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Invasive parasites, habitat change and heavy rainfall reduces breeding success in Darwin's finches

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1. Abstract

Invasive alien parasites and pathogens are a major and growing threat to biodiversity worldwide, which can significantly contribute to the extinction of vulnerable endemic species. On the Galápagos Islands, the invasive parasite *Philornis downsi* and other introduced predators pose a precarious threat to endemic bird species. Here, we investigated the influence of these invasive species on the breeding success of two endemic Darwin's finches: the warbler finch (*Certhidea olivacea*) and the sympatric small tree finch (*Camarhynchus parvulus*). The warbler finch has experienced a dramatic decline in population size, dropping by over 50% in the last 15 years on Santa Cruz Island, while the small tree finch has remained stable over the last decade. To address this differing population development, we aimed to identify whether warbler finches, in comparison with small tree finches, are particularly vulnerable during the breeding cycle, and if so, to look which stages were most affected. Furthermore, we wanted to determine whether low breeding success caused by parasites and predators contributed to the rapid decline of this species. We found that the introduced parasite *Philornis downsi* had a high negative influence on breeding success in both the arboreal finches. Our data does, however, suggest that extreme climatic conditions, such as heavy rain and control of invasive plant species with herbicides, may have an important additive negative impact on both species. We assume that these factors influence food supply during chick rearing, which in turn results in mortality in chicks that are already weakened by parasitism. The yearly variation in heavy rainfall during the breeding season may also explain the different magnitudes of *Philornis* effect on chick growth and mortality found in previous studies. Our data support the hypothesis that low breeding success leads to population decline in the warbler finch as well as in the small tree finch. For the latter species, counting data show a less stable population over the last few years, as well as an apparent change in age structure, with a higher prevalence of older birds suggesting low reproduction.

2. Introduction

Studies on Darwin's finches, which are endemic to the Galápagos Islands, have provided the inspiration for some of the most important ideas in evolutionary biology. Unlike populations of land birds on other tropical archipelagos, the Galápagos bird community has remained remarkably unaltered following human colonization. However, the introduction of predators, pathogens and parasites have led to increasing pressures affecting several Darwin's finch species (e.g. Thiel et al. 2005, Kleindorfer & Dudaniec 2006, Deem et al. 2008, Wiedenfeld & Jiménez-Uzcátegui 2008, Fessl et al. 2010). One of the biggest threats to the Galápagos avifauna is the obligate bird parasite *Philornis downsi* (Causton et al. 2006), which was first discovered on the archipelago in 1997 (Fessl & Tebbich 2002). Adult flies lay their eggs in bird nests where the parasitic larvae then hatch (Fessl et al. 2006a). The first instar larvae usually develop within the chicks' nostrils, whereas the second and third instar larvae are found in the bottom layer of the nest and suck blood from the nestlings during the night (Dudaniec & Kleindorfer 2006, Fessl et al. 2006a, O'Connor et al. 2010a, own observations). Correlative as well as experimental studies have shown that *Philornis downsi* has a negative impact on nestling growth, haemoglobin levels and fledgling success (Dudaniec et al. 2006, Fessl et al. 2006b, Huber 2008, Kleindorfer & Dudaniec 2009, Koop et al. 2011). The mortality caused by *Philornis downsi* varies from 16 to 95% of all finch nests (reviewed in O'Connor et al. 2010b).

The highest prevalence and intensity of *P. downsi* infestation on the Galápagos Islands was found on Santa Cruz Island (Wiedenfeld et al. 2007). Here, finch population numbers have decreased continuously over the last 15 years (Dvorak et al. 2012), and in some species this decrease has been dramatic**.** A quantitative survey of Darwin's finches and other land birds on Santa Cruz Island, between 1997 and 2010, revealed that six of nine investigated species declined significantly. This decline was most pronounced at higher elevations in humid native forest and in agricultural areas (Dvorak et al. 2012). Notably, these two habitat types have been most affected by introduced species and direct human impact. The greatest decline was observed in the warbler finch (*Certhidea olivacea*). This insectivorous species is an arboreal finch and is the smallest of the Darwin's finches. The warbler finch population has shrunk by 50% in the humid native *Scalesia* forest and by up to 75% in the agricultural zone (Dvorak et al. 2012). A pre-study in 2010 (Tebbich et al. unpublished data) suggests that the warbler finch decline may be explained, at least to some extent, by low breeding success. In 2010, only 50% of warbler finch nests produced at least one fledgling. Different factors may be responsible for this low breeding success and thus the population decline of the warbler finch.

Warbler finches could be affected more strongly by *Philornis* parasitism than other Darwin's finch species for two reasons. Firstly, their small body and clutch size may enhance mortality due to parasitism (Dudaniec et al. 2007, Kleindorfer & Dudaniec 2009). Secondly, this species is restricted to the humid highlands where conditions for *Philornis* are better than in the lowlands (e.g. higher host nesting density and better year-round food supply for adult flies) (Wiedenfeld et al. 2007, O'Connor et al. 2010c). In line with this proposition, *Philornis* intensity was significantly higher in the highlands than in the lowlands on Floreana Island (O'Connor et al. 2010c), however this effect was not found on Santa Cruz Island (Dudaeniec et al. 2007).

The influence of parasitism on breeding success in Darwin's finches is highly variable from year to year (reviewed in O'Connor et al. 2010b). The reasons for this high variation are, so far, poorly understood. A possible natural source of variation could relate to differences in precipitation within and between years (Dudaniec et al. 2007). Such interaction between rainfall and *Philornis* prevalence and intensity has also been found in *Philornis* sp. which affect various bird species in Puerto Rico (Arendt 2000) and Argentina (Antoniazzi et al. 2011). The Galápagos archipelago is characterised by a highly seasonal climate with pronounced wet and dry seasons, as well as extraordinary yearly variation in rainfall (Grant & Grant 1989). Periods of intense rain (El Niño years) and severe draughts reoccur at irregular intervals, though Darwin's finches have adapted to these extreme weather conditions over at least 1-2 million of years (Grant & Grant 2008). In ground finches, mortality is high during droughts with populations recovering during El Niño years, due to higher breeding success and an extended breeding season (Grant et al. 2000). *Philornis* may undermine this capability to buffer short-term declines during unfavourable climatic conditions by significantly reducing breeding success during dry as well as humid periods. Indeed, Darwin's finch nests have been found to suffer from a higher *Philornis* intensity in El Niño years (Dudaniec et al. 2007), which may reduce any positive influence by favourable weather conditions on the finches' reproduction.

Other than parasitism, the loss of primary habitat could be a possible reason for the population decline. By 2009, the endemic humid *Scalesia* forest was reduced to only 2% of its original area (Mauchamp & Atkinson 2011). Additionally, introduced trees and shrubs have invaded these remnant *Scalesia* forest patches (Rentería & Buddenhagen 2006, Jäger et al. 2007). The *Scalesia* forests are most affected by the introduced plant species *Rubus niveus*. High cover by *R. niveus* has significantly reduced richness and available cover for native plant species, as well as lead to changes in the *Scalesia* forest structure (Rentería et al. 2012). As a result, the National Park has set up a program to control these invasive neophytes, in particular *R. niveus*. Strong herbicides, such as "round-up", are sprayed throughout areas in the *Scalesia* zone,

which lead to temporary removal of the entire understory. Such dramatic habitat degradation may have led to changes in plant communities and species composition of invertebrates, which could also negatively influence the insectivorous bird species. Finally, introduced predators, especially rats (*Rattus rattus*), may negatively affect bird species. For example, a study on mangrove finches found that rats can cause significant brood loss (Fessl et al. 2010). Furthermore, rats may have a stronger influence on the warbler finch over the other species, as warbler finch nests are built lower down in the tree's canopy (own unpublished data). It is possible that, rather than being attributable to a single factor, a combination of different unfavourable conditions and stressors are responsible for the bird population declines.

The warbler finch population decline provides a good exemplar of the decline of the insectivorous passerines on Santa Cruz Island. These species include the vermilion flycatcher (*Pyrocephalus rubinus nanus*), yellow warbler (*Dendroica petechia aureola*) and woodpecker finch (*Camarhynchus pallidus*). All of these species produce small clutches and are predominantly insectivorous. With the exception of the woodpecker finch, they also each have a small body size. In studying the warbler finch, we could provide evidence regarding the relative importance of two particular factors that may be key to understanding the decline of all these bird species. The first of these two factors refers to the impact of *Philornis*, since this parasite has a stronger impact on species with small body and clutch size (Dudaniec et al. 2007). Secondly, we can explore how change in habitat structure may affect food abundance and/or availability for chicks and adults.

The aim of the study was therefore to investigate warbler finch breeding success, specifically to explore possible reasons for nesting failure, with a particular focus on the influence of *Philornis* parasitism, habitat structure, predation and climatic conditions. In order to get a clearer picture of the extent to which these factors can explain the dramatic population decline in the warbler finch, we also looked at the breeding success of the small tree finch. This species is a Darwin's finch, which is sympatric to the warbler finch, but differs in that it has a stable population (Dvorak et al. 2012). Warbler finches should be more affected by *Philornis* parasitism, than small tree finches, because of their smaller body size (Dudaniec et al. 2007). In relation to this, warbler finch nests have been found to have higher *Philornis* intensities than those of small tree finches (Kleindorfer & Dudaniec, 2009). Furthermore, warbler finch nests should be more vulnerable to predation (by rats) due to their lower nesting position (Kleindorfer & Dudaniec 2009, own data). In addition, changes in habitat structure (use of herbicides to control invasive plants) may result in low insect abundance. Thus the insectivorous warbler finch should be more affected by habitat structure changes than the small tree finch, which exploits a broader

diet (Tebbich et al. 2004). We therefore predict that the declining warbler finch will have a lower breeding success than the stable small tree finch.

3. Methods

3.1 Study site

The study was conducted during the main breeding season (January to end of March 2012) in the highland area around Los Gemelos (0°37'34" S, 90°23'10" W) on Santa Cruz Island, Galápagos. This area is dominated by the endemic tree *Scalesia pedunculata* and is thus called the *Scalesia* zone. In some areas of our study site, the National Park applies strong herbicides to control the invasion of *R. niveus*, which results in the removal of the whole forest understory.

3.2 Population survey

We continued the population survey, which started in 1997 in the *Scalesia* zone, of the two focal species, warbler finch (*Certhidea olivacea*) and small tree finch (*Camarhynchus parvulus*), by conducting point counts following the same method used by Dvorak et al. (2012). The data was collected from the 18th to 21st February 2012 by Michael Dvorak and Birgit Fessl. Within the *Scalesia* forest, point counts, lasting 5 minutes each, were conducted between 06:30 and 10:30 am – when Darwin's finches show the highest singing activity. The 26 points were spaced at least 70 m apart. The number of singing birds (presumed to be territory holding males) and the distance of each singing individual to the observer were recorded for each point. However, in order to measure the population trends over the whole period from 1997 to 2012, only the number of singing males per point was used. In addition to point counts, we recorded the age structure of the small tree finch population in the *Scalesia* forest. The brownish head coloration of young small tree finch males turns black in a specific moulting pattern as the subjects age (Kleindorfer 2007). Each small tree finch male found displaying near its nest (irrespective if it was already paired or not) was therefore assigned to one of two categories following Kleindorfer's (2007) coloration categories (0-5). These were: (i) brown (young) males, whose black plumage is maximally extended from around the beak to the eye region (categories 0-3),

and (ii) black (old) males, whose black plumage has already extended to the throat and the back part of the head and nape (categories 4-5).

3.3 Nest monitoring and parasite abundance

We monitored the nests of both Darwin's finch species – warbler finch and small tree finch – in an area of approximately 2 ha within the *Scalesia* forest. Nest status was determined at different intervals depending on the current breeding status (nest building: 5 days interval, incubation: 3 days interval, feeding: 2 days interval, close to fledging: daily) by inspecting the inside of the nests with a small endoscopic video camera, which allowed recordings of clutch as well as brood size. Successful nests (breeding success) were defined as nests that produced at least one fledgling. Nests that failed were assigned to the following categories: (1) abandoned (pair stopped incubating, no chicks present in the nest), (2) dead chicks (all chicks dead but still in the nest), (3) empty nest (previously active nest, chicks ≤ 6 days, found empty, most likely dead chicks thrown out by parents), (4) predated (nest destroyed or intact and empty, previously contained chicks ≥ 7 days – too big to be thrown out by parents) and (5) others (e.g. nesting tree collapsed, nest fallen down due to wind).

The chicks' age (in days) of successful and failed nests was calculated by combining information from nest inspections with a series of images of growing nestlings (when inspections coincided with hatching). Hatching date was calculated as the last observation date minus chick age. Where possible, the calculated hatching date was cross-checked with observational data from nest inspections. In total, 43 nests were found before incubation started and were successfully incubated until the chicks' hatched. The incubation time was calculated for each nest as the time period (in days) from date of first incubating observation to hatching date. The mean incubation time was 13.7 ±2.0 SD days (n=27, median 14 days) for the warbler finch and 13.6 ±2.0 SD days (n=16, median 14) for the small tree finch. Thus, for all nests, date of starting incubating was defined as hatching date minus 14 days. For abandoned nests that had been found before incubation started, the date of first incubating observation was used as date started incubating.

All monitored nests were collected in separate sealed plastic bags following nesting failure or chicks fledging. Eggs found in failed nests were inspected to identify the developmental stage of the embryo (undeveloped: no signs of developed embryo, developed embryo: first tissues of small embryo visible, and developed embryo close to hatching: embryo showing feathers and

nest monitoring suggested end of incubation). Nests were later dismantled in the laboratory in order to count *P. downsi* larvae, pupae and empty puparia. After the accidental discovery of *P. downsi* larvae in abandoned incubating nests, all abandoned nests where systematically checked for parasites thereafter (in total 17 warbler finch nests and 9 small tree finch nests). Parasite abundance was calculated as the total number of parasites (*P. downis* specimens) per nest or per chick of a given nest irrespective if it was infected or not (after Bush et al. 1997). There is no numerical difference in parasite abundance and intensity (*P. downsi* specimens per infected nest or chick of a given infected nest after Bush et al. 1997) for nests with hatchlings, because for these nests prevalence was 100%. As the number of parasites can be only counted by destroying the nest, parasite abundance was assigned to the age of the chicks at the time breeding activity terminated at a given nest. Parasite intensities increase with chick age because of multiple infections of nests with *P. downsi* (Dudaniec et al. 2010). This leads to the contradictory finding that successful nests have the highest *Philornis* intensities. Therefore *Philornis* abundance (or intensity) could not predict breeding success and thus was excluded from further analysis.

3.4 Habitat parameters and daily rainfall

For each nest encountered, nesting height, maximum and average canopy height, as well as vegetation cover of herb-layer, bush-layer (including *R. niveus*), *R. niveus* separately and canopy-layer (vegetation >3 m), of the surrounding area (5 m radius) were estimated. Height levels were estimated in one meter intervals and vegetation covers in %-categories of 10% intervals. Furthermore, the nesting location was assigned to (i) *Rubus* controlled site (area around the nest, 5 m radius, still showed clear signs of herbicide usage) or (ii) not controlled sites (no signs of herbicide usage detected, usually dense understory). Data of daily rainfall were provided by the Charles Darwin Station from the meteorological station near Santa Rosa (0°39’16,45’’ S, 90°24’12,96’’ W, elevation 500 m a.s.l.) about 3.5 km from our study site. Within the relevant study period of 101 days (date of starting incubation at the first nest to the date of the last nest inspection), it rained more than 10 mm per day on 26 days. These days were defined as “heavy rain days”.

3.5 Estimation of rat predation

Black rats (*Rattus rattus*) and Norway rats (*Rattus norvegucus*) have been introduced on all inhabited Galápagos Islands (Jiménez-Uzcátegui et al. 2007). Due to their climbing skills and omnivorous diet, the black rats in particular are considered a threat to the Galápagos avifauna (e.g. Grant & Grant 1997, Dvorak et al. 2004, Fessl et al. 2010, O'Connor et al. 2010b). In March 2012, we conducted an artificial nest experiment to identify potential nest predators and estimate nest predation rates following the method developed by Fessl et al. 2010. The artificial nests were made from coconut fibre. Each nest contained two Plasticine eggs (Acrilex modelling clay) dipped in egg albumen resembling finch eggs, which were tied to the nest. All nests and eggs were handled with surgical gloves to avoid them being tainted with human odour. A total of 30 artificial nests were systematically placed along two transects (15 nests per transect), with a minimum distance of at least 30 m between nests, and about 3 m height, mainly in *Scalesia* trees. To examine the effect of *Rubus* control (understory removal), one transect was located in a controlled area with a 5 m bush cover around the nest of 21% ±27 (mean ±SD), whilst the other was in a non-controlled area with a bush cover of 87% ±15 (mean ±SD). Nests were revisited after 3, 6 and 9 days before being removed. Eggs with possible signs of predation were removed from nests and replaced with new Plasticine eggs, resulting in a total of 180 possible egg predation events. Traces on artificial eggs were assigned to (1) rats, if clear rat tooth marks were present, (2) birds, if single punctures were visible, or (3) unidentified. We calculated the percentage of predated individual nests over the whole 9-day period for each transect. Furthermore, we measured the number of predated eggs and, of these eggs, calculated the percentage that had been predated by rats.

3.6 Analysis

As breeding pairs did re-nest within one breeding season, especially after a breeding failure, it is likely that we monitored different nests from the same breeding pair. Nests found in close proximity of a monitored nest, where a breeding attempt had recently terminated, were considered to belong to the same breeding pair. To reduce such pseudo-replication, only one randomly chosen nest per breeding pair was included in the analysis. We monitored a total of 142 active nests, though excluded 13 nests because of possible re-nesting, resulting in a dataset of 129 nests (74 warbler finch nests, 55 small tree finch nests).

To assess population trends for both species, non-parametric correlations and t-tests were calculated to compare bird numbers over specific years. We computed Chi²-tests and Fisher exact tests, when the sample size was too small, to compare different distributions (e.g. age structure of the small tree finch population at different time periods, species differences in breeding success, breeding success and predation of artificial nests in *Rubus* controlled compared with uncontrolled sites). Species differences in *Philornis* abundance were tested with two tailed Student t-tests. For the multivariate analyses of the breeding success, we constructed Generalized Linear Models (GLMs) with binomial error structure and a logit-link function. Successful nests were defined as nests with at least one fledged young, while all other nesting attempts were counted as failures. Since stepwise methods may produce inflated Type I errors, we present full models with all variables entered (Mundry & Nunn 2009) and reduced models that retained only the significant predictor variables. To avoid multi-colinearity (Tabachnick & Fidell 2007), we chose among predictor variables that were highly correlated (Spearman rank correlation $r>0.4$), the one that seemed to be of higher biological relevance. Predicted variables were breeding success (fledged young or not), predictor variables were height of the nest (m), cover of canopy (%), the day-of-year (ordinal date) of the start of incubation, and the percentage of heavy rain days during the incubation and nestling period. We tested the effect of *Rubus* control on the breeding success separately using Chi²-test because of inter-correlation with other habitat variables and low sample size. Statistical analyses were done with R 3.0.1.

3.7 Ethics statement

Permission to conduct this study was granted by the Galápagos National Park and the Charles Darwin research station (Project PC-54-11, Permit Nr. PR.CDS.ACI.P01.R02). As our study was purely appetitive, strictly non-invasive and based exclusively on behavioural observations, they are classified as non-animal experiments in accordance with the Austrian Animal Experiments Act (§ 2. Federal Law Gazette No. 501/1989).

4. Results

4.1 Population survey

Point counts showed that the warbler finch population significantly decreased over the last 15 years (Spearman's Roh=-0.964, n=7, p<0.01, data from Dvorak et al. 2012 and Dvorak unpublished data). Compared to 1997, the number of singing males significantly dropped to 58% (two tailed Student t-test: T=11.318, p<0.001; Figure 1). Over the whole period from 1997 to 2012, the small tree finch population remained more or less stable (Spearman's Roh=-0.643, n=7, p=0.12), though did increase from 1997 to 2005 by 38% (two-tailed Student t-test: T=3.324, p=0.002, data from Dvorak et al. 2012 and Dvorak unpublished data) and thereafter decrease by 39% until 2012 (two-tailed Student t-test: T=6.380, p<0.001, Figure 1). Additionally, the age structure of the small tree finch population significantly changed between 2000-2004 (Kleindorfer 2007) and 2012 (Chi^2-test: Chi^2=10.396, p=0.001; Figure 2). The population of 2000-2004 consisted of 72% "young" males and 28% "old" males, whereas in 2012, the proportion of "old" males increased to 51%.

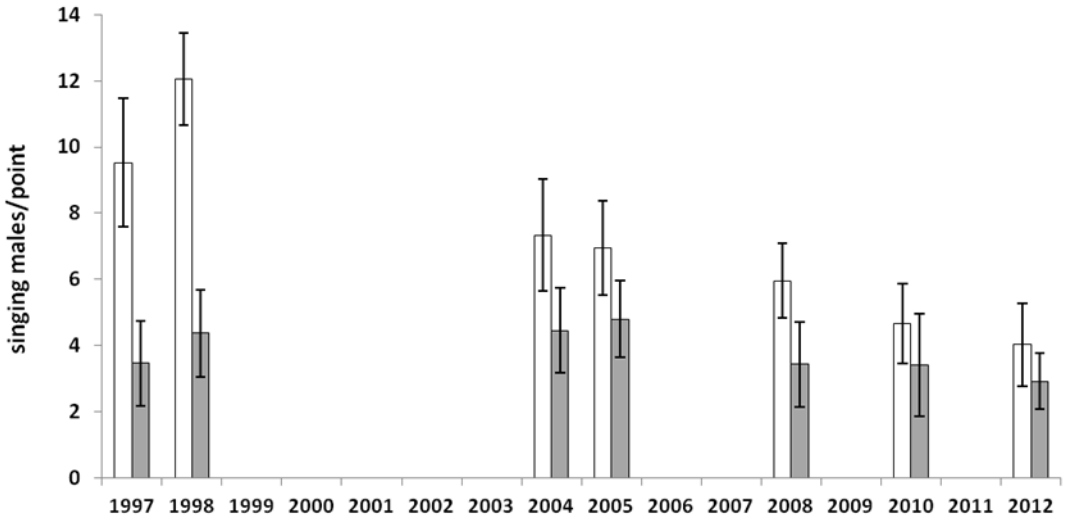

Figure 1: Mean (± SD) number of singing warbler finch (white bars) and small tree finch males (grey bars) per point count of the *Scalesia* zone on Santa Cruz, Galápagos, of the years 1997, 1998, 2008, 2010 (data from Dvorak et al. 2012), 2004 and 2005 (Dvorak et al. unpublished data) and 2012.

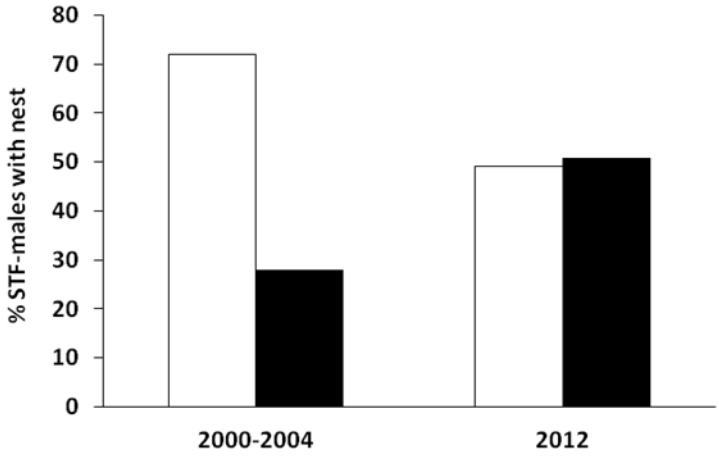

Figure 2: Percentage of brown/young (white bars) and black/old (black bars) displaying small tree finch males of the *Scalesia* zone population in 2000-2004 (n=132, Kleindorfer 2007) and 2012 (n=63) on Santa Cruz, Galápagos.

4.2 Breeding success

At least one chick fledged in 14.5% of the small tree finch nests in comparison with 36.5% of the warbler finch nests (Figure 3). Although the breeding success was low in both species, it was significantly higher for warbler finches than small tree finches (Chi^2-test: $Chi^2=6.123$, p=0.002).

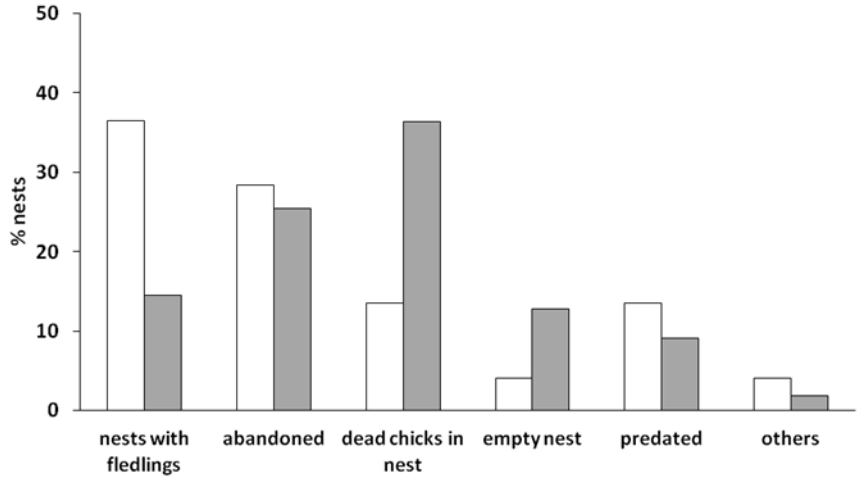

Figure 3: Proportional nesting outcome for the breeding season 2012 of warbler finch nests (white bars, n=74) and small tree finch nests (grey bars, n=55) of the *Scalesia* zone population on Santa Cruz, Galápagos.

Breeding success was significantly influenced by measures of *Rubus* control. In areas where the National Park had sprayed herbicides, breeding success of warbler finches was significantly lower than in areas that were not managed (Chi²-test: Chi²=6.735, p=0.014, Figure 4). Due to the overall low breeding success of the small tree finch, this analysis could not be run for this species.

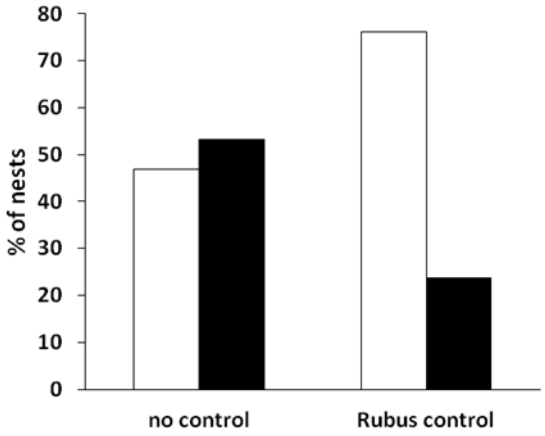

Figure 4: Percentage of failed (white bars) and successful (black bars) warbler finch nests in areas with no control measures by the National Park (no control, n=32) and in areas where the National Park recently sprayed herbicides to control the invasive *Rubus niveus* (*Rubus* control, n=42).

For both species the majority of failed breeding attempts were assigned to the following three categories: “abandoned nest”, “predated nest” and “dead chicks in the nest”.

Most of the small tree finch nests that lost their total brood did so when the chicks were 6 days old or younger (71%, Figure 5). In the warbler finch, two distinct age classes showed the highest percentage of nests with total brood loss (Figure 5): 38% failed when chicks were 1-3 days old and 33% failed when chicks were 7-9 days old. For both species, the main categories of breeding failure in the age class 1-3 days was “dead chicks in the nest” and “empty nest” (18 nests out of 20). If nests with chicks were predated (n=9), chicks were in all but one case at least 7 days old (other – 5 days old).

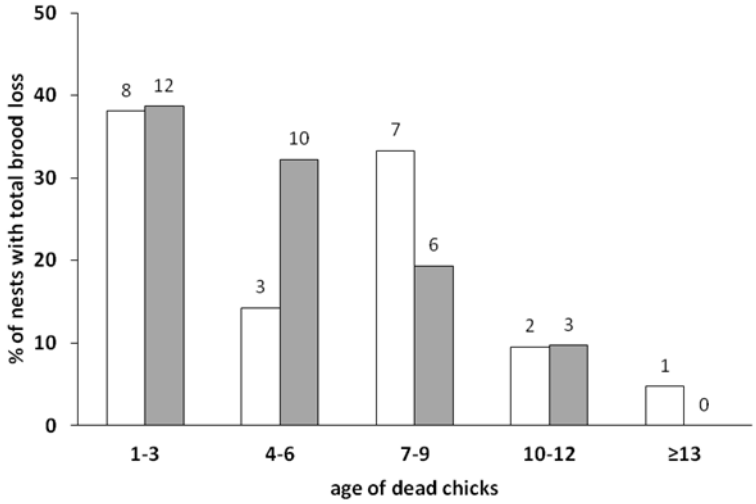

Figure 5: Percentage of nests with total brood loss (dead chicks in the nest, empty nest, predated) depending on the age that the last chick died in the nest. Warbler finch (white bars, n=21), small tree finch (grey bars, n=31). Numbers above bars indicate total numbers of cases.

4.2.1 Abandoned nests

In total, 21 warbler finch nests and 13 small tree finch nests were abandoned before the chicks hatched, thus still containing eggs (Figure 3). Several possible reasons for nest abandonment during incubation were identified: nest containing undeveloped eggs (33% of abandoned warbler finch nests, 19% of small tree finch nests) and (ii) developed chicks close to hatching, which did not manage to hatch (19% of warbler finch nests, 15% of small tree finch nests). In 88% of abandoned warbler finch (15 out of 17) and 22% of small tree finch nests (2 out of 9), *P. downsi* larvae of different larval stages were found. This species difference was significant (Fisher exact test: p=0.002). Furthermore, in both species, abandoned nests experienced a significantly higher percentage of heavy rain days during incubation than those in which chicks hatched (two tailed Student T-test: warbler finch T=2.698, p=0.009; small tree finch T=2.129, p=0.038).

4.2.2 Predation and artificial nest experiment

Predation as a cause for nesting failure was observed in 9.1% of small tree finch nests and 13.5% of warbler finch nests (Figure 3). Potential predators observed in the study area were the short-eared owl (*Asio flammeus galapagoensis*, endemic), the smooth-billed ani (*Crotophaga ani*, introduced) and the black rat (*Rattus rattus*, introduced). The artificial nest

experiment revealed similar results. Over the whole experimental period (9 days), eggs from 7 out of the 30 artificial nests (23.3%) showed signs of predation at least once. There was no difference in predation rate between the *Rubus* controlled area (3 of 15 predated artificial nests) and the non-controlled area (4 of 15 predated artificial nests, Fisher exact test: p=1.000). In total, 20 Plasticine eggs of the possible 180 eggs showed signs of predation. Of these eggs, 18 had clear rat tooth marks.

4.2.3 Nesting failure and Philornis infestation

A high percentage of nests contained dead chicks or were empty, though showed no signs of predation (both categories combined: warbler finch 17.6% and small tree finch 49.1% of the nests, Figure 3). Since all these nests suffered high parasite loads and no other cause of death was found, we attributed these nesting failures to *Philornis* parasitism. If we include the fledging nests that also contained dead chicks (partial brood loss), then 73% of small tree finch and 44% of warbler finch chicks most likely died due to *Philornis* parasitism.

All nests that contained nestlings were infested with *P. downsi,* which resulted in 100% prevalence. However, the two finch species were affected differently. Small tree finches, the species with significantly lower breeding success, had significantly more *Philornis* specimens per nest and per chick than the warbler finch (two tailed Student T-test: *Philornis*/nest, T=-2.577, p=0.012; *Philornis*/chick, T=-3.205, p=0.002, Figure 6). These significant differences in *Philornis* intensity were already present in nests with chicks of 6 days and younger (Student T-test: *Philornis*/nest, T=-2.222, p=0.034; *Philornis*/chick, T=-2.631, p=0.014, Figure 6). They were also still present in nests with chicks of 7 days and older (two tailed Student T-test: *Philornis*/nest, T=-3.934, p<0.001; *Philornis*/chick, T=-4.295, p<0.001, Figure 6).

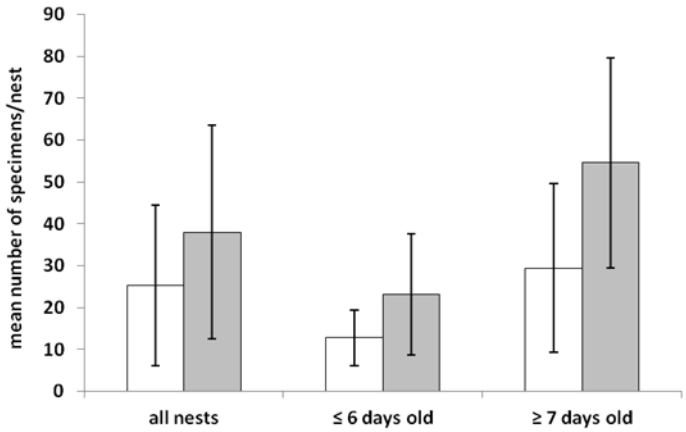

Figure 6: Mean (±SD) number of *Philornis downsi* specimens (larvae, pupae and puparia) per nest of warbler finches (white bars) and small tree finches (grey bars) for all nests, nests with chicks of six days and younger and with chick of seven days and older.

Because of the 100 % prevalence of *Philornis* larvae, we are not able to test whether a lower infection rate at early nestling stage results in a higher probability of a successful nest. However, parasitism may not be the only reason for breeding failure, and so we analysed whether other factors may also influence breeding success. We found that the only factor to significantly negatively influence breeding success in both species was the percentage of heavy rain days during the nestling period (full and reduced model, Table 1). Warbler finch nests were also successful significantly more often later in the season (full and reduced model, Table 1).

Table 2. Variables that explained variation in breeding success of warbler finches and small tree finches by GLMs with a binomial error structure. Significant variables are marked in bold.

Dependent variable: Breeding success (n=44)	**Warbler finch**			
Predictors	Estimate	SE	z	P
Full model				
Intercept	-4.79	4.07	-1.18	0.24
% Heavy rain days in nestling phase	-0.21	0.07	-3.15	0.002
% Heavy rain days in incubation phase	6.41	4.18	1.53	0.13
Nest height	0.22	0.40	0.54	0.59
Canopy cover	0.04	0.02	1.64	0.10
Date of incubation start	**0.13**	**0.06**	**2.06**	**0.04**
Reduced model				
Intercept	3.05	1.54	1.98	0.05
% Heavy rain days in nestling phase	**-14.21**	**6.02**	**-2.36**	**0.003**
Date of incubation start	**0.08**	**0.03**	**2.33**	**0.02**

Dependent variable: Breeding success (n=33)	**Small tree finch**			
Predictors	Estimate	SE	z	P
Full model				
Intercept	-2.94	10.54	-0.28	0.78
% Heavy rain days in nestling phase	**-0.21**	**0.10**	**-2.19**	**0.03**
% Heavy rain days in incubation phase	3.32	8.93	0.37	0.71
Nest height	-0.12	0.32	-0.37	0.71
Canopy cover	0.01	0.03	0.34	0.73
Nesting date	0.14	0.19	0.75	0.46
Reduced model				
Intercept	3.05	1.54	1.98	0.05
% Heavy rain days in nestling phase	**-14.21**	**6.02**	**-2.36**	**0.02**

5. Discussion

In both species breeding success was negatively influenced by *Philornis* parasitism, heavy rain days and the use of herbicides on surrounding habitat, whilst predation only had a minor influence. We assessed the influence of these factors by analysing the cause for brood loss in areas with and without invasive plant control. For both species, the main causes for brood loss were dead chicks in the nest and abandoned nests. Although the direct cause of death of dead chicks in the nest could not be identified, it is very likely that parasitism by *P. downsi* played a major role in the death of 73% of small tree finch and 44% of warbler finch chicks. Indirect evidence for the role of *Philornis* comes from the comparison of breeding success in relation to parasite intensity between the small tree finch and the warbler finch: the nests of the small tree finch, the species which had significantly lower breeding success, had a significantly higher *Philornis* abundance than the nests of the warbler finch. This difference was already present in the early nestling phase, in which mortality was particularly high. However, only experimentally manipulating parasite abundance can reveal the impact of *Philornis* on mortality. In an experimental study on Darwin's ground finches, where parasites were eliminated in the nests, mortality was reduced from 66% to only 14% (Fessl et al. 2006b). In a similar study by Koop et al. (2011) mortality decreased from 96% to 67% as parasite abundance was reduced.

The higher parasite loads and lower breeding success of small tree finch compared with warbler finch nests were contradictory to our predictions and to previous findings, which

report higher *Philornis* intensities in the warbler finch (Dudaniec et al. 2007, Kleindorfer & Dudaniec 2009). In the small tree finch the mean *Philornis* intensity per nest (52.9 ±6.0, mean ±SE, n=18) and per chick (26.0 ±3.1, n=18) for nests with nestlings of ≥6 days old was also higher than previously reported (Dudaniec et al. 2007: mean *Philornis*/nest: 36.2 ±2.4, n=33; mean *Philornis*/chick: 20.5 ±2.3, n=29). The parasite load is comparable with those of the large-bodied large tree finch and woodpecker finch. This is surprising because *Philornis* intensity is positively correlated with host body size (Dudaniec et al. 2007, O'Connor et al. 2010b) and nest size (Kleindorfer & Dudaniec 2009). One possible explanation could be that *Philornis* intensity increased over the last years in general and thus, the mentioned species would show increased parasite loads as well. However, that does not explain the fact that *Philornis* intensity decreased in warbler finch nests (mean *Philornis*/nest: 29.4 ±3.4, mean ±SE, n; mean *Philornis*/chick: 13.0 ±1.4; n=37) compared to pooled data from 1998 to 2005 (Dudaniec et al. 2007: mean *Philornis*/nest: 42.2 ±4.6, n=21; mean *Philornis*/chick: 21.2 ±2.5, n=15). Changes in warbler finch females breeding behaviour, which seem to react to parasitism, could explain lower parasite loads (see below), which possible resulted in higher breeding success (36.5% in 2012 compared to 27% pooled data 1998-2005, Dudaniec et al 2007). Another factor increasing parasites in the nest is the number of neighbouring nests of any bird species (mixed nesting associations, Kleindorfer & Dudaniec 2009). We have no data on nesting aggregations in 2012 and thus we cannot rule out this factor. The low breeding success of small tree finches may additionally be explained by limiting ecological conditions, such as availability of suitable prey for chick rearing, which in turn impacts on their ability to compensate for the adverse effects of parasitism. Preliminary data on breeding phenology suggests that small tree finches start breeding later and are more synchronic than the warbler finches, which are more opportunistic breeders. Future studies focusing on breeding phenology and detailed foraging observations may highlight some key factors, such as special food sources, which have been overlooked so far.

In both species, a high percentage of nests (small tree finch 25%, warbler finch 28%) were abandoned during incubation (before the chicks hatched). Studies on Darwin's finches on several other islands have previously reported much lower values (e.g. Fessl & Tebbich 2002: 1.8-6.7%; Kleindorfer 2007: 7%; Fessl et al 2010: up to 10%). However, O'Connor et al. (2010c) found 30.4% (data of 2004 and 2006 combined) of small ground finch nests abandoned in the lowlands, and in 2005, 25% abandoned nests in the highlands of Floreana Island. At least for 2005, it was suggested that extreme drought conditions lead to this high percentage of abandoned nests. Our data suggest that nest abandonment during the incubation stage may be

increased by heavy rain days. Thus, in both cases, extreme weather conditions are related to abandonment of the nest in the incubating stage.

It seems plausible that arboreal finches similarly start to breed when the rain starts, but then interrupt their breeding attempts when rainfall suddenly stops and so insect abundance does not increase as expected. In Darwin's ground finches, gonadal activity is triggered by rain (Hau et al. 2004), which optimizes their breeding activity, as insect abundance starts to increase about 10 days after the first rains on the Galápagos Islands (Grant & Grant 1989). The finding that warbler finch breeding success increased later in the breeding season fits well with the reported interaction between onset of the rainy season and increase in food abundance thereafter. Alternatively, intense rains may negatively affect nest temperature and humidity, thus leading to nest abandonment. This may be linked to a higher energy cost for the incubating female since clutches will cool more rapidly in a wet nest (reviewed in Heenan 2013).

In addition to an influence of adverse weather conditions, our findings suggest that *Philornis* parasitism in nests that were still being incubated may indicate another potential reason for nest abandonment. To our knowledge, this is the first study to report *Philornis* larvae of all stages and pupae in incubating nests. Darwin's finches rarely reuse their nests during further breeding attempts. We also know the history of some of these nests and therefore can exclude that the larvae were remnants of previous breeding attempts. Tebbich & Fessl (2002) explicitly state that no *Philornis* larvae were found in abandoned incubating nests. Similarly, O'Connor et al. (2010a) only observed *P. downsi* larvae in nests with nestlings. It had previously been assumed that first instar larvae only develop in the nostrils of chicks (Fessl et al. 2006a), so this finding is particularly important. It remains unclear whether this finding represents a recent change in parasite behaviour – the flies are now laying their eggs in incubating bird nests – or if the search effort was insufficient in previous studies.

An alternative explanation would be that these nests are not directly infested by *P. downsi*, but that the birds are using infested nesting material from other nearby nests. Warbler finches have been observed stealing nesting material from other birds' nests (S. Keindorfer, personal communication). It is unclear whether they would also take material from inside the bottom of the nest, where *Philornis* larvae are found (Fessl et al. 2006a). However, this does not explain why larvae of different stages have not been found previously. In any case, our findings strongly suggest that chicks are not obligatory for the successful life-cycle of *P. downsi*. This notion is supported by preliminary stable isotope data (in preparation), which suggests that the first

instar larvae were feeding on bird blood. *Philornis* larvae of different developmental stages found in abandoned incubating nests most likely suck blood from the incubating females. Adult medium ground finches have significantly higher *Philornis*-specific antibody levels during the nesting period and females showed higher levels than males (Huber et al. 2010). These findings suggest that incubating or brooding females are at least occasionally attacked by *Philornis* larvae.

Another interesting aspect of *Philornis* parasitism in abandoned incubating nests is that we found significantly more parasitized warbler finch than small tree finch nests. There are two possible explanations for this outcome. Firstly, incubated warbler finch nests, irrespective whether they are abandoned or not, show higher parasite prevalence because they are more attractive to *P. downsi* than small tree finch nests. This explanation seems unlikely, because nests with nestlings show the opposite infestation pattern – small tree finch nests contained significantly higher parasite intensities than warbler finch nests. Secondly, there is no difference in *P. downsi* prevalence between incubating warbler finch and small tree finch nests, however incubating warbler finches abandoned infested nests while small tree finches did not. This hypothesis is supported by the significantly higher *P. downsi* intensities in small tree finch nests with chicks of six days and younger. Despite this, we did find a similar percentage of abandoned nests in both species. Thus, if warbler finches mainly abandon the nests because of parasitism by *Philornis*, small tree finches must be reacting to other factors (e.g. they are more sensitive to heavy rainfalls).

Rubus control with herbicides also negatively affected breeding success. Warbler finches had a significantly lower breeding success in areas where herbicides had recently been applied compared with uncontrolled areas. The usage of strong herbicides by the National Park to control the invasion of *R. niveus* leads to removal of more or less the entire understory (own observations). This may have lead to changes in abundance and invertebrate species composition, which could negatively affect the insectivorous bird species. The fact that four of the six declining species are insectivorous (Dvorak et al. 2012) supports this notion.

The effect of predation on breeding success was lower than expected. However, our data showed that nests with nestlings of seven days and older are more vulnerable to predation. This is most likely because, at this age, chicks start to beg acoustically and so become more conspicuous for predators such as the short-eared owl (native) and black rat (introduced).

In previous studies on Santa Cruz, the percentage of predated warbler finch and small tree finch nests was higher than in the present study (warbler finch 13.5%, small tree finch 9.1%

nests). Fessl & Tebbich (2002) investigated four Darwin's finch species (warbler finch, small tree finch, woodpecker finch and small ground finch) and found 26.3% in 1998, and 51.2% in 2000 of nests were predated across the four species. Pooled data from 1998, 2000, 2001, 2002, 2004 and 2005 revealed that 50% of small tree finch nests and 37.1% of warbler finch nests failed because of predation (Dudaniec et al. 2007, similar datasets in Kleindorfer 2007 and Kleindorfer et al. 2009). Mangrove finches on Isabela Island suffered even higher predation rates (Fessl et al. 2010). In the breeding season of 2006/2007, about 72% of mangrove finch nests were predated, which dropped to about 45% after intense rat control. Although these findings could in part by attributed to differing definitions of depredated nests and calculations, it is likely that, overall, predation decreased. The results of the artificial nest experiment further supports this conclusion. In the *Scalesia* forest of Santa Cruz, 23% of artificial nests were depredated compared with 77-87% at two breeding sites of mangrove finches on Isabela Island (Fessl et al. 2010). However, after rat control in mangrove finch breeding sites, the proportion of depredated artificial nests significantly dropped to 28% (at least in one of the two study sites), which corresponds with the recent impact of rat predation measured by us in the *Scalesia* forest of Santa Cruz.

5.1 Conclusions and future plans

We found three factors that negatively influenced the breeding success of both finch species: adverse climatic conditions (heavy rain days), *Philornis* parasitism and habitat change due to control of invasive plant species. We hypothesize that the combination of these factors, rather than one single factor, leads to breeding failures. For instance, the negative role played by *Philornis* parasitism may be increased by occurrence of intense rainfall (natural stressor) and major habitat changes, leading to low breeding success. The parents may be able, at least to some extent, compensate for energy losses due to parasitism when food abundance is high. However, as soon as food abundance decreases, either naturally because of heavy rainfalls or due to humans through *Rubus* control, parents may be unable to overcome the negative impact of parasitism. During intense rain, parents may be less efficient in foraging or even stop searching for food as insects are more difficult to find. This temporary lower food abundance likely leads to lower feeding rates by the parents and thus poses stress on chicks, especially those that are very young and so require regular feeding. Furthermore, heavy rain may directly influence the nest environment by increasing humidity and decreasing the temperature in the nest. This hypothesis should be investigated in future studies e.g. by selectively manipulating

parasite abundance through use of insecticides in areas with invasive plant species control compared with uncontrolled areas. This data could then be combined with daily weather conditions.

It is still unclear whether the low breeding success measured in this study can explain the dramatic decline of the warbler finch population (down 58% compared to 1997) in the *Scalesia* forest on Santa Cruz, as reliable population models are still missing. However, one could argue that an increase in the mean age of a population reflects lower presence of young individuals, which can result from low reproductive success. This argument is supported by data on population sizes, age structure and reproductive success of the small tree finch. The change in age structure of the small tree finch population studied goes in parallel with a significant decrease in the population since 2005 as well as low reproductive success in 2010 (Tebbich et al. unpublished data) and 2012. To date, there is no data on the age structure, juvenile survival and dispersal behaviour of the warbler finch population available. Thus, future studies should aim to collect this relevant information in order to be able to develop meaningful population model, which are helpful tools for evaluating possible conservation measures. Furthermore, more information regarding breeding ecology and foraging behaviour are needed to further explore the relationship between the three identified factors (heavy rains, *P. downsi* parasitism, *Rubus* control with herbicides) and their negative influence on breeding success.

6. Literature

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8. Zusammenfassung

Invasive eingeschleppte Krankheitserreger und Parasiten stellen weltweit eine immer größer werdende Bedrohung der Biodiversität dar. Sie können massiv zur Ausrottung von gefährdeten endemischen Arten beitragen. Die invasive parasitische Fliege *Philornis downsi* und andere eingeschleppte Prädatoren bedrohen die endemische Vogelwelt der Galapagos Inseln. In dieser Studie untersuchten wir den Einfluss dieser eingeschleppten Arten auf den Bruterfolg zweier Darwin Finken, dem Laubsängerfink (*Certhidea olivacea*) und dem Kleinen Baumfink (*Camarhynchus parvulus*). Die Population des Laubsängerfinken auf der Insel Santa Cruz ist in den letzten 15 Jahren um mehr als die Hälfte geschrumpft, wohingegen die Population des Kleinen Baumfinken mehr oder weniger stabil blieb. Ziel der Studie war es, zu untersuchen, ob der Laubsängerfink im Verglich zum Kleinen Baumfink während des Brutgeschäfts besonders sensibel auf verschiedene potentielle Stressfaktoren reagiert. Des Weiteren wollten wir feststellen, ob der niedrige Bruterfolg bedingt durch Parasiten und Prädatoren zum rapiden Rückgang dieser Art beiträgt. Der eingeschleppte Parasit *Philornis downsi* hatte einen negativen Einfluss auf den Bruterfolg beider untersuchten Vogelarten. Der Prädationsdruck war relativ gering. Unsere Daten weisen ebenfalls darauf hin, dass extreme Wetterbedingungen, wie Starkregenereignisse, und der Einsatz von Herbiziden zur Bekämpfung von invasiven Pflanzenarten sich zusätzlich negativ auf den Bruterfolg beider Darwin Finken auswirkten. Wir vermuten, dass beide Faktoren die Nahrungsverfügbarkeit während der Jungenaufzucht negativ beeinflussen, was die Mortalität der bereits durch Parasiten geschwächten Küken erhöht. Die jährlichen Schwankungen von Starkregen während der Brutsaison würden auch das unterschiedliche Ausmaß von *P. downsi* auf das Wachstum und die Mortalität der Jungen in vorherigen Studien erklären. Unsere Daten stützen die Hypothese, dass der geringe Bruterfolg zum Populationsrückgang beim Laubsängerfink und Kleinen Baumfink beiträgt. Zähldaten für den Kleinen Baumfink zeigen auch bei dieser Art einen Abwärtstrend in den letzten Jahren, sowie eine Veränderung in der Altersstruktur mit einer Zunahme von älteren Vögeln, was für einen geringeren Reproduktionserfolg spricht.

9. *Curriculum Vitae*

Name:	**Arno Cimadom**
E-Mail:	arno.cimadom@hotmail.com
Date of birth:	January 29th, 1986 in Bressanone (BZ), South Tyrol, Italy
Citizenship:	Italian

Education

March 2013	Master degree obtained at the University of Vienna, in "Etholoy, Neurobiology and Cognition".
since 2008	Master course of "Ethology, Neurobiology and Cognition" and Master course of "Nature Conservation and Biodiversity Management" at the University of Vienna, Austria
2005-2008	Bachelor course of Biology at the University of Innsbruck, Austria
2000-2005	High school "Realgymnasium J. Ph. Fallmerayer", Bressanone, Italy

Research Experience

2012-2013	MSc Thesis: Investigating the decline of the Warbler finch on Santa Cruz Island, Galápagos. Supervisor: Dr. Sabine Tebbich (University of Vienna, Austria)
2010	Research practical: The attitude to nature and nature conservation at the urban fringe. Supervisor: Dr. Thomas Wrbka, Dr. Stefan Schindler (both University of Vienna, Austria)
2009-2012	MSc Thesis: String pulling and discrimination learning in jackdaws (*Corvus monedula*) and New Caledonian crows (*Corvus moneduloides*). Supervisor: Uni. Prof. Mag. Dr. Ludwig Huber, Dr. Gyula K. Gajdon (both University of Vienna, Austria), Dr. Auguste von Bayern (University of Oxford, Great Britain)
2009	Research practical: How much do keas (*Nestor notabilis*) rely on perceptual motor feedback when solving the string pulling task. Supervisor: Dr. Gyula K. Gajdon (University of Vienna, Austria)
2008	BSc Thesis: Development of a method to force the occurrence of

	chimerea in regeneration of *Dorvillea bermudensis* (Annelida). Supervisor: Mag. Dr. Bernhard Egger (University of Innsbruck, Austria)
2006	BSc Thesis: Differences of the activity-pattern of Northern Bald Ibises (*Geronticus eremita*) during Zugunruhe. Supervisor: Dr. Johannes Fritz (University of Vienna, Austria)

Employment History

since 2012	Coordination and textual elaboration of information boards for two nature parks and one national park of the province of Burgenland, Austria
2011-2012	Textual elaboration of the exhibition “Love in the reeds” on the reproductive strategies of reed breeding birds, Purbach am Neusiedler See, Austria
Summer 2010	Construction assistant at the new research station “Haidlhof” of the Department of Cognitive Biology, University of Vienna, Austria
2010	Certificated National Park Ranger of the “Nationalparks Austria”
since 2009	Guide at the Neusiedlersee – Seewinkel National Park, Austria
2006	Hand rearing of two Night herons (*Nicticorax nicticorax*) for the Austrian documentary “UNIVERSUM”
2006-2008	Collaborator of the research project “waldrappteam” (Dr. Johannes Fritz). Research assistant, public relations, communication with the Italian partners, assistant at two human led migrations

Scholarships

2011	Scholarship (Förderungsstipendium) of the University of Vienna, Austria, for the field trip to Galapagos
2011	Performance Scholarship for the academic year 2009/2010 of the University of Vienna, Austria
2009	Performance Scholarship for the academic year 2007/2008 of South-Tyrol, Italy
2008	Performance Scholarship for the academic year 2006/2007 of South-Tyrol, Italy

Publications

Cimadom A., Nemeth E., Fessl B., Tebbich S. (in prep.): Invasive parasites, habitat change and heavy rainfall reduces breeding success in Darwin's finches.

Schindler S., Cimadom A., Wrbka T. (2011): The attitude to nature and nature conservation at the urban fringe. *Innovation – the European Journal of Social Science Research*, 24, 379-390

Talks

Cimadom A., Tebbich S., Fessl B., Hood-Novotny R. (2012): The need of basic biological information to effectively control an invasive parasitic fly (*Philornis downsi*) on the Galápagos Islands. 6th European Conference of Behavioural Biology, Essen, Germany

Posters

Cimadom A., Tebbich S., Fessl B., Hood-Novotny R. (2013): Behavioural changes in hosts and parasite in a newly established host parasite interaction on the Galápagos Islands. Behaviour 2013, 33rd International Ethological Conference, Newcastle, Great Britain.

Cimadom A., Gajdon GK., von Bayern AMP., Huber L. (2013): Investigating information seeking behaviour of jackdaws (*Corvus monedula*). 3rd Transfer-of-Knowledge Conference (CompCog), Vienna, Austria.

Tebbich S., Cimadom A., Fessl B., Hood-Novotny R. (2013): The need of basic biological information to effectively control an invasive parasitic fly (*Philornis downsi*) on the Galápagos Islands. Online Conference, Ethology investigates: Invasive species.

Languages

German: native language

Italian: very good knowledge in writing and speaking

English: very good knowledge in writing and speaking

Spanish: basic knowledge in speaking