

Distribution and abundance of Darwin's finches and other land birds on Santa Cruz Island, Galápagos: evidence for declining populations

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Abstract Population monitoring is a vital tool for conservation management and for testing hypotheses about population trends in changing environments. Darwin's finches on Santa Cruz Island in the Galápagos archipelago have experienced habitat alteration because of human activity, introduced predators, parasites and disease. We used point counts to conduct systematic quantitative surveys of Darwin's finches and other land birds between 1997 and 2010. The temporal analysis revealed that six of the nine species investigated declined significantly and that this decline was most pronounced at higher elevations in humid native forest and agricultural areas; the highland areas have been most affected by introduced species or direct human impact. Five of the six declining species are insectivorous, which suggests that changes in insect abundance or insect availability are a critical factor in the declines. Further study is required to test this idea. Other factors including habitat alteration and introduced parasites or pathogens may be contributing to the observed declines.

Keywords *Camarhynchus*, *Certhidea*, Darwin's finches, distance sampling, Galápagos, *Geospiza*, population estimate, Santa Cruz Island

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Introduction

Fourteen species of Darwin's finches (Geospizinae) occur in the Galápagos archipelago, representing 47%

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of the 30 resident species of land birds (Parent et al., 2008). Although several island populations of Darwin's finches and mockingbirds have been lost since the arrival of humans (Steadman, 1986), no land bird species in the Galápagos has gone extinct in historic times (Dvorak et al., 2004; Grant & Grant, 2008b; O'Connor et al., 2010c). However, three species, mangrove finch *Camarhynchus heliobates*, medium tree-finch *Camarhynchus pauper* and Floreana mockingbird *Mimus trifasciatus*, are categorized as Critically Endangered on the IUCN Red List of Threatened Species (IUCN, 2010).

Human activity over the past 500 years has dramatically altered most of the Galápagos islands. Santa Cruz Island was the last island to be colonized by humans; its first settlers arrived in the 1920s. The following decades saw the almost complete disappearance of the native humid forest on Santa Cruz and its replacement with introduced vegetation. Since the 1990s the ecological impact of human presence has accelerated because of drastic ecological and social changes (Watkins & Cruz, 2007; González et al., 2008). Santa Cruz now receives the highest number of tourists per year in the Galápagos and exhibits the second highest degree of degradation in several of its vegetation zones (Watson et al., 2010).

Here we use quantitative census data to describe the distribution and abundance of the land birds of Santa Cruz. By comparing data for 1997–1998 with data for 2008–2010 we analyse population changes and discuss the effects of drastic ecological changes on bird populations. To evaluate the impact of these changes for conservation of individual species we estimated population sizes for 2008, the year with the most complete survey coverage.

Study area

The 986 km² Santa Cruz Island, which has a maximum altitude of 864 m, is the second largest island in the Galápagos archipelago, with 88% of its surface protected as part of the Galápagos National Park (Servicio Parque Nacional Galápagos, 2006). As a result of precipitation and temperature patterns, several vegetation zones occur along an altitudinal gradient. Besides the coastal strip the following zones are commonly distinguished (Wiggins & Porter, 1971; Fig. 1): (1) Dry zone, southern slope (0–120 m, 531.7 km²),

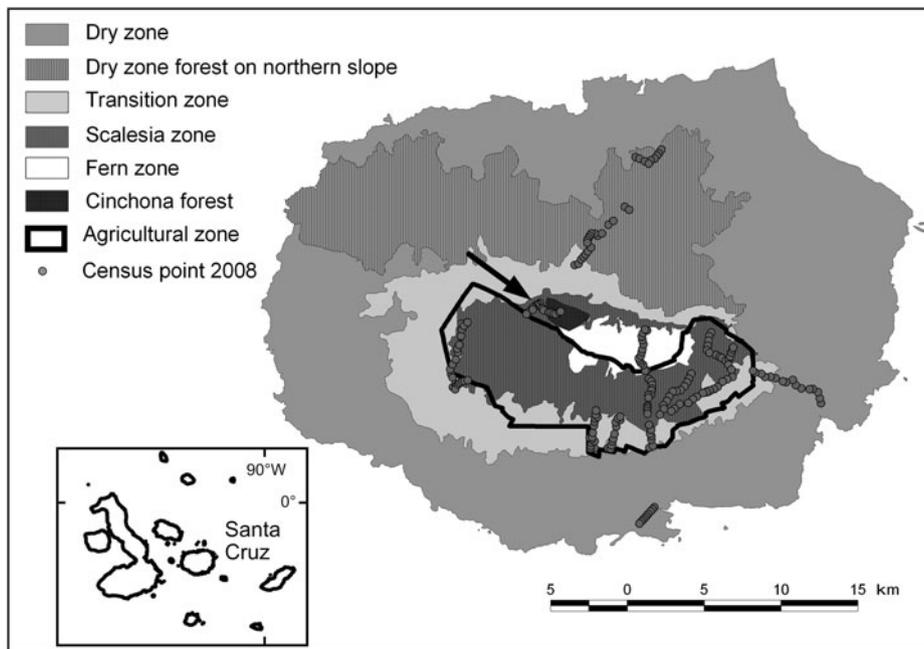


FIG. 1 The extent and location of the vegetation zones on Santa Cruz Island, based on data from Huttel (1990), and the locations of the 233 survey points (Table 1) used in 2008. The inset indicates the location of Santa Cruz in the Galápagos archipelago.

characterized by dry forest and scrub land dominated by deciduous trees, mainly palo santo *Bursera graveolens*, cacti *Opuntia echios*, *Jasminocereus thouarsii* and various species of scrubs. (2) Dry zone, northern slope (191.5 km²), covered by high palo santo forest. (3) Transition zone (120–300 m, 99.2 km²), a dense, mainly deciduous forest dominated by the endemics pega-pega *Pisonia floribunda*, guayabillo *Psidium galapagei* and matazarno *Piscidia carthagenensis*. (4) Scalesia zone (300–650 m, 1.8 km²), an evergreen forest dominated by treelike *Scalesia pedunculata*; trunks and branches are densely covered with epiphytes (mosses, liverworts, ferns and others); most of this zone and smaller parts of the transition and fern zones have been converted to agriculture. (5) Agricultural zone (114.2 km²), mainly farms and grazing land, with introduced trees and shrubs (e.g. *Psidium guajava*, *Cedrela odorata*, *Rubus* spp.), almost completely confined to the wetter southern side of the island. (6) Fern zone (above 650 m, 17.7 km²), where vegetation consists mostly of ferns, grasses and the shrub *Miconia robinsoniana*; many of the introduced plant species from adjacent farmland have invaded the fern zone (Watson et al., 2010). (7) Cinchona zone (12 km²), areas of the fern zone that are now overgrown with forests of *Cinchona pubescens* (Jäger et al., 2009).

Methods

Nomenclature of Darwin's finches follows Petren et al. (1999).

Data collection

Point counts were used for all surveys. Data were collected during the early breeding season of land birds in 1997 (17 January–20 March), 1998 (15 January–17 February), 2008 (29 January–15 March) and 2010 (13 January–10 March) by MD (all years), BF (all but 2010) and EN (2010). Counts lasted for 5 minutes between 07.00 and 11.00. Darwin's finches and other land birds on the Galápagos show high singing activity during the breeding season and mostly inhabit areas of dense vegetation, and therefore direct observations are unreliable. As our aim was to calculate relative and absolute densities in a comparable way we noted only singing birds (presumed to be territory holding males) to avoid counts of non-singing females or juveniles. For Galápagos mockingbird *Mimus parvulus*, Galápagos flycatcher *Myiarchus magirostris* and smooth-billed ani *Crotophaga ani* all observations (except overflying individuals) were tallied. However, the first two species have a tendency to follow an observer and we did not therefore include these species in the between year comparison (Table 3). The dark-billed cuckoo *Coccyzus melacoryphus* was also excluded from this analysis because its singing activity seems to be less correlated with breeding activity and territories than other species and is dependent on other, unknown, factors. Distances of the birds to the observers were estimated to the nearest 5 m between 0 and 20 m, and to the nearest 10 m beyond 20 m. In all years we started with calibration sessions for distance estimation.

A snapshot approach was used. At the beginning we counted all singing birds as rapidly as possible; then, during the remaining minutes, we counted any additional birds in the context of the position and behaviour of the individuals already registered. Using this approach we decreased the risk of counting the same individuals twice (e.g. while moving around) and increased the probability of recognizing new birds that were silent during the initial phase. We avoided counting birds that were obviously not present at the point initially, such as individuals moving into the area during the 5-minute counting period. Points were generally counted once per year as it was assumed that the census period covered the main phase of singing activity. In 1997 and 1998 some points were counted twice; in this case the count with the highest bird numbers was used. Points covered all vegetation zones and altitudes on Santa Cruz (Table 1). Because of the difficulties of accessing some parts of the island points could not be located randomly but were placed along existing paths and small roads (we avoided counting along busy and wide roads). Points were spaced at least 500 m apart in all habitats except in the Scalesia zone, where smaller distances had to be used. Coverage of vegetation zones was uneven between years, with an emphasis on the agricultural and Scalesia zones. In 2008 we added additional survey points in the dry northern slope and Cinchona zones (Table 1). We repeated point counts in the agricultural and Scalesia zones in 2010 to test the validity of the results from 2008.

Data analysis

To examine temporal variation we used the numbers of birds per point to calculate relative abundance in each vegetation zone. We calculated a one-way ANOVA with year as the factor and performed pair-wise comparisons among years with a Bonferroni post-hoc test.

Bird densities for 2008 were calculated with *Distance v. 5* (Thomas et al., 2006) using techniques recommended by Buckland et al. (2001) and Thomas et al. (2006). Density estimation from point count data analysed with *Distance* is now widely used for surveys in tropical and insular environ-

TABLE 1 Number of sample points for birds in each vegetation zone and year on Santa Cruz Island (see Fig. 1 for the locations of the 233 points in 2008).

Zone	1997	1998	2008	2010
Dry southern slope	25		28	
Dry northern slope			19	
Transition	13	14	24	
Scalesia	17	16	27	24
Agricultural	41	41	113	115
Fern	13		16	
Cinchona			6	
<i>Total</i>	111	71	233	139

ments (Marsden et al., 1997; Marsden, 1999; Cramp et al., 2009). Densities (singing males per km²) were calculated for each individual species in each vegetation zone; 95% confidence intervals were calculated using bootstrapping methods. All observations were entered into *Distance* in grouped format; intervals of either 10 or 20 m were used in the analyses. Estimated distances were inspected for outliers that could make model fit problematic, and any found were excluded. Combinations of all key models and adjustments provided by *Distance* were tested. The detection curve based on the model that best fitted the data was chosen automatically by *Distance* using Akaike's Information Criterion. Detection curves were fitted to the data separately for each year and each vegetation zone if there were enough data (60–80 records, as recommended by Buckland et al., 2001). In the case of fewer observations, a composite detection curve using data from two or more zones was used.

To estimate populations, mean bird densities in each vegetation zone were multiplied by the estimated area of the zone. Figures for all zones were summed for each bird species; in this way we calculated an estimate for the breeding population of the entire island. For some species, such as the shy dark-billed cuckoo for which song seems to have limited territorial function, our calculations could be underestimates. The extent of each vegetation zone was derived from geographical information system data using satellite imagery (Huttel, 1990).

Results

We encountered 17 bird species during our censuses. Calculation of relative abundances and densities for four species was not possible because of small sample sizes: vermilion flycatcher *Pyrocephalus rubinus* (27 observations), paint-billed crake *Neocrex erythrops* (10), Galápagos rail *Laterallus spilonotus* (9), and large ground-finch *Geospiza magnirostris* (3). The latter may have very specific habitat requirements and thus be more abundant outside our study sites. Smooth-billed anis were encountered frequently at census points but were not included in the analysis because of their behavioural differences and consequent problems with the counting method used.

Distribution and density

Table 2 provides the density estimates for 12 species in 2008, the year with the most complete survey coverage, in the seven vegetation zones.

Dry zone, southern and northern slope The two most abundant species were the small ground finch *Geospiza fuliginosa* and medium ground finch *Geospiza fortis*; common cactus finch *Geospiza scandens* was common but restricted to areas with cacti (at c. 100 m altitude).

TABLE 2 Estimates of the density of singing males per ha (with 95% confidence intervals in parentheses) of 12 bird species in 2008, including eight species of Darwin's finches, in the seven vegetation zones on Santa Cruz Island (Fig. 1). P (present) indicates a species was recorded in low numbers; empty fields indicate the species was not detected. Confidence intervals were calculated with *Distance*, using bootstrapping methods.

	Dry southern slope	Dry northern slope	Transition	Agricultural	Scalesia	Fern	Cinchona
Small ground finch <i>Geospiza fuliginosa</i>	3.8 (2.8–5)	3.7 (2.9–4.7)	4.5 (3.4–6.1)	5.7 (4.5–7.2)	4.7 (3.5–6.5)	1.0 (0.6–1.6)	P
Medium ground finch <i>Geospiza fortis</i>	3.4 (2.6–4.4)	3.7 (2.9–4.7)	1.3 (0.9–2)	0.6 (0.4–0.8)	P		
Common cactus finch <i>Geospiza candens</i>	1.8 (1.2–2.7)	1.3 (1–1.7)					
Small tree finch <i>Camarhynchus parvulus</i>	0.9 (0.5–1.6)	2.3 (1.6–3.3)	3.9 (3.1–5)	3.3 (2.4–4.4)	6.5 (5–8.5)	0.9 (0.5–1.6)	4.8 (3.1–7.5)
Large tree finch <i>Camarhynchus psittacula</i>	0.01 (0.00–0.03)	P	0.1 (0.03–0.3)	0.4 (0.3–0.5)	0.7 (0.5–0.9)		0.6 (0.3–1)
Woodpecker finch <i>Camarhynchus pallidus</i>	0.02 (0.01–0.05)	P	0.2 (0.1–0.4)	0.6 (0.4–0.8)	1.0 (0.8–1.2)	0.1 (0.08–0.2)	1.1 (0.06–1.9)
Vegetarian finch <i>Platyspiza crassirostris</i>	0.7 (0.4–1.2)	P	0.3 (0.1–0.7)	0.1 (0.05–0.2)	P		
Warbler finch <i>Certhidea olivacea</i>	P		2.1 (1.2–3.4)	0.9 (0.6–1.3)	18.3 (16.6–20.1)	5.6 (4.1–7.6)	9.3 (6.9–12.5)
Yellow warbler <i>Dendroica petechia</i>	0.8 (0.5–1.3)	1.3 (1.0–1.7)	4.3 (2.8–6.6)	3.8 (3.1–4.8)	1.5 (1.1–2.1)	1.2 (0.5–3)	0.6 (0.3–1.3)
Galápagos flycatcher <i>Myiarchus magnirostris</i>	2.2 (1.5–3.3)	1.3 (0.7–2.1)	1.2 (0.7–2)	0.3 (0.2–0.5)	P	P	P
Galápagos mockingbird <i>Mimus parvulus</i>	0.9 (0.7–1.3)	0.9 (0.6–1.2)	0.8 (0.5–1.2)	0.3 (0.2–0.4)	P		
Dark-billed cuckoo <i>Coccyzus melacoryphus</i>	0.04 (0.01–0.07)	0.2 (0.08–0.2)	0.015 (0.01–0.35)	0.03 (0.01–0.07)	0.1 (0.04–0.2)		P

The large ground finch was confined to the dry and lower transition zone but in low numbers. The dry zone is the main habitat of the vegetarian finch *Platyspiza crassirostris*, Galápagos mockingbird and flycatcher, although the former is rare on the northern slope. Of the tree finches only the small tree finch *Camarhynchus parvulus* was common, whereas woodpecker finch *Camarhynchus pallidus* and large tree finch *Camarhynchus psittacula* were both sparsely distributed and restricted to areas with tall palo santo trees. Warbler finch *Certhidea olivacea* occurred locally down to c. 150 m altitude. The density of the yellow warbler *Dendroica petechia* was low.

Transition zone The four most common species were small ground finch, yellow warbler, small tree and warbler finches; all other species occurred at much lower densities. Vegetarian finch and Galápagos mockingbird both reached the upper limit of their distribution at 250–300 m in this zone.

Scalesia zone The little that remains of the once expansive Scalesia forest still holds the highest densities of warbler, small tree, large tree and woodpecker finches. The small ground finch is a common breeding bird in this zone. This zone, at c. 550 m at Los Gemelos and its surroundings, is the most important remaining breeding site of the vermilion flycatcher.

Agricultural zone The natural vegetation of the higher transition zone, most of the Scalesia zone, and parts of the fern zone have been converted to agricultural land, and changes are ongoing. These areas hold the majority of the breeding populations of several species of tree finches. Woodpecker and large tree finches were locally common in stands of higher trees, mainly Cuban cedar *Cedrela odorata*, avocado *Persea americana*, and small woodlands. Small tree and small ground finches and yellow warbler were all widespread and common in semi-open and open farmland. Vegetarian finch, Galápagos mockingbird and flycatcher, and medium ground finch were confined to lower elevations up to 300 m. Warbler finch still occurred locally in the higher elevation zones but its status has changed dramatically (see below).

Fern zone The warbler finch was common and the small tree and small ground finches and yellow warbler were widely distributed but at low densities.

Cinchona zone In this zone the three tree finch species and warbler finch reach densities comparable to the Scalesia forest zone.

Population changes between 1997 and 2010

We calculated changes in relative abundance for eight species of Darwin's finches and the yellow warbler (Table 3,

TABLE 3 Trends in the relative abundance of eight species of Darwin's finches and the yellow warbler across five of the seven vegetation zones (trends cannot be examined for the dry northern and Cinchona zones as there are data for only 1 year) on Santa Cruz Island (Fig. 1). Black shading indicates that the species was not observed, grey that the species occurred irregularly (Table 2). We tested for significant differences in abundance across years and zones with an ANOVA using Bonferroni post-hoc corrections. Arrows indicate significance at $P < 0.05$ (one arrow), < 0.01 (two) and < 0.001 (three) and direction of change; arrows in both directions indicate fluctuating significance between years. Empty fields indicate no significant change between years.

Species	Dry southern slope	Transition	Agricultural	Scalesia	Fern
Small ground finch			⇓⇓⇓	⇓⇓	
Medium ground finch	⇓⇓				
Common cactus finch					
Small tree finch					
Large tree finch	⇓⇓		⇓		
Woodpecker finch	⇓		⇓⇓⇓	⇓⇓	
Vegetarian finch			⇓⇓⇓		
Warbler finch		⇓⇓⇓	⇓⇓⇓	⇓⇓⇓	
Yellow warbler	⇓⇓⇓	⇓⇓⇓	⇓⇓⇓	⇓⇓⇓	⇓⇓⇓

Appendix) in five of the vegetation zones. For the dry northern slope and Cinchona zones no comparative data are available (Table 1). The medium ground finch in the dry zone more than doubled between 1997 and 2008 ($F = 35.3$, $P < 0.001$). Small ground finch, a foraging generalist, increased significantly from 1997/1998 to 2008 in both the agricultural and Scalesia zones, followed by a significant decrease in 2010 (Scalesia: $F = 17.9$, $P < 0.001$; agricultural: $F = 4.8$, $P < 0.01$). The small tree finch, another foraging generalist, remained stable in all five vegetation zones. Large tree finch and vegetarian finch decreased in the dry zone and the agricultural zone, respectively, but these zones were not the species' strongholds (Tables 2–3). Three insectivorous species decreased significantly in several zones. Woodpecker finch declined significantly in the dry zone ($> 65\%$, $F = 6.4$, $P < 0.05$), the Scalesia forest ($> 20\%$, $F = 5.88$, $P < 0.01$), and the agricultural zone ($> 50\%$, $F = 17.66$, $P < 0.001$; Fig. 2). Warbler finch declined significantly in three of five zones (transition: $> 75\%$, $F = 30.65$, $P < 0.001$; Scalesia: $> 45\%$, $F = 66.83$, $P < 0.001$, agricultural zone: $> 85\%$, $F = 64.39$, $P < 0.001$; Fig. 2); the abundance of this species did not change in the fern zone and only few data are available for the dry zone. The yellow warbler exhibited negative trends in all vegetation zones, with significant declines in the dry ($> 85\%$, $F = 85.07$, $P < 0.001$), agricultural ($> 35\%$, $F = 38.67$, $P < 0.001$) and fern zones ($> 70\%$, $F = 17.87$, $P < 0.001$).

Population estimates for 2008

The total population of 12 of the land bird species on Santa Cruz Island in 2008 was estimated to be 1.44 million breeding pairs (assuming a 1:1 sex ratio); c. 1 million of these were Darwin's finches (Table 4). The five species with $> 10\%$ of total abundance were small ground finch (26.7%), medium ground finch (18.8%), small tree finch (12.3%), Galápagos flycatcher (10.9%) and yellow warbler

(10.8%). Although the warbler finch has declined dramatically during the last 10 years in the agricultural zone it still had a comparatively large breeding population with c. 55,500 singing males because of its high density in the fern zone. Vegetarian finch occurred everywhere at a low density but had a total of c. 41,300 singing males because of its wide range in the dry and transition zones. Population sizes of woodpecker finch and large tree finch, both largely confined to higher altitudes, were lower at c. 12,000 and 9,000 singing males, respectively. The breeding population of large ground finch could not be estimated but was probably in the low thousands and the vermilion flycatcher probably numbers < 200 pairs.

Discussion

The most alarming finding of our study was the dramatic decline of at least four insectivorous bird species on Santa

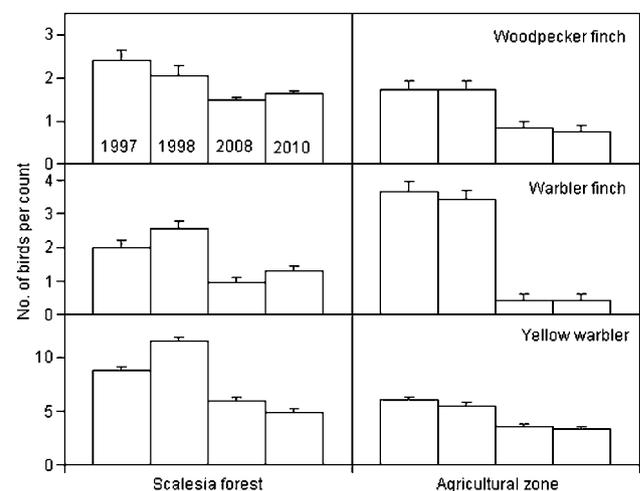


FIG. 2 Mean (\pm SE) number of birds per point count for woodpecker and warbler finches and yellow warbler in 1997, 1998, 2008 and 2010 in the Scalesia forest and agricultural zones of Santa Cruz Island (Fig. 1). Note the different y-axis scales. These three species showed the strongest declines in these zones.

TABLE 4 Estimates of the mean total population of singing males (with confidence intervals in parentheses) of 12 bird species in 2008, including eight species of Darwin's finches, on Santa Cruz Island (Fig. 1). Values calculated with *Distance* for each vegetation zone were multiplied by the respective area and then summed for the entire island. Values are rounded to the nearest 100.

Species	Mean (CI)
Small ground finch	388,300 (291,200–504,500)
Medium ground finch	271,400 (207,300–352,900)
Common cactus finch	95,700 (63,800–143,600)
Small tree finch	176,800 (120,900–261,500)
Large tree finch	8,900 (4,300–11,100)
Woodpecker finch	11,600 (6,400–18,600)
Vegetarian finch	41,300 (22,800–73,000)
Warbler finch	55,500 (37,300–80,600)
Yellow warbler	156,300 (110,200–228,200)
Galápagos flycatcher	157,200 (102,400–241,200)
Galápagos mockingbird	76,500 (56,000–108,600)
Dark-billed cuckoo	6,500 (2,300–11,900)

Cruz Island between 1997 and 2010 (warbler and woodpecker finches, yellow warbler and vermilion flycatcher, the latter already detected by Wiedenfeld, 2006). The population size of the formerly common vermilion flycatcher is now too small to be censused reliably with point counts. We found significant decreases, in at least one vegetation zone, of the large tree and vegetarian finches but sample sizes were low. Only three species (small ground, medium ground and small tree finches) either increased or appeared to be stable.

The majority of the populations that declined did so in the humid areas of Santa Cruz (upper transition, agricultural and Scalesia zones). These environments are the stronghold of the warbler and tree finches and have been, directly or indirectly, altered by human activity. The endemic Scalesia forest is estimated to have covered almost 100 km² on Santa Cruz (Stewart, 1915) but was reduced to c. 20% of its original size by the 1980s (Huttel, 1990) and 1–2% by 2009 (Mauchamp & Atkinson, 2011). These remnant Scalesia forest patches, which are now of only 1–2 km², have been invaded by introduced trees and shrubs such as *C. odorata*, *C. pubescens* and *Rubus niveus* (Rentería & Buddenhagen, 2006; Jäger et al., 2007). Invasion by *R. niveus* has accelerated and may have been triggered by the El Niño event of 1997–1998 (Mauchamp & Atkinson, 2011). Many bird species consume the fruits of *R. niveus* and other weed species now present in the humid zones (Kleindorfer et al., 2006; Guerrero & Tye, 2009). This change in the plant community could have resulted in an alteration of the composition of the bird community by favouring seed eaters and generalist species such as the small tree finch because they can increase seed and fruit intake and therefore counter a possible limitation in insect abundance. The intense use of herbicides to control these

invasive plant species may have led to altered plant communities with reduced or altered invertebrate abundance, which could impair foraging by insectivorous bird species.

Santa Cruz has the highest human population (estimated to be 18,000; Ch. Grenier, pers. comm.) of the Galápagos and, after San Cristobal, the largest proportion of its land area modified (14%; Watson et al., 2010). Urban development is rapid and is closely followed by rural development (González et al., 2008). The heterogeneous agricultural zone is a suitable secondary habitat for many bird species but is not within the National Park and undergoes constant changes.

A major factor affecting land birds are introduced species acting as predators, competitors or parasites, or carrying and transmitting diseases, such as rats (Fessl et al., 2010), mosquitoes (Whiteman et al., 2005) and the parasitic fly *Philornis downsi* (Fessl & Tebbich, 2002). *P. downsi* larvae in finch nests were first discovered in 1997 (Fessl et al., 2001) and, since then, several studies have demonstrated their negative impact on nesting success (Dudaniec et al., 2006; Fessl et al., 2006; Huber, 2008; Kleindorfer & Dudaniec, 2009; O'Connor et al., 2010c). The fly occurs at higher densities in moist habitats (Wiedenfeld et al., 2007; O'Connor et al., 2010a) and birds with smaller clutch sizes (such as tree finches in general and birds in the humid zone in particular) have higher nestling mortality (Dudaniec et al., 2007). The two species with the highest prevalence of *P. downsi* in their nests (woodpecker and warbler finches; Dudaniec et al., 2007) are also the species that showed the strongest declines in our study. No data are available on the impact of *P. downsi* on yellow warbler nests. Exotic diseases are a significant factor in the decline of threatened species (Smith et al., 2006; Barbosa & Palacios, 2009) and for the Galápagos fauna in particular (Wikelski et al., 2004; Deem et al., 2008; Levin et al., 2009). Avian pox (Thiel et al., 2005; Kleindorfer & Dudaniec, 2006) and other pathogens transmitted by mosquitoes (Bataille et al., 2009) are of particular importance. Since 1998 the number of medium ground finches in the highlands has increased (authors, pers. obs.) and small ground finches now regularly breed in the Scalesia zone (Kleindorfer, 2007). Small ground finch numbers fluctuate annually, indicating possible changes in movement patterns and the possibility of carrying diseases to immunologically naive highland bird populations. Highland woodpecker finches brought to captive facilities in the lowlands immediately contracted avian pox (S. Tebbich et al., unpubl. data), indicating a high susceptibility in these populations.

Climate fluctuations or climate change could cause changes in bird populations and could also magnify the impact of humans and invasive species on an ecological system. In the Galápagos in particular rainfall patterns are a driving force for breeding activity and patterns of species'

interactions (Grant & Grant, 2008a). During our survey period from 1997 to 2010 the Galápagos experienced 2 years of high rainfall (1998, 2008) and otherwise persistent drought conditions with annual rainfall < 300 mm (except for 2002 with 577 mm) in the lowlands of Santa Cruz (CDF, 2010). The strong El Niño in 1998 (1,752 mm annual rainfall at 0 m) and the moderate El Niño in 2008 (769 mm) could have led to an increase in male singing activity and an increase in population sizes as Darwin's finches are known to produce multiple clutches in El Niño years. However, our data indicate neither outcome. The census data in 1998 were similar to the data in 1997, which was a year of normal rainfall. Also, the strong rainfall of 2008 did not lead to a measurable population increase in 2010. While these findings are surprising, most recent data suggest that high rainfall periods depress finch populations via an increase in parasite prevalence (Antoniazzi et al., 2011; J. O'Connor & S. Kleindorfer, unpubl. data; S. Tebbich, unpubl. data). The overall dry conditions since 1997 could possibly have contributed to the decline of several species.

Our findings indicate the significant decline in abundance and density of at least four passerine species on Santa Cruz. The greatest decline is that of the warbler finch, now estimated to comprise 55,000 singing males compared to > 1 million at the beginning of the 20th century (considering the original extent of forest on the island). There is evidence of changes in species' abundances and bird community composition on other inhabited Galápagos islands. A survey on Floreana Island indicated a stable population of ground finches and small tree finches but a decline in large-bodied birds, including the medium tree finch (O'Connor et al., 2010c), and the grey warbler finch *Certhidae fusca*, which is morphologically and ecologically very similar to the warbler finch (Petren et al., 2005), is extirpated or nearly so (Grant et al., 2005). Preliminary data for San Cristobal indicate that the population of the grey warbler finch there is in the low 10,000s (M. Dvorak & E. Nemeth, unpubl. data). On San Cristobal Island the vermilion flycatcher is considered locally extinct (Vargas, 1996; Wiedenfeld, 2006).

No bird census data exist for Isabela and Santiago Islands, the other two elevated islands on which introduced herbivores have destroyed or degraded most of the native forest (Henderson & Dawson, 2009). We suspect that this has had a large negative impact on the warbler, woodpecker and large tree finches. At present these three species are considered to be at low risk of population decline (IUCN, 2010) but this may not be the case if we infer their potential population trajectory given comparable habitat loss on Santa Cruz, Isabela and Santiago.

We recommend the implementation of a full-scale monitoring programme for land birds on the inhabited islands of the Galápagos archipelago. Human impacts on these islands have been multifaceted and extensive yet there

have been few bird surveys and, since 1997, there have been successful eradication efforts for alien plant species on some of the Galápagos islands and future eradication programmes are planned (Campbell & Donlan, 2005; Carrión et al., 2007; Donlan et al., 2007). Bird surveys would facilitate the monitoring of the impact of disease and habitat change and assessment of the effects of island restoration projects on bird communities. We are preparing a proposal for such a survey on San Cristobal Island.

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References

- ANTONIAZZI, L.R., MANZOLI, D.E., ROHRMANN, D., SARAVIA, M.J., SILVESTRI, L. & BELDOMENICO, P.M. (2011) Climate variability affects the impact of parasitic flies on Argentinian forest birds. *Journal of Zoology*, 283, 126–134.
- BARBOSA, A. & PALACIOS, M.-J. (2009) Health of Antarctic birds: a review of their parasites, pathogens and diseases. *Polar Biology*, 32, 1305–1315.
- BATAILLE, A., CUNNINGHAM, A.A., CEDEÑO, V., PATIÑO, L.C., CONSTANTINO, A., KRAMER, L.D. et al. (2009) Natural colonization and adaptation of a mosquito species in Galápagos and its implications for disease threats to endemic wildlife. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10230–10235.
- BUCKLAND, S.T., ANDERSON, D.R., BURNHAM, K.P., LAAKE, J.L., BORCHERS, D.L. & THOMAS, L. (2001) *Introduction to Distance Sampling*. Oxford University Press, Oxford, UK.
- CAMPBELL, K. & DONLAN, C.J. (2005) Feral goat eradications on islands. *Conservation Biology*, 19, 1362–1374.
- CARRIÓN, V., DONLAN, C.J., CAMPBELL, K., LAVOIE, C. & CRUZ, F. (2007) Feral donkey (*Equus asinus*) eradications in the Galápagos. *Biodiversity and Conservation*, 16, 437–445.
- CDF (2010) *Charles Darwin Foundation Weather Data Base*. [Http://www.darwinfoundation.org/datazone/darwin_weather](http://www.darwinfoundation.org/datazone/darwin_weather) [accessed 4 July 2010].
- CRAMP, R.J., PRATT, T.K., MARSHALL, A.P., AMIDON, F. & WILLIAMS, L.L. (2009) Recent status and trends of the land bird avifauna on Saipan, Mariana islands, with emphasis on the endangered nightingale reed warbler *Acrocephalus luscinius*. *Bird Conservation International*, 19, 323–337.

- DEEM, S.L., CRUZ, M., JIMÉNEZ-UZCÁTEGUI, G., FESSL, B., MILLER, R.E. & PARKER, P.G. (2008) Pathogens and parasites: an increasing threat to the conservation of Galapagos avifauna. In *Galápagos Report 2007–2008* (ed. F.C. Darwin), pp. 125–130. Puerto Ayora, Galápagos, Ecuador.
- DONLAN, C.J., CAMPBELL, K., CABRERA, W., LAVOIE, C., CARRIÓN, V. & CRUZ, F. (2007) Recovery of the Galápagos rail (*Laterallus spilonotus*) following the removal of invasive mammals. *Biological Conservation*, 138, 520–524.
- DUDANIEC, R., FESSL, B. & KLEINDORFER, S. (2007) Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. *Biological Conservation*, 139, 325–332.
- DUDANIEC, R., KLEINDORFER, S. & FESSL, B. (2006) Effects of the introduced ectoparasite *Philornis downsi* on haemoglobin level and nestling survival in Darwin's small ground finch (*Geospiza fuliginosa*). *Austral Ecology*, 31, 88–94.
- DVORAK, M., VARGAS, H., FESSL, B. & TEBBICH, B. (2004) On the verge of extinction: a survey of the mangrove finch *Cactospiza heliobates* and its habitat on the Galápagos islands. *Oryx*, 38, 1–9.
- FESSL, B., COURI, M.S. & TEBBICH, S. (2001) *Philornis downsi* Dodge and Aitken, new to the Galápagos Islands (Diptera, Muscidae). *Studia dipterologica*, 8, 317–322.
- FESSL, B., KLEINDORFER, S. & TEBBICH, S. (2006) An experimental study on the effects of an introduced parasite in Darwin's finches. *Biological Conservation*, 127, 55–61.
- FESSL, B. & TEBBICH, S. (2002) *Philornis downsi*—a recently discovered parasite on the Galápagos archipelago—a threat for Darwin's finches? *Ibis*, 144, 445–451.
- FESSL, B., YOUNG, H.G., YOUNG, R.P., RODRIGUEZ-MATAMOROS, J., DVORAK, M., TEBBICH, S. et al. (2010) How to save the rarest Darwin's finch from extinction: the mangrove finch on Isabela Island. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 365, 1019–1030.
- GONZÁLEZ, J.A., MONTES, C., RODRÍGUEZ, J. & TAPIA, W. (2008) Rethinking the Galápagos Islands as a complex social-ecological system: implications for conservation and management. *Ecology and Society*, 13, 13.
- GRANT, B.R. & GRANT, P.R. (2008a) Fission and fusion of Darwin's finches. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 363, 2821–2829.
- GRANT, P.R. & GRANT, B.R. (2008b) *How and Why Species Multiply. The Radiation of Darwin's Finches*. Princeton University Press, Princeton, USA.
- GRANT, P.R., GRANT, R.B., PETREN, K. & KELLER, L.F. (2005) Extinction behind our backs: the possible fate of one of the Darwin's finch species on Isla Floreana, Galápagos. *Biological Conservation*, 122, 499–503.
- GUERRERO, A.M. & TYE, A. (2009) Darwin's finches as seed predators and dispersers. *The Wilson Journal of Ornithology*, 121, 752–764.
- HENDERSON, S. & DAWSON, T.P. (2009) Alien invasions from space observations: detecting feral goat impacts on Isla Isabela, Galápagos Islands with the AVHRR. *International Journal of Remote Sensing*, 30, 423–433.
- HUBER, S.K. (2008) Effects of the introduced parasite *Philornis downsi* on nestling growth and mortality in the medium ground finch (*Geospiza fortis*). *Biological Conservation*, 141, 601–609.
- HUTTEL, C. (1990) Cartografía de la vegetación en las islas Galápagos. In *Botanical Research and Management in the Galápagos Islands* (eds J.E. Lawesson, O. Hamann, G. Rogers, G. Reck & H. Ochoa), pp. 67–78. Missouri Botanical Garden, Saint Louis, USA.
- IUCN (2010) *Red List of Threatened Species v. 2010.1*. <http://www.iucnredlist.org> [accessed 20 June 2010].
- JÄGER, H., KOWARIK, I. & TYE, A. (2009) Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation. *Journal of Ecology*, 97, 1252–1263.
- JÄGER, H., TYE, A. & KOWARIK, I. (2007) Tree invasion in naturally treeless environments: impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos. *Biological Conservation*, 140, 297–307.
- KLEINDORFER, S. (2007) The ecology of clutch size variation in Darwin's small ground finch *Geospiza fuliginosa*: comparison between lowland and highland habitats. *Ibis*, 149, 730–741.
- KLEINDORFER, S., CHAPMAN, T., WINKLER, H. & SULLOWAY, F.J. (2006) Adaptive divergence in contiguous populations of Darwin's small ground finch (*Geospiza fuliginosa*). *Evolutionary Ecology Research*, 8, 357–372.
- KLEINDORFER, S. & DUDANIEC, R. (2006) Increasing prevalence of avian poxvirus in Darwin's finches and its effect on male pairing success. *Journal of Avian Biology*, 37, 69–76.
- KLEINDORFER, S. & DUDANIEC, R. (2009) Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches. *Behavioral Ecology and Sociobiology*, 63, 731–739.
- LEVIN, I.L., OUTLAW, D.C., VARGAS, F.H. & PARKER, P.G. (2009) *Plasmodium* blood parasite found in endangered Galápagos penguins (*Spheniscus mendiculus*). *Biological Conservation*, 142, 3191–3195.
- MARSDEN, S.J. (1999) Estimation of parrot and hornbill densities using a point count distance sampling method. *Ibis*, 141, 377–390.
- MARSDEN, S.J., JONES, M.J., LINSLEY, M.D., MEAD, C. & HOUNSOME, M.V. (1997) The conservation status of the restricted-range lowland birds of Buru, Indonesia. *Bird Conservation International*, 7, 213–233.
- MAUCHAMP, A. & ATKINSON, R. (2011) Pérdida de hábitat rábida, reciente e irreversible: los bosques de Scalesia en las islas Galápagos. In *Informe Galápagos 2009–10* (eds A.M. Luna, L.J. Cayot & M.V. Toral Granda), pp. 111–114. Puerto Ayora, Galápagos, Ecuador.
- O'CONNOR, J., DUDANIEC, R.Y. & KLEINDORFER, S. (2010a) Parasite infestation and predation in Darwin's small ground finch: contrasting two elevational habitats between islands. *Journal of Tropical Ecology*, 26, 285–292.
- O'CONNOR, J., ROBERTSON, J. & KLEINDORFER, S. (2010b) Video analysis of host–parasite interactions in nests of Darwin's finches. *Oryx*, 44, 588–594.
- O'CONNOR, J., SULLOWAY, F.J. & KLEINDORFER, S. (2010c) Avian population survey in the Floreana highlands: is Darwin's medium tree finch declining in remnant patches of *Scalesia* forest? *Bird Conservation International*, 20, 1–11.
- PARENT, C.E., CACCONI, A. & PETREN, K. (2008) Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, 363, 3347–3361.
- PETREN, K., GRANT, B.R. & GRANT, P.R. (1999) A phylogeny of Darwin's finches based on microsatellite DNA length variation. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 266, 321–329.
- PETREN, K., GRANT, P.R., GRANT, B.R. & KELLER, L.F. (2005) Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. *Molecular Ecology*, 14, 2943–2957.
- RENTERÍA, J.L. & BUDDENHAGEN, C.E. (2006) Invasive plants in the *Scalesia pedunculata* forest at Los Gemelos, Santa Cruz, Galápagos. *Noticias de Galápagos—Galápagos Research*, 64, 31–35.

- SERVICIO PARQUE NACIONAL GALÁPAGOS (2006) *Plan de manejo*. Parque Nacional Galapagos, Santa Cruz, Galapagos.
- SMITH, K.F., SAX, D.F. & LAFFERTY, K.D. (2006) Evidence for the role of infectious disease in species extinction and endangerment. *Conservation Biology*, 20, 1349–1357.
- STEADMAN, D.W. (1986) Holocene vertebrate fossils from Isla Floreana, Galápagos, Ecuador. *Smithsonian Contributions to Zoology*, I–IV, 1–104.
- STEWART, A. (1915) Some observations concerning the botanical conditions on the Galápagos Islands. *Transaction of the Wisconsin Academy of Science and Arts and Letters*, 18, 272–340.
- THIEL, T., WHITEMAN, N.K., TIRAPÉ, A., INES BAQUERO, M., CEDEÑO, V., WALSH, T. et al. (2005) Characterization of canarypox-like viruses infecting endemic birds in the Galápagos Islands. *Journal of Wildlife Diseases*, 41, 432–453.
- THOMAS, L., LAAKE, J.L., STRINDBERG, S., MARQUES, F.F.C., BUCKLAND, S.T., BORCHERS, D.L. et al. (2006) *User's Guide Distance 5.0 Release 2*. Research Unit for Wildlife Population Assessment. University of St Andrews, St Andrews, UK.
- VARGAS, H. (1996) What is happening with the avifauna of San Cristobal? *Noticias de Galápagos*, 57, 23–24.
- WATKINS, G. & CRUZ, F. (2007) *Galápagos at Risk: A Socio-economic Analysis of the Situation in the Archipelago*. Charles Darwin Foundation, Puerto Ayora, Galápagos.
- WATSON, J., TRUMAN, M., TUFET, M., HENDERSON, S. & ATKINSON, R. (2010) Mapping terrestrial anthropogenic degradation on the inhabited islands of the Galapagos Archipelago. *Oryx*, 44, 79–82.
- WHITEMAN, N.K., GOODMAN, S.J., SINCLAIR, B.J., WALSH, T., CUNNINGHAM, A.A., KRAMER, L.D. et al. (2005) Establishment of the avian disease vector *Culex quinquefasciatus* Say, 1823 (Diptera: Culicidae) on the Galápagos Islands, Ecuador. *Ibis*, 147, 844–847.
- WIEDENFELD, D.A. (2006) Aves, the Galápagos Islands, Ecuador. *Checklist*, 2, 1–27.
- WIEDENFELD, D.A., JIMENEZ, U., GUSTAVO, A., FESSL, B., KLEINDORFER, S. & VALAREZO, J.C. (2007) Distribution of the introduced parasitic fly *Philornis downsi* (Diptera, Muscidae) in the Galápagos Islands. *Pacific Conservation Biology*, 13, 14–19.
- WIGGINS, I.L. & PORTER, D.M. (1971) *Flora of the Galápagos Islands*. Stanford University Press, Stanford, USA.
- WIKELSKI, M., FOUFOPOULOS, J., VARGAS, H. & SNELL, H. (2004) Galápagos birds and disease: invasive pathogens as threats for island species. *Ecology and Society*, 9, 5.

Appendix

The appendix for this article is available online at <http://journals.cambridge.org>

Biographical sketches

MICHAEL DVORAK is coordinating and conducting research on threatened bird species and protected areas for BirdLife Austria. BIRGIT FESSL is a freelance behavioural ecologist with a particular interest in conservation biology. She investigated the impact of *Philornis downsi* and was field manager of the mangrove finch project from 2006 to 2009. ERWIN NEMETH is part of the Social Communication Group at the Max Planck Institute for Ornithology and has worked on bioacoustics and conservation of birds. SONIA KLEINDORFER studies *Philornis* parasitism and tree finch evolution on the Galápagos Islands and avian population ecology and behaviour in Australia. SABINE TEBBICH is studying the relationship between feeding ecology and cognition in Darwin's finches and corvids and is also involved in studies of the conservation of Darwin's finches.