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Population status and trend of the Critically Endangered Montserrat Oriole

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Summary

Many island endemics are of great conservation concern due to small range and population sizes. The Montserrat Oriole *Icterus oberi* is a forest passerine endemic to the Caribbean island of Montserrat, where recent volcanic activity has destroyed a large proportion of suitable forest habitat. From 1997 to 2000 the Montserrat Oriole population declined dramatically even in the remaining forest habitat, leading to its classification as 'Critically Endangered'. We present trend estimates of the Montserrat Oriole population from 2000 to 2013, and estimate the world population size in 2012 based on repeat point counts and beta-binomial mixture models. Montserrat Orioles recovered between 2003 and 2005, and we found no evidence for a continuing population decline. However, there was large uncertainty around trend estimates, and the power to detect a shallow negative trend was very low. Based on the comparison of count data at 42 points, the Montserrat Oriole population in 2013 was less than half as large as in 1998. To improve future trend estimates a new monitoring design was introduced in 2011, and applied to all subpopulations of the species in 2012. The world population in 2012 was estimated to hold between 307 (95% credible interval 212–503) and 690 birds (476–1131) birds in the two forest fragments on Montserrat, depending on whether the sampling area around each point count was assumed to encompass 100 m or 150 m. Based on these estimates, the Montserrat Oriole currently does not meet the IUCN criteria for 'Critically Endangered', and we recommend a revision of the species' conservation status.

Introduction

Single island endemic species are of great conservation concern due to their limited range and generally small populations that render them vulnerable to extinction by environmental stochasticity. The islands in the Caribbean are home to nine oriole species of the genus *Icterus*, of which four are endemic to single islands (Garrido *et al.* 2005, Price and Hayes 2009). Two of the Caribbean oriole species are classified as 'Critically Endangered', the Bahama Oriole *Icterus northropi* (Price *et al.* 2011), and the Montserrat Oriole *I. oberi* (Arendt *et al.* 1999, Hilton *et al.* 2003).

The Montserrat Oriole is endemic to the volcanic island of Montserrat in the Lesser Antilles, and is considered Critically Endangered due to a rapid population decline between 1997 and 2000 (Arendt *et al.* 1999, Bowden *et al.* 2001, Hilton *et al.* 2003). This population decline was most likely due to an ongoing volcanic eruption, which started in July 1995 and continued into 2013. During the first two years of this volcanic activity almost 60% of the Montserrat Oriole's original habitat in semi-deciduous and evergreen moist forests were destroyed (Arendt *et al.* 1999, Hilton *et al.* 2005). Since 1997, the Montserrat Oriole has been restricted to two small forest remnants on Montserrat, the Centre Hills (11 km^2) and a much smaller remnant (2.7 km^2) in the South Soufrière Hills (Allcorn *et al.* 2012). Following the initial volcanic destruction of habitat in 1996 and 1997, the population in the Centre Hills forest declined further until 2003, presumably because of low adult survival and poor reproductive output that may have been caused by volcanic ash fall, drought, and nest predation (Hilton *et al.* 2003, Marske *et al.* 2007, Allcorn *et al.* 2012, Oppel *et al.* 2013). However, an apparent recovery occurred between 2003 and 2005 (Dalsgaard *et al.* 2007), but no information is available on recent trends and the current size of the Montserrat Oriole population. In February 2010, the Soufriere Hills Volcano displayed the most vigorous activity since 1995, leading to massive ash fall on the island (Scientific Advisory Committee 2010). Subsequently, Montserrat Orioles were observed at lower elevations than ever before, and there was concern about the effects of this most recent episode of volcanic activity on the Montserrat Oriole population.

In this study, we examine the population trend of Montserrat Orioles between 2000 and 2013 using a state-space model to account for random observation error. We further introduce a revised monitoring approach that is designed to estimate abundance while accounting for imperfect detection. Lastly, we use detailed observations of colour-ringed individuals to assess average movement distances of territorial birds, and use this information to extrapolate the size of the global population of Montserrat Orioles.

Methods

Study area

Montserrat (16°45′N, 62°12′W; 104 km^2) lies at the northern end of the Lesser Antilles in the eastern Caribbean Sea. The Centre Hills are the largest forest area remaining on the island, a contiguous block of mostly secondary forest covering the steep-sided valleys of a dormant volcanic cone rising to a maximum elevation of 737 m above sea level (Hilton *et al.* 2003, Allcorn *et al.* 2012). A smaller forest remnant exists in the South Soufriere Hills, to the south of the active volcano. This forest area lies in a volcanic exclusion zone where volcanic hazards prevent regular public access, but the forest is separated from the active volcano by a deep valley and thus not vulnerable to recurring pyroclastic flows. The natural vegetation in both forests is tropical moist broadleaf forest above 200–300 m, with small areas of elfin forest on exposed ridges at high elevations. Canopy heights of 15–25 m are typical, and the understorey is frequently dominated by *Heliconia* plants.

Bird monitoring

Montserrat Orioles were monitored using point counts between 2000 and 2013 by the Montserrat Department of Environment. Because bird detection is challenging in tropical forests, a distance sampling approach was employed in the surveys before 2012 to account for imperfect detection (Hilton *et al.* 2003). However, most forest birds including the Montserrat Oriole are only recorded acoustically, and the distance sampling approach may lead to highly biased population estimates (Hilton *et al.* 2003, Alldredge *et al.* 2007a, 2007b). Recent analytical developments allow the estimation of detection probability from repeated counts rather than from estimated distances between birds and observer (Royle and Nichols 2003, Kéry *et al.* 2005, Royle *et al.* 2005, Kéry 2008, Chandler and King 2011). Thus, a new survey protocol was established in 2011 to overcome the complications associated with estimating the distance to a vocalising bird in dense tropical forest habitat.

From 2000 to 2013, bird monitoring was conducted at fixed census stations in the Centre Hills during the breeding season of Montserrat Orioles between late March and mid-July (Allcorn *et al.* 2012). A total of 90 census stations were originally established throughout the Centre Hills along accessible walking routes (Hilton *et al.* 2003, Dalsgaard *et al.* 2007), however, some of the census stations were too close together to provide independent observations for Montserrat Orioles, and others were in unsuitable habitat. For the analysis of long-term trends, we chose a subset of 50 permanent census stations that were all at least 200 m apart, did not change between

2000 and 2013, and at which Montserrat Orioles were observed at least once during the 13 years of monitoring.

We counted birds during 10-min point counts after a 3-min settling down period upon arrival at a census station. All counts were conducted between 05h45 and 14h00 local time, and detailed descriptions of the bird surveys can be found elsewhere (Hilton *et al.* 2003, Dalsgaard *et al.* 2007).

From 2011 to 2013, we employed a new survey protocol during which each of 70 point count stations were surveyed 2–3 times within a 3-week period. These 70 stations were all > 200 m apart and were a combination of existing points from previous surveys and newly established points spread throughout the entire Centre Hills forest. The repeat surveys followed the same 10-min point count protocol described above, and were conducted at the beginning of the breeding season (last week of March and April) to ensure that the Montserrat Oriole population was demographically closed during the survey period. In 2012, volcanic hazards were lower than in any of the previous years (Scientific Advisory Committee 2012), allowing us to access the South Soufriere Hills. We established 19 census stations that were > 200 m apart and conducted two repeat surveys at these stations in mid April 2012.

Estimation of movement distances of territorial orioles

In May 2011 and 2012 we individually colour-ringed adult territory-holding orioles and observed their movements during 15 days of intense observations. During these intense observations the focal individual was observed from a distance of 10–20 m, which was subjectively assessed to minimally influence the behaviour of the bird. The focal individual was then followed through the forest for as long as possible, and all movements were logged with a handheld GPS unit (Garmin eTrex HS). These observations yielded a minimum movement radius for territorial birds from a fixed focal point (i.e. the nest) in their territory during the breeding season.

Estimation of population trend and population size

Previous analyses of Montserrat Oriole population trends used raw count data (Hilton *et al.* 2003, Dalsgaard *et al.* 2007) because several of the assumptions underlying the distance sampling approach may be violated during Montserrat Oriole surveys (Hilton *et al.* 2003). We followed these previous approaches and used the raw census data to estimate a population trend for count data from 2000 to 2013. In addition, we compared the raw count data at 42 points in the Centre Hills that were surveyed both in late March 1998 and in early April 2013 with a paired samples Mann-Whitney *U*-test to assess the change in population size between 1998 and 2013.

We used the total number of Montserrat Orioles counted at the census stations in a given year. In all years, some of the census stations could not be surveyed because certain parts of the Centre Hills forest were formally closed due to volcanic hazards. We thus divided the number of orioles by the number of census stations surveyed to calculate the number of orioles per census station as an annual population index. This population index is a composite metric of true population abundance and detection probability, and thus includes errors associated with the observation process. To estimate a trend we used a hierarchical state-space model that decomposed the observed time series of Montserrat Oriole observations into a population process and an observation error component (De Valpine 2003, Clark and Bjørnstad 2004, Kéry and Schaub 2012). Briefly, a state-space model consists of two equations that link the unobserved process of interest (annual population size) with the observed data in a hierarchical fashion. Because each component includes an error term, the model can account for both environmental stochasticity (process error) and measurement uncertainty (observation error). State-space models allow a more accurate estimate of a population trend than standard GLMs, which assume zero process error and may therefore underestimate the uncertainty in a trend (Wilson *et al.* 2011, Kéry and Schaub 2012).

The trend estimates derived from this model are only accurate if no systematic change in detection probability occurred over the course of the study, and false-negative and false-positive observations cancel out on average. We believe that this is a reasonable assumption for the Montserrat Oriole count data because the same staff members were involved in all surveys between 2000 and 2013, and neither the forest environment nor weather parameters that may affect the detection process have systematically changed during those 13 years. We fitted state-space models using Markov chain Monte Carlo methods in a Bayesian framework (Kéry and Schaub 2012). We ran three Markov chains each with $5*10^5$ iterations and discarded the first 10^5 iterations. From the remaining iterations we only used every 5^{th} iteration for inference. Because posterior estimates were highly skewed, we report results as the posterior median and 95% credible intervals. Convergence was tested using the Gelman-Rubin diagnostic (Brooks and Gelman 1998).

Because the state-space model cannot estimate the probability of detection and thus true population size, we used the repeated surveys in 2011–2013 to estimate true Montserrat Oriole abundance and detection probability using binomial mixture models (Royle and Nichols 2003, Kéry *et al.* 2005, Royle *et al.* 2005). These models use the repeated observations at a given sampling station to estimate separately the probability to detect birds and the number of birds that use the habitat around the sampling station. Briefly, these models consist of two components which link the ecological state of interest (abundance of birds) and the observation process (detection probability) in a hierarchical fashion. The abundance component is modelled as a random Poisson process and estimates the size of the 'superpopulation' of birds, conceptually the total number of birds whose home range overlaps the radius around a sampling station where they can be detected by observers (Royle and Nichols 2003, Kéry *et al.* 2005, Kéry and Schaub 2012). The observation model component is conditional on the number of birds estimated at each sampling station, and estimates the probability of detection based on repeated counts at a given site using binomial trials for each bird. A critical assumption for these models is that the population is closed over the period during which the repeat surveys are conducted. To satisfy this assumption, we conducted repeat surveys of the same sampling station within 2-3 weeks.

Montserrat Orioles frequently travel around in pairs (Allcorn *et al.* 2012), and acoustic detection of one member of a pair can often lead to the partner being detected as well. Hence, the detection of two birds at a given point count station is not necessarily independent, and we therefore used beta-binomial mixture models that account for the non-independence of multiple detections during a given survey (Martin *et al.* 2011). This model formulation introduces another parameter into the binomial mixture model described above, and thus modifies the binomial trials that are used to estimate detection probability to allow subsequent trials to be correlated (Martin *et al.* 2011). The correlation parameter mimics the calling behaviour of birds, which is the most common cue for detection. To assess whether the beta-binomial mixture model fit the data, we applied a Bayesian posterior predictive check (Gelman *et al.* 2004), and we report the Bayesian *P*-value as an indicator of model fit (Kéry and Schaub 2012). We ran three Markov chains each with 100,000 iterations and discarded the first 20,000 iterations, and report posterior mean estimates for abundance and detection probability. We fit all state-space and binomial mixture models in WinBUGS 1.4 via the R2WinBUGS package (Sturtz *et al.* 2005, Kéry and Schaub 2012) in R 2.15.3 (R Development Core Team 2010).

Binomial mixture models provide an estimate of abundance at the survey sites. To estimate global population size of Montserrat Orioles, we had to extrapolate the estimated abundances at our survey sites to the suitable forest area available on Montserrat, which required an assessment of the radius over which birds would be detected around census stations. We used the intensive observations of individually colour-ringed birds to assess the maximum movement radius from a focal territorial point (i.e. the nest), and previous assessments of detection distance which considered it unlikely that birds could be detected beyond 50 m (Hilton *et al.* 2003). We then assumed that the number of Montserrat Orioles estimated to use a given survey point reflected the number of birds in a circle around the survey point with a radius equal to the mean maximum distance moved by colour-ringed Montserrat Orioles, plus the maximum detection distance of 50 m.

We used a GIS layer of forest cover on Montserrat to calculate the area of suitable forest within this radius of all sampling points, and divided this area by the total area of suitable forest available in the Centre Hills (1,110 ha) and the South Soufriere Hills (269 ha). We used the mean posterior abundance estimate from the beta-binomial mixture model to estimate global population size by scaling the abundance estimate to the ratio of surveyed/total forest area on Montserrat. This extrapolation is highly sensitive to the radius chosen around each sampling point, and we therefore repeated this extrapolation with a radius twice as large as the one we recorded from bird movements to assess the magnitude of change in our global population estimate.

Results

Population trend 2000–2013

We observed between 8 and 85 Montserrat Orioles per year at 16–46 census stations in the Centre Hills between 2000 and 2013, resulting in a range of 0.46–2.19 Montserrat Orioles per census station. At 42 points in the Centre Hills that were surveyed both in 1998 and in 2013 we recorded 1.19 (± 1.70 SD) Montserrat Orioles per point in 1998, and 0.45 (± 0.63) in 2013, a reduction of > 60% (Mann-Whitney *U*-test $P = 0.01$).

The state-space model indicated large observation variance (standard deviation of observation process = 17.9) compared to the mean estimate of Montserrat Orioles at all census stations (40.6 birds). However, there were also substantial population fluctuations, and the coefficient of variation for the observation error (0.44) was only slightly larger than the coefficient of variation for the population process (0.35). The overall population growth rate between 2000 and 2013 was 1.03 (95% credible intervals 0.82–1.29), but due to the large variance around estimates there was little power to determine a long-term population increase or decline (Figure 1).

Estimates of detection probability and true abundance in 2011–2013

The probability of detecting Montserrat Orioles at a census station on a given visit was 0.30 (95% credible intervals 0.13–0.46) in 2011, 0.33 (0.19–0.46) in 2012, and 0.29 (0.14–0.43) in 2013. In 2011, the estimated abundance of Montserrat Orioles that used the forest around sampling stations in the Centre Hills was 142 (88–282), while it was 107 (75–176) in 2012, and 138 (89–256)

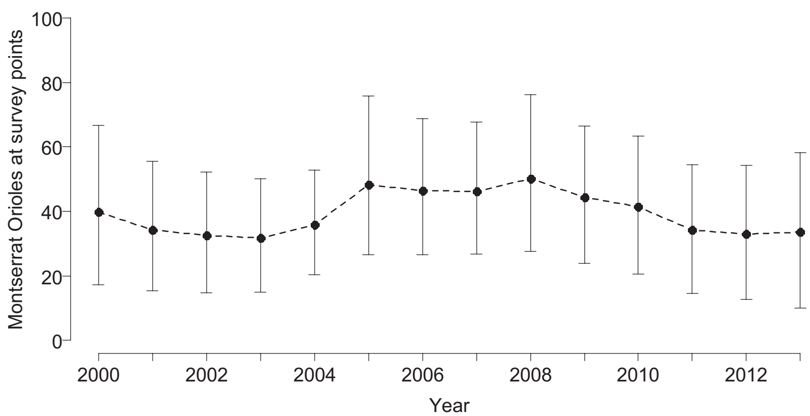

Figure 1. Estimated number of Montserrat Orioles at 50 survey points in the Centre Hills of Montserrat in 2000–2013. Points represent posterior median estimates from a state-space model accounting for random observation error between years, lines indicate 95% credible intervals.

in 2013. The estimated abundance around sampling stations in the South Soufriere Hills was 34 (22–55) Montserrat Orioles in 2012. We obtained Bayesian *P*-values of 0.44, 0.46, and 0.64 for the beta-binomial mixture models in 2011–2013, respectively, indicating that there was no evidence of lack of fit for these models.

Extrapolation of global population size in 2012

We intensively observed 10 adult Montserrat Orioles that were individually colour-ringed. The mean maximum movement distance of these birds from a known central location in their territory was 51.7 m. Based on these movements we assumed that point counts at census stations in the forest of Montserrat would sample Montserrat Orioles whose territory centres would lie within a 100 m radius around each point. The area of forest habitat available in a 100 m radius around all census stations surveyed in 2012 was 218 ha in the Centre Hills (at 70 stations) and 60 ha in the South Soufriere Hills (19 stations). Thus, our effectively surveyed area comprised 19.6% of the Centre Hills and 23.5% of the South Soufriere Hills forest areas, respectively. We divided the estimated abundance at census stations by the proportion of forest area surveyed, and thus extrapolated a total population size of Montserrat Orioles of 546 (382–897) individuals in the Centre Hills, and 143 (94–234) individuals in the South Soufriere Hills. Thus, the estimated world population size of Montserrat Orioles in the wild was 690 birds (476–1,131) in 2012.

Because the global population size extrapolations are sensitive to the assumed radius around census stations, we also applied a radius of 150 m to demonstrate the effect on our population estimates. Under this extended radius assumption, our effectively surveyed area would comprise 44% of the Centre Hills and 53% of the South Soufriere Hills. The total population size of Montserrat Orioles would then be 243 (170–399) individuals in the Centre Hills, and 64 (42–104) individuals in the South Soufriere Hills, resulting in a world population of 307 birds (212–503). Thus, a two-fold increase of the assumed movement radius of birds resulted in a > 50% reduction in the global population estimate.

Discussion

The Montserrat Oriole population in 2013 was lower than in 1998, but there was no clear evidence for an ongoing population decline between 2000 and 2013, despite ongoing volcanic activity and the persistent presence of alien and native nest predators. However, suboptimal survey design led to very large confidence intervals around trend estimates, and the power to detect a mild population decline would have been extremely low. The current world population is estimated to be 476–1131 individuals, and the two forest remnants where the Montserrat Oriole breeds are either formally or informally protected. While we acknowledge that there is large uncertainty associated with the estimated population trend between 2000 and 2013, it appears that the Montserrat Oriole currently does not meet the IUCN category of 'Critically Endangered' (http://www.iucnredlist.org/static/categories_criteria_3_1): the population is likely larger than 250 mature individuals, the area of occupancy is slightly larger than 10 km^2, there is no continuing population decline or a decline of > 80% over the past 10 years, and there are no extreme fluctuations in the population size or area of occupancy. Thus, we recommend re-assessing the conservation status of this species.

Despite the lack of an ongoing population decline, the Montserrat Oriole population is still confined to a small range (< 2,000 ha), and monitoring the population is vitally important to assess the effect of ongoing environmental perturbations. The state-space model employed here to estimate a population trend was able to account for random observation error, but resulted in very wide confidence limits for the estimated trend. While such models are useful for basic monitoring data, the monitoring of rare and endangered species should aim at higher precision to ensure that even small population changes can be detected. Given the large observation and process variance estimated in our model, only very strong declines could be detected statistically, which is an undesirable property for a small and vulnerable population like the Montserrat Oriole (Wilson *et al.* 2011). Thus, the adoption of more powerful monitoring approaches that are able to detect smaller changes in population size is critical for this and other species with small population sizes (Kéry *et al.* 2009, Chandler and King 2011, Schmidt *et al.* 2013).

The new monitoring approach that we adopted in 2011 yielded satisfactory estimates of detection probability and abundance, with much greater precision than the state-space model or previous distance-sampling based approaches (Hilton *et al.* 2003). Because the new monitoring approach relied on repeated visits to the same counting stations, it required 2-3 times more field effort than the distance sampling approach employed from 1997 to 2010. We argue that this additional effort is a useful investment to avoid future ambiguities over the population trajectory of a rare island endemic, and we recommend that annual monitoring is carried out with this revised design.

While the repeated counts are valuable for annual monitoring, extrapolating the estimated abundance from point count stations to derive an estimate of global population size is challenging. Besides the movement radius of birds, which could substantially affect our estimates of total population size, our extrapolations may be inaccurate if a substantial number of floaters occur in the Montserrat Oriole population. Floaters may move longer distances throughout the forest and thus occur at several point count stations, which would lead to an overestimate of population size because the same birds would be counted multiple times. The number or proportion of floaters is extremely difficult to estimate, and to our knowledge no quantitative estimates exist for tropical forest passerines. Newton and Rothery (2001) estimated 0.28 floaters per breeder in European Sparrowhawks *Accipiter nisus*, and a similar proportion of floaters in the Montserrat Oriole population could result in significant bias if these floaters move large distances and are recorded at several point count stations. However, floaters in songbird populations often have restricted movement ranges to rapidly occupy a territory as soon as it becomes vacant (Stutchbury 1991, Zack and Stutchbury 1992, Eikenaar *et al.* 2007), and the number of floaters that would be recorded at multiple point count stations may therefore be negligible.

Given the methodological differences between our approach and previous attempts to estimate Montserrat Oriole population size, it is difficult to compare our population estimate in 2012 (382–897 individuals in the Centre Hills) with previous estimates ranging from 244–503 pairs based on intensive territory mapping in 1998 (Hilton *et al.* 2003). Our comparison of raw count data indicated that the number of orioles observed in 2013 was > 60% lower than in 1998, and we therefore conclude that the population size of Montserrat Orioles in the Centre Hills was lower in 2013 than it had been in 1998. We hypothesise that two non-exclusive processes may explain this lack of obvious population recovery. The first process that may prevent population recovery is ongoing volcanic activity with episodic ash fall events. Particularly the massive volcanic activity in February 2010 may have led to similar mortality as volcanic events in 2001 and 2003, and our state-space model indeed estimated the lowest population growth rate between 2010 and 2011 for all the years in our study (Figure 1). While Montserrat Orioles may recover in years with heavy rain and no volcanic activity (Oppel *et al.* 2013), the re-occurrence of volcanic ash falls will continue to set the population back until volcanic activity diminishes (Allcorn *et al.* 2012), which is not expected for the next 25 years (Scientific Advisory Committee 2011).

The second process that may prevent apparent recovery is potentially inflated population size in the Centre Hills after 1997. We speculate that some of the population decline observed between 1997 and 2003 may have been a result of the Centre Hills population relaxing to carrying capacity, after having received an influx of displaced birds from the Soufriere Hills volcano. The first volcanic activity that led to forest loss in the Soufriere Hills occurred in July 1995, and was followed by subsequent activity that destroyed all of the forest covering the Soufriere Hills volcano by June 1997 (Robertson *et al.* 2000). Many birds inhabiting the forest habitat on the Soufriere Hills at that time may have had the opportunity to escape pyroclastic flows and volcanic debris, and seek refuge in the Centre Hills forest, which is only 5 km to the north and did not at the time require travel through unvegetated terrain. Thus, the gradual destruction of the Soufriere Hills forest may not have led to the immediate death of all birds inhabiting this forest, but may have resulted in a mass exodus to the only large intact forest area remaining on the island. Because the forest area lost was larger than the forest area currently remaining in the Centre Hills, the displaced Montserrat Oriole population may have been larger than the resident population in the Centre Hills at that time. Such a mass exodus could therefore have led to a two-fold increase in Montserrat Orioles in the Centre Hills, which may explain the high densities observed in December 1997 (Hilton *et al.* 2003). Because the Centre Hills could not support such a high density of birds, populations declined to approach the carrying capacity of the forest, and the Montserrat Oriole population may have fluctuated around this lower level since 2000.

Although the Montserrat Oriole currently does not appear to be in immediate danger of extinction, the small area of suitable habitat, and its limited range make it vulnerable to extreme stochastic events. The suitable forest on Montserrat is continually degraded by the presence of invasive feral livestock, and conservation measures to protect the forests on Montserrat should focus on removal of invasive mammals (Allcorn *et al.* 2012). We stress that the continuation of a robust annual monitoring is critical to understand Montserrat Oriole population fluctuations and inform future conservation management.

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References

Allcorn, R. I., Hilton, G. M., Fenton, C., Atkinson, P. W., Bowden, C. G. R., Gray, G. A. L., Hulme, M., Madden, J., Mackley, E. K. and Oppel, S. (2012) Demography and breeding ecology of the critically endangered Montserrat Oriole. *Condor* 114: 227–235.

Alldredge, M. W., Simons, T. R. and Pollock, K. H. (2007a) Factors affecting aural detections of songbirds. *Ecol. Appl.* 17: 948–955.

Alldredge, M. W., Simons, T. R. and Pollock, K. H. (2007b) A field evaluation of distance measurement error in auditory avian point count surveys. *J. Wildl. Manag.* 71: 2759–2766.

Arendt, W. J., Gibbons, D. K. and Gray, G. (1999) Status of the volcanically threatened Montserrat Oriole *Icterus oberi* and other forest birds in Montserrat, West Indies. *Bird Conserv. Internatn.* 9: 351–372.

Bowden, C. G. R., Fenton, C., Gray, G. A. L., Mackley, L., Hilton, G. M. and Atkinson, P. W. (2001) The Montserrat oriole: In trouble again. *Dodo* 37: 100.

Brooks, S. P. and Gelman, A. (1998) General methods for monitoring convergene of iterative simulations. *J. Computational and Graphical Statistics* 7: 434–455.

Chandler, R. B. and King, D. I. (2011) Habitat quality and habitat selection of golden-winged warblers in Costa Rica: an application of hierarchical models for open populations. *J. Appl. Ecol.* 48: 1038–1047.

Clark, J. S. and Bjørnstad, O. N. (2004) Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85: 3140–3150.

Dalsgaard, B., Hilton, G. M., Gray, G. A. L., Aymer, L., Boatswain, J., Daley, J., Fenton, C., Martin, J., Martin, L. and Murrain, P. (2007) Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. *Ibis* 149: 298–312.

De Valpine, P. (2003) Better inferences from population-dynamics experiments using Monte Carlo state-space likelihood methods. *Ecology* 84: 3064–3077.

Eikenaar, C., Richardson, D., Brouwer, L. and Komdeur, J. (2007) Parent presence, delayed dispersal, and territory acquisition in the Seychelles warbler. *Behav. Ecol.* 18: 874–879.

Garrido, O. H., Wiley, J. W. and Kirkconnell, A. (2005) The genus *Icterus* in the West Indies. *Ornitol. Neotrop.* 16: 449–470.

Gelman, A., Carlin, J. B., Stern, H. S. and Rubin, D. B. (2004) *Bayesian data analysis*. Boca Raton, FL: Chapman & Hall/CRC.

Hilton, G., Atkinson, P., Gray, G., Arendt, W. and Gibbons, D. (2003) Rapid decline of the volcanically threatened Montserrat oriole. *Biol. Conserv.* 111: 79–89.

Hilton, G. M., Gray, G. A. L., Fergus, E., Sanders, S. M., Gibbons, D. W., Bloxam, Q., Clubbe, C. and Ivie, M. (2005) *Species Action Plan for the Montserrat Oriole, Icterus oberi*. Sandy, UK: Royal Society for the Protection of Birds.

Kéry, M. (2008) Estimating abundance from bird counts: binomial mixture models uncover complex covariate relationships. *Auk* 125: 336–345.

Kéry, M., Dorazio, R. M., Soldaat, L., van Strien, A., Zuiderwijk, A. and Royle, J. A. (2009) Trend estimation in populations with imperfect detection. *J. Appl. Ecol.* 46: 1163–1172.

Kéry, M., Royle, J. A. and Schmid, H. (2005) Modeling avian abundance from replicated counts using binomial mixture models. *Ecol. Appl.* 15: 1450–1461.

Kéry, M. and Schaub, M. (2012) *Bayesian population analysis using WinBUGS*. Oxford, UK: Academic Press.

Marske, K. A., Ivie, M. A. and Hilton, G. M. (2007) Effects of volcanic ash on the forest canopy insects of Montserrat, West Indies. *Envir. Entom.* 36: 817–825.

Martin, J., Royle, J. A., Mackenzie, D. I., Edwards, H. H., Kéry, M. and Gardner, B. (2011) Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Meth. Ecol. Evol.* 2: 595–601.

Newton, I. A. N. and Rothery, P. (2001) Estimation and limitation of numbers of floaters in a Eurasian Sparrowhawk population. *Ibis* 143: 442–449.

Oppel, S., Hilton, G. M., Allcorn, R., Fenton, C., Matthews, A. J. and Gibbons, D. (2013) The effects of rainfall on different components of seasonal fecundity in a tropical forest passerine. *Ibis* 155: 464–475.

Price, M. R. and Hayes, W. K. (2009) Conservation taxonomy of the Greater Antillean Oriole (*Icterus dominicensis*): diagnosable plumage variation among allopatric populations. *J. Caribbean Ornithol.* 22: 19–26.

Price, M. R., Lee, V. A. and Hayes, W. K. (2011) Population status, habitat dependence, and reproductive ecology of Bahama Orioles: a critically endangered synanthropic species. *J. Field Ornithol.* 82: 366–378.

R Development Core Team (2010) *R: A language and environment for statistical computing*. Available at: http://www.R-project.org/. Vienna, Austria: R Foundation for Statistical Computing.

Robertson, R. E. A., Aspinall, W. P., Herd, R. A., Norton, G. E., Sparks, R. S. J. and Young, S. R. (2000) The 1995–1998 eruption of the Soufriére Hills volcano, Montserrat, WI. *Philos. Trans. A Math. Phys. Eng. Sci.* 358: 1619–1637.

Royle, J. A. and Nichols, J. D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84: 777–790.

Royle, J. A., Nichols, J. D. and Kery, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos* 110: 353–359.

Schmidt, J. H., McIntyre, C. L. and MacCluskie, M. C. (2013) Accounting for incomplete detection: What are we estimating and how might it affect long-term passerine monitoring programs? *Biol. Conserv.* 160: 130–139.

Scientific Advisory Committee (2010) *Assessment of the hazards and risks associated with the Soufriere Hills Volcano, Montserrat*. In Fourteenth Report of the Scientific Advisory Committee on Montserrat

Volcanic Activity. Montserrat: Montserrat Volcano Observatory.

Scientific Advisory Committee (2011) *Assessment of the hazards and risks associated with the Soufriere Hills Volcano, Montserrat*. In Fifteenth Report of the Scientific Advisory Committee on Montserrat Volcanic Activity. Montserrat: Montserrat Volcano Observatory.

Scientific Advisory Committee (2012) *Assessment of the hazards and risks associated with the Soufriere Hills Volcano, Montserrat*. In Sixteenth Report of the Scientific Advisory Committee on Montserrat Volcanic Activity. Montserrat: Montserrat Volcano Observatory.

Sturtz, S., Ligges, U. and Gelman, A. (2005) R2WinBUGS: a package for running WinBUGS from R. *J. Statistical Software* 12: 1–16.

Stutchbury, B. J. (1991) Floater behaviour and territory acquisition in male purple martins. *Anim. Behav.* 42: 435–443.

Wilson, H. B., Kendall, B. E. and Possingham, H. P. (2011) Variability in population abundance and the classification of extinction risk. *Conserv. Biol.* 25: 747–757.

Zack, S. and Stutchbury, B. J. (1992) Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour*: 194–219.

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