecrowns on Róbinson Crusoe, these factors may favour the Green-backed Firecrown. It is also possible that the latter are more likely to abandon the nest at the approach of danger (Barros 1952) than are Juan Fernández Firecrowns. The ease of capture of the endemic hummingbird by humans also suggests poor adaptation to escape from predators (Busse 1971, J. C. Torres-Mura *in litt.*). Johnson & Goodall (1967) report that the naturalist Federico Johow captured ten pairs of Juan Fernández Firecrowns with a butterfly net.

Ecological theory (Holt 1977, 1984) suggests that, when two or more prey species (e.g. the two hummingbird species plus black rats) have a predator in common (e.g. the coati), a high population of one of the prey species (initially rats, currently the Green-backed Firecrown) will lead to a decrease in the population of the other prey species (the Juan Fernández Firecrown), especially if individuals of the latter are more easily captured or they reproduce more slowly. The phenomenon is quite independent of any competition for resources among the prey species. Essentially, the alternative prey sustain larger populations of the predator, with disproportionate impact on the most vulnerable and slowest-reproducing prey. Atkinson (1985) documents this phenomenon specifically for the role of introduced predators feeding on both endemic birds and introduced rats on other oceanic islands.

If Guzman Parada (1951) is correct about coati predation on black rats, then, initially, the coati population may have risen quickly on an originally abundant diet of black rats. If the rats declined as a result, the numerous hungry (and longer lived) coatis may have been forced to turn increasingly to a diet of wild birds. If the coati population is indeed now on the decline (F. G. Stiles *in litt.*), then the Juan Fernández Firecrown may eventually recover in some degree, given time, but much more study is required before any such optimistic prediction could be justified.

Conclusions

Even if hummingbird population densities on the Juan Fernández Islands were to stabilize indefinitely at present levels, the risk of extinction for the Juan Fernández

Firecrown is great simply because of the dangerously low absolute size of the single remaining population on Isla Róbinson Crusoe. The historical record indicates clearly that densities of this species in forested areas of the island were once many times greater, well into the present century, and that the species continued to thrive in spite of many threats. Moreover, extensive parts of the island are still covered with relatively undisturbed native forests. There is still hope for the recovery of the Juan Fernández Firecrown.

On the basis of historical and biological data, I have conjectured that the control or elimination of coatis—and perhaps of bramble—would be the most effective interventions, but further studies are urgently required before any programme is undertaken. A long-term study of the biology and population status of the Juan Fernández Firecrown by Javiera Meza (under the auspices of the Corporación Nacional Forestal, Chile) is currently underway.

Even more urgently, protection of the Juan Fernández Islands themselves—which comprise both a National Park and an International Biosphere Reserve—from destructive development (CODEFF 1987) requires the attention of the international scientific and conservation communities. Perhaps the Juan Fernández Firecrown can serve as a catalyst and symbol for the conservation of the habitats and biota of the Juan Fernández Islands.

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References

ANONYMOUS. 1745. Providence displayed: Or, a very surprising Account of one Mr. Alexander Selkirk . . . Harlein Miscellany 5: 402–406.

ATKINSON, I.A.E. 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *In* Moors, P.J. (ed.), Conservation of Island Birds, ICBP Technical Publication No. 3: 35–81. Cambridge: International Council for Bird Preservation.

BARROS, R. 1952. Nuestros picaflores del género *Sephanoides*. An. Acad. Chil. Cién. Nat. 17: 145–156.

BONAPARTE, C.L. 1850. Conspectus Generum Avium. Leyden: E.J. Brill.

BOURNE, W.R.P. 1983a. New Zealand ornithological survey of Juan Fernandez, South Pacific. Ibis 125: 595.

BOURNE, W.R.P. 1983b. Preliminary report on the ornithological situation at Juan Fernandez. Unpubl. Report to the International Council for Bird Preservation.

BRIDGES, E.L. 1948. The Uttermost Part of the Earth. New York: E.P. Dutton.

BROOKE, M. DE L. 1987. The birds of the Juan Fernandez Islands, Chile. ICBP Study Report No. 16. Cambridge: International Council for Bird Preservation.

BÜRGER, O. 1922. Die Robinsoninsel. Leipzig: Dieterich.

BUSSE, K. 1970. Nota preliminar sobre las poblaciones de colibries de las Islas de Juan Fernández. Boletín Ornitológico 2: 2–3.

BUSSE, K. 1971. Wilde Kolibris sassen auf meiner Hand: Die Kolibris der Robinsoninsel. Das Tier 11: 4–9.

CARPENTER, F.L. 1976. Ecology and evolution of an Andean hummingbird (*Oreotrochilus estella*). Univ. Calif. Publ. Zool. 106: 1–74.

CHAPIN, J.P. 1936. Islands west of South America. Nat. Hist. 38: 31–55.

CODEFF, 1987. Preocupación por intervención masiva en Juan Fernández. Actual No. 5 (28 December 1987). Santiago, Chile: Comite Nacional pro Defensa de la Fauna y Flora (CODEFF).

COLLAR, N.J. 1985. Red data bird: the Juan Fernández Firecrown. World Birdwatch 7: 5.

COLWELL, R.K. In press. A morphometric study of adaptive radiation in hummingbirds. Fieldiana.

CONAF/FAO. 1976. Plan de manejo del Parque Nacional Juan Fernández. Document Técnico de Trabajo No. 22. Santiago, Chile: Corporación Nacional Forestal (CONAF) and U.N. Food and Agriculture Organisation (FAO).

COOKE, E. 1712. A Voyage to the South Sea, and round the World. London: B. Lintot, R. Gosling, A. Bettesworth and W. Innys.

CUADRADO, A. 1971. El Archipiélago de Juan Fernández, Chile, Santiago, Chile: Elicier Parada.

DABBENE, R. 1929. Los picaflores de Chile. Revista Chilena de Historia Natural 33: 489–503.

DE SCHAUENSEE, R. M. 1970. A Guide to the Birds of South America. Wynnewood, Penn.: Livingston.

DE VOS, A., MANVILLE, R.H. & VAN GELDER, R.G. 1956. Introduced mammals and their influence on native biota. Zoologica 41: 163–194.

ENDLER, J.A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76–91.

ERMEL, A. 1889. Eine Reise nach der Robinson-Crusoe-Insel. Hamburg: L. Friederichsen.

FEINSINGER, P. & COLWELL, R.K. 1978. Community organization among neotropical nectar-feeding birds. Am. Zool. 18: 779–795.

FUNNELL, W. 1707. A Voyage round the World. London: W. Botham. [Facsimile published as Bibliotheca Australiana No. 57, 1969. Amsterdam: N. Israel.]

GERLACH, D.C., HART, S.R., MORALES, V.W.J. & PALACIOS, C. 1986. Mantle heterogeneity beneath the Nazca plate: San Felix and Juan Fernández Islands. Nature 322: 165–168.

GOODALL, J.D., JOHNSON, A.W. & PHILIPPI, R.A. 1957. Suplemento de las Aves de Chile. Buenos Aires: Platt.

GOULD, J. 1861. Humming-birds. London: Taylor.

GOULD, J. 1870. On a supposed new species of humming-bird from the Juan-Fernández group of islands. Ann. Mag. Nat. Hist. 6: 406.

GRAHAM, M. 1824. Journal of a Residence in Chile during the Year 1822. London: Longman, Hurst, Rees, Orme, Brown, Green and Murray.

GRANT, P.R. 1986. Ecology and Evolution of Darwin's Finches. Princeton, NJ: Princeton University Press.

GRAY, G.R. 1840. A List of the Genera of Birds. London: R. & J.E. Taylor.

GUZMAN PARADA, J. 1951. Cumbres oceánicas: Las Islas de Juan Fernández. Santiago, Chile: Bustos y Letelier.

HELLMAYR, C.E. 1932. The Birds of Chile. Zoology Vol. 19. Chicago: Field Museum of Natural History.

HEMSLEY, W.B. 1884. Report on the Botany of Juan Fernandez, the South Eastern Moluccas, and the Admiralty Islands. Voyage of *H.M.S. Challenger*, Botany, Part III. London: Challenger Office.

HERNÁNDEZ, R. & MONLEON, J. 1975. La comunidad de pescadores de Juan Fernández. *In* Orellana, M., Medina, A., Morel, P., Ruh, M., Hernández, R. & Monleon, J. (eds), Las Islas de Juan Fernández: 137–153. Santiago, Chile: Departamento. Ciéncias Antropológicas y Arqueológicas, Universidad de Chile.

HOLT, R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theor. Pop. Biol. 12: 197–229.

HOLT, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. Am. Nat. 124: 377–406.

HOWARD, R. & MOORE, A. 1980. A Complete Checklist of the Birds of the World. Oxford: Oxford University Press

HOWELL, J. 1829. The Life and Adventures of Alexander Selkirk. Edinburgh: Oliver & Boyd.

JOHNSON, A.W. & GOODALL, J.D. 1965. The Birds of Chile, Vol. 1. Buenos Aires: Platt.

JOHNSON, A.W. & GOODALL, J.D. 1967. The Birds of Chile, Vol. 2. Buenos Aires: Platt.

JOHOW, F. 1893. Las plantas de cultivo en Juan Fernández. Anales de la Universidad de Chile 84: 939–972.

JOHOW, F. 1896. Flora de las Islas de Juan Fernández. Santiago, Chile: Cervantes.

KAUFMAN, J.H. 1962. Ecology and social behavior of the coati, *Nausa narica*, on Barro Colorado Island, Panama. Univ. Calif. Publ. Zool. 60: 95–222.

KING, P.P. 1831. [Notes on birds collected by Capt. King in Chile.] Proc. Zool. Soc. Lond. 1830–31: 29–30.

KING, P.P. 1839. Narrative of the Surveying Voyages of His Majesty's Ships *Adventure* and *Beagle*. (R. Fitzroy, ed.), Vol. I. London: Henry Colburn.

KUNKEL, G. 1968. Robinson Crusoe's Island. Pacific Discovery 21: 1–8.

LESSON, R.P. 1828. Manuel d'Ornithologie, ou Description des Genres et des Principales Espèces d'Oiseaux. Paris: Rovet.

LESSON, R.P. 1831. Les Trochilidées ou Colibris et les Ouiseau-mouches. Paris: A Bertrand.

LESSON, R.P. & GARNOT, P. 1830. Catalogue des oiseaux recueillis dans l'expédition de la Coquille. *In* Duperrey, L. I. (ed.), Voyage autour du monde executé. . . sur la corvette. . .la Coquille, pendant des années 1822, 1823, 1824 et 1825, Vol. I, Part 2, Livr. 15. Paris: A. Bertrand.

LÖNNBERG, E. 1920. The birds of the Juan Fernandez Islands. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. III, Part 1: 1–17. Uppsala: Almquist and Wiksells.

LOOSER, G. 1927. La zarzamora (*Rubus ulmifolius* Schott) en Juan Fernández. Revista Chilena de Historia Natural 31: 84–85.

MACARTHUR, R.H. 1972. Geographical Ecology. New York: Harper and Row.

MEDINA, A. 1975. El piloto Juan Fernández y las islas que llevan su nombre. *In* Orellana, M., Medina, A., Morel, P., Ruh, M., Hernández, R. & Monleon, J. (eds), Las Islas de Juan Fernández: 23–81. Santiago, Chile: Departamento Ciéncias Antropológicas y Arqueológicas, Universidad de Chile.

MILLER, J. 1829. Memoirs of General Miller. London: Longman, Rees, Orme, Brown and Green.

MILLER, S. & ROTTMANN, J. 1976. Guía para el Reconocimiento de Mamíferos Chilenos. Santiago: Mistral.

MOSELEY, H.N. 1879. Notes by a Naturalist on the 'Challenger.' London: MacMillan.

MUÑOZ PIZARRO, C. 1969. El Archipiélago de Juan Fernández y la conservación de sus recursos naturales renovables. Boletín de la Academia de Ciencias, Instituto de Chile 1: 83–103. [Reprinted in Museo Nacional de Historia Natural (Santiago, Chile), Serie Educativa, No. 9: 17–69, 1974.]

MURPHY, R.C. 1936. Oceanic Birds of South America, Vol. I. New York: American Museum of Natural History.

OEHRENS, E. & GARRIDO, N. 1985. On the possibility of the biological control of wild blackberry in the Juan Fernandez Archipelago, Pacific Ocean. Boletín Sociedad Biológica de Concepción 57: 205–206.

ORELLANA, M. 1975. Historia de los primeros poblamientos de la Isla Róbinson Crusoe. *In* Orellana, M., Medina, A., Morel, P., Ruh, M., Hernández, R. & Monleon, J. (eds), Las Islas de Juan Fernández: 9–22. Santiago, Chile: Departemento Ciéncias Antropológicas y Arqueológicas, Universidad de Chile.

ORTIZ-CRESPO, F.I. 1986. Consideraciones sobre las migraciones de dos picaflores neotropicales. El Hornero 12: 298–300.

PERRY, R. 1984. Juan Fernandez Islands: a unique botanical heritage. Environ. Cons. 11: 72–76.

PETERS, J.L. 1945. Check-list of Birds of the World, Vol. 5. Cambridge, Mass.: Harvard University Press.

REED, E.C. 1874. Remarks on the birds of Juan Fernandez and Mas-a-fuera. Ibis (3) 4: 81–84.

REED, E.C. 1883. Field Notes; Chapter XIV–XVIII. *In* Vicuña Mackenna, B., Juan Fernández, Historia Verdadera de la Isla de Róbinson Crusoe: 251–258. Santiago, Chile: Jover.

ROGERS, W. 1712. A Cruising Voyage round the World. London: A. Bell and B. Lintot.

ROSS, A. 1965. Introduction. *In* Defoe, D. Robinson Crusoe: 7–21. London: Penguin Books.

RUH, M. 1975. Alfredo de Rodt, Subdelegado en Juan Fernández 1877–1905. *In* Orellana, M., Medina, A., Morel, P., Ruh, M., Hernández, R. & Monleon, J. (eds), Las Islas de Juan Fernández: 97–136. Santiago, Chile: Departamento Ciencias Antropológicas y Arqueológicas, Universidad de Chile.

SALVIN, O. & HARTERT, E. 1892. Catalogue of the Picariae in the Collection of the British Museum. London: Longmans.

SANDERS, R.W., STUESSY, T.F. & MARTICORENA, C. 1982. Recent changes in the flora of the Juan Fernandez Islands, Chile. Taxon 31: 284–289.

SANDERS, R.W., STUESSY, T.F., MARTICORENA, C. & SILVA O., M. 1987. Phytogeography and evolution of *Dendroseris* and *Robinsonia*, tree-Compositae of the Juan Fernandez Islands. Opera Botanica 92: 195–215.

SCHMITT, W.L. 1928. A voyage to the island home of Robinson Crusoe. National Geographic 54: 353–370.

SCLATER, P.L. 1866. [Report that *Eustephanus stokesi* is the female of *E. fernandensis*.] Proc. Zool. Soc. Lond. (1866) 556–557.

SCLATER, P.L. 1871. On the land birds of Juan Fernandez. Ibis (3) 1: 178–183.

SCLATER, P.L. & SALVIN, O. 1878. Reports on the collections of birds made during the voyage of H.M.S. 'Challenger.' No. 9. On the birds of Antarctic America. Proc. Zool. Soc. Lond. 28: 431–438.

SHELVOCKE, G. 1726. A Voyage round the World. London: Cassell.

SIMMONS, J. 1982. Alexander Selkirk, the monarch of San Juan Fernandez Island. Oceans 15: 49–54.

SIMON, E. 1921. Histoire Naturelle des Trochilidae (Synopsis et Catalogue). Paris: L. Mulo.

SKOTTSBERG, C. 1922. The phanerogams of the Juan Fernandez Islands. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. 2, Part 2: 95–240. Uppsala: Almquist and Wiksells.

SKOTTSBERG, C. 1928. Pollinationsbiologie und Samenverbreitung auf den Juan-Fernandez-Inseln. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. 2, Part 4: 503–547. Uppsala: Alquist & Wiksells.

SKOTTSBERG, C. 1938. On Mr C. Bock's collection of plants from Masatierra (Juan Fernandez), with remarks on the flowers of *Centaurodendron*. Meddn. Göteborgs. Bot. Trädg. 12: 361–373.

SKOTTSBERG, C. 1953. The vegetation of the Juan Fernandez Islands. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. 2, Part 6: 793–960. Uppsala: Almquist and Wiksells.

SKOTTSBERG, C. 1954. A geographical sketch of the Juan Fernandez Islands. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. I, Part 2: 89–192. Uppsala: Almquist and Wiksells.

SKOTTSBERG, C. 1956. Derivation of the flora and fauna of Juan Fernandez and Easter Island. *In* Skottsberg, C. (ed.), The Natural History of Juan Fernandez and Easter Island, Vol. I, Part 3: 193–438. Uppsala: Almquist and Wiksells.

SOKAL, R.R. & ROHLF, J. 1981. Biometry. San Francisco: W.H. Freeman.

STEELE, R. 1713. The Englishman. No. 26 (1–3 December).

STILES, F.G. 1987. Observaciones sobre la situación actual del Picaflor Rojo de Juan Fernández (*Sephanoides fernandensis*), con recomendaciones para un estudio integral de su ecología y biología poblacional. Documento no. 2, serie Intercambio Técnico. (Report to Corporación Nacional Forestal [CONAF]and U.N. Food and Agriculture Organisation [FAO]. Santiago, Chile: Oficial Regional Forestal de la FAO.

STUESSY, T.F, FOLAND, K.A., SUTTER, J.F., SANDERS, R.W. & SILVA O.M. 1984. Botanical and geological significance of potassium–argon dates from the Juan Fernandez Islands. Science 225: 49–51.

SUTCLIFFE, T. 1843. Crusoniana, or Truth vs. Fiction, Elucidated in a History of the Island of Juan Fernandez by a Retired Governor of that Colony. Manchester: P. Grant

VALENZUELA, R. 1978. La protección jurídica del património ambiental de las islas oceánicas chilenas. Valparaiso, Chile: Ediciones Universitarias de Valparaíso.

VICUÑA MACKENNA, B. 1883. Juan Fernández, Historia Verdadera de la Isla de Róbinson Crusoe. Santiago, Chile: Jover.

WALLACE, A.R. 1878. Tropical Nature and Other Essays. London: Macmillan.

WALTER, R. & ROBINS, B. 1748. A Voyage round the World by George Anson. [Reprinted 1974. London: Oxford University Press.]

WOODWARD, R.L., JR. 1969. Robinson Crusoe's Island: a history of the Juan Fernandez Islands. Chapel Hill, N. Carolina: University of N. Carolina Press.