

## Article

# Effects of Deforestation on Foraging Behavior, Ectoparasites, and Adult Survival in the Vulnerable La Selle Thrush, *Turdus swalesi*, in Haiti

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**Abstract:** Although range-restricted Neotropical bird species are highly endangered, little is known about their ability to cope with environmental disturbance. We studied the vulnerable, Hispaniola-endemic La Selle Thrush (LST), *Turdus swalesi*, in a protected forested area in Haiti threatened by agriculture, livestock and logging. We used capture–mark–recapture, visual observations, and camera traps to document foraging ecology and estimate adult survival over 26 months. LST foraged mainly in deciduous woodlots. However, some individuals regularly foraged on or around dung pats in fallow pastures, whereas no other ground-dwelling bird species was observed to do so. Coincidentally, 16.5% of 79 mist-netted LST harbored Ixodid ticks, compared to none of the 2131 individuals belonging to 29 other species mist-netted in the area. This suggests that infestation with ticks might come as a cost of opportunistically exploiting a new food resource. Apparent annual adult survival rate was independent of sex, and varied between 0.393 and 0.440, depending on the inclusion of a transience effect in our models. This low value was possibly due to “permanent” emigration from the site during the study. We discuss the potential effects of deforestation on the ecology and demography of LST and make recommendations for future conservation-oriented research in Haiti.

**Keywords:** adult survival; conservation; deforestation; ectoparasites; foraging innovation; Ixodid ticks; neotropical bird species; *Turdus swalesi*



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## 1. Introduction

Of the 1227 bird species worldwide that are currently considered threatened with extinction, 79% occur in lowland and mountain tropical forests [1]. Deforestation, overexploitation, pollution, invasive species, and diseases have been identified as major threats for Neotropical forest bird species [1–3], and recent evidence [4] further indicates that their decline can take place in relatively large and protected areas. Knowledge about the ecology, behavior, and key demographic parameters is therefore of crucial importance for their conservation [5–7]. This is even truer of endemic and range-restricted species, as they are at greater extinction risk from localized events such as introduction of alien species or extreme climatic events [8,9]. However, the available information on Neotropical forest bird species mostly comes from species of minor or no conservation concern, with relatively wide geographical distribution areas [7,10–16]. In contrast, data on threatened and range-restricted bird species are scarce [17,18].

The vulnerable La Selle Thrush, *Turdus swalesi*, is one such range-restricted species, endemic of the island of Hispaniola in the Greater Antilles, where its distribution range

is limited to three mountain chains in Haiti and the Dominican Republic [19–21]. It is a sexually monomorphic turdid species, with a black, rufous and white plumage, and yellow-to-orange bill and eye-ring [22]. It has limited sexual dimorphism regarding size, with only wing chord and tail tending to be longer in males than in females [23]. This diurnal species can be observed in the dense vegetation of mountain forests, particularly in rainy and cloudy deciduous forests, and, more rarely, in pine forests [21,24,25]. Its mixed diet consists of fruits and berries, and invertebrates [21,26].

The La Selle Thrush was considered to exist in reasonably large numbers until about 1986 [19,27,28]. However, since then, a sharp decline in its abundance and distribution has been reported [29], possibly as a consequence of ongoing forest conversion to agriculture on Hispaniola, including in supposedly protected areas [30,31]. Despite the conservation status of the La Selle Thrush and the fragile state of its restricted distribution area, very limited quantitative information exists on its population dynamics and behavioral ecology. In particular, little is known about how the species is affected by deforestation. Such data are, however, of prime importance to assess population viability and develop effective conservation plans to prevent the species from further decline and contribute to its recovery.

Considering this urgent need, we developed a research and monitoring program of the La Selle Thrush in southeastern Haiti. First results recently allowed us to assess the extent of sexual dimorphism and to provide evidence for a strongly male-biased sex ratio in our study population [23]. Here, we report new and original results on the behavioral ecology and demography of the La Selle Thrush in Haiti in relation to deforestation. We particularly assessed spatial and temporal variation in foraging activity and foraging habitat use, prevalence of infection with ectoparasites, and adult survival rate based on captures and marking of individuals, visual observations and data obtained from camera traps. We discuss our results in relation to the ability of the species to adapt to environmental perturbations and we provide some recommendations for future research.

## 2. Materials and Methods

### 2.1. Study Area

The presence of the La Selle Thrush has been previously documented in several protected areas in the La Selle ridge [28,32]. In order to select our study site, we carried out four preliminary surveys, for a total of 16 days between January and September 2019 throughout the Haitian side of the area, particularly within Parc National Forêt des Pins and Parc National La Visite. Based upon observed spatial variation in observed density, accessibility and logistical constraints, we selected the so-called “Tête Opaque” site (18°20.928' N, 72°14.347' W, with an altitude varying between 2146 and 2260 m) as our study site (see [23]). The site is located within Parc National La Visite, to the north of the first municipal district of Baie d’Orange, commune of Belle Anse, in Haiti’s South-East department. It is close to Morne Cabaïo, the highest peak in Parc La Visite. Access to the study area was limited to the rugged mountain road running from Port-au-Prince through Furcy and Ca Jacques (see [23]). The surrounding vegetation mainly consists of deciduous wooded lots, considered as the main type of habitat for La Selle Thrush, with coniferous trees, *Pinus* spp., being the most dominant tall trees (see [33]) for a detailed account of the local vegetation). The presence of 42 migratory and resident bird species was previously recorded in the area [33], including several endemic ones, as well as exotic mammals such as the small Indian mongoose (*Urva auropunctata*), feral domestic cats (*Felis catus*), stray dogs (*Canis lupus familiaris*), and rats (*Rattus* spp.). Although Parc La Visite is officially a protected area, the forest ecosystem in the park is threatened by human activities such as agriculture, livestock and logging (see [30,33] for details).

### 2.2. Data Collection

We carried out 13 consecutive capture sessions at our field site between December 2019 and January 2022. However, because of COVID-19 pandemic restrictions and safety issues, we were unable to conduct capture sessions from April to August 2020. On each

capture session, we deployed mist nets (Ecotone<sup>®</sup>, Gdynia, Poland, 6 × 3 m, 19 mm mesh, most suitable for capturing La Selle Thrush and Ecotone<sup>®</sup> 12 × 3 m, 30 mm mesh) along footpaths created by humans and pre-existing openings in vegetation corresponding to abandoned agricultural plots. In order to minimize interference with current agricultural activities by local people, we rotated locations over a total distance varying between 800 and 1000 m, such that our study area covered about 268 ha (see [23]). Due to various logistic constraints, we were unable to maintain a constant capture effort during the course of the study. First, the duration of capture sessions varied from 3 to 15 days (mean = 11.08; median = 12.5), partly depending on weather conditions. Second, the total length of the mist nets increased progressively from 12 m to 96 m from the first to the last session, while the total time spent catching birds in mist nets per capture session ranged from 20 to 108 h (see [23] for details about capture effort per session). Each captured bird was banded with an aluminum leg band engraved with an alphanumeric code and a unique combination of colored plastic rings (see [23] for details) and was visually inspected (for about one min) for the presence of ectoparasites. In addition, we took standard biometric measurements and measured weight to the nearest gram using a Pesola<sup>®</sup> (Schindellegi, Switzerland), 500 g spring scale. Blood and/or feather samples were collected as a source of DNA to allow subsequent molecular sexing (see [23] for details). However, we immediately released birds after ringing when captured late in the day (about the time they are roosting for the night), such that data on sex and morphology were obtained for only a subset of all ringed birds.

Data collection was completed by regular observations of banded and non-banded La Selle Thrushes using binoculars (KITE (Jabbeke, Belgium) 8 × 23) during each session. In addition, starting on the third session, we used camera traps (Moultrie (Bristol, UK) M8000i) that remained active 24 h d<sup>-1</sup> in order to both increase the recapture rate of banded individuals and to document variation in diel activity of La Selle Thrushes. The number of cameras increased from 5 to 17 from the third to the last session, as additional funding became available to purchase additional units during the course of the study (see [33] for details). Each single camera was attached to a robust tree in areas where the vegetation was not too dense. Camera-trap parameters (shutter sensitivity, height above the ground, and distance of detection range) were set so as to maximize the probability that ground-dwelling bird species, such as the La Selle Thrush, present in the study area would be detected (see [33] for details). In order to avoid multiple photographs of the same individual over short time periods, we programmed each camera trap on a 30 s delay between trigger events, with one picture per detection event. Time of day was automatically recorded by the camera trap on each detection event.

### 2.3. Data Analysis

#### 2.3.1. Foraging Behavior

We documented ground-dwelling foraging activity using both visual observations and data from camera traps. First, direct observations of individuals allowed us to qualitatively assess to what extent La Selle Thrushes exploited different forested (pine woodlots and deciduous woodlots) and deforested (crops and fallow lands used to pasture livestock) patches in our study area, and to establish comparisons with other avian species observed there (see [33]). Second, photos obtained from camera traps allowed us to quantitatively assess diel variation in the ground-dwelling activity of La Selle Thrushes at our study site. The pattern of diel activity, i.e., the distribution of activity throughout the daily cycle, is an important aspect of animal behavior that is influenced by various environmental constraints such as resource availability, predation risk, and level of disturbance [34–36]. We visualized patterns of daily ground-dwelling activity in forested habitat from the frequency distribution of photos of La Selle Thrushes obtained during the course of the study according to time of day. To that end, we pooled photos from all sessions without time transformation, as our study area is located below 20° latitude (see [37]). We then relied on a dip test [38] to assess deviation from a unimodal distribution, using the dip test function available in the dip test package [39] in the R Statistical Software 4.2.0 [40]. Third, we

analyzed daily variation in body mass of birds at first capture, as a clue to the daily routine of mass gain [41]. Based on evidence in other bird species [42], including turdids [43], we expected body mass at capture to increase from dawn to dusk. As the distribution of captures of weighed birds during the day was clearly bimodal (see results) and weight was normally distributed (see [23]), we compared the weight of first-captured individuals between the morning and afternoon using a *t*-test. We then checked for an increase in body mass with time of capture separately among birds captured in the morning and among birds captured in the afternoon using a one-tailed Spearman rank order correlation test.

### 2.3.2. Prevalence, Intensity and Consequences of Infection with Ectoparasites

Using records on ectoparasites on captured individuals, we calculated the prevalence (percentage of infected individuals) and intensity of infection (number of ectoparasites per infected individuals). We then used a Fisher's exact test to compare the prevalence of infection between males and females, based on a subset of sexed individuals [23].

### 2.3.3. CMR Modelling of Adult Survival Rate

Using package RMark 2.2.7 [44] in the R Statistical Software 4.2.0 [40], as an inter-phase of MARK 9.0 [45], we relied on the Cormack–Jolly–Seber (CJS) model structure for open populations [46] to separately estimate recapture probability ( $p$ ) and apparent survival probability ( $\phi$ ). We first built individual capture histories using data collected from captures and recaptures with mist nets, visual observations of banded individuals using binoculars, and photos of banded individuals taken by camera traps. One assumption of mark–recapture modelling is that the period of marking (and re-sighting) should be short, relative to the period over which survival is measured [47], although violating this assumption results in relatively small bias [48,49]. Following Robinson et al. [50], and since several individuals were resighted several times in a given session, we rearranged the data into 13 consecutive sessions, separated by a two-month time interval from December 2019 to January 2022 (see Appendix A), assuming that birds survived from the mid-point of one time interval to the mid-point of the next, two months later. In order to take into account the interruption of field work in spring 2020 (see above), we included two “virtual” bimonthly sessions (session 3: April–May 2020 and session 4: June–July 2020), for which we fixed  $p$  to zero in the CMR analyses [51]. We tested for trap-dependence, i.e., individuals captured at  $t$  have a significantly higher or lower probability of being captured at  $t + 1$  than individuals not encountered at  $t$ , test 2CT in program U-CARE [52]. Because we had no evidence as to whether mist-netted birds were year-long residents or were just transiting through the study area, we were interested in estimating the proportion of transients in the population [53]. The transience effect corresponds to a lower expectation of re-observation of individuals marked for the first time as compared to other individuals [53,54]. To that end, in addition to test 3SR in program U-CARE [52], we considered models with two age classes, where  $\phi_1$  is the apparent survival of first-captured individuals and  $\phi_2$  is the apparent survival of previously captured individuals. The proportion of transients among the marked individuals can then be obtained as  $1 - (\phi_1 / \phi_2)$  [53].

Because sex could not be determined for all captured individuals ( $n = 79$ ), we first evaluated the effect of sex and transience on  $\phi$  and  $p$  on a data subset containing only the capture histories of 66 sexed individuals (45 males and 21 females [23]). We compared the goodness-of-fit of models including the null, constant, additive or interactive effects of sex, time, and transience (55 models), using the Akaike information criterion for small sample sizes (AICc, [55]). We retained the model with the lowest AICc value as the best model out of the total set of models, and considered all models that differed by fewer than two AICc units from the best one ( $\Delta\text{AICc} < 2$ ) to have substantial support [56]. As sex had no significant effect on either  $\phi$  or  $p$  (see Results), we then included all captured and banded individuals in the data set for further analyses. We used the same procedure as described above to compare models including the null, constant, additive or interactive effects of transience and time interval between two bimonthly sessions on both  $\phi$  and  $p$ .

From the best model, we calculated the probability of survival between two bimonthly sessions,  $\phi_b$ , as the logit transformation of the beta estimator of survival,  $\beta$ , with  $\phi_b = 1/(1 + e^{-\beta})$ . We then calculated the annual survival rate as  $\phi_b^6$  and the mean lifespan in months as  $[-2/\log(\phi_b)]$ .

#### 2.4. Ethical Note

Access to the protected area of “Parc National La Visiste”, capture and handling of birds and collection of biological samples (blood and feathers) were carried out with the agreement of the Direction of Biodiversity, Haitian Ministry of the Environment (authorization 28 July 2023). The study complied with relevant laws and guidelines for the capture and banding of birds, as well as with rules for collecting genetic data.

### 3. Results

#### 3.1. Foraging Activity

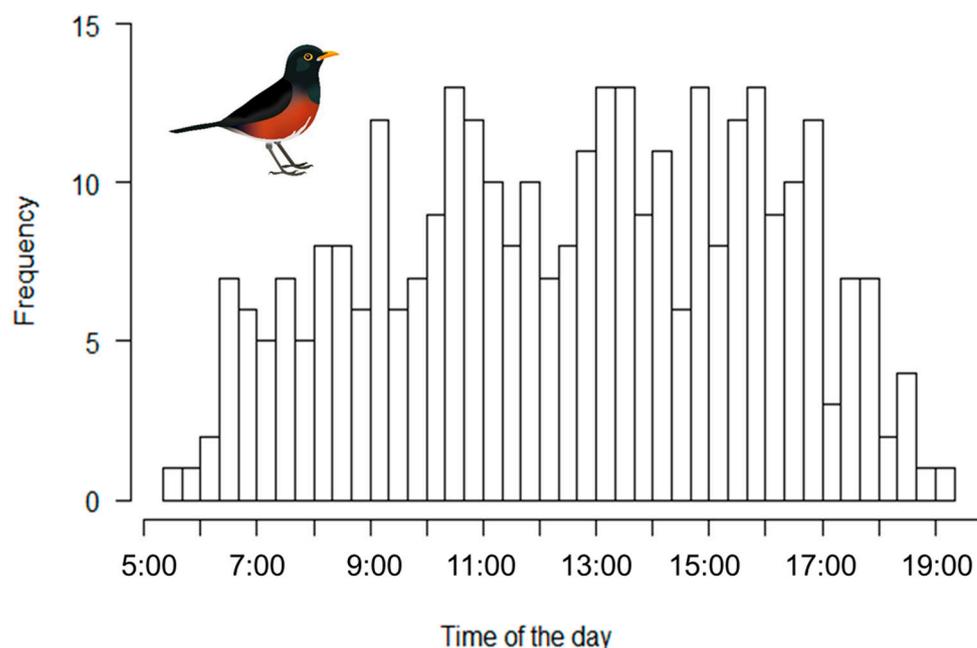
We visually observed La Selle Thrushes foraging on the ground on the edges of deciduous forest woodlots. In contrast, we never observed the species foraging in pinewoods. La Selle Thrushes were occasionally foraging in croplands, soon after plowing and/or following rainfall. Finally, we regularly observed them in fallow lands used to pasture livestock, mostly in the early morning and the late afternoon, where they fed upon insects flushed out by cattle as they graze, and on and around dung pats. Dung exploitation was peculiar to the La Selle Thrush, as it was not recorded in any of the 29 other bird species that we observed foraging in pastures during the study period [33]. Although we did not proceed to any quantitative assessment, we did not notice any difference in the intensity of use of the different foraging habitats through time. Most individuals were observed foraging alone, although some flocks of up to five birds were occasionally seen feeding in croplands or pastures.

Using camera traps, we obtained 323 photos of La Selle Thrushes foraging or standing on the ground within deciduous woodlots (Figure 1).



**Figure 1.** Camera trap photographs of banded male (a) and non-banded (b) La Selle Thrushes foraging within deciduous woodlots at Tête Opaque, Haiti.

Out of these, only one photo was taken of two individuals foraging on the ground at close distance, whereas all other photos showed only one individual. Thirteen photos (4%) showed one of eight banded individuals (three males, three females and two birds of unknown sex), whereas all other showed non-banded birds. The frequency distribution of photos according to time of day (Figure 2) was unimodal (Dip test,  $D = 0.01$ ,  $P = 0.984$ ), and was indicative of a regular increase in activity/number of birds foraging on the ground from dawn to about 10:00 a.m., followed by a plateau and a sharp decrease from about 5:00 p.m. to dusk.



**Figure 2.** Frequency distribution of photos of La Selle Thrushes made with camera traps according to time of day.

Body mass of birds at first capture was normally distributed, and ranged from 90 to 120 g (see [23]). However, time of capture followed a bimodal distribution (Dip test,  $D = 0.10$ ,  $P = 0.0005$ ), with 35 individuals captured between 5:30 and 8:20 a.m., and 15 individuals captured between 3:25 and 7:30 p.m. Birds captured in the afternoon were on average 8.8% heavier than birds captured in the morning (mean body mass  $\pm$  s.d. in grams, morning:  $114 \pm 11$ , afternoon:  $124 \pm 13$ ;  $t$ -test,  $t = 2.71$ , d.f. = 48,  $P = 0.0094$ ). In addition, body mass of birds at first capture increased through the daytime, both in the morning (one-tailed Spearman rank order correlation test,  $r_s = 0.32$ ,  $n = 35$ ,  $P = 0.0311$ ) and in the afternoon ( $r_s = 0.55$ ,  $n = 15$ ,  $P = 0.0117$ ).

### 3.2. Prevalence, Intensity and Consequences of Infection with Ectoparasites

Overall, 13 out of the 79 mist-netted adult La Selle Thrushes harbored hard ticks identified as *Ixodes* spp., corresponding to a prevalence of 16.5%. The intensity of infection ranged from one to five ticks, with seven individuals (50%) harboring one single tick, four individuals harboring two ticks, one individual harboring three ticks, and one individual harboring five ticks. All ticks were located on the head of infected individuals, attached to the skin on the eye ring or on the corner of the beak (Figure 3). Based on the subset of sexed individuals, we found no significant difference in prevalence of infection between males (13%,  $n = 45$ ) and females (33%,  $n = 21$ ;  $P = 0.0940$ ). The probability of recapture of individuals infected with ticks at first capture (53.8%) did not differ significantly from that of uninfected ones (36.4%; Fisher's exact test:  $P = 0.3517$ ). Interestingly, we did not observe ticks on any of the 2131 mist-netted birds belonging to 29 other species during the course of our study.



**Figure 3.** Infection with Ixodid ticks in the La Selle Thrush at Tête Opaque: camera trap photograph of a banded individual (a) and close sight of a captured individual (b). Ticks are visible inside the white circles.

### 3.3. Adult Survival Rate

We found no heterogeneity in the data when assessing the goodness of fit of the time-dependent CJS model structure with the data, using the R2ucare package [57] of the R Statistical Software 4.2.0 [40].

The model that provided the best fit with the subset of data consisting of 66 sexed individuals retained a constant survival probability across sessions, with no effect of sex or time, and a constant probability of recapture (model  $[\phi(\cdot), p(\cdot)]$ ). The second-best model ( $\Delta\text{AICc} = 1.744$ ) included a transience effect on survival and a constant recapture rate (model  $[\phi(\text{age}), p(\cdot)]$ ). The best model retaining an effect of sex (on the probability of recapture) was not informative ( $\Delta\text{AICc} > 2$ ). We therefore used the whole data set, consisting of individual capture histories of 79 individuals, to estimate adult survival.

Using the whole data set of captured individuals, we found no evidence for a trap-dependence effect (Test 2CT, sign test = 0.205, d.f. = 7,  $P = 0.5880$ ) or a transient effect (Test 3SR, sign test = 0.863, d.f. = 7,  $P = 0.6970$ ). However, test 3SR had low power because of limited sample size. Following model selection, the best model included constant adult survival and time-dependent recapture rate (model  $[\phi(\cdot), p(\text{time})]$ ). From this model, the probability of adult survival between two bimonthly sessions,  $\phi$  ( $\pm$ s.d. and 95% CI), was 0.856 ( $\pm 0.046$  [0.740–0.925]), corresponding to an apparent annual adult survival rate of 0.393 (95% CI: [0.164–0.626]) and a mean lifespan of 12.9 months (95% CI: [6.6–25.7]). The probability of recapture differed between sessions, ranging from 0.077 ( $\pm 0.045$ ) to 0.612 ( $\pm 0.156$ ). However, the second-best model ( $\Delta\text{AICc} = 2.28$ ) retained an effect of transience on survival and time-dependent recapture rate (model  $[\phi(\text{age}), p(\text{time})]$ ), whereas all other models were clearly non informative ( $\Delta\text{AICc} > 12.56$ ). From the second model, apparent survival of first-captured birds,  $\phi_1$  ( $\pm$ s.d. and 95% CI), was 0.804 ( $\pm 0.126$  [0.460–0.952]), while apparent survival of previously captured birds,  $\phi_2$  ( $\pm$ s.d. and 95% CI), was 0.872 ( $\pm 0.060$ ; [0.704–0.951]). Based on  $\phi_2$ , annual adult survival rate was 0.440 (95% CI: [0.122–0.740]), with a mean lifespan of 14.6 months (95% CI: [5.7–39.8]). The proportion of transients among the marked individuals was estimated to be 7.8%.

## 4. Discussion

Our study of the La Selle Thrush in Parc La Visite covers a 26-month period, during which difficulties inherent to the safety situation in Haiti and various logistic constraints (see [23]) limited the access to a large sample size of captured individuals and to maintaining a constant sampling effort in the field. However, combining capture and banding of individuals with direct visual observations and photos taken by camera traps allowed us to document for the first time several interesting aspects of the natural history and demography of a vulnerable and poorly known Neotropical bird species endemic on Hispaniola. This information is particularly important in connection with the evidence

recently provided for a decline of insectivorous avian species with a high level of forest-dependency over the last 15 years in our study area [33].

#### 4.1. Foraging

Although the La Selle Thrush is primarily a forest-dwelling species, our observations indicate that it can exploit opportunistically the deforested areas. Similarly, Guilherme and Lima [58] reported that the forest-dependent Hauxwell's Thrush, *T. hauxwelli*, can be encountered in cultivated clearings. Considering together diurnal activity assessed from camera traps and data on daily variation in body mass provides some insights on the foraging ecology of the La Selle Thrush. First, both direct visual observations and the data obtained from camera traps indicate that individuals were most of the time foraging alone, even during the reproductive season. Although the species is socially monogamous, mated pairs may thus partition their foraging territory to increase foraging efficiency, as reported for the closely related American Robin, *T. migratorius* [59]. Second, the observed pattern of foraging activity and the continuous mass gain during the day are suggestive of a more or less continuous foraging activity from dawn to dusk, with the percentage of weight gain during the day being in the range of what is known for free-ranging birds [42]. In particular, the unimodal pattern of activity within deciduous woodlots contrasts with the rather bimodal pattern of activity in pastures that we directly observed, but, unfortunately, did not measure quantitatively. However, such a difference is suggestive of a certain flexibility in daily activity between foraging habitats possibly related to disturbance levels, as recently shown by [35] in 16 avian species inhabiting temperate rainforests of southern Chile. One way to improve on the present results in the future would be to record fat scores [60], in addition to body mass, on a larger sample of individuals. A more intense and more regular camera-trapping effort would allow for the comparison of activity in woodlots vs. cultivated patches in order to better understand the daily routines of foraging activity in the La Selle Thrush and its variation in relation to season or level of disturbance (see [41]).

The observation of La Selle Thrushes foraging on or near dung pats in pastures deserves further consideration. The same behavior has been observed in various bird species [61–63], including, more recently, in turdids [64,65]. However, we did not observe it in other avian species during our study, suggesting that only the La Selle Thrush has learned to exploit a new and profitable resource. Indeed, although conversion of forest to agriculture and livestock areas may directly threaten the avian avifauna in Parc La Visite [23], cattle deposit dung in pastures, which may locally increase both arthropod and earthworm abundance around dung pats [66,67]. The value of dung pats for insectivores might be particularly high at Tête Opaque, as local people are too poor to purchase pesticides to protect crops or anti-helminthic treatments for cattle (J.M. Exantus, pers. obs.), such that dung pats may support high insect abundance [68]. Regular monitoring of the population in the future may help to assess whether the exploitation of dung pats concerns a growing number of La Selle Thrushes or remains limited to a few specialized individuals. In addition, it would be important to assess the costs and benefits of exploiting dung pats in pastures, compared to foraging in forested areas in terms of both foraging efficiency (i.e., energy gain per time spent foraging) and predation risk, particularly by the Red-tailed Hawk, *Buteo jamaicensis* (see [33]).

#### 4.2. Infection with Ectoparasites

Careful observations of mist-netted birds during our study allowed us to document for the first time infection with Ixodid (hard) ticks in Haiti. The exact number of different tick species in Haiti is still elusive, as literature reviews provide contradictory information [69–72]. The ticks collected on La Selle Thrushes were therefore provisionally identified as *Ixodes* sp., based on general morphology, awaiting a species identification based on more refined morphological and molecular investigations.

Interestingly, we observed infection with *Ixodes* sp. only in the La Selle Thrush, although we examined a reasonably large sample of birds belonging to different species during the course of our study. Infection with Ixodid ticks has been previously reported in a few turdid species from countries with temperate [73], continental [74], or subtropical climates [75–77]. Turdid species are actually known to show particularly high prevalence and intensity of infection with Ixodid ticks, compared to other bird species. In a study on the prevalence and intensity of infection by *Ixodes pari*, a bird-specific tick, among 32 different avian species in western and central France, Doby [78] found that turdid species were, by far, the most frequently and intensively infested hosts, with, on average, 16.7 ticks per infected individual ( $n = 35$ ) in *T. merula*. Taragel'ová et al. [79] found that two thrush species, *T. merula* and *T. philomelos*, had the highest levels of tick infestation among 38 avian species examined in Slovakia (with 95.7% prevalence of infestation), while Sormunen et al. [80] reported that turdid species generally had the highest mean *I. ricinus* load in both spring migrants and local resident avian species in Finland. Outside of Europe, Choi et al. [81] found that the Pale Thrush, *T. pallidus*, was the most important host for Ixodid ticks among 75 species of migratory birds on Jeju Island in Korea.

The high susceptibility of turdid species to infection with Ixodid ticks is often seen as a consequence of their ground-dwelling behavior, through which they are regularly exposed to juvenile ticks residing in ground vegetation and litter [82,83]. However, this explanation does not fit with our results. First, infestation with ticks was observed only in the La Selle Thrush, although we checked mist-netted individuals belonging to several other ground-dwelling forest species [33]. These included one species in particular, the Ovenbird, *Seiurus aurocapilla*, in which heavy infection with Ixodid ticks has been previously reported [84], and another turdid species, the Red-legged Thrush, *T. ardosiaceus*. Both species were photographed on several occasions by camera traps in forested sites where the presence of the La Selle Thrush was also recorded. Second, the observed prevalence and intensity of infection by Ixodid ticks in the La Salle Thrush at Tête Opaque remains moderate, compared to what has been reported for other neotropical turdid species in which prevalence can reach 60% [77] and even up to 100% [85].

We are therefore inclined to think that the infection with Ixodid ticks in the La Selle Thrush at Tête Opaque might be the consequence of foraging in pastures on or nearby dung pats. Ixodid ticks can remain in and around pastures, often in the root networks of bush and grass clumps or in the cracks formed along the roots where humidity remains high, even in the dry season, as observed in Guadeloupe [86]. Thrushes could become infected simply by passing close enough to ticks that have climbed aerial parts of plants and waiting for a potential host to attach onto it. Thrushes could also become infected with ticks through the consumption of dung beetles. Different species of dung beetles have been recorded in Haiti, including in the La Selle ridge [87]. Some evidence shows that Ixodid ticks can be occasional phoronts on coprophagous beetles [88]. Although we did not identify prey consumed by La Selle Thrushes when feeding near or on dung pats, several thrush species are known to prey upon dung beetles (reviewed in [89]).

Whatever the mechanism by which La Selle Thrushes become infected with ticks, its potential consequences deserve consideration. Although ticks can contaminate their avian hosts with various pathogens [83], most knowledge of tick-borne pathogens in the insular Caribbean is limited to a few common mammal ones [71]. Experimental and observational data suggest that Ixodid ticks can have some harmful effects on the health status of small passerine hosts [90]. In particular, several species of ticks can cause avian tick paralysis, a potentially deadly polyneuropathy characterized by progressive motor paralysis, and associated with a neurotoxin present in the female tick's salivary glands [91]. However, infection with ticks appears to have most often mild or no detectable effects on bird body condition and health, especially at low intensity [92,93]. We could not assess the effect of infestation with ticks on bird fitness in the present study, as only a low proportion of individuals were infected and because we removed ticks from most infected individuals for later identification and molecular analyses. However, the probability of recapture of first-

captured birds infected with ticks did not differ from that of uninfected ones. In addition, the recapture of one individual on which ticks had not been collected on first capture allowed us to observe that birds can get rid of ticks over time. Although La Selle Thrushes are probably unable to remove ticks attached to their head by themselves, non-nidicolous ticks are known to detach from hosts in environments that are suitable for reproduction and survival [94]. Given the uncertainty regarding the harmfulness of infection with ticks for La Selle Thrushes, we recommend closely monitoring infection dynamics, possibly on a larger sample of individuals and a longer time period, to better assess its causes and consequences.

#### 4.3. Adult Survival Rate and Transience

Our estimates of recapture rate varied extensively, most probably due to variation in both capture and observation effort between field sessions, due to logistic constraints (see [33]), but were, on average, in the range of values previously reported for turdid species [50,95,96]. In contrast, our estimate of adult survival rate was low compared to other turdid species measured using the Cormack–Jolly–Seber method [50,95–99]. This is particularly true considering the tendency for adult survival to be higher for tropical turdid species compared to temperate ones [99–103]. The estimate was, however, slightly higher after taking into account the presence of transients (i.e., individuals leaving the study area shortly after banding). Although we estimated the proportion of transients to be about 8%, to the best of our knowledge no data on other tropical forest turdid species are available for comparison. However, Whitaker et al. [104] observed large variation in the proportion of transients among three turdid species in boreal forest landscapes, with a slight tendency for transience to be more important in areas fragmented by clearcut areas. Importantly, we could not distinguish mortality from permanent dispersal, which resulted in estimating apparent survival, not actual survival. Our estimate must therefore be considered as an underestimation of true survival. Indeed, one adult bird captured and banded in the first session was captured again in mist nets in the last session, i.e., 26 months later. We therefore contend that the observed adult survival rate is low, not necessarily because of high adult mortality, but, instead, because of “permanent” emigration (different from transience, as some individuals may leave permanently the study area after having been recaptured at least once) during our relatively short study period. This might arise as a consequence of movements in response to increased human disturbance in our study area [105,106]. Indeed, we regularly witnessed clearing and burning of woodlots at Tête Opaque during the course of our study, including by very young children who are not enrolled at school and must make a living on their own. To what extent movement patterns underlying both transience and emigration can contribute to the resilience of La Selle Thrushes to localized disturbance (see [104]) remains to be evaluated. Therefore, future monitoring of the La Selle Thrush in Haiti should cover a larger area within Parc La Visite, and be extended to other protected areas such as Forêt des Pins, in order to better document movements of individuals [107]. In addition to banding and recapture, light-weight transmitters (<5% of body mass) could be attached to a certain number of individuals, as this technique has proved to be both efficient in the same habitat type and safe for turdid species [108].

Although the overall sex ratio in our subset of sexed birds was significantly male-biased, with about 2.25:1 male-to-female ratio [23], and thus suggestive of potential sex-related differences in survival [109], we found no evidence for a significant effect of sex either on adult survival or on recapture rate. This is contrast to what has been observed in the endangered Hawaiian Thrush, *Myadestes palmeri*, in which survival was significantly higher for wild adult males than for wild adult females [98]. On the other hand, it is in agreement with what has been observed in the European Blackbird, *T. merula* [50,96]. Exantus et al. [23] observed, however, that the sex ratio differed between the breeding and non-breeding season, with a more balanced sex ratio at the time of reproduction, i.e., from early April to the end of July. This suggests that females may be more likely than males to move away from the study area during the non-breeding season, although we

did not detect a significant sex effect on the probability of recapture or on transience. Our sample size might, however, have been too low to have enough power to detect a moderate difference in survival or recapture probability between sexes. Alternatively, as we only estimated adult survival, the observed biased sex ratio [23] might be related to sex-related differences in fledging success and/or juvenile survival.

## 5. Conclusions and Perspectives

Our study provides new and valuable information on the status of the vulnerable La Selle Thrush in part of its range. It confirms the ecological dependency of the species on deciduous forest and, at the same time, reveals the unshared ability of the species, at the local scale, to adapt to drastic changes in its environment by using newly available foraging habitats and food resources. However, this feeding innovation might come with a hidden cost in the form of infestation with ticks (see [110]). Our results thus suggest that the species could be, to a certain extent, tolerant of human-altered habitats, as observed in other Neotropical passerine species [18], but this needs to be confirmed by measuring the balance between costs and benefits. In addition, the low value obtained for apparent adult survival rate and male-biased sex ratio in our study population [23] provides an incentive to develop a more comprehensive and long-term research and monitoring program, developed with close cooperation between researchers in Haiti and in the Dominican Republic, to better assess the conservation status of the species. Although La Selle Thrush is often presented as a shy bird remaining hidden from sight in the forest understory, our study shows that combining different techniques of investigation can be very efficient to document its natural history and demography.

Even though the development of slash-and-burn agriculture in protected areas appears to be a major threat to the Haitian avifauna [23], its precise impact on the La Selle Thrush remains to be evaluated, as little evidence exists for a direct negative effect of forest thinning and burning on Neotropical thrush species [111]. To that end, we need to acquire information on several important parameters (such as first-year survival, mean clutch size, partial clutch or brood loss and sex ratio at hatching), as the observed adult survival rate is unlikely to support a viable population. However, obtaining reliable data on reproduction might be difficult. Although we searched for nests in deciduous woodlots during the breeding season at our study site, we could not find any. Birds were actually nesting in deciduous forests located on very steep cliffs to which access was very difficult, if not perilous, without proper equipment. Further surveys should therefore be conducted elsewhere in the La Selle ridge and in the Dominican Republic to locate areas of reproduction and evaluate to what extent breeding performance can be measured without too much disturbance. Finally, transnational cooperation would be particularly efficient in measuring genetic structuration between the Haitian and Dominican population and assess the extent of gene flow.

In the meantime, we recommend maintaining the conservation status of the species as “vulnerable”, awaiting detailed information on population trends and levels of genetic diversity. The current tragic situation in Haiti is likely to stimulate further emigration of the poorest people from cities to rural areas, thus increasing human pressure on protected areas. In addition, the La Selle Thrush might be exposed to predation by exotic mammal species. Although our camera traps regularly recorded the presence of small Indian mongoose and feral cats in our study area, their predatory impact on the La Selle Thrush, and more generally on the ground-dwelling avifauna, remains undocumented. Similarly, potential predation by rats, also photographed with camera traps during our study, on nests and incubating adults should be assessed.

Haiti has a rich and vulnerable tropical avifauna [20,21,28,29]. Unfortunately, very little research has been carried out on the basic biology and ecology of resident birds, in particular on the 33 bird species endemic to the island [112,113]. The present study, however, shows that knowledge gaps could be relatively easily and more effectively filled through funding tertiary education of local young researchers and regional cooperation,

instead of promoting parachute science [114–116]. In particular, significant funding should be allocated to the training of Haitian students in conservation biology at the master and PhD levels, and to giving them access to modern tools of investigation, including remote-sensing techniques and molecular analyses. In that respect, international and regional conservation organizations willing to contribute to wildlife conservation in Haiti may want to reconsider their policies.

**Author Contributions:** J.-M.E. was involved in study design and methodology, data collection, part of the statistical analysis, and the writing up of the article. A.V. was involved in all CMR data analyses and the writing up of the article. F.C. was involved in study design, supervision, project administration, statistical analysis and the writing up of the article. All authors have read and agreed to the published version of the manuscript.

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**Data Availability Statement:** Data will be made available on reasonable request.

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## Appendix A

Dates: number of first captures ( $n = 79$ ) and number of recaptures ( $n = 42$ ) of *Turdus swalesi* per bimonthly session, in the La Selle ridge, Haiti. No data were collected during sessions 3 and 4, due to logistic constraints.

Session	Dates	First Captures	Recaptures
1	1–15 December 2019; 25–27 January 2020	5	-
2	22–26 February 2020	2	0
3	Missing session April 2020	0	0
4	Missing session July 2020	0	0
5	26 September–10 October 2020	9	0
6	15–19 November 2020	11	7
7	17–31 January 2021	7	4
8	28 March–11 April 2021	8	12

Session	Dates	First Captures	Recaptures
9	22–31 May 2021	4	7
10	6–13 July 2021	2	3
11	2–13 August 2021; 5–18 September 2021	16	9
12	8–17 November 2021	12	5
13	24–31 January 2022	3	3

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