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"Effect of an introduced parasite and food availability on the breeding success of the Little Vermilion Flycatcher *Pyrocephlaus nanus* in the Galápagos"

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Celina Leuba, Bsc

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Abstract

Although most bird species live on continents, the majority of avifauna extinctions have been on islands. The Galápagos islands, thus far considered well preserved, experienced its first bird extinction, the endemic Least Vermilion Flycatcher, *Phyrocephalus dubius*. Its close congener, the endemic Little Vermillion Flycatcher, *Pyrocephlaus nanus*, is also declining: originally distributed on ten islands, this species has recently gone locally extinct on Floreana Island and is close to local extinction on Santa Cruz Island. Identifying the leading causes of population decline is key to develop efficient conservation strategies. In this study, we investigated the causes of breeding failure of the Little Vermillion Flycatcher. We compared breeding success of the Little Vermillion Flycatcher, infection intensity by the parasitic fly *Philornis downsi*, predation, and food availability between three study sites that differed in the level of habitat alteration. To test for the causal role of parasitism, we reduced the number of *P. downsi* larvae in 50% of the nests.

Our results show that *P. downsi* parasitism caused high brood loss, but only in nests with high *P. downsi* abundance. Parasitism also influenced parental feeding rate, as nestlings of highly infested nests were fed less frequently by their parents. The small population of the Little Vermilion Flycatcher on Santa Cruz Island had a very low breeding success due to abandonment during the incubation phase, when nests were not yet infested by *P. downsi*. At this study site, which is highly invaded by the blackberry plant, *Rubus niveus,* prey attack rates, defined as number of preys caught by individual birds, was low and indicates low food availability. Additionally, Little Vermillion Flycatchers used higher perches and foraged at higher heights in the vegetation at this site when compared to the other two study sites. Alien predators only seem to play a minor role in brood loss as levels of nest predation were equally low at all three study sites.

Zusammenfassung

Während die meisten Vogelarten auf Kontinenten leben, ist der größte Teil der Vogelwelt auf Inseln ausgestorben. Die Galápagos-Inseln, die bislang als gut erhalten galten, erlebten kürzlich ihr erstes Vogelaussterben: der endemische San-Cristóbal-Rubintyrann, *Phyrocephalus dubius*. Die Populationen seines engen Verwandten, der endemische

Galápagos-Rubintyrann, *Pyrocephlaus nanus*, gehen ebenfalls zurück: ursprünglich auf zehn Inseln verbreitet, ist diese Art vor kurzem lokal auf der Insel Floreana ausgestorben und auf der Insel Santa Cruz vom Aussterben bedroht. Um effiziente Erhaltungsstrategien zu entwickeln, ist die Identifizierung der Hauptursachen für den Populationsrückgang essenziell. In dieser Studie untersuchten wir die Ursachen für das Zuchtversagen des Galápagos-Rubintyrann. Wir verglichen den Bruterfolg des Galápagos-Rubintyrann, die Infektionsintensität durch die parasitäre Fliege *Philornis downsi*, die Prädation und die Futterverfügbarkeit zwischen drei Untersuchungsstandorten, die sich im Ausmaß der Lebensraumveränderung unterschieden. Um die kausale Rolle des Parasitismus zu testen, haben wir die Anzahl der *P. downsi*-Larven in 50% der Nester reduziert.

Unsere Ergebnisse zeigen, dass *P. downsi*-Parasitismus einen hohen Brutverlust verursachte, jedoch nur in Nestern mit hohem *P. downsi*-Vorkommen. Parasitismus beeinflusste auch dieFütterungssrate der Eltern, da Nestlinge von stark befallenen Nestern weniger häufig von ihren Eltern gefüttert wurden. Die kleine Population des Galápagos-Rubintyrann auf der Insel Santa Cruz hatte einen sehr geringen Bruterfolg: die meisten Nester wurden während der Inkubationsphase aufgegeben als diese noch nicht von *P. downsi* befallen waren. An diesem Untersuchungsort, der stark von der Brombeerpflanze *Rubus niveus* befallen ist, war die Beuteangriffsrate, definiert als die Anzahl gefangener Beute von einzelnen Vögeln pro Minute, niedrig. Dies weist auf eine geringe Futterverfügbarkeit hin. Darüber hinaus verwendete der Galápagos-Rubintyrann in diesem Untersuchungsort höhere Sitzstangen und fing seine Beute höher in der Vegetation im Vergleich zu den anderen beiden Untersuchungsorten. Nicht heimische Raubtiere scheinen beim Brutverlust nur eine untergeordnete Rolle zu spielen, da der Grad der Nistprädation an allen drei Untersuchungsorten gleich niedrig war.

Acknowledgments

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Introduction

The Galápagos Islands is one of the most renowned natural sites with unique fauna and flora (Steinfartz 2011). Due to late colonization by humans, the archipelago has remained in a nearly pristine condition and still retains 95% of its original species (Tye et al. 2002). However, due to a rapid increase in tourism and permanent human population size in the last century, the Islands, particularly the four inhabited islands (Santa Cruz, San Cristobal, Isabela, and Floreana) are increasingly affected by habitat alteration and invasive species (Lindström et al. 2004). This also affects the unique land bird fauna of the Galápagos with population declines in 21 of the 34 endemic and native bird species (Dvorak et al. 2012, 2017, 2019, Fessl et al. 2017). Accordingly, 16 species are considered threatened by the International Union for Conservation of Nature (IUCN) (IUCN 2016) and one species, the Least Vermilion Flycatcher, *Phyrocephalus dubius* of San Cristóbal, considered extinct (Dvorak et al. 2019). Its close congener, the endemic Little Vermilion Flycatcher (LVF) *Pyrocephalus nanus*, originally distributed on ten islands, has recently gone extinct on Floreana (Merlen 2013, Dvorak et al.

2017) and has been reduced to approximately 40 breeding pairs in the highlands of Santa Cruz Island. In the lowlands this species has almost disappeared (Fessl et al. 2017). Considered as proper species in 2016 (Carmi et al. 2016), the Little Vermilion Flycatcher was classified as "Vulnerable" by the IUCN red list (IUCN 2016).

Identifying the reasons for the rapid decline and extinction of these populations is a precondition for developing efficient conservation strategies. Previous studies on Darwin's finches (Fessl et al. 2010, Cimadom et al. 2014) and the Little Vermilion Flycatcher (Mosquera et al. submitted) point towards three potential reasons a) reduced food availability on inhabited islands due to anthropogenic habitat change b) predation by alien predators, and c) parasitism by the invasive parasitic fly *Philornis downsi.*

This invasive neotropical fly was recorded in land bird nests on the Galápagos Islands for the first time in 1997 (Fessl et al. 2001) though retrospective analysis of insect collections found that it had been present already in the 1960s (Causton et al. 2006, Kleindorfer et al. 2016). The hematophagous larvae are obligate bird parasites of several land bird species (Fessl et al. 2018). Larvae start to develop in the chick's nostrils, then live in the bottom layer of the nest, and feed on blood until they pupate (Fessl et al. 2006; O'Connor et al 2010). *P. downsi* parasitism reduces hemoglobin concentrations and body mass gain in nestlings and can cause high mortality (reviewed in Fessl et al. 2018). A previous study on a LVF population in the south of Isabela, demonstrated that *P. downsi* caused complete brood loss during the late breeding season over three consecutive years (Mosquera et al. submitted).

Another cause of low breeding success might be reduced food availability due to anthropogenic change on inhabited islands. The LVF is insectivorous and mainly forage close to the ground using low perches. The highlands of the four inhabited islands have been heavily altered by agriculture and invasive plants (Watson et al. 2010). One of the most problematic invasive plant species is the fast-growing blackberry, *Rubus niveus,* that forms dense vegetation in the understory, hindering native plant species to grow (Renteria and Buddenhagen 2006, Rentería et al. 2012, Jäger et al. 2017). The dense understory may also prevent the LVF to access arthropods near the ground.

The reasons for the rapid decline could be due to single factors as well as the interaction of parasitism with poor habitat conditions (Cimadom et al 2019, Mc New et al. 2019). Cimadom at al 2019 found an interaction between parasitism and habitat quality for the Green Warbler-finch *Certhidea olivacea* in the highlands of Santa Cruz. The study reveals that Green Warbler-

finches tolerate *P. downsi* under good habitat conditions but not when insect availability was temporarily reduced. The reduction was due to a blackberry control program by the Galápagos National Park Directorate which involves the removal of the entire understory resulting in a temporary reduction of arthropod abundance.

Predation by invasive species might also be a threat for the LVF. Feral and domestic cats, *Felis catus* are found on the four islands with permanent human populations, and three species of rodents - black rat, *Rattus rattus*, Norwegian rat, *Rattus norvegicus*, and the house mouse, *Mus musculus* - are found on the majority of islands (Phillips et al. 2012). Nests in the incubation phase are known to be particularly vulnerable to predation by rats. For example, 54% of nests of the critically endangered Mangrove Finch *Camarhynchus heliobates*, breeding in the mangrove forests of Isabela Island, have been depredated before the rat control program was implemented in 2007 (Fessl et al. 2010).

To assess the potential influences of habitat quality we compared three study sites that are located in the highlands at a similar level of altitude but differ in the level of habitat alteration (Alcedo / Isabela Island, El Cura / Isabela Island, Mina Roja / Santa Cruz Island). Alcedo, the most pristine study site, is located in the center of the Island Isabela, remote from human settlement and so far, not invaded by alien plant species (Rivas-Torres et al. 2018). El Cura is situated in the south of Isabela, close to human settlements and mainly covered by farmland area dominated by pasture, and trees. Mina Roja is situated in the middle of Santa Cruz, in a *Scalesia* forest situated above the farmland area. It is highly altered by the invasive blackberry and invasive tree species. We hypothesize that the three habitats differ in prey abundance and/or prey accessibility. As the bird's perception of prey availability depends on arthropod mobility, crypsis, and palatability, sampling methods by humans could be inadequate to measure food availability (Sherry 1984, Hutto 1990, Wolda 1990, Lovette and Holmes 1995). Thus in our study, we used adult prey attack rate, foraging success and parental feeding rates as an index for food availability (Hutto 1990, Lovette and Holmes 1995).

The three study sites might also differ in *P. downsi* parasitism and predation. We measured predation pressure with the help of artificial nests containing Plasticine eggs. We measured *P. downsi* prevalence and tested the causal role of parasitism for brood loss by experimentally reducing *P. downsi* larvae randomly in half of the nests.

If *P. downsi* is the main cause for breeding failure, we predicted that the breeding success would be lowest in areas with highest *P. downsi* abundance and prevalence and would be

significantly higher in experimentally treated nests than untreated nests. If habitat quality is the main factor for brood loss, we predicted the lowest breeding success in areas with the lowest prey attack rate, foraging success, and parental feeding rates. If higher food availability allows parents to compensate for the negative impacts of parasitism, we predicted that parasitism will have less effect on breeding success in areas with higher parental provisioning rate.

Methods

Study areas

The study was performed during the breeding season of the LVF from February to April 2018, and data was collected by different teams in parallel on three study sites on the Galápagos Islands, Ecuador (Fig.1). All three sites are situated in the humid zone: Volcano Alcedo in central Isabela, El Cura in Southern Isabela (Volcano Sierra Negra) and Mina Roja on Santa Cruz Island. Vegetation maps for the three sites were realized using QGIS version 2.18.13 and were based on The Vegetation Map of the Galápagos v.2016 by Gonzalo Rivas-Torres (Rivas-Torres et al. 2018) (see appendix, vegetation maps). All three study areas have been invaded by the fly *P. downsi*, by cats, and by three species of rodents, the black rat, the Norwegian rat and the house mouse (Phillips et al. 2012).

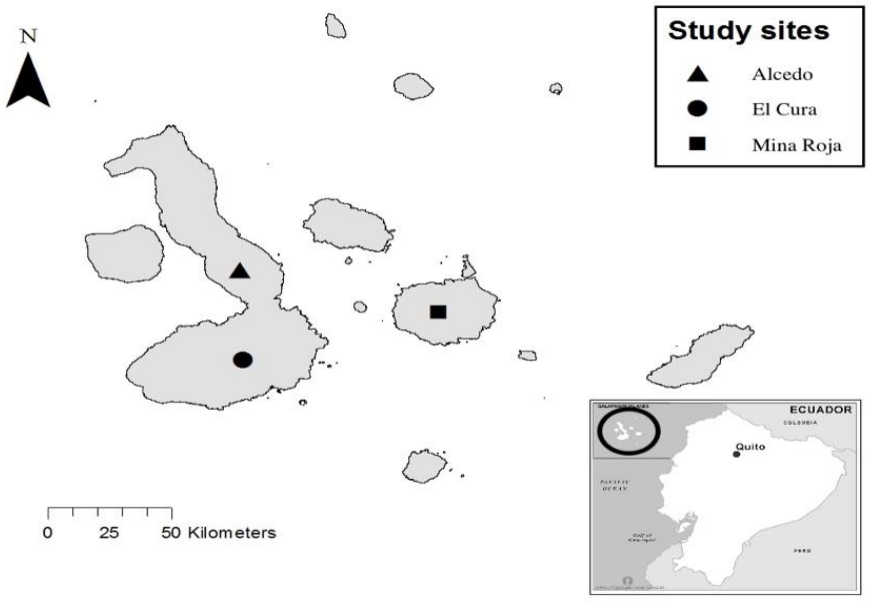

Figure 1. The three study sites on the Galápagos Islands.

Alcedo study site

Located in the center of the Isabela island, Alcedo is one of the six shield volcanoes of this island. The study was conducted on the southern rim of the volcano on an area of 3.6 km^2, between 760- and 1100-meters altitude (0°27'35"S, 91° 6'59"W). Alcedo is part of the Galápagos National Park and uninhabited. So far Alcedo's habitat is not threatened by plant species invasion and is considered as natural and near pristine (Rivas-Torres et al. 2018). The dominating plant species are Scalesia trees *Scalesia microsephalia*, soldier bush *Tournifortia pubescens*, bromeliad *Tillandsia insularis*, fern, and herbs (all natives) (Rivas-Torres et al. 2018). Alcedo is covered mainly by humid grasslands at the highest elevations, whereas shrubs and low trees (3-7m) dominate the hilly terrain (Van der Werff in 1978). Herbage cover is high especially during the rainy season and vegetation is maintained low by grazing giant tortoises.

El Cura study site

The monitored area of 5.5 km^2 is located on the slope of Sierra Negra volcano. A small area is within the Galápagos National Park, and the rest on private farmland (0°50'0"S, 91° 5'0"W) (see vegetation map in appendix). The area reaches a maximum altitude of 1000 meters close to the crater and a minimum of 650 meters descending through the farmland area. El Cura is dominated by cattle pastures covered by invasive guava trees *Psidium guayaba* of varying densities and delimited by walnut tree rows *Juglans neotropica* (introduced). Other dominating plants are bromeliad, fern and herbs (see appendix with vegetation maps). Blackberry is present in small patches but has not invaded the area yet. Guava trees are mainly managed by fumigation or manual control by the farmers.

Mina Roja study site

The study zone at "Mina Roja" is situated in the highlands of Santa Cruz in the humid Scalesia zone and comprises a total of 6.5 km^2 between 580- and 670-meters altitude (0°37'37"S, 90°22'4"W). Mina Roja is situated in the Galápagos National Park, close to the farmland area and human settlements. It has been highly invaded by exotic plants and represents a dense forest dominated by endemic Scalesia *Scalesia penduculata,* the several invasive plants including guava, quinine *Cinchona pubescens*, sauco *Cestrum auriculatum,* cedrela *Cedrela*

odorata trees, elephant grass *Pennisetum purpureum* and the fast growing blackberry dominating the understory (Itow 2003, Jäger et al. 2017) see appendix with vegetation maps).

Nest monitoring, manipulation of *P. downsi* load, and parental feeding observations

During the breeding season, we searched actively for LVF and their nests. Each encountered individual and nest was marked with waypoints in the GPS and the nest status was determined by both behavioral observation and filming of the nest. Nests being built could be identified by the direct observations of males and females bringing nest material to the nest. When incubation or feeding behavior was observed, the nest was additionally filmed with an endoscopic camera (dnt Findoo 3.6) attached to fishing rods to check the number of eggs or chicks.

Nests were monitored at intervals depending on breeding status. Following the method of Cimadom et al (2014), building nests were observed every five days, incubation nests every three days, and feeding nests every two days. Nests were assigned to the following categories: successful (nest produced at least one fledgling), abandoned (female stopped incubating the eggs), predated (empty nest with signs of predation: broken egg shells in or under nest, destroyed nest), empty nest (no signs of predation of a previously active nest), dead chicks (dead chicks found inside the nest), others (e.g. nest fallen down, tree collapsed) (Cimadom et al. 2014).

To measure the influence of *P. downsi* on breeding success, we experimentally reduced the parasite load in 33 nests (11 in Alcedo, 16 in El Cura, 6 in Mina Roja) using a 0.5% permacap solution (Permethrin MC microencapsulated). Permethrin is a neurotoxin targeting adults and larvae of many species of invertebrates (Causton and Lincango 2014). Nontoxic to birds, it has been successfully used in other studies to reduce *P.downsi* abundance in Galápagos land bird nests (Knutie et al. 2013, 2016, Koop et al. 2014, Kleindorfer and Dudaniec 2016). The treatment was performed by injecting the solution into the nest base using a 5 ml syringe. To optimize the distribution of the solution in the nest base, the injection was performed twice from opposite angles. From each side 0.75ml of the solution was injected. In lower nests that could be easily reached with the help of a ladder (up to ~3.5m), the solution was manually injected. For higher nests (until approximately 5.5 m) two superposed fishing rods were used

in addition to the ladder. The method has been developed by Cimadom et al. in 2014 (Cimadom et al. 2019) and consists in fixing the syringe at the end of a 3 m fishing pole into which a thinner pole was inserted. Once the syringe needle was introduced into the nest bottom, the thinner rod was pushed against the plunger of the syringe to release the insecticide. Nests were treated once between the 7. day of incubation and the 2nd day of feeding (mean incubation time is 15.05 days ± 3.82 SD). In Alcedo and El Cura, the permacap treatment significantly reduced the average number of Philornis larvae per nest (Wilcoxon test, El Cura, $n_{treated}$= 12, $n_{untreated}$ = 9,W = 105.5, P< 0.001, Alcedo , $n_{treated}$= 9, $n_{untreated}$ = 10, W = 70.5, P=0.034). Mina Roja could not be included into the analysis due to a very low number of monitored nests (n=5).

Once nest activity ceased, nests were collected in plastic bags and inspected for *P. downsi* parasitism the same day. We dismantled the nest and counted the number of *P. downsi* pupae, puparia and larvae.

To assess the importance of food availability on breeding success, we conducted parental feeding observations for 48 nests (24 nests in Alcedo, 22 nests in El Cura, and 2 in Mina Roja). For thirty-minutes, we recorded the frequency of courtship feeding by the males and parental provisioning by both male and female. The parental provisioning rate was defined as the total feeding events where parents provide food to their chicks. The observations were carried out randomly over the day and repeated twice for each nest. As feeding events are known to increase with the age of chicks (Grundel 1987, Barba et al. 2009), we limited the observation to chicks aged between two and seven days (mean fledgling age: 17.84 days). To avoid any disturbance that could influence the food provisioning behavior, the nests were filmed after the observation only. We used photographs and videos to determine the number and age of chicks where hatching date was unknown.

Foraging behavior observations

We recorded three different elements of foraging: 1) first foraging, 2) first type of prey and 3) continuous foraging observation. Individuals were not color banded but were identified by plumage characteristic (females have yellow plumage and males red, but males show noticeable variation in red colorations) and location. As LVF individuals remain in their territory during the breeding season (Mosquera et al, submitted), each individual observed near a nest was considered to be part of the territorial pair.

1) First foraging observation is defined as the first time a bird is observed foraging. Following the methods of Filek et al. (2018), we recorded perch and foraging height, foraging technique, and foraging success. Foraging techniques were categorized as “sally” (attacking in the air) or “collect” (prey caught from a surface). Foraging success was recorded as “successful”, “failed”, or “unknown” when it could not be clearly seen if the prey was successfully caught.

2) First type of prey was defined as the first type of identifiable prey.

3) To measure the prey attack rate of a bird we used “continuous foraging” observations**.** Following Lovette and Holmes (1995) we defined prey attack rate as the total number of foraging events performed per minute foraging time. The observer followed the bird as close as possible at a distance of 5 -10 meters. This distance often allowed identification of prey type but did not disturb the birds in their foraging behavior. We recorded all foraging events (either successfully, unsuccessfully or unknown) during a minimum of one minute and a maximum of five minutes observation time. As soon as the sight on the individual was lost, or when the individual stopped foraging for more than 15 seconds, the observation was stopped. Where possible, the prey type and size were also recorded.

Egg predation experiment

To compare predation pressure between the study sites, we conducted an artificial nest predation experiment. By following the method of Fessl et al. (2010), we fixed semi-open nests made of coconut fiber on tree branches at about two meters above ground. In each nest we placed 2 plasticine eggs covered by egg albumen. To avoid any contamination with human odor, all handling used plastic gloves. In each study site, a total of 16 nests at a distance of 30 meters were placed along a transect line. Nests were checked every three days and removed after nine days. Depredated eggs were replaced by new ones at day three and day six. Predation type was identified by the marks found on the eggs and classified into the following categories: 1) rat, when showing clear signs of rat teeth 2) bird predation, when showing puncture marks and 3) unknown, when marks could not be identified.

Statistical Analysis

We did not include the study site Mina Roja into the analysis for *P. downsi* prevalence and abundance, parental feeding rate and breeding success due to a very low number of monitored nests (n=5) and no permutation of treatments.

***P. downsi* prevalence and abundance in Alcedo and El Cura**

Because of small sample sizes we used non-parametric tests to compare differences of *P. downsi* prevalence and abundance of untreated nests between sites. We performed a Fisher's exact test to compare *P. downsi* prevalence (n_{Alcedo}=10, $n_{El\ Cura}$=8). We defined *P. downsi* prevalence as presence or absence of *P.downsi* in the nest (yes/no). *P. downsi* abundance defined as number of *P. downsi* individuals per nest, was compared in feeding status nests with a Wilcoxon Test (n_{Alcedo}=10, $n_{El\ Cura}$=11).

Breeding success in Alcedo and El Cura

To compare hatching success (yes/no) between the study sites Alcedo and El Cura. we performed a chi-square test (n_{Alcedo}=29, $n_{El\ Cura}$=30). Hatching success is defined as successful when at least one egg hatched. Because permethrin treatment was performed in the late incubation phase (mean incubation time is 15.05 days ± 3.82 SD), we used treated and untreated nests for this analysis. Two nests that were abandoned after treatment were excluded. To compare fledgling success (yes/ no) between the study sites Alcedo and El Cura we performed a Fisher exact test. Fledgling success is defined as successful when at least one chick fledged. For this analysis we included only untreated nests with chick status (n_{Alcedo}=10, $n_{El\ Cura}$=9).

The influence of permethrin treatment on breeding success

Both site and treatment had a significant effect on breeding success. However, there was no breeding success in untreated nests in El Cura and only two unsuccessful nests in Alcedo. Because of this missing variance and because of small sample sizes it was not possible to test the interaction of both variables in a single model. Thus, we tested the effect of treatment on breeding success separately for each with a chi square test. (n_{Alcedo}=19, $n_{El\ Cura}$=21).

Parental feeding rate in Alcedo and El Cura

To determine the factors influencing the parental feeding rate of chicks, we calculated a generalized linear model with Poisson error structure. For the response variable we used the observed parental feeding events per observation period. One observation period lasted for 30 minutes; for 38 nests we had two observation periods and for seven nests we had one

observation period. The number of observations was used as an offset variable in the model. Predictors were study site (Alcedo and El Cura), permethrin treatment, number of chicks, and the interaction term study site x treatment. Age of chicks can be a relevant factor and that parental feeding rate increases with age of chicks (Grundel 1987, Barba et al. 2009). However, in our case, chick ages within a nest varies only between three- and five-days, and it showed no effect in our model and so we omitted this variable.

Diet composition, prey attack rate and foraging success in all three study sites

We used a Fisher exact-test to compare diet composition between the study sites (n_{Alcedo}=93, $n_{El\ Cura}$=54, $n_{Mina\ Roja}$=31). We categorized prey to the following classification level: "*Arachnida*", "*Annelida*", "*Coleoptera* and *Hemiptera*", "*Dermaptera*", "*Diptera*", "*Formicidae*", "*Gastropoda*", "Insect larvae" (larvae from all type of insects including caterpillars), "*Lepidoptera*", "*Myriapoda*", and "*Orthoptera*".

To compare the prey attack rate between the three study sites, we performed a one-way analysis of variance (ANOVA, n_{Alcedo} = 47; $n_{El\ Cura}$ = 59; $n_{Mina\ Roja}$ = 11) followed by a Tukey HSD post hoc test. Prey attack was log-transformed to obtain normally distributed residuals.

To compare perch and foraging height used by birds between the three study sites we used a Kruskall-Wallis Test, followed by a Wilcoxon signed-rank test (n_{Alcedo} = 59; $n_{El\ Cura}$ = 110; $n_{Mina\ Roja}$ = 45).

To identify the factors influencing foraging success, we calculated General linear models with binomial family structure (n = 194). The response variable was foraging success (successful/failed). Predictor variables were study site, perch height, foraging height and foraging technique. Observations for which foraging success was recorded as unknown were not used. As perch and foraging height were correlated ($r_{Pearson\ correlation}$ = 0.820), two separate General linear models for each variable were performed.

Egg predation

We compared the number of nests showing clearly identifiable rat marks on a at least one egg between the study sites with a Fisher exact test (n=16x3).

The statistical analyses were performed using RStudio version 1.0.153 and packages lme4, stats, car, ggplot2 and jtools.

Results

P. downsi prevalence and abundance

Whereas all nests containing chicks were infested by *P. downsi* in any site, we found significant differences in parasite prevalence for nests in incubation stage. In Alcedo, only one out of ten nests were infested, whereas seven out of eight nests were infested in El Cura (Fisher exact test: P<0.003). *P. downsi* abundance for nests in feeding phase was higher in the study site El Cura than in Alcedo (*P.downsi*/nest (mean ± SD): El Cura 16.4 ± 9.7; Alcedo 7.2 ± 9.7, Wilcoxon Test: W = 18.5, p-value = 0.011) (Fig.2) even though nests in Alcedo were generally collected later (when chicks already fledged) and expected *P. downsi* numbers to be higher compared to nests in El Cura that were collected earlier as young chicks died.

In Mina Roja, two of four incubation nests contained *P. downsi* and no measure for *P. downsi* abundance could be collected due to the low number of nests that had chicks.

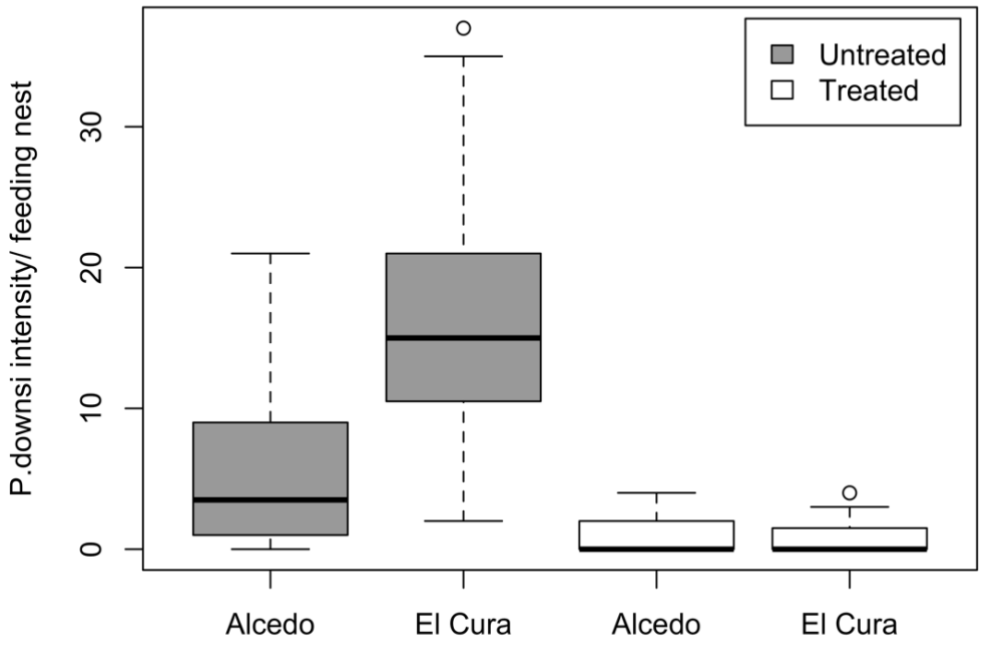

Figure 2. Mean number of *P. downsi* specimens per feeding nests respectively in treated and untreated nests in the study sites Alcedo and El Cura (Isabela island). The data show the interquartile range (box), mean (bar), data extent (whiskers) and outliers (black squares)

Breeding success in Alcedo and El Cura

Hatching success was similar in Alcedo and El Cura: in Alcedo 65.5% egg nests reached the chick status and in El Cura it was 70.0 % (Chi- squared test= 0.008, df = 1, p-value = 0.928) (Fig.3). Fledgling success was higher in Alcedo than in El Cura: in Alcedo 80% of feeding nests reached the fledgling status whereas in El Cura none of the chicks fledged when the nests were not treated (Fig.3) (Fisher's exact test; p-value = 0.0007). In Mina Roja, breeding success was very low: most nests failed during the incubation period because of abandonment (80%, n=5). The five monitored breeding pairs had between two to four breeding attempts. Only two nests were successful (one treated and non-treated nest).

The influence of treatment on breeding success

At El Cura only treated nests produced fledglings whereas in Alcedo there was no difference in fledgling success between treated and non-treated nests (El Cura Chi^2-test: $\chi^2 = 8.94$, df = 1, p = 0.003; Alcedo Chi^2-test: $\chi^2 = 3.6$ e-31, df = 1, p = 1) (Fig.3).

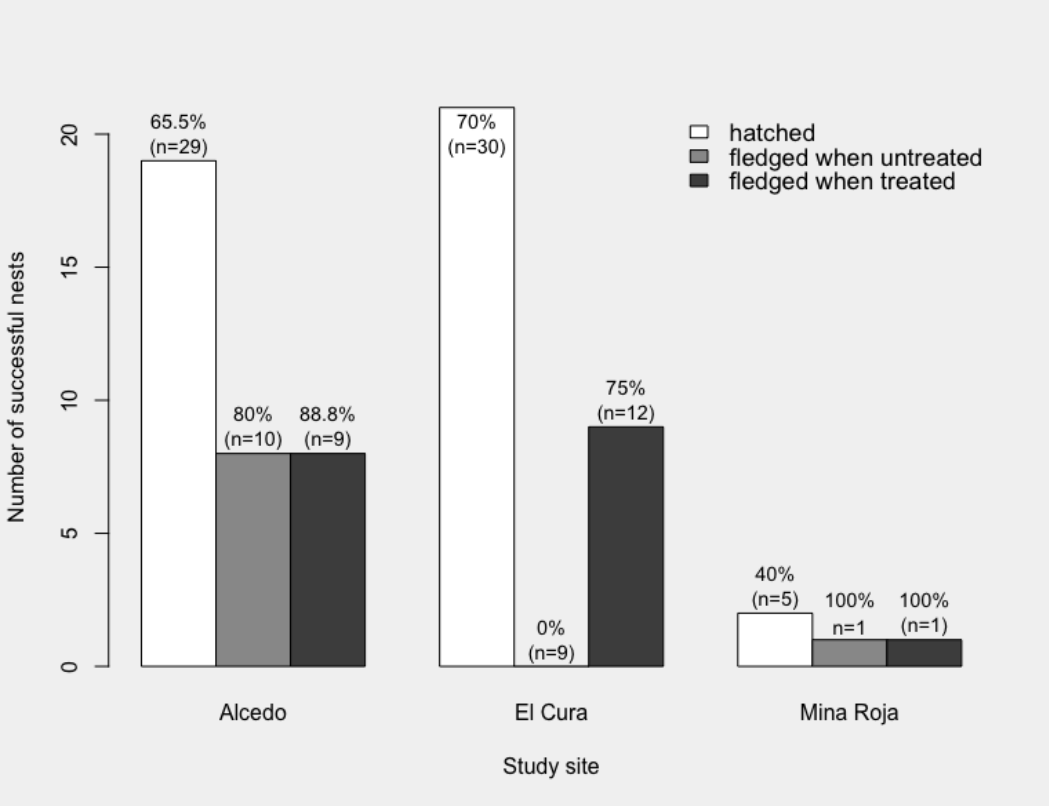

Figure 3 Hatchling success, fledgling success of treated and non-treated nests separately for each study sites. Sample size and % are provided above the bars.

Parental feeding rate

The parental feeding rate was higher in Alcedo than in El Cura (Alcedo: mean= 5.28, (± 2.93 SD); El Cura: mean 2.84, (± 1.88 SD). Study site (Alcedo and El Cura), the number of chicks, and the study site x treatment interaction had significant effects on parental feeding rates (Table 1). The significant interaction showed that the effect of treatment depended on the study site. Parental feeding rates in El Cura were higher in treated than in untreated nests (Table 1, Fig.4)

Table 1: Variables that explained parental feeding in Alcedo and El Cura by GLM with a poisson error structure

Dependent variable: parental feeding (N=45)				
Predictors	**Estimate**	**SE**	**z**	**P**
Intercept	1.83225	0.25735	7.12	**1.08e-12 *** **
Study site	-1.00326	0.18636	-5.383	**7.31e-08 *** **
Treatment	0.01488	0.12998	0.114	0.9089
Number of chicks	**0.27209**	**0.11828**	**2.301**	**0.0214 ***
Study site x Treatment	**0.51633**	**0.23547**	**2.193**	**0.0283 ***

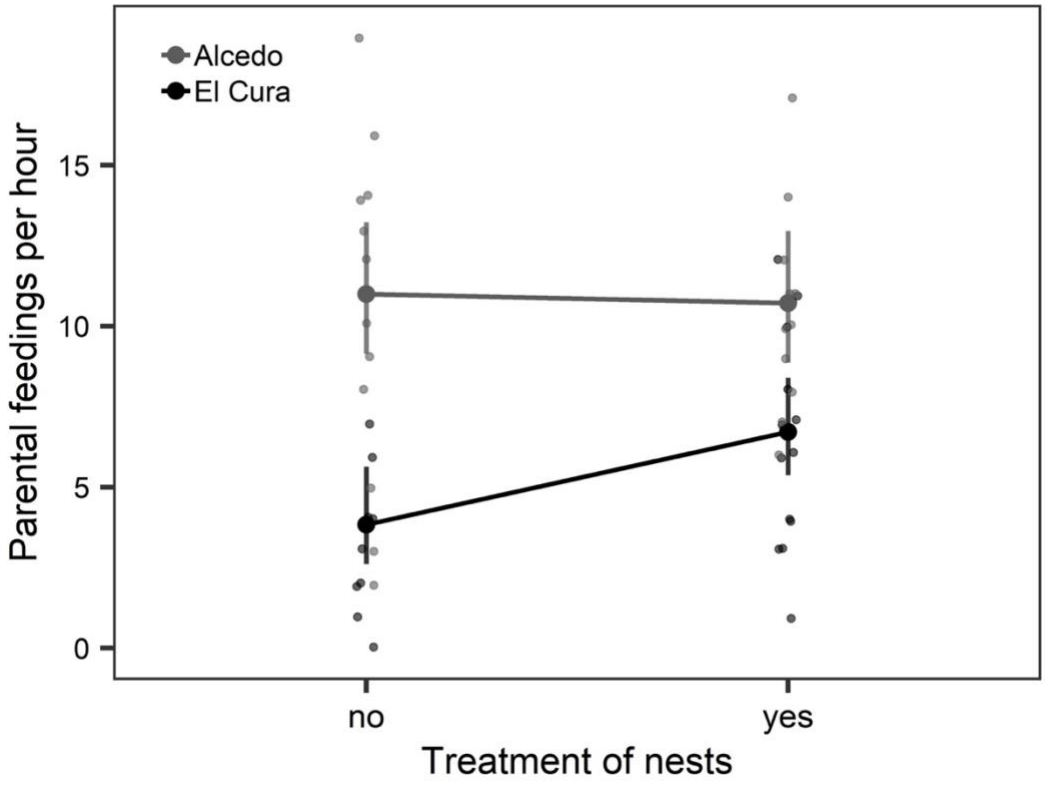

Figure 4. Predicted parental provisioning/hour in treated and non-treated nests (+/- 95% CI) separately for Alcedo (grey) and El Cura (black). Vertical lines indicate model's predicted values, dots represent observed values of the independent variables.

Diet composition

Study sites differed significantly in diet composition (Fisher exact test: $p<0.001$).LVF from El Cura and Mina Roja had a similar diet composition foraging mainly on insect larvae, Lepidoptera and Diptera (Table 2). Alcedo differed from the other two sites: LVF mainly caught Dipteran, insect larvae and Orthoptera (Table 2).

Prey attack rate

Birds from the three study sites differed in prey attack rate (one-way ANOVA F=5.979, p=0.003)(Fig.4). Post hoc analysis revealed that the prey attack rate was significantly lower in Mina Roja than in El Cura (p= 0.003), whereas there was no significant difference between Alcedo and Mina Roja (p= 0.179) nor between Alcedo and El Cura (p= 0.096).

Perch height, foraging height and foraging success

Perch and foraging height differed significantly between the three study sites (Kruskal-Wallis chi-squared = 3978.4, df = 77, p-value < 2.2e-16). Birds in Mina Roja used higher perches and foraged higher when compared to the two other sites (Wilcoxon test: foraging height MR vs Alcedo: W = 885, p-value = 0.002; MR vs EC: W = 1927, p = 0.027; perch height MR vs. Alcedo: W = 975.5, p = 0.019; MR vs EC: W = 2037.5, p = 0.084). Alcedo and El Cura did not differ in perch and foraging height (Wilcoxon test: foraging height: W = 2833, p-value = 0.154; perch height: W = 2844, p-value = 0.184) (Fig.4).

Foraging success was not affected by study site, perch height, foraging height, or foraging technique in all three study sites. The GLMs including the variable perch height showed no significant effect on foraging success. Similarly, for the GLMs including the variable foraging height, none of the predictors remained significant.

Table 2. Comparative diet composition of the LVF in Alcedo (Isabela island), El Cura (Isabela island) and Mina Roja (Santa Cruz). Values represent total number and proportion for each prey category.

	Alcedo	**El Cura**	**Mina Roja**	**% Alcedo**	**% El Cura**	**% Mina Roja**
Arachnida	4	0	1	4,30%	0,00%	3,23%
Annelida	0	0	2	0,00%	0,00%	6,45%
Dermaptera	1	0	0	1,08%	0,00%	0,00%
Formicidae	0	1	1	0,00%	1,85%	3,23%
Gastropoda	0	1	0	0,00%	1,85%	0,00%
Insect larvae	21	25	10	22,58%	46,30%	32,26%
Lepidoptera	12	15	11	12,90%	27,78%	35,48%
Myriapoda	1	3	2	1,08%	5,56%	6,45%
Orthoptera	19	1	0	20,43%	1,85%	0,00%
Coleoptera and Hemiptera	7	1	0	7,53%	1,85%	0,00%
Diptera	28	7	4	30,11%	12,96%	12,90%
Total	93	54	31	100,00%	100,00%	100,00%

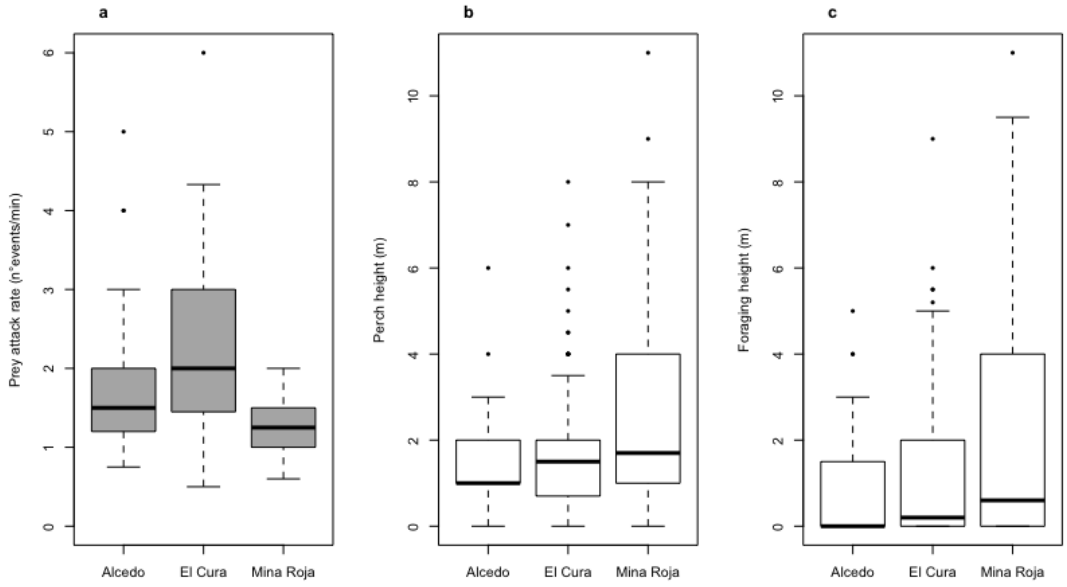

Figure 4. (a) Prey attack rate of LVFs in Alcedo (Isabela island), El Cura (Isabela island) and Mina Roja (Santa Cruz island). (b) Perch height used by LVFs when foraging, respectively in the three study sites. (b) Height at which LVFs caught their preys, respectively in the three study sites. The data show the interquartile range (box), mean (bar), data extent (whiskers) and outliers (black squares)

Predation

Predation pressure was low at all study sites. Only a few natural nests showed signs of predation: 13% of nests in Alcedo (n=29), 6.6% in El Cura (n=30), and none in Mina Roja (n=5) were depredated. The artificial egg nest experiment demonstrated low rat predation across all study sites. Over the whole experimental period, few nests were predated by rats: 6.25% nests in Mina Roja and 25.00% in Alcedo and El Cura (n=16 for each site, Fisher exact test p=0.34).

Discussion

Our results showed that breeding success of untreated nests varied between the three study sites with the highest breeding success at the pristine study site on Vulcan Alcedo and no or close to zero breeding success at the other two sites, El Cura and Mina Roja. We found difference in *P. downsi* parasitism abundance and habitat quality among the sites, whereas predation pressure was generally low across sites.

P. downsi abundance was twice as high in El Cura even though nests were collected earlier and we had expected *P. downsi* number to be lower. In line with our first prediction we found lower breeding success in El Cura. The result of our parasite removal experiment supported the hypothesis that *P. downsi* is a major cause of breeding failure when *P. downsi* abundance is high. However, treatment had no effect at Alcedo which suggests that the LVF is able to cope with low to medium *P. downsi* abundance. A similar result is found in El Cura early in the breeding season (from October/November) when *P. downsi* abundance is lower (Mosquera et al. 2019).

The difference in host vulnerability between the two sites El Cura and Alcedo could be explained by differences in the timing of infestation. In El Cura most nests with eggs already contained *P. downsi*. As a result, the freshly hatched chicks in El Cura are exposed to larger larvae than in Alcedo. Previous studies on finches demonstrated that *P. downsi* had a higher impact when chicks are still small (Tebbich et Cimadom submitted). A similar effect was found in host parasite interaction between *Philornis deceptivus* and Pearly-Eyed Thrashers *Margarops fuscatus* (Arendt 1985). It is known that the size and number of larvae can lead to

higher vulnerability to parasites and as consequence, to reduced breeding success e.g (Kleindorfer and Dudaniec 2016). Additionally, long term studies on Darwin finches showed that timing of *P. downsi* infestation has advanced in the breeding cycle (nests are infested earlier) (Cimadom et al. 2016), and thus the detrimental effect of *P. downsi* might have and could increase in the future.

The lower *P. downsi* abundance and later infestation of nests found in Alcedo might be explained by its isolation from human activities and/or higher elevation. Alcedo is isolated from the human activities that represent the points of the fly's introduction, and *P. downsi* levels might not have reached high levels yet. Another explanation may be the higher altitude of the Alcedo site. Wiedenfeld et al. 2007 examined the occurrence of *P. downsi* at different elevations among the Galapagos islands and found that *P. downsi* abundance increased with elevation due to increased moisture. However, at high altitudes like the Alcedo area, climates become arid again (Wiedenfeld et al. 2007) and thus might represent unfavorable conditions for *P. downsi* survival and dispersion. The higher elevation also leads to lower air temperatures which is known to be a limiting factor for *P. downsi's* ecology. A previous study on the El Cura population demonstrated that *P. downsi* prevalence decreased with decreasing temperature (Mosquera et al. submitted). The negative effect of low temperatures on insect development and flight activity is well established (Taylor 1963, Ratte et al 1985, Reznik et al. 2009). Also, a recent study in Santa Cruz demonstrated low *P. downsi* activity at low temperatures: male catching rate was close to zero in the highlands when temperatures were below ~19–21°C (Causton *et al.* submitted)

We also investigated the relationship between habitat quality and breeding success and predicted the lowest breeding success in areas with the lowest prey attack rate, foraging success, and parental feeding rates. Our results indicate that Alcedo has a higher habitat quality compared to the two other sites. Prey attack rate of the population of Alcedo was similar to the other sites but prey diversity was higher. Specifically, Orthoptera, which is a large prey for the LVF, were not observed in El Cura and Mina Roja. This difference may be linked to the transformed vegetation composition as it is known from other studies that the diversity of invertebrates is reduced by alien plant species (Olckers and Hulley 1991, Samways et al. 1996). As arthropods vary greatly in terms of macro and micro-nutritional composition,

changes in diet composition can cause the decline of insectivorous birds (Britschgi et al. 2006). Additionally, the parental feeding analysis indicates that quantity of food for chick rearing is better in Alcedo than in El Cura as the parental feeding rate in Alcedo was higher independently of whether the nests were treated or not. In sum, the pristine Alcedo site seems to provide better conditions for chick rearing, which could be the reason for the higher breeding success in this area.

However, an interaction between parasitism and habitat quality is possible. As study on the Green Warbler-finch found that parents can compensate for parasitism when insect abundance was high (Cimadom et al. 2019, McNew et al. 2019). As Alcedo and El Cura differ simultaneously in *P. downsi* abundance and habitat quality, their interaction and their relative influence on breeding success cannot be separated.

Food availability could also influence parent's ability to compensate for the negative impacts of parasitism. Contrary to our prediction, there was no increase in food provisioning in parasitized nests. In Alcedo parental feeding rates did not differ between treated and untreated nests and in El Cura nestlings of untreated nests were significantly less fed than those of treated nests. This indicates that the LVF is not able to compensate for high parasite abundance with parental food provisioning. This is in line with previous studies on other land bird species as the Small Tree-Finch *Camarhynchus parvulus* (Heyer et al. submitted) and the Small Ground-Finch *Geospiza fuliginosa* (O'Connor et al. 2014) but see Knutie et al 2016. Reduced parental feeding rate in the presence of parasites might be caused by reduced begging of weakened chicks (O'Connor et al. 2014) and/or an increased trade-off between parents and offspring fitness (Szép and Møller 1999, Morrison and Johnson 2002, Johnson et al. 2016). The conflict of parent survival and reproduction and offspring may arise when parental care costs increase. As a result, self-preservation is favored over costly parental care (Trivers 1974).

The study site Mina Roja could not be included into the analysis on breeding success because of a very low number of breeding pairs. The extremely high brood loss occurred in the incubation phase due to abandonment by the female. These nests were not infested, thus *P. downsi* parasitism is not the primary reason for abandonment. We hypothesize that low habitat quality may play a role in nest abandonment at Mina Roja. The adult bird foraging

observations reveal that Mina Roja probably has the lowest food availability as prey attack rate was only half as high compared to El Cura although diet composition was similar. This could be explained by low resource abundance caused by alien species (Litt et al. 2014) or low resource accessibility. As the area in and around Mina Roja is heavily invaded by invasive blackberry and elephant grass that are covering the understory, LVF probably have less accesses to the ground. The transformed habitat might also explain the different foraging behavior observed in Mina Roja compared to the other sites. It is known from other studies that foraging behavior of birds is influenced by the structural complexity of the surrounding environments (Robinson, Scott K., Holmes 1982, Whelan 2018). Birds in Mina Roja used higher perch and foraging heights compared to the two other sites. In Alcedo and El Cura, birds foraged from low perches in an area dominated by low growing pastures created by giant tortoises or cows.

Additionally, open areas might increase food abundance and be beneficial for different arthropods. Open patches offer direct sun exposure that are favorable for thermophilic arthropods (Liu et al). Also flying insects such as moths benefit from open areas as their dispersal depends on finding new feeding grounds (Young 1977).

However, neither perch height nor foraging height nor foraging technique affected the foraging success. One reason might be that our measure of foraging success was too crude as while we could often identify whether prey had been captured, we could not identify it when the prey was very small and we then had to categorize the prey as unknow. Thus, prey attack rate might be the more accurate measure for habitat quality.

Conclusion

Our data suggest that the LVF is not able to compensate for high *P. downsi* infestation but is able to cope with low to medium parasitism. At the remote Alcedo site and at the El Cura site, which is predominately farm area, LVFs frequently hunted by flying from low perches to the ground, in areas where grass was maintained at low heights by grazers (giant tortoises in Alcedo, cows in El Cura). This also indicates that anthropogenically transformed habitats with pastures, as encountered in El Cura, are favorable for the LVF when *P. downsi* abundance is reduced. Conservation strategies should take this into account and could combine habitat management with *P. downsi* control.

However, *P. downsi* might not be the primary reason for the low breeding success in Santa Cruz, given that most of the nests were abandoned during the incubation phase and not infested with *P*. *downsi*. We found some indication that invasion by blackberry has a negative influence on prey availability. Low food availability could be a reason for nest abandonment by the incubating females because parents with lower energy reserves have poor prospects for offspring production (Wiggins et al. 1994). This could be investigated in the future by experimental habitat management. Additionally, the population on Santa Cruz Island is so small (approximately 40 breeding pairs) that the low breeding success could be a result of a genetic bottleneck that can cause loss of heterozygosity and inbreeding depression (Kirkpatrick and Jarne 2000), among other effects. Consequently, environmental changes might have a larger effect on the population on Santa Cruz Island. Further studies are necessary to measure the possible influence of these factors

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Appendix: Vegetation maps

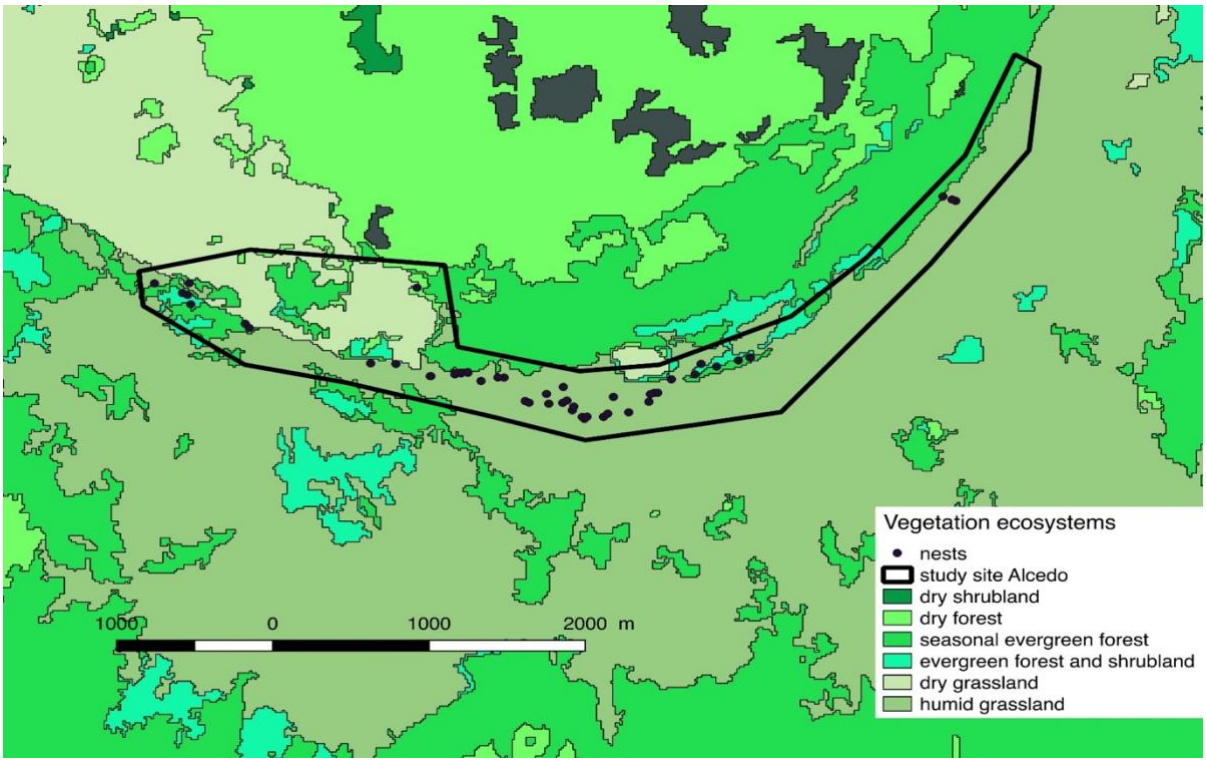

Figure 5. Map presenting the study site Alcedo. The study area (3.6 km2, delimited by the black line) is located within the Galápagos National Park on the southern rim of Volcano Alcedo in central Isabela (0°27'35"S, 91° 6'59"W). Black dotes represent nests that were monitored during the breeding season 2018. Dominated vegetation units are distinguished by colors. (map source © Gonzalo Rivas-Torres, PhD , University of San Francisco Quito).

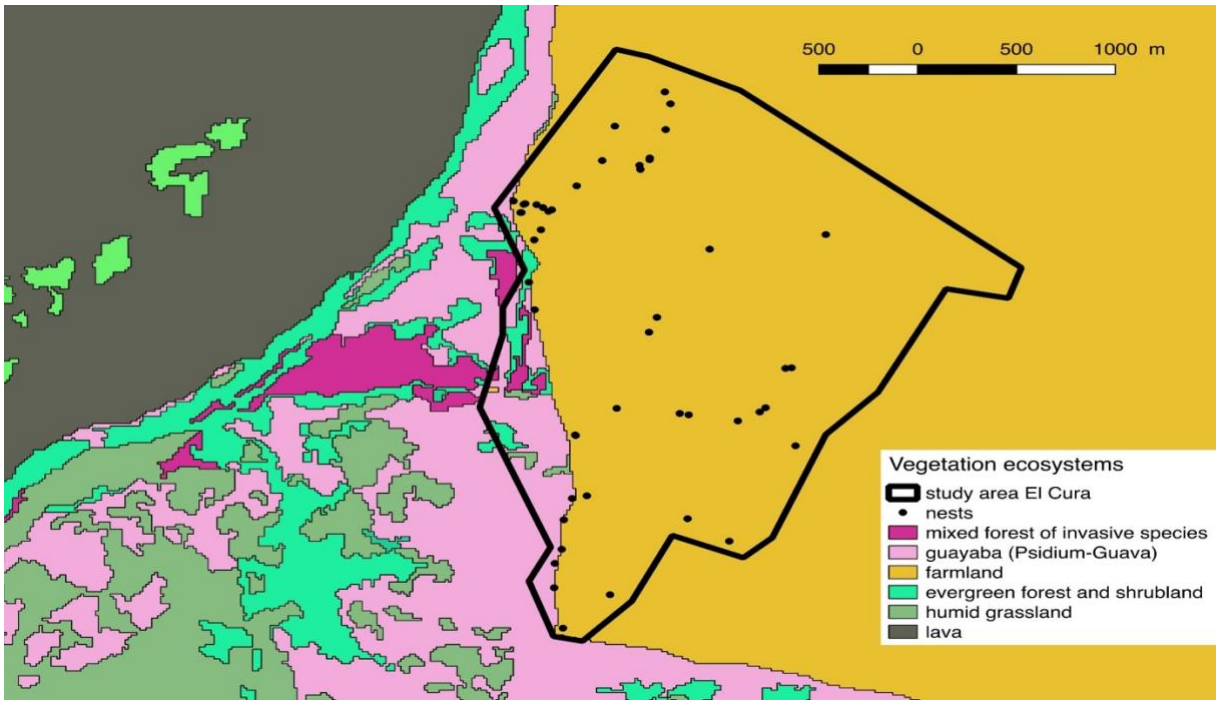

Figure 6. Map presenting the study site El Cura. Located on the slope of Sierra Negra volcano, Isabela island (0°50'0"S, 91° 5'0"W), the study area (5.5 km2, delimited by the black line) is mostly covered by private farmland whereas a minor part is within the Galápagos National Park. Black dotes represent nests that were monitored during the breeding season 2018. Dominated vegetation units are distinguished by colors. Note that the farmland area is dominated by the invasive guava, from low to high densities depending on the management intensity (map source © Gonzalo Rivas-Torres, PhD , University of San Francisco Quito).

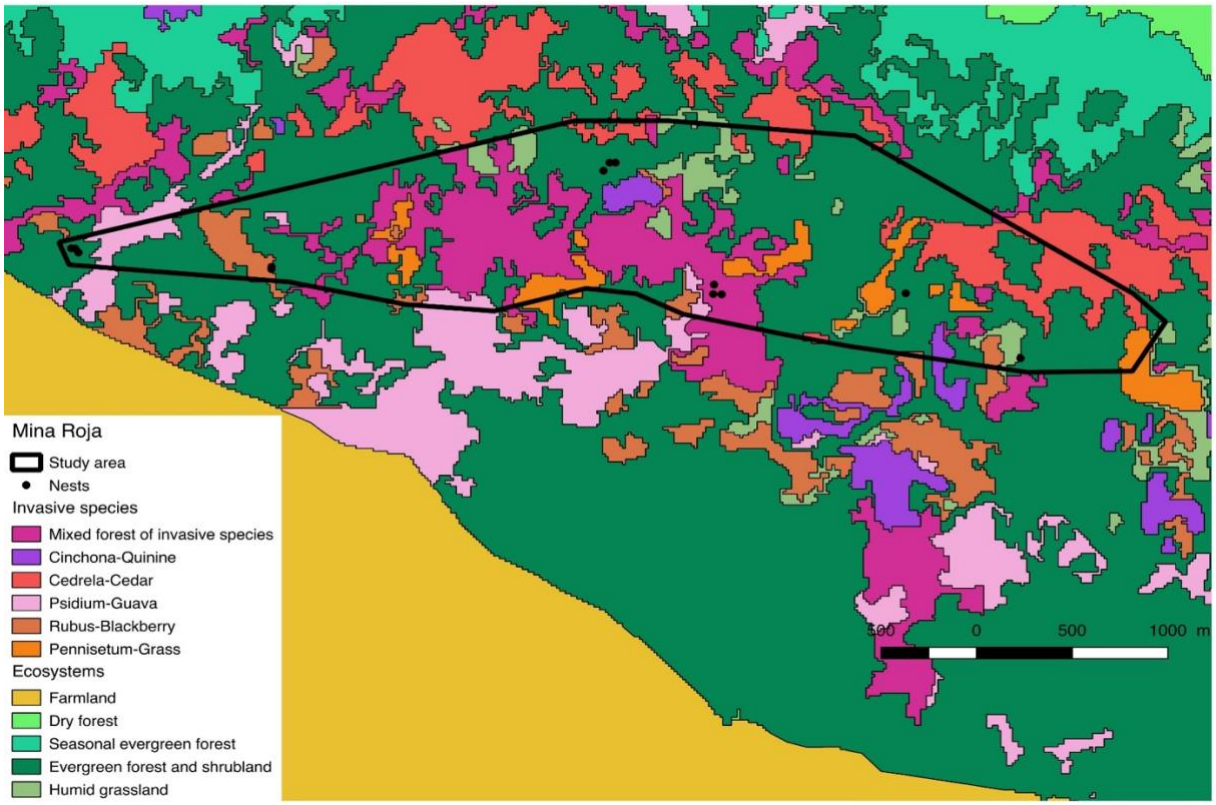

Figure 7. Map presenting the study site Mina Roja. Located in the highlands of Santa Cruz island (0°37'37"S, 90°22'4"W), the study area (6.5 km2, delimited by the black line) is situated within the Galápagos National Park, close to the farmland area and human settlements. Black dotes represent nests that were monitored during the breeding season 2018. Dominated vegetation units are distinguished by colors (map source © Gonzalo Rivas-Torres, PhD , University of San Francisco Quito).