

Research Article

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Habitat restoration to conserve the Little Vermilion Flycatcher *Pyrocephalus nanus* on Santa Cruz Island, Galapagos

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Summary

The endemic Little Vermilion Flycatcher (LVF) *Pyrocephalus nanus* has suffered a drastic decline on Santa Cruz Island, Galapagos, where it was common 30 years ago. Currently, fewer than 40 individuals remain in the last remnants of natural humid forest in the Galapagos National Park on the island. This small population has low reproductive success, which is contributing to its decline in Santa Cruz. Previous studies have identified Avian Vampire Fly *Philornis downsi* parasitism, changes in food sources, and habitat alteration as threats to this species. In Santa Cruz, invasive plants may strongly affect the reproductive success of LVF because they limit accessibility to prey near the ground, the preferred foraging niche of these birds. Since 2019, we restored the vegetation in seven plots of 1 ha each by removing invasive blackberry plants and other introduced plant species. In all nests that reached late incubation, we also reduced the number of Avian Vampire Fly larvae. In this study, we compared foraging and perch height, pair formation, incubation time, and reproductive success between managed and unmanaged areas. As predicted, we found significantly lower foraging height and perch height in 2021 in managed areas compared with unmanaged areas. In 2020, the daily failure rate (DFR) of nests in the egg stage did not differ between management types; however, in 2021, the DFR in the egg stage was significantly lower in managed areas than in unmanaged areas. The DFR during the nestling stage was similar between managed and unmanaged areas in 2020, but in 2021, only nests in managed areas reached the nestling stage. Females brooded significantly more during the incubation phase in managed areas. Additionally, we found significantly higher reproductive success in managed areas compared with unmanaged areas in 2021, but not in 2020. Habitat restoration is a long-term process and these findings suggest that habitat management positively affects this small population in the long term.

Introduction

Recent studies raise concerns about the drastic decline of many avian species worldwide (BirdLife International 2022). One of the main groups of birds affected is the group that feeds on arthropods (Tallamy and Shriver 2021). Frequently identified causes for such declines include habitat loss and use of pesticides, which result in a reduction of arthropods, the birds' main food supply (Forister et al. 2019; Mahmood et al. 2016; Sekercioglu 2002; Wagner et al. 2021; Wauters et al. 2017). In the Galapagos Islands, declines of insectivorous birds are becoming more common (Dvorak et al. 2012, 2017, 2020). The original habitat of landbirds on several islands in the Galapagos has changed dramatically since colonisation by humans (Alomía et al. 2022; Geladi et al. 2022; Lundh 2006; Watson et al. 2010), altering food sources and adding further pressure on many vulnerable species.

The genus of birds with the most dramatic decline on the Galapagos Islands is *Pyrocephalus*, which originally included two endemic taxa, Little Vermilion Flycatcher *Pyrocephalus nanus* and Least Vermilion Flycatcher *Pyrocephalus dubius* (Carmi et al. 2016). The Least Vermilion Flycatcher, endemic to San Cristobal Island, is now considered “Extinct” (IUCN 2023); thus, it is the first extinction of an avian species in recent history in the Galapagos (Dvorak et al. 2020). Long-term monitoring of landbird populations has revealed that the Little Vermilion Flycatcher (hereafter LVF) is disappearing from several islands of the Galapagos archipelago. This species originally inhabited 10 large islands but has disappeared from two islands (Santa Fe and Floreana Islands) and is in sharp decline on Santiago Island (Fessl et al. 2017). The LVF is currently classified as “Vulnerable” in the IUCN Red List (IUCN 2023).

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On Santa Cruz Island, the second largest island in the archipelago (986 km²), LVF was abundant until 30 years ago (Merlen 2011). Since then, the population has decreased rapidly, with an estimate of fewer than 30–40 breeding pairs left in 2016 (Fessl et al. 2017). Small population sizes favour the mating of genetically close individuals, leading to inbreeding and increased hatching failure (Kruuk et al. 2002), which could add more stress to this population. Santa Cruz has the largest human population in the Galapagos and large areas of native forest have been cleared for agriculture (Alomía et al. 2022; Benitez-Capistros et al. 2014; Espinoza De Janon 2013, Geladi et al. 2022). The remaining LVF population in Santa Cruz has taken refuge in the forest in the humid zone (550–720 m a.s.l.) in a 7-km² area in the Galapagos National Park. Despite being protected, this area has been invaded by several invasive plant species such as blackberry *Rubus niveus*, guava *Psidium guajava*, orange cestrum *Cestrum auriculatum*, quinine *Cinchona pubescens*, cedrela *Cedrela odorata*, grasses *Paspalum conjugatum* and *Cenchrus purpureus*, and ferns *Dennstaedtia globulifera* and *Ctenitis sloanei*, reducing its habitat quality (Carrión-Klier et al. 2022; Rivas-Torres et al. 2018).

Recent studies comparing populations of LVFs on Santa Cruz and Isabela Island suggest that the decline in Santa Cruz is associated with altered arthropod diversity and accessibility due to habitat change (Leuba et al. 2020), caused by the invasive blackberry plant (Renteria et al. 2021). The blackberry is spreading aggressively within humid zones, where it competes with native and endemic plants, preventing them from regenerating (Renteria et al. 2012, 2021; Walentowitz et al. 2021). Blackberry brambles form a dense, tangled understorey up to 4 m in height (Renteria et al. 2012), leaving few open areas near the ground where LVFs can hunt for arthropods (Leuba et al. 2020). Due to restricted access to the ground on Santa Cruz, LVFs usually capture prey above invasive plants. However, in areas with no invasive blackberry on Isabela, they take their prey very close to the ground and have a higher foraging success than on Santa Cruz (Leuba et al. 2020).

Another major threat to LVFs is the invasive Avian Vampire Fly (Vampire Fly) *Philornis downsi* (Leuba et al. 2020; Mosquera et al. 2022). Its larval stages feed on the blood and tissue of nestlings, causing blood loss, anaemia, beak deformations, and nestling mortality (Fessl et al. 2018). When Vampire Fly parasitism was experimentally reduced in LVF nests, they had higher breeding success than in highly parasitised nests. This suggests Vampire Fly parasitism significantly decreases the LVFs' breeding success and may be one of the main factors influencing its population declines. Furthermore, the effects of Vampire Fly parasitism may be mediated by habitat quality as Leuba et al. (2020) found higher LVF breeding success and food provisioning rates in a more preserved site compared with a site with lower quality habitat.

However, Vampire Fly parasitism does not seem to be the main reason for breeding failure in Mina de Granillo Rojo in Santa Cruz. We found that 33 out of 56 nests were abandoned at an early stage of incubation, without any signs of predation or parasitism by the Vampire Fly (Leuba et al. 2020; Charles Darwin Foundation (CDF), unpublished). We hypothesise that the high percentage of nest abandonment and overall poor breeding success in Santa Cruz is linked to altered habitat quality (Kitaysky et al. 1999; Ouyang et al. 2012) caused by invasive plants, especially blackberry, which reduce prey accessibility.

To test this hypothesis, we carried out an experimental habitat management in seven plots of 1-ha each. In collaboration with the Galapagos National Park Directorate (GNPD), we cleared the invasive understorey from these plots and compared managed

and unmanaged areas with respect to: (1) foraging height and perch height of LVF; (2) pair formation; (3) daily nest failure rate at egg and nestling stages; (4) incubation time; (5) breeding success. We predicted that managed areas would have lower foraging and perch height, more successful pair formation, lower nest failure rate, and higher breeding success than unmanaged areas.

Methods

Study area

This study took place in a cloud forest in the humid zone in the centre of Santa Cruz Island (90°21'30.69"W, 0°37'58.45"S) between 550 m and 720 m a.s.l. This area, called Mina de Granillo Rojo, covers approximately 700 ha, with 37 km of trails, which were used to search for birds and nests (Figure 1). The climate is seasonal, with a warm and humid climate from December to May and a cooler, dry climate during the remaining months.

Study species

The LVF has marked sexual dimorphism. The adult male has bright red and black feathers; however, during transition to adulthood, the immature male's plumage changes successively from yellow/brown (juvenile) to orange and a dull red colour (first-year breeding), with pronounced individual variation. In contrast, females have brown and yellowish plumage, with some individuals having sporadic orange feathers on the head. LVFs feed exclusively on arthropods (Guerrero and Tye 2011; Leuba et al. 2020), and prefer to forage by sallying from perches into open and semi-open areas both on the ground and in the air (Leuba et al. 2020). The birds build an open cup nest using lichens, moss, and tree bark as materials (D.J.A. personal observations) (Supplementary material Figure S1).

Habitat management

The plots for experimental management were selected using maps of vegetation types and previous sightings of LVFs. Seven plots of 1-ha each were selected for management. Plots were chosen based on accessibility and the presence of existing territories (Figure 1), not selected randomly. Invasive plants, including blackberry, orange cestrum, quinine, grasses, and ferns, were controlled and removed along with their roots to prevent regrowth. Workers used machetes and heavy cutting iron blades (*barretones*). Herbicides were not used to avoid any potential secondary impact on arthropods. From the beginning of the restoration in January 2019 to May 2021, each plot was cleaned every three to four months to prevent invasive plants from recolonising. The vegetation was cut at a height between 10 cm and 20 cm above the ground to mimic the vegetation structure at sites grazed by Galapagos Giant Tortoises *Chelonoidis niger*, which are the natural top herbivore in the Galapagos (Froyd et al. 2014; Hunter et al. 2021), but absent from our study area. This allowed native plants to germinate and grow faster.

Foraging and perch height

We collected data throughout the entire nesting season, which runs from December to May, when arthropod availability increases. To limit the effect of variation in foraging behaviour, observations took place at random, from 07h00 to 11h30, when the birds have the highest foraging activity. We did not conduct observations during

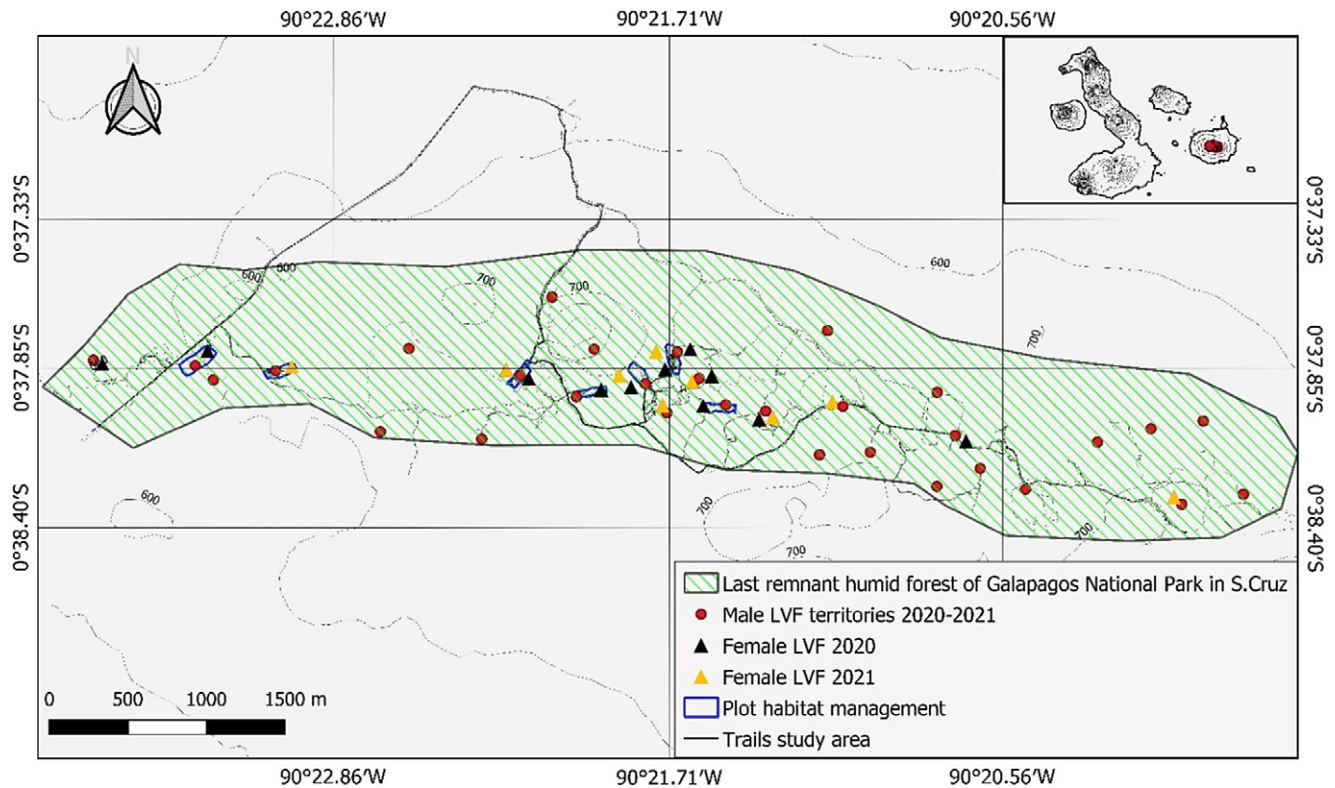


Figure 1. Study area and location of the last remnant of the Little Vermilion Flycatcher *Pyrocephalus nanus* population in Santa Cruz Island.

rainy weather because bird activity is usually limited. Upon entering an individual's territory, observers carefully followed the focal individual from afar using binoculars to avoid disturbance. The first time that an observed individual was seen foraging was referred to as a "first foraging observation". Each observation terminated after the first foraging attempt was recorded. Individuals were identified by plumage differences and by using combinations of colour rings; 11 males and six females were colour ringed during 2020 and 2021, which represents an estimated 50% of the males and females observed. Records of unringed breeding birds in a territory within one breeding season were assumed to be of the same individual. After a first foraging attempt (successful or not) during an observation, we recorded the height at which it foraged, the height of the perch from which the foraging sally was launched, and the type of surface where it captured its prey (e.g. ground, trunk, branches, leaves, air). The type of prey was recorded to the level of order if it was possible to identify it before the bird ate it.

Nest monitoring

Nest searching was conducted along 37 km of trails. These trails went through areas with managed and unmanaged habitat (Figure 1). In addition, narrow paths were opened in unmanaged areas to make these more accessible. Equal search effort was dedicated to managed and unmanaged areas. Five days per week, from 7h00 to 11h30, two teams of two people each simultaneously searched for birds and collected data in managed and unmanaged areas. The probability of detecting a territorial pair was high in both areas due to this intensive monitoring. Additionally, the behaviour of the LVF male is very noticeable, as they frequently fly above the canopy to display a territorial song. Also, males call the females during the mating phase, which was one of the main behaviours

used to find an active territory. Pair formation was identified by the presence of an aggressive male and an aggressive female or a male and a female interacting and/or copulating. Breeding seasons spanned two successive calendar years. The season running from December 2019 to 15 March 2020 is referred to as "2020". The breeding season of the LVF continued until the end of May 2020, but it was not possible in 2020 to continue monitoring nests for the whole season due to the Covid-19 pandemic and GNPDR restrictions. In the second year, "2021", data were collected during the whole breeding season from December 2020 to May 2021.

After an active nest was found, it was visited every three days during the incubation and feeding phases until its activity ended. Any effect that the observer could have on the behaviour of the adults near/at their nest was minimised as much as possible. During each visit, the nest was first observed with binoculars from a distance of 15–20 m and then filmed with an endoscopic camera when the birds left the nest to forage. The process of filming the open cup nests took ~20–30 seconds. By filming from above, we could count the number of eggs or nestlings and determine whether there were any changes since the previous visit. After filming, we waited at a distance until the female returned to the nest. Our methodology followed Leuba et al. (2020), which found no abandonment attributed to observations and nest filming. The total number of active days for a nest was determined by the start of the incubation phase to the last date of activity.

Incubated nests (42 nests: 25 in 2020, 17 in 2021) were observed every three days for one hour to record the total time the female was inside the nest. We could not compare parental feeding rate of nestlings between managed and unmanaged territories because most nests in unmanaged areas were abandoned during incubation. The outcome of each nest was categorised as follows. (1) Fledged (at least one nestling fledged) or failed; a fledgling was defined as a

nestling that left the nest and stayed around the nest waiting to be fed by the parents. Failed nests during the incubation phase were categorised as (2) Abandoned: when eggs were intact in the nest, (3) Empty during the incubation phase; a nest previously containing eggs and found empty (ejection by wind/rain), or (4) Predated: a destroyed or partially destroyed nest, and/or broken eggshell remains. As nests of the LVF are fragile and small (8–9 cm diameter) in comparison to all potential predators, predation events leave visible destruction of the nest (Leuba *et al.* 2020; D.J.A. personal observations).

Failed nests during the nestling phase were categorised as follows. (5) Empty during nestling phase: a nest previously containing nestling(s) and found empty before the end of the nestling period (ejection by wind or removal of dead nestlings by parents can be causes of this). (6) Dead nestling(s): one or more nestlings found dead in the nest. (7) Predated: remains of nestlings' body parts or remains of feathers or down (see above), and/or destroyed or partially destroyed nest. (8) Unknown: nests that failed due to unknown reasons. For five nests, we could not establish the reason of failure, as we could not enter the field site during the weeks they failed due to pandemic regulations. Once we confirmed on three nest visits that activity had ceased, each nest was collected for a detailed examination.

Eggs

If a nest failed or was abandoned, the eggs were collected to check whether they were fertile and to see if abandonment was likely due to egg infertility. We candled eggs using a flashlight in a darkened room to check for the presence of embryos. However, if an egg contained a small embryo, this method was unreliable, so we opened eggs with no visibly large embryo and inspected the contents carefully in a Petri dish.

Control of Vampire Fly infestation in LVF nests

To minimise the influence of Vampire Fly parasitism on breeding success, we reduced the number of larvae from all nests that reached late incubation by injecting Permacap[®] (Controlled Release Permethrin) into the nest. Permacap is an insecticide used to target and kill Vampire Fly larvae in nests of Galapagos landbirds (Cimadom *et al.* 2019; Leuba *et al.* 2020; Mosquera *et al.* 2022). Approximately 5 ml of a 0.5% (by volume) aqueous solution of Permacap was injected into the base of the nest. A second injection of 1–3 ml of Permacap was applied if some of the solution ran off from the nest during the initial application. The solution was applied using a syringe secured to the end of a carbon fibre tube extending up to 7 m. The solution in the syringe was pushed out by a pressurised air pump. Each nest was treated in the late stage of incubation from days 11 to 15 (mean number of days of incubation for LVF is 16 days). Injection of the insecticide solution was carried out while standing on a ladder for closer proximity to each nest. No nest abandonment was observed after the treatment.

Of the 42 nests monitored, only 20 nests (15 nests in managed and five nests in unmanaged areas) were treated against Vampire Fly parasitism because the other nests did not reach the late incubation stage. After nest activity ceased, nests were collected, dismantled in the laboratory, and the number of Vampire Fly pupae or larvae and their larval stage were recorded. Treated nests had an average of $1.80 \pm \text{SD } 3.8$ larvae/nest. In previous studies on this species in an unmanaged, anthropogenic habitat (El Cura, Isabela), the average number of larvae was $16.4 \pm \text{SD } 9.7$ (Leuba *et al.* 2020).

Of the treated nests, 15 nests had no detectable Vampire Fly parasites when examined after the end of the breeding attempt and 5 nests had Vampire Fly parasites (3, 4, 5, 10, 14 larvae or pupae). Of those five nests, only one was identified as possibly failing due to Vampire Fly parasitism (with 14 larvae). Two nests that had 10 and three Vampire Fly larvae were successful, while two nests with low numbers of Vampire Fly larvae (four and five) were probably destroyed by wind and heavy rain. Of the 22 nests that were not treated because they did not reach the late incubation stage (15 managed, seven unmanaged), 17 nests did not have Vampire Fly larvae. The other five nests that reached mid incubation stage had Vampire Fly larvae (2, 2, 4, 7, and 10 larvae); all five nests were in managed areas. The one nest with 10 larvae failed during heavy rain conditions and it is not known with certainty whether parasitism or rain influenced the abandonment.

Statistical analysis

Foraging and perch height

We ran robust linear mixed models (RLMMs) using the “*rlmer*” function from the *robustlmm* package (Koller 2016) in R, version 4.2.1 (R Core Team 2022) to analyse foraging height and perch height as dependent variables in separate models. For the analysis, “first foraging observation” data were used and foraging observations with incomplete data were excluded. For fixed effects, management (binary variable: yes/no) was included as the main independent variable and sex was included as a binary covariate. Individual ID was modelled as a random factor “to account for pseudoreplication”. This model was chosen due to non-normality of residuals and heteroscedasticity. Only data from 2021 were used in this analysis because these data were collected during the entire breeding season.

Pair formation

We used a Fisher's exact test for a 2×2 table to compare the number of paired and unpaired males in managed and unmanaged areas. Only data from 2021 were used in this analysis because these data were collected during the entire breeding season.

Daily failure rate at egg and nestling stages

We examined the effects of habitat management on the daily probability of failure of nests, the daily failure rate (DFR), at the egg and nestling stages using an extension of the method of Mayfield (1975), which allows for variation among nests and nesting stages in the period during which the outcome was monitored. We followed Aebischer (1999) in using a generalised linear model (GLM) with a logistic link function and binomial error term to fit logistic regression models in which the number of binomial trials in the analysis is the number of days for which each nest was monitored and on which its outcome (survival or failure) on each day was observed. The total number of binomial trials per nest was therefore the number of exposure-days of the nest in the Mayfield method; for further details see Aebischer (1999). We adapted the approach by taking the binary dependent variable to be the outcome on each exposure-day to be failure (1 = failed) or survival (0 = survived). Exposure-days and failure events for each nest were partitioned between the egg stage and nestling stage and a binary independent variable representing stage (0 = egg stage; 1 = nestling stage) was included in the model for each exposure-day to account for the possible effect of stage on DFR. For the purposes of modelling, we assumed that nests that failed did so at the midpoint between the penultimate and final nest check. Our principal

objective was to model DFR in relation to two independent variables, i.e. habitat management and breeding season, both recorded as binary variables (unmanaged = 0, managed = 1, 2020 = 0, 2021 = 1).

Studies of DFR often find differences between the egg stage and the nestling stage, so we would ideally have fitted separate models to data from these two stages. However, this was not possible because no nesting attempts survived to hatching in unmanaged territories in 2021. Instead we analysed egg-stage and nestling-stage data together in the same models using the logistic regression method described above and assumed that the effect of stage on logit (DFR) was independent of season and management treatment. We fitted five models including main effects, in addition to stage, of (1) season or (2) habitat management included separately, (3) both of these main effects included together, (4) both of the main effects and their two-way interaction, and (0) the null model with no covariates except for stage. For each fitted model, we used the residual deviance and number of fitted parameters to calculate the small-sample Akaike Information Criterion (AIC_c) (Burnham and Anderson 2002). We selected the model with the lowest AIC_c value.

The survival of breeding attempts from the first-egg date (FED) to hatching and from hatching to fledging was calculated by raising the daily attempt survival rates (1-DFR) estimated from Model 4 to the power of the mean duration in days of FED to hatching (16.8 days) and hatching to fledging (20.4 days) periods. These two survival rates were multiplied together to give the probability of survival of a nesting attempt from FED to fledging. We multiplied these probabilities by the mean number of young per fledged brood to obtain the mean number of fledglings per breeding attempt. There were insufficient observations of the size of fledged broods to calculate means separately for each year and management treatment category, so we multiplied by the mean number of young per fledged brood for both treatments combined, which was 2.0 in both seasons.

Incubation time per hour

We fitted a linear least-squares mixed model (LMER) in R using the *lme4* package (Bates et al. 2015) with female attendance in nest (in minutes per hour) as the dependent variable and management type and year as independent variables modelled as fixed effects, both being taken to be binary variables (untreated = 0, treated = 1, 2020 = 0, 2021 = 1). Nest ID was modelled as a nested random factor with pair ID to account for pseudoreplication. A variance inflation factor (VIF) test was conducted to test for collinearity among predictors. Additionally, the model was checked for normally distributed residuals using the Shapiro–Wilk test for normality and by visually observing the Q–Q plot of the residuals. Homoscedasticity of residuals was also confirmed via visual inspection of scaled residuals and by conducting a studentised Breusch–Pagan test using the “bptest” function from the *lmtest* package (Zeileis and Hothorn 2002). *T* values and *P* values were obtained using the *lmerTest* package (Kuznetsova et al. 2017).

Season-long breeding productivity

The preceding analyses allowed us to estimate the mean number of fledglings per breeding attempt, but individual pairs were observed to make several breeding attempts in the same season, often replacing failed attempts. Ideally, we would also have estimated season-long breeding productivity by using a simulation model of nesting (Beintema and Muskens 1987; Green et al. 1997), but there were insufficient data to estimate all the relevant parameters

separately for the two seasons and two habitat treatments. We therefore divided the total number of fledglings recorded for each season per treatment combination by the number of territories monitored to give the mean season-long productivity. We expect this approach to be accurate, even if we did not find and record every breeding attempt in every territory. That is because breeding attempts that survived the 37 days from FED until fledging would be highly likely to be detected at some time during this lengthy period.

Of the nesting attempts that were recorded as hatching ($n = 12$), the first record of eggs being present in the nest was obtained within four days of FED in all cases (mean 1.7 days; range 0–4 days), even though the duration of incubation was 17 days. Although sample sizes were small, there was no indication of any marked difference in this interval between nests in unmanaged and managed plots (unmanaged: mean 2.5 days; range 1–4 days; $n = 2$; managed: mean 1.5 days; range 0–3 days; $n = 10$). In addition, nests were often found during building before eggs were laid. We concluded that our simple measure of season-long productivity is likely to have been accurate for both unmanaged and managed territories.

Results

Foraging and perch height

Of 242 foraging observations of males and females, 160 observations (of 10 individuals) were in managed areas and 82 observations (of 15 individuals) were in unmanaged areas. We recorded the foraging height of 237 observations and perch height of 236 observations. The RLMM showed that management type had a significant effect on foraging height ($t = -3.72$, $P < 0.001$, $n = 237$), with birds having a $1.39 \pm \text{SE } 0.37$ m lower foraging height in managed areas. Perch height was also significantly lower in managed areas ($t = -3.87$, $P < 0.001$, $n = 236$), with a $1.16 \pm \text{SE } 0.30$ m lower perch height in managed areas (Figure 2). Sex of individuals did not significantly affect foraging height ($t = 0.47$, $P = 0.64$), nor perch height ($t = 0.69$, $P = 0.49$). Of the 242 foraging observations, we were able to identify 70 prey items as Lepidoptera in larval stage (caterpillars) (36% managed, 16% unmanaged), followed by 31 prey items as adult stage Lepidoptera (moths/butterflies) (12% managed, 13% unmanaged), two prey items as Diplopoda (millipedes), and one item as Coleoptera (ladybugs) (2% managed, 1% unmanaged). A total of 138 observations that were categorised as unknown prey (50% managed, 71% unmanaged) were small invertebrates that were immediately swallowed by the bird when hunting in the air.

Pair formation

In managed areas, we found four males with a mate and three males without a mate, while in unmanaged areas, we found five males with a mate and 11 males without a mate. Two of these pairs in unmanaged areas did not nest. There was no significant difference in pair formation between managed and unmanaged areas (Fisher’s exact test, two-tailed, $P = 0.36$).

DFR at the egg stage

DFR at the egg stage was similar in the two management types in 2020, but was much higher in managed than in unmanaged territories in 2021 (Table 1). Nestling-stage DFR was very similar in unmanaged and managed territories in 2020. No nests were

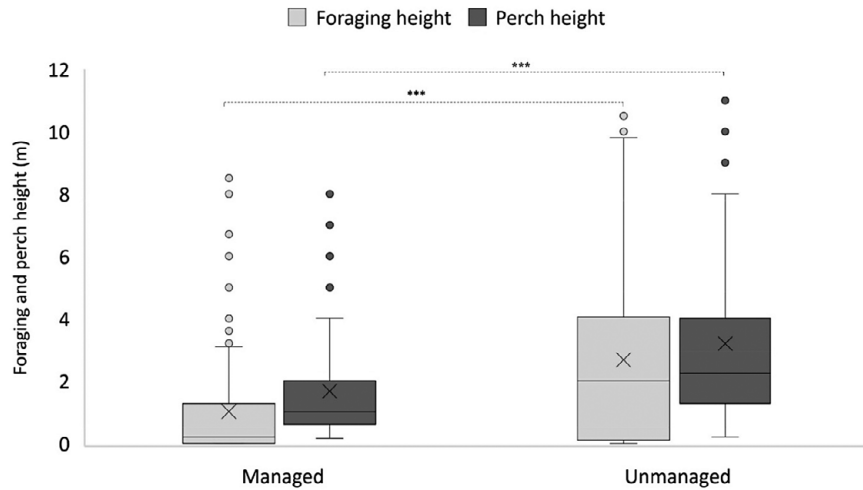


Figure 2. Foraging height and perch height of Little Vermilion Flycatcher *Pyrocephalus nanus* in managed versus unmanaged areas. The coloured circles in the graph represent the outliers of the collected data. The upper boundary of the boxplot reflects the third quartile, the lower boundary reflects the value of the first quartile, and the whisker lines show the least and greatest values. The line inside the boxplot reflects the median and the x symbol denotes the mean.

Table 1. Breeding success of Little Vermilion Flycatcher *Pyrocephalus nanus* on Santa Cruz in 2020 and 2021 in relation to habitat management in territories to control invasive plant species. DFR values are from stage-specific data for each treatment class and year and not from logistic regression models. No eggs hatched in monitored nets in 2021 in unmanaged territories, so the DFR could not be estimated. The probability of a breeding attempt surviving from FED to fledging was calculated from Model 4 (see text). The number of fledglings recorded per monitored territory recorded during the whole season is also shown. DFR = daily failure rate; FED = first-egg date

Parameter	2020		2021	
	No	Yes	No	Yes
Habitat management				
Breeding territories monitored	3	7	3	4
Attempts monitored at egg stage	7	18	5	12
Egg-stage DFR	0.0806	0.0733	0.1852	0.0337
Nestling-stage DFR	0.0500	0.0476	–	0.0263
Attempt survival probability: FED to fledge	0.0556	0.0745	0.0000	0.3033
Mean number of fledglings per attempt	0.111	0.149	0.000	0.607
Total fledglings recorded per territory	1.000	0.429	0.000	2.000

monitored at the nestling stage in unmanaged territories in 2021, so unmanaged and managed territories could not be compared. Logistic regression modelling identified the model of DFR at both nesting stages with main effects of breeding season, habitat management, and their two-way interaction (Model 4) as having the lowest AIC_c value of the five models compared (Table S1). The 95% confidence interval (CI) for the interaction term between season and management treatment provided strong evidence for a difference in the effect of treatment between seasons (95% CI for the interaction term for logit DFR: -3.318 to -0.180), there being no evidence for an effect of treatment on logit DFR in 2020 (95% CI for the treatment term: -1.072 to 0.881), but strong evidence for a negative effect of treatment in 2021 (95% CI for the treatment term: -3.135 to -0.613).

DFR at the nestling stage

Nestling-stage DFR was very similar in unmanaged and managed territories in 2020. No nests were monitored at the nestling stage in unmanaged territories in 2021, but nestling-stage DFR was considerably lower in managed territories in 2021 than in 2020. However,

the sample sizes were small and this apparent difference between years was non-significant ($\chi^2_{(1)} = 0.36, P = 0.55$) (Table 1). Overall, nests in managed areas were active longer (mean $15.77 \pm SE 2.00$ days, $n = 30$) than nests in unmanaged areas (mean of $8.25 \pm SE 2.94$ days, $n = 12$) (Figure 3).

Incubation time

In areas with vegetation management, females spent significantly more time in the nest compared with unmanaged areas ($t = 2.74, P = 0.018, n = 116$), namely on average $12.18 \pm SE 4.45$ minutes longer per hour of observation (Figure 4). Year did not have a significant effect on the time the female spent in the nest ($t = -0.88, P = 0.40, n = 116$) (Figure 3).

Per-attempt nest success and season-long breeding productivity

As a consequence of the results obtained from the DFR analysis, per-attempt nest success was similar in unmanaged and managed territories in 2020, but there was a large difference in 2021, with

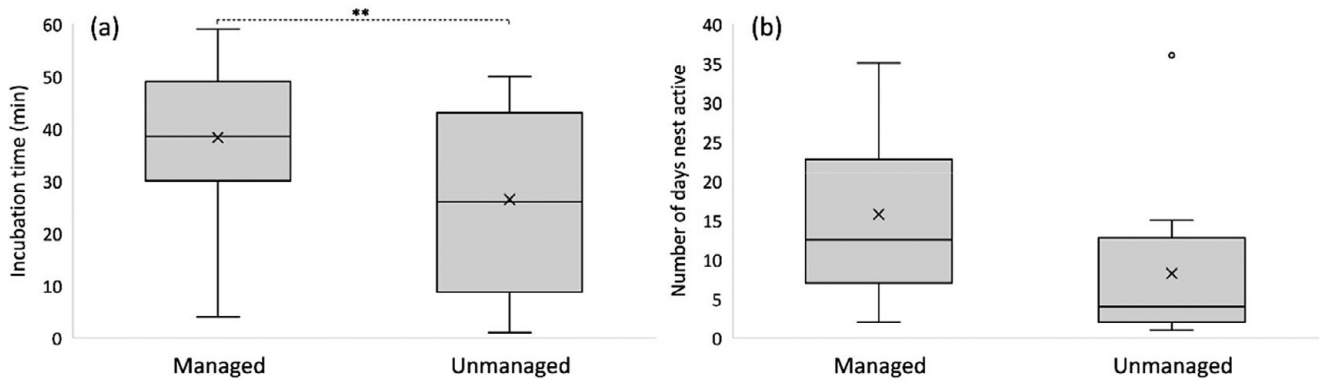


Figure 3. (a) Length of time (in minutes per hour) the female spent sitting on the nest for each management type. (b) Number of days that the nests were active in habitat managed versus unmanaged areas during the 2020 and 2021 breeding seasons combined. The upper boundary of the boxplot reflects the third quartile, the lower boundary is the value of the first quartile, the whisker lines indicate the least and greatest values. The line inside the boxplot reflects the median and the x symbol denotes the mean.

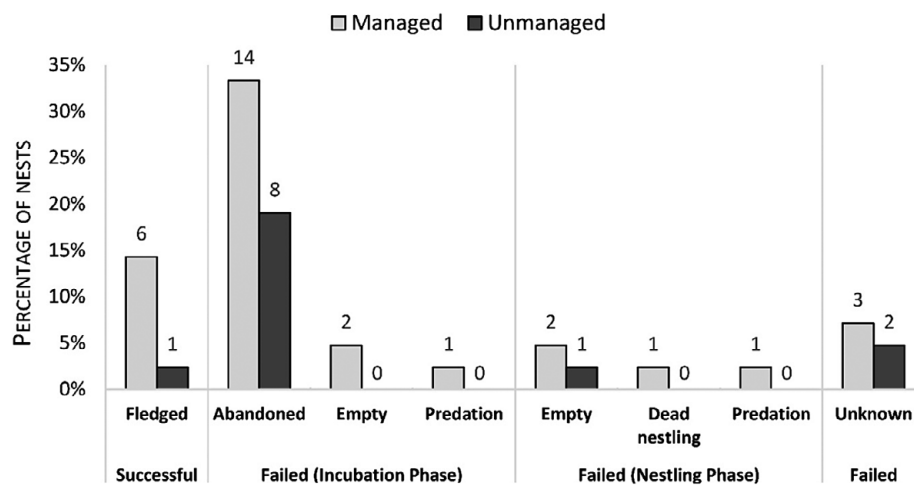


Figure 4. Nest outcome of Little Vermilion Flycatcher *Pyrocephalus nanus* in Santa Cruz during the 2020 and 2021 breeding seasons.

success being zero in unmanaged territories and substantially higher in managed territories than it was in managed territories in 2020 (Table 1). A similar pattern was seen for season-long breeding productivity (Table 1).

Nest outcome

In total, we observed 42 breeding attempts (30 in managed and 12 in unmanaged areas) from at least 10 breeding pairs. Not all the birds in our study were ringed, therefore, it could not be verified if they were the same breeding pairs in both years. Overall, seven successful nests were monitored during both years with 14 fledglings in total, including six nests in managed areas and one nest in an unmanaged area (Figure 4). Abandonment (with intact eggs) during the incubation phase was the main reason for breeding failure in both managed and unmanaged areas (Figure 4). During the nestling phase, one nest was found with a dead nestling and Vampire Fly parasitism and/or heavy rain probably caused this nest to fail. Predation seemed to play only a minor role, as only two nests showed obvious signs of predation (one nest in the incubation phase and one nest in the nestling phase). However, a more detailed study with trap cameras would be important in order to assess the level of predation.

Eggs

Most (60%) of the 78 eggs that were laid were fertile in both breeding seasons. Only one egg during those seasons was infertile. The fertility of 30 unhatched eggs could not be determined. Of these, 18 eggs were lost when they fell from the nests during nest collection from high tree branches and could not be found on the forest floor and 12 eggs were in early development, so we could not determine their fertility.

Discussion

Habitat management had a delayed positive effect on the breeding success of LVF. Although habitat management did not have a significant effect on pair formation, pairs that were in managed areas nests survived longer, pairs had more breeding attempts, longer incubation bouts, and higher breeding success in 2021. We hypothesise that this was mainly influenced by increased food availability in the managed areas, since we recorded a significantly lower perch and foraging height in managed territories in 2021. These results are similar to those of Leuba et al. (2020), who reported that a lower perch height in the near pristine site Alcedo was associated with higher foraging success. It would have been

valuable in our study to also measure foraging success as prey captures per unit time or the provisioning rate to nestlings, but we were unable to collect sufficient good quality data to do this.

Forests that have open areas, whether they are man-made or natural, generally have higher numbers of flycatchers than closed forest areas (Mannan 1984), since flycatchers generally prefer open areas to closed forests with dense vegetation (Beedy 1981; Mannan 1984). This may be due to the flycatchers' need for areas with perches and unobstructed airspace, which allows them to visually scan a large area for invertebrates on the ground or in the understory (Beedy 1981). Given this, in open areas, researchers may be able to detect LVFs better and their conspicuous display behaviour, their tendency to approach humans, and their bright coloration increase detectability. Although the dense bramble thickets in unmanaged areas may have reduced our ability to detect unpaired females, our intensive search effort and the conspicuous behaviour of paired males render it unlikely that we missed breeding attempts or that our estimate of productivity was affected by the different visibility in managed and unmanaged areas. The detectability of birds during foraging is unlikely to have affected foraging height data. We understand that further concerns could arise with data from unmanaged areas where dense vegetation may have prevented sightings of foraging birds. However, we made detailed observations on LVF behaviour in areas with dense vegetation in prior years (Charles Darwin Foundation, unpublished data), which showed that LVFs preferred to move quickly to hunt by surprise, flew quickly or perched over vegetation, and foraged above it. They were not observed trying to manoeuvre their way through the dense vegetation.

Food availability plays an important role in bird breeding decisions and behaviour (O'Brien and Dawson 2011; Rubenstein 2007). In line with these studies, we recorded significantly more breeding attempts, longer nest duration, and longer incubation bouts in managed areas. In House Sparrows *Passer domesticus*, females prolonged their bouts of attendance at their nests in habitats with more food sources compared with areas with fewer food sources (Václav *et al.* 2003). Higher food density in territories may allow adults to avoid travelling far in the search for food and reduce the chance of extra pair copulation, which may also influence the time invested in the nest (Davies and Lundberg 1984). Likewise, a higher density of food may allow adults to increase their food delivery to nestlings and increase nest success.

Habitat restoration and effect on breeding success

Even though we found a positive effect of habitat management on DFR at the egg stage and on the probability that a nest would survive from egg laying to fledging, this effect was not apparent until 2021. This might be because regeneration of Galapagos native and endemic plants and their associated invertebrate fauna takes time after invasive plant removal (Cimadom *et al.* 2019). Management of habitat is a long-term investment and several forest restoration projects reported that birds increase their reproduction in these areas over time (Gaines *et al.* 2007; Hartung and Brawn 2005; Ortega-Álvarez and Cisneros 2012).

Despite habitat restoration efforts, many LVF nests failed during the early incubation phase in managed areas in the 2020 season, continuing a similar pattern observed since 2017. The first weeding of plots started in January 2019 and, during that whole year, there was more disturbance at the study site. Therefore, we initiated this study in 2020 to allow the native vegetation to regrow. However, it is likely that in 2020, nest abandonment was higher in managed areas

as the vegetation and associated invertebrates were likely still recovering from the initial cutting of vegetation. In 2021, we did not record nest abandonment in early incubation and the birds remained very active and committed to their nests. This could suggest an improvement in habitat conditions over time in managed areas.

Weather and predation also played a role in nest failure. In both breeding seasons, torrential rains and strong winds affected the success of six LVF nests, including five nests in managed areas and one in an unmanaged area. Strong wind and rain can have a negative effect on passerine nests in the Galapagos, as the nests become wet and the eggs and nestlings get cold quickly (Cimadom *et al.* 2014). Additionally, Heyer *et al.* (2021) found that heavy rains can prevent foraging and nestling provisioning in Darwin's finches. Also, during the two years of monitoring, only two out of 42 nests were predated, suggesting predation only has a minor effect, as reported in prior studies (e.g. Leuba *et al.* 2020).

Despite factors influencing nest failure in both managed and unmanaged areas, currently the highland Scalesia forest may be the most suitable habitat for LVFs. In the past, LVFs were distributed throughout Santa Cruz Island in different and more open types of ecosystems (Merlen 2011; Rothschild and Hartert 1899). However, habitat reduction, highly intensive agriculture, and use of pesticides might have reduced prey sources. Additionally, another possible reason why the Santa Cruz LVF population persists in the highlands is that there is a lower Vampire Fly parasitism intensity at the beginning of the breeding season in higher, colder areas (Mosquera *et al.* 2022), which could have alleviated the pressures of parasitism.

Fertility and small population size

Contrary to expectations that the fertility of a small population would decrease due to a bottleneck effect, such as inbreeding (Jamieson and Ryan 2000), this appears not yet to be a frequent problem in this population since most eggs were fertile. The small number of individuals (30 birds in 2020 and 32 in 2021), with twice as many males as females observed, is of great concern. Perhaps some females or males were not detected, which could have affected the sex ratio. However, half of the males observed in our study were unmated and competed to mate with the few females we observed, which suggests that there are a limited number of females at the study site. Small populations are at higher risk of experiencing random imbalance of their sex ratio due to demographic and environmental stochasticity (Frankham and Wilcken 2006; Robinson *et al.* 2014). Male LVFs' distinct red plumage and courtship/territorial behaviours can make them more vulnerable to natural predators; however, this could also increase detectability for researchers. Contrastingly, females have cryptic plumage and are more evasive; however, they are more vulnerable while brooding in open cup nests, where predators could attack more easily. In general, for many threatened avian species, females have higher mortality rates than males (reviewed in Donald 2007). Females spend a lot of energy, laying up to five clutches with two to three eggs per season. Most of these nests were not successful, but they continued to make repeated attempts. This high-energy investment by the female required for egg development (Meijer *et al.* 1989) and the reduction of favourable food sources could influence their long-term survival and overall fitness (Hanssen *et al.* 2005).

Given the positive effect of habitat restoration in this study, habitat management and removal of invasive plants appears to be a valuable tool for the recovery of the LVF population. Based on our study and knowledge of the pressures on this population, we believe

that the most important management objectives for improving the breeding success and stabilising the population are as follows: (1) continued persistent control of Vampire Fly parasitism; (2) restoration of endemic forests without the use of pesticides and avoidance of additional habitat reduction; (3) continued controlling of any potential predation from invasive species, such as rats, cats, and possibly the invasive Smooth-billed Ani *Crotophaga ani*; (4) evaluation of the impact of diseases on LVF; (5) reduction in mortality from car impacts on birds; (6) evaluation of the consequences of the bottleneck effect on this population; (7) after the factors that are causing the LVF's decline are controlled, the evaluation and review of the possibility of translocation of individuals from other populations to Santa Cruz to increase genetic diversity if proven necessary.

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