

The Forest Thrush *Turdus lherminieri* prefers mature mesic forest with dense canopy

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Summary

Habitat loss, the primary driver for loss of biodiversity worldwide, is of special concern for species that have a small area of occurrence, such as those restricted to islands. The Forest Thrush *Turdus lherminieri* is a 'Vulnerable' (VU) species endemic to four islands in the Caribbean, and its population has declined dramatically over the past 15 years. Because this decline is poorly understood, we studied its habitat associations on Montserrat. We conducted three repeat point count surveys and measured forest structure and habitat at each of 88 randomly placed locations in the largest forest area remaining on the island. We related Forest Thrush abundance to habitat using binomial mixture models that account for imperfect detection. Detection probability was a function of survey time, survey date, location of the survey point, and wind. Local habitat structure had the greatest influence on Forest Thrush abundance, with birds being more abundant at mid-elevations under closed canopies. We conclude that the Forest Thrush prefers mature mesic and wet forests on Montserrat. Assuming similar habitat selection in the rest of its range, the species's long-term future depends on good protection of these natural forests on all four islands where it occurs.

Introduction

Habitat loss is the primary driver for the loss of biodiversity worldwide (Gaston *et al.* 2003, Pimm *et al.* 2006, Brook *et al.* 2008), and is of special concern for species that have small ranges and therefore small populations, such as those restricted to islands (BirdLife International 2000). More than 90% of bird species extinctions since 1800 have occurred on islands (Johnson and Stattersfield 1990, Banko *et al.* 2013). Moreover, islands account for 48% of all Endemic Bird Areas, with more than 600 globally threatened bird species being confined to them (Stattersfield *et al.* 1998, Ricketts *et al.* 2005, Dallimer and King 2007). An understanding of the habitat requirements of threatened island-endemic species is therefore crucial to our ability to provide effective management for their long-term conservation.

The Caribbean islands harbour a rich biodiversity and were identified as one of 25 globally important biodiversity hotspots (Myers *et al.* 2000). Habitat conversion and invasive species threaten native taxa, many of them endemic to these islands, yet little is known about their habitat requirements. The Forest Thrush *Turdus lherminieri* is restricted to forests on four islands in the Lesser Antilles: Montserrat, Guadeloupe, Dominica and St Lucia (Collar 2005, Eraud *et al.* 2012), with each island assumed to hold distinct subspecies, *T. l. montserrati*, *T. l. lherminieri*, *T. l. dominicensis* and *T. l. sanctaeluciae*, respectively (Clement and Hathway 2000, Zuccon 2011). The subspecies on St. Lucia may have recently become extinct (last sighting 2007; BirdLife International 2013). Owing to a dramatic overall decline in its population over the last

15 years, the species is listed as globally 'Vulnerable' (BirdLife International 2013), but the causes of its precarious status on each island are largely a matter of speculation.

Generally, however, the Forest Thrush is believed to be threatened by habitat loss, nest predators and hunting on Guadeloupe (Eraud *et al.* 2012, BirdLife International 2013). On Guadeloupe the species occurs in areas of continuous rainforest from 110 to 1,400 m above sea level and wet coastal forests (Eraud *et al.* 2012, Arnoux *et al.* 2013). While previous studies have mainly investigated morphological and genetic differentiation (Arnoux *et al.* 2013, 2014), no study has quantified the habitat preferences of the Forest Thrush. A better understanding of the species's habitat requirements is needed to assess the extent of habitat loss and guide conservation management.

Animals of dense tropical forests are generally difficult to detect. Many studies of habitat associations in birds ignore the fact that some individuals may have been missed during surveys (Kéry *et al.* 2005, 2009, Kéry 2008). Imperfect detection may affect abundance estimates and habitat inferences if aspects of habitat structure with potential to affect species presence or abundance also affect the ability of an observer to detect the species (Kéry 2008). Two common approaches to account for imperfect detection are distance sampling and repeat surveys using multiple visits or observers (Nichols *et al.* 2009). Of these, distance sampling is problematic in tropical forests where dense vegetation precludes accurate determination of radial distances, leading to inaccurate density estimations (Allredge *et al.* 2007, Simons *et al.* 2007, Oppel *et al.* 2014a). However, repeat surveys combined with binomial mixture models allow the estimation of detection probability and provide an excellent basis for analysing habitat preferences (Royle 2004, Kéry *et al.* 2005, Kéry 2008).

Here we use binomial mixture models to elucidate the habitat associations of the Forest Thrush while accounting for the imperfect detection process in a dense tropical forest. We conducted this study on Montserrat, which holds a significant proportion of the Forest Thrush world population. We use the information about habitat preferences of the Forest Thrush to make recommendations for the conservation of the species and to inform future land management on Montserrat.

Methods

Study area

Montserrat (16°45'N, 62°12'W) is an island of 104 km², located at the northern end of the Lesser Antilles in the Greater Caribbean Basin. It experiences a moist tropical climate, with an annual rainfall of 1,000–2,500 mm per year (Hilton *et al.* 2003). There are three main hill ranges: Silver Hills, Soufrière Hills and Centre Hills, the latter two rising to 700–900 m asl (Young 2008). A range of habitats occur on the island, including dry, mesic and wet forests, and elfin woodland on exposed ridges at high elevations. Following volcanic activity in the Soufrière Hills that started in 1995, almost 60% of the island's forest habitat was lost, and now the largest remnant exists in the Centre Hills, with an area of 11 km² (Young 2008).

Bird monitoring

Bird surveys were carried out during the breeding season of the Forest Thrush in April 2013. We conducted 10-minute point counts between 06h00 and 14h00 Atlantic Standard Time (AST), during which all visual and acoustic detections of the Forest Thrush were recorded. Point counts were carried out three times per point over a three-week period at 88 survey points located randomly within the Centre Hills forest, with a minimum of 200 m between points (for details see Dalsgaard *et al.* 2007, Oppel *et al.* 2014a).

Habitat data

Based on previous work on related species (Jones *et al.* 1995, Dallimer and King 2007, Rangel-Salazar *et al.* 2008), we recorded geographical and habitat variables that might influence Forest

Thrush abundance at each point (Table 1). Land cover type at the survey point, distance to permanent water sources and distance to forest edge or clearing (roughly 10 m² or larger) were obtained from high-resolution aerial images available on a GIS web-platform (<http://landinfo.gov.ms/>, accessed 14 April 2013) (Table 1).

Data analysis

We aimed to relate the abundance of the Forest Thrush to various habitat variables. While habitat or landscape variables usually influence species occurrence and abundance, some habitat features and other variables (e.g. wind, rain, sampling time) may affect an observer's ability to detect the species (Royle and Dorazio 2008, Nichols *et al.* 2009). To account for imperfect detection in our data we used binomial mixture models (BMM), which are a class of hierarchical models that require spatial as well as temporal replication of counts (Royle and Nichols 2003, Kéry *et al.* 2005, Royle *et al.* 2005); they have already been used with forest bird monitoring data on Montserrat (Opell *et al.* 2014a). A critical assumption for BMMs is that the population is demographically closed over the period during which the repeat surveys are conducted. To satisfy this assumption, repeat surveys of the same survey points were conducted within 2–3 weeks, during which demographic closure is highly likely.

BMMs consist of a hierarchy of two Generalised Linear Models (GLMs), the first of which models the observation process to estimate detection probability while the second models true abundance in relation to environmental variables, given that not all birds are detected (Kéry and Schaub 2012). We modelled the abundance component as a random Poisson process to estimate the size of the local 'superpopulation' of birds whose home range overlaps the radius around a

Table 1. Definitions of survey-specific detection covariates, geographical and habitat variables recorded at 88 survey points across the Centre Hills on Montserrat in 2013.

Variable	Metric	Definition
Survey-specific detection/observation covariates		
Rain	categorical	0 = no rain, 1 = rain during the count
Wind	categorical	Strength of wind during count in two categories: calm/light or moderate/strong
Survey date	date	Date when survey was conducted
Survey time	time	Time at which survey was conducted
Geographical variables		
Elevation	m	Metres above sea-level recorded by GPS (Garmin GPSmap 60s)
Location	categorical	Two categories: valley/midslope or ridge
Land cover type	categorical	Type of vegetation cover at the survey point in three categories—dry forest, mesic forest, and wet forest. Elfin woodland was recorded at only three points and was classed as 'wet forest'.
Distance to forest edge/clearing	m	Distance of survey point from forest edge or manmade clearing
Distance to permanent water source	m	Distance of survey point from permanent ghaut or river
Habitat variables		
Canopy cover	%	Cover of tree canopy estimated with a spherical densiometer
Tree density	trees/m ²	Calculated using Point-Centered Quarter method (Cottam and Curtis 1956). We defined a tree as a plant with woody trunk at breast height and >5 m in height.
Tree height	m	Mean of heights of tallest tree in each of four 90° quadrants around the survey point, measured with a range finder, within a maximum radius of 30 m

sampling station. We used a Poisson rather than a negative binomial distribution, as the negative binomial distribution generally yields larger and less precise estimates for count data of common species (Kéry *et al.* 2005, Joseph *et al.* 2009, Hunt *et al.* 2012). The observation model component was conditional on the number of birds estimated at each sampling station, and calculated the probability of detection based on repeated counts at a given site using binomial trials for each bird.

We constructed multiple biologically plausible candidate models in three hierarchical steps. First, we tested models describing the detection process, while keeping abundance constant. We considered that wind, survey time, survey date, rain and location of the survey point might affect detection probability, and explored all possible combinations of these variables, including quadratic effects of survey date to account for non-linear change in detection probability (Schmidt *et al.* 2013). In the second step, we explored all possible combinations of site-specific habitat covariates (elevation, tree height, tree density, canopy cover) as well as a quadratic effect of elevation on Forest Thrush abundance in a suite of models that included all detection covariates from the most parsimonious detection model. For sedentary forest species such as the Forest Thrush local habitat is usually the primary factor affecting abundance, while landscape-scale variables have a weaker secondary effect (Dolman 2012). Hence, in a third step, we added landscape effects (distance to forest edge, distance to permanent water source, land cover type) to the most parsimonious local habitat model, while retaining the detection covariates. Because some landscape variables were strongly correlated with elevation ($r > 0.5$; land cover type and distance to forest edge), we omitted combinations of these correlated variables in the third step. Across the three steps, we constructed a total of 841 models to test detection covariates and habitat relationships of the Forest Thrush. We used an information-theoretic approach to select the most parsimonious model from all three steps (Burnham and Anderson 2002) and used the most parsimonious model for inference to avoid overestimation of variable importance based on model weights (Galipaud *et al.* 2014).

All numeric site and survey-specific covariates were standardised by rescaling so that all predictors had zero mean and unit variance, in order to enhance the convergence of the numerical optimisation algorithm (Kéry *et al.* 2005). All categorical variables were structured as ordered factors, except for location of point and land cover type, which were structured simply as factors. All models were fitted using the 'pcount' function in the 'unmarked' package (Fiske and Chandler 2011), and models with combinations of terms were tested using the 'dredge' function in the 'MuMIn' package (Barton 2014) in R version 3.1.0 (R Development Core Team 2014).

The goodness of fit of the most parsimonious model was assessed with Pearson's χ^2 statistic via 200 simulations using parametric bootstrap. If the observed statistic is not too extreme (beyond the 0.05 percentile of the reference distribution), then the model fits (Silllett *et al.* 2012). In addition, lack of model fit was quantified using the overdispersion parameter \hat{c} as follows:

$$\hat{c} = X_{obs}^2 / \bar{X}_B^2$$

where \bar{X}_B^2 is the average of the test statistics obtained from the parametric bootstrap. If the model is an adequate description of the data, then \hat{c} should be approximately 1 (MacKenzie and Bailey 2004).

Although the average home range size of 30 radio-tracked male Forest Thrushes during the breeding season on Guadeloupe was 0.08–0.2 km² and the maximum distance covered in a day was < 200 m (Eraud *et al.* 2012), the distance between points may not have been sufficient to ensure complete spatial independence of point counts, which would affect the inference drawn from models. We therefore examined spatial independence of samples by calculating Moran's I of the most parsimonious model residuals using the function 'moran.test' in the R-package 'spdep'.

Results

We counted 480 Forest Thrushes at the 88 survey points during the three repeat surveys, with 0–6 birds encountered during each point count and most detections (> 90%) being aural. The best detection model included wind, time, location of point and survey date, and indicated that detection probability was generally low (mean \pm SD = 0.16 \pm 0.06, range 0.05–0.30) and decreased

later in the morning, with stronger wind, and when point count stations were located on ridges, but increased in the middle of the month-long field survey (Figure 1, Table 2). Including these detection covariates, there was overwhelming support for elevation and canopy cover as determinants of Forest Thrush abundance (Tables 2, 3). Predicted Forest Thrush abundance ranged from 1–15 birds per point (mean \pm SD = 11 \pm 3 birds), increased with canopy cover, and was highest at intermediate elevations (Figure 1). The bootstrap P value for the most parsimonious model based on Pearson’s χ^2 statistic was 0.71, suggesting that it provided an adequate fit to the data. The over-dispersion parameter $\hat{c} = 0.94$ indicated that there was no evidence for a lack of fit of this model. There was no spatial autocorrelation of the model residuals (Moran’s $I = -0.011$, $P = 0.49$).

There were ten models across the three steps of the model selection process, which were within three AICc units of the most parsimonious model (Table 2). These models provided some evidence that tree height and distance to a permanent water source could affect the abundance of Forest Thrush. While tree height had a positive effect on abundance (abundance parameter estimate 0.096 ± 0.066 SE), Forest Thrushes appeared to be marginally less abundant in areas farther from a water source (-0.0524 ± 0.057 SE), but the effect size of these two variables was lower than for the variables in the most parsimonious model (Table 3).

Discussion

Canopy cover and elevation influence Forest Thrush abundance on Montserrat, with birds being more abundant at mid-elevations, dominated by closed canopies. Since land cover type and habitat

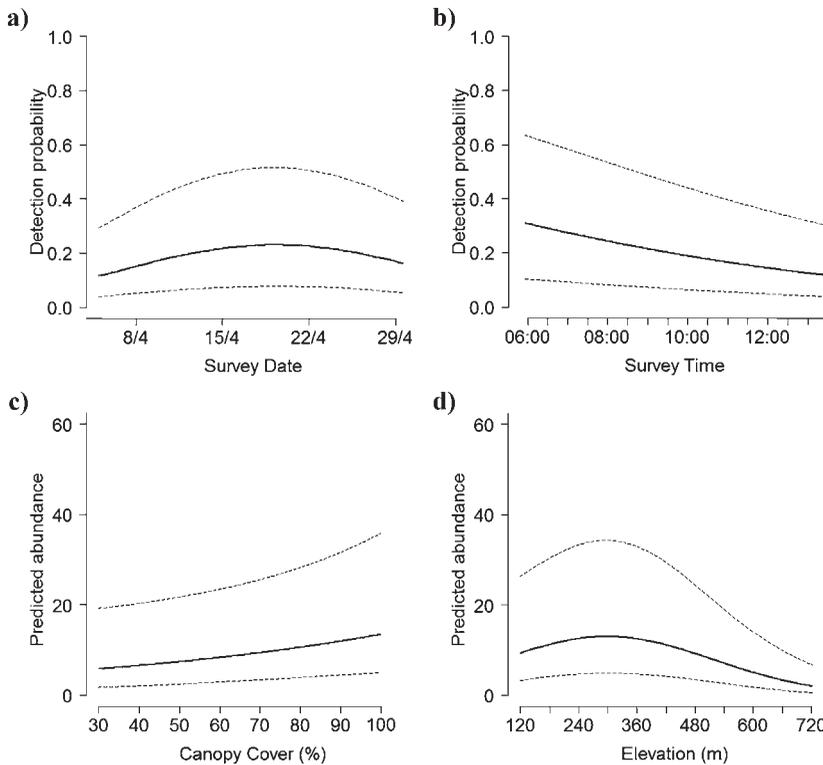


Figure 1. Factors influencing detection probability (a-b), and habitat variables influencing Forest Thrush abundance (c-d) in the Centre Hills of Montserrat, 2013, from the most parsimonious binomial mixture model. Dotted lines represent 95% confidence intervals.

Table 2. Top ten candidate binomial mixture models across all three steps of the model selection process, describing the detection and ecological processes involved in explaining abundance of Forest Thrush at 88 survey points in the Centre Hills of Montserrat in 2013. Covariates influencing abundance (λ) and detection probability (p) in each model are listed. Squared terms indicate quadratic effects.

Model no.	λ	P	No. of parameters	AICc	Δ AICc
1	elev + elev ² + canopy	date + date ² + loc + time + wind	10	808.54	0.00
2	elev + elev ² + canopy + treeheight	date + date ² + loc + time + wind	11	809.08	0.54
3	elev ² + canopy	date + date ² + loc + time + wind	9	809.73	1.19
4	elev ²	date + date ² + loc + time + wind	8	809.93	1.39
5	elev + elev ² + canopy + dist_to_water	date + date ² + loc + time + wind	11	810.29	1.75
6	elev + elev ²	date + date ² + loc + time + wind	9	810.43	1.89
7	elev ² + canopy + treeheight	date + date ² + loc + time + wind	10	810.91	2.37
8	elev + elev ² + canopy + treedens	date + date ² + loc + time + wind	11	811.12	2.58
9	elev ² + treeheight	date + date ² + loc + time + wind	9	811.40	2.86
10	elev + elev ² + treeheight	date + date ² + loc + time + wind	10	811.49	2.95

AICc = Corrected Akaike information criterion.

canopy = % canopy cover, date = survey date, dist_to_water = distance to permanent water source, elev = elevation, loc = location of survey point, time = survey time, treedens = tree density, treeheight = tree height, wind = strength of wind (see Table 1 for details of measurements).

type change along an elevational gradient, elevation was used as a proxy to make inferences about the type of forest that the species prefers. On Montserrat, the elevational habitat gradient is probably driven by moisture, as higher elevations receive more rainfall (Barclay *et al.* 2006). Forest

Table 3. Parameter estimates from the most parsimonious binomial mixture model explaining abundance of forest thrush at 88 survey points in the Centre Hills of Montserrat in 2013. All variables were standardised (to unit mean and variance) for comparability of parameters.

Submodel and coefficient	Estimate	Standard error
Abundance (λ):		
Intercept	2.53	0.50
Elevation	-0.16	0.08
Elevation ²	-0.23	0.06
Canopy cover	0.13	0.06
Detection (p):		
Intercept	-1.41	0.63
Strong wind	-0.28	0.09
Location on ridge	-0.54	0.24
Survey time	-0.27	0.07
Survey date	0.10	0.06
Survey date ²	-0.23	0.06

Thrush abundance was greatest at elevations of 200–400 m, which are dominated by mature secondary mesic forests, and declined slightly with further increase in elevation. There was also some evidence that Forest Thrushes were more abundant in areas with taller trees and closer to permanent water sources, but these effects were less pronounced than canopy cover and elevation. Overall, our findings provide quantitative support for qualitative descriptions of Forest Thrush distribution and habitat elsewhere (Eraud *et al.* 2012).

Many forest- and woodland-dwelling thrush species are strongly adapted to forage terrestrially in leaf-litter, but generally breed and sometimes feed in the canopy (Collar 2005). Because leaf-litter is thickest and supports a greater abundance of animal life in relatively level ground under a dense canopy, where low light conditions discourage obstructive undergrowth (Canham *et al.* 1990, Bartels and Chen 2013), the greater abundance of Forest Thrushes in such habitat probably reflects better foraging habitat. Dense canopy cover and reduced lighting may also increase nesting success by reducing visual detection by nest predators (in this case, Pearly-eyed Thrashers *Margarops fuscatus*), as has been found in Ruddy-capped Nightingale-thrushes *Catharus frantzii* in Mexico, which enjoy higher nesting success under closed canopies (Rangel-Salazar *et al.* 2008).

Unsurprisingly, detection probability in our study decreased with increasing strength of wind, and use of ridges as survey points: birds are less audible in windy conditions (Simons *et al.* 2007), and ridges hold inappropriate foraging substrates while their steep slopes reduce audibility. If not accounted for, this artifact of the observation process might have been mistaken for low Forest Thrush abundance on ridges. It therefore highlights the value of using binomial mixture models to study habitat preferences (Kéry 2008). We also found that detection probability decreased with time of day, which is a well-known phenomenon among songbirds, which often change their vocal activity through the day (Bibby *et al.* 2000, Schmidt *et al.* 2013). However, as singing intensity increased in the second half of April we observed an intermittent increase in detection probability during the breeding season. Because the monitoring programme on Montserrat was originally designed for a different species with a slightly earlier breeding period, the first round of point count surveys recorded very few singing Forest Thrushes and it is therefore not surprising that detection probability increased over time.

The estimated abundance of birds per survey point in our study was quite large (> 15 birds/point, Fig. 1), a fact that has been recognised in other applications of binomial mixture models (Hunt *et al.* 2012). Binomial mixture models estimate the size of a 'super-population', which is the number of birds that use the habitat around a counting station (Nichols *et al.* 2009, Kéry and Schaub 2012). Thus, overlapping home ranges of several pairs, which has been recorded for radio-tracked individuals on Guadeloupe (Eraud *et al.* 2012), will lead to several pairs using the same forest area and would thus explain the high estimated abundance per point. Although we are not able to convert our estimates of abundance into density and thus total population size of Forest Thrushes on Montserrat, we are confident that these estimates are reliable to infer habitat associations and to model population changes over time (Parashuram 2013).

Our study has important implications for the conservation of the Forest Thrush. The preferred forest habitat for the species includes tall mesic forests with closed canopies, which have matured after forest clearance for agriculture in previous centuries and more recent natural disasters (Lugo *et al.* 1981, Arendt 1990, Dalsgaard *et al.* 2007). Both natural and semi-natural forests are still threatened by human development on all islands in the range of the Forest Thrush (BirdLife International 2014). In addition, intense grazing pressure from feral livestock may alter the forest structure and inhibit regeneration, with potentially negative consequences for the Forest Thrush (Peh *et al.* 2014). For the long-term survival of this and other island species, it is critical to retain as much forest cover as possible to allow for population shifts in response to stochastic environmental events such as hurricanes and volcanic eruptions, which are frequent in the Caribbean (Tanner *et al.* 1991) and have led to major distributional shifts of birds, especially on Montserrat, in the last two decades (Arendt *et al.* 1999, Oppel *et al.* 2014b). While our study has clarified the habitat associations of the Forest Thrush on Montserrat, urgent work is now needed to establish forest management programmes that protect significant areas of mature forest from damage from overgrazing and losses to human development.

Acknowledgements

We thank L. Martin, J. Boatwain, A. Homer and L. Bambini for assistance with fieldwork and data entry. L. Rogers of the Montserrat Physical Planning Unit kindly granted access to the high-resolution aerial images and GIS resources of the island. The Montserrat Department of Environment provided invaluable logistical support.

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Received 11 August 2014; revision accepted 21 November 2014;
Published online 2 February 2015