

Rapid decline of the volcanically threatened Montserrat oriole

Geoff M. Hilton^{a,*}, Phil W. Atkinson^{a,b}, Gerard A.L. Gray^c,
Wayne J. Arendt^d, David W. Gibbons^a

^aRoyal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

^bCurrent address: British Trust for Ornithology, National Centre for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

^cMinistry of Agriculture, Lands, Housing and Environment, PO Box 272, Brades, Montserrat

^dUSDA Forest Service, International Institute of Tropical Forestry, Sabana Field Research Station, PO Box 490, Palmer, 00721 Puerto Rico

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Abstract

Prior to 1995, the Montserrat oriole (*Icterus oberi*) was confined to ca. 30 km² of hill forest on the Lesser Antillean island of Montserrat, but was not listed as globally threatened. Since then, the eruption of the Soufriere Hills volcano has destroyed more than half of the species' range. Recent intensive monitoring has indicated that the species has also declined dramatically within the remaining intact forest, and is now critically threatened. Different monitoring and analytical methods indicate a decline of 8–52% p.a., and a remaining global population of ca. 100–400 pairs. This case study justifies the use of the restricted range criterion in designating threatened species. Despite intensive monitoring and the use of several analytical methods, it has proved surprisingly difficult to estimate the magnitude of the oriole's decrease, or to control for potential artefacts in the census method. We discuss the reasons for this. The cause(s) of population decline in the intact forest are unclear, though two hypotheses appear plausible: a decrease in arthropod food, a result of volcanic ash fall, and an increase in nest predation as a result of increases in populations of opportunistic omnivores.

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1. Introduction

It is a paradigm of conservation biology that species with geographically small ranges, particularly those that are confined to a single site, are vulnerable to extinction due to rare catastrophic events (Caughley and Gunn, 1995). For this reason, IUCN threat criteria include a 'Very Small Range' criterion, which allows a species to be designated as globally threatened if its area of occupancy is < 100 km², regardless of population density or trends within that range (Hilton-Taylor, 2000). Natural disaster is perceived to be a threat to 135 of the world's 1186 globally threatened bird species; for 48 of these species the entire population is at risk (BirdLife International, 2001). However, examples of species that have gone extinct because of natural disasters are rare in the modern era. In a review of the 128 bird species thought to have become extinct since 1500, natural disasters are

mentioned as a potential contributory cause for only two species, and in both cases were not the major or final factor (BirdLife International, 2000). Extant species that are in a high threat category because of recent natural disasters include Cozumel thrasher (*Toxostoma guttatum*), which has suffered massive population reductions as a consequence of recent hurricanes, and northern royal albatross (*Diomedea sanfordi*), whose major nesting island was devastated by a storm in 1985, and which has subsequently suffered greatly reduced reproductive output (BirdLife International, 2000).

In the Caribbean region, major natural disturbances in the form of hurricanes and volcanic eruptions are relatively frequent events, and indeed are a major driver of ecological processes (Tanner et al., 1991). Moreover, the region's biota is particularly sensitive to localised catastrophe, because of the high proportion of restricted-range species and single-island endemics (Stattersfield et al., 1998; Myers et al., 2000). The eruption of the Soufriere Hills volcano on the Lesser Antillean island of Montserrat since 1995 has provided a classical case

* Corresponding author. Fax: +44-0-1767-683211.

E-mail address: geoff.hilton@rspb.org.uk (G.M. Hilton).

study of a natural catastrophe impacting populations of single-island endemics.

The eruption has been characterised by pyroclastic flows that have covered large areas of the island in mud and ash, and ash clouds that have repeatedly deposited ash over all of the island, and more widely in the Caribbean region (Young et al., 1998). The southern half of the island is now uninhabited, and the capital, Plymouth, is buried under several metres of mud and ash. Volcanic activity peaked (to date) in late 1997, but renewed high levels of seismic activity and dome growth during 2000 suggest that the eruption may continue for some years (Montserrat Volcano Observatory, September 2001); there was a further major eruption in July 2001. The island currently holds at least three endemic reptile species, and two endemic plants (Johnson, 1988). The impact of the volcanic eruption on these species is poorly documented at present, but for the island's only endemic bird, the Montserrat oriole (*Icterus oberi*), information is much more complete. Here we report on the effect of the volcano on the oriole population.

A forest and edge species, the Montserrat oriole probably occurred throughout the main hill ranges prior to anthropogenic forest clearance (Arendt and Arendt, 1984; Fig. 1). In the lowlands, it probably occurred in the wetter forests of the west and south of the island, particularly along the steep river valleys,

known locally as ghauts. Most forest habitat, including the hill forests, was destroyed by clearance for plantation agriculture during the eighteenth and nineteenth centuries (Beard, 1949). However, with the decline of the plantations, secondary forest developed over most of the hill ranges. The core area of available habitat prior to 1995 is estimated as ca. 3,000 ha of hill forest, with some small, scattered occupied areas in the lowlands (Arendt and Arendt, 1984). The species therefore qualified as globally 'Vulnerable', under the 'Very Small Range' criterion (BirdLife International, 2000). The volcanic eruption destroyed the majority of the forest in the Soufriere and South Soufriere Hills, although in July 2001 it was discovered that one forest patch of ca. 200 ha has survived intact in the extreme south-east of the island, and is occupied by Montserrat orioles (Fig. 1). The main area of remaining hill forest occupies ca. 1400 ha in the Centre Hills. These surviving forests have suffered periodic heavy ash falls throughout 1995–2001, most intensively in 1997 and 1998 (Young et al., 1998; Robertson et al., 2000).

At the peak of the eruption in late 1997, there was concern for the short-term survival of the Montserrat oriole, and therefore an emergency census was carried out in the Centre Hills (Arendt et al., 1999). This gave a relatively reassuring population estimate of 4000 individuals (95% CI 1500–7800)—higher than pre-eruption estimates (Arendt and Arendt, 1984), and suggested that ash falls in the intact forests were not having an immediately catastrophic effect. Arendt et al. (1999) concluded that the oriole population in the Centre Hills "seems reasonably secure", and recommended that the species be considered 'Endangered', as a result of the inevitable population reduction brought about by destruction of more than half of the habitat. In this paper, we describe subsequent changes in the species' status during the period 1997–2000 when volcanic activity was in general decline.

2. Study area and methods

Montserrat (16°N, 62°W, 109 km²) is a UK Overseas Territory lying at the northern end of the Lesser Antilles. It has a tropical climate, rainfall varying between 1000 and 2500 mm per year (Blankenship, 1990). The natural climax vegetation is a succession from xerophytic scrub, through seasonal forest, rainforest, and elfin woodland as precipitation and altitude increases. There are three main hill ranges—the South Soufriere Hills, Soufriere Hills, and Centre Hills, rising to 700–900 m asl. Prior to 1995, hill forests covered most land above ca. 300 m in the hill ranges, with very limited forest cover at lower elevations.

The first main oriole census was conducted in December 1997 (Arendt et al., 1999). A second, identical census

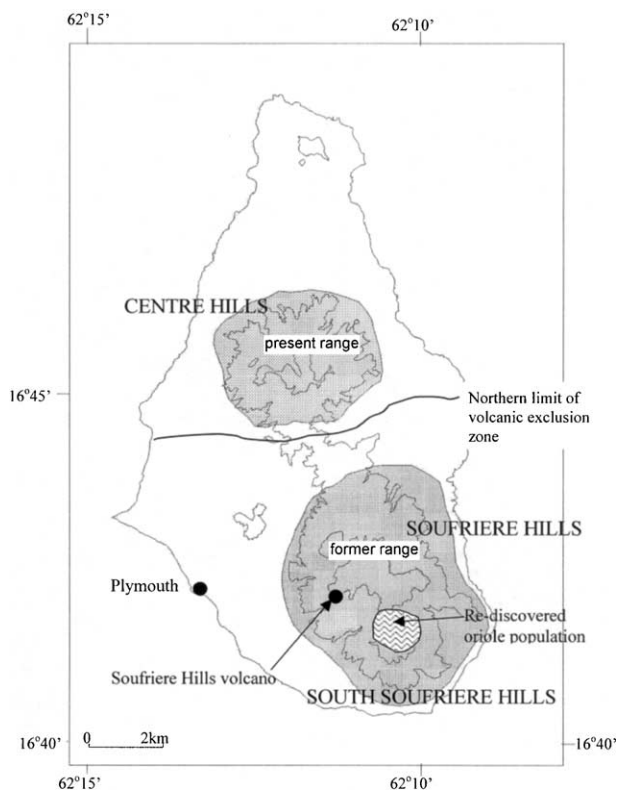


Fig. 1. Map of Montserrat, showing past and present range of the Montserrat oriole, the location of the volcano, and the main hill ranges. Contour lines are marked at 305 and 615 m asl.

was conducted in December 1999. In addition, smaller quarterly censuses were conducted, using identical methods, between December 1997 and September 2000, using a sub-set of the main census points. Territorial pairs were mapped in selected study areas during the breeding seasons of 1998 and 2000. Territory mapping followed conventional methods (Bibby et al., 1992); pairs were mapped using repeated visits to pre-defined study plots (areas ranging between 6.8 and 19.1 ha) in April–September 1998 (> 10 visits per site), and during June 2000 (1–4 visits per site). Oriole pairs are relatively conspicuous. Site visits in 2000 were prolonged compared to those in 1998, with a minimum of 6 h spent in each site. However, the shorter time-period for study, and fewer site visits, mean that in 2000 it is possible that some pairs were missed.

2.1. *Main oriole censuses*

The two main censuses were performed between 3 and 10 December 1997, and 30 November–10 December 1999. Methods employed during the 1997 census are described in detail in Arendt et al. (1999). The 1999 census was an identical repeat of the 1997 census. Briefly, 137 points were surveyed on a systematic grid laid out over a 1440-ha area of the Centre Hills. This area comprised the entire known range of the species, (although note the subsequent discovery of ca. 200 ha of occupied habitat in the South Soufriere Hills). Distance-sampling point counts were employed, and all orioles detected during a 10-min silent period at each point were recorded. The exact distance from the observer to a detected oriole was measured in the 1997 census. During the 1999 census, orioles were ascribed to one of five circular distance bands: 0–5 m from the observer, 5–10, 10–20, 20–40, and > 40 m. Counting stations were separated by ca. 250–400 m. After the 10-min silent period, a recording of an oriole song was played for three minutes on a portable tape recorder. The same original master recording was used in all censuses, though the tapes used in the field were replaced periodically. All orioles detected during this three-minute period were recorded in the same way as during the silent period.

The two censuses are directly comparable: (1) The same key personnel were involved throughout, although not all points were done by an identical team; (2) the dates were almost identical; (3) in most cases the exact point that was visited in 1997 was re-located, while in all cases the 1999 observers would have been within 100 m of the equivalent point from 1997; and (4) the same oriole recordings were used.

2.2. *Quarterly oriole censuses*

Thirty-eight points taken from the main oriole census grid were adopted for use in quarterly censuses, together

with nine points that were visited during pilot studies in December 1997. These points were not chosen at random. Rather they were chosen to create a series of routes that could be walked in a single day and to cover a representative sample of habitats in the Centre Hills. In practice, this means that they are slightly spatially autocorrelated, and tend to be in relatively accessible areas of the forest. However, overall they give good coverage of the Centre Hills and the major habitats contained along the altitudinal, exposure and rainfall gradients, in roughly equal proportions to the main census. These range from dry evergreen and seasonal forest in the lowlands, through rainforest to palm brake, elfin woodland and montane thicket (Beard, 1949). Data are available for 12 quarterly censuses between December 1997 and September 2000; three censuses were conducted in each of four 'seasons': December–January (start dates between 30/11–01/01), March–April (01/03–23/03), June–July (08/06–30/06), and September–October (04/09–19/10). Start dates of successive censuses were 59–111 days apart, thus the representation in Fig. 2 of the quarterlies as an evenly spaced time-series is a simplification.

Census methods were identical to those employed in the main censuses. However, in most censuses, a few points were missed, due mainly to a failure to re-locate them in dense forest (40–47 points were completed per census)—no systematic bias is associated with these missed points.

2.3. *Data analysis*

In order to test whether the number of orioles per point differed significantly between the main censuses in 1997 and 1999, paired Wilcoxon Signed-Rank Tests were performed on the number of orioles recorded per point. To investigate the magnitude of the difference, we bootstrapped (999 iterations) the number of orioles per point, and compared the distribution of bootstrap values for each census.

Data from the point counts consist of (1) birds recorded during the 10-min silent period, (2) birds recorded during the subsequent 3-min tape-playing period, and (3) data for both periods combined. Birds recorded during the tape-playing period include those that were also recorded during the preceding silent period, and new birds that were detected for the first time during the tape-playing period. Where the data for both periods are combined, we sum the number of birds recorded during the silent period to the number of *new* birds recorded during the tape-playing period.

Indices of abundance for the 12 quarterly censuses were calculated by summing the number of orioles seen on all 47 points and scaling the final count to 100; values for missing counts were imputed using the Underhill method (Underhill and Prys-Jones, 1994). In order to

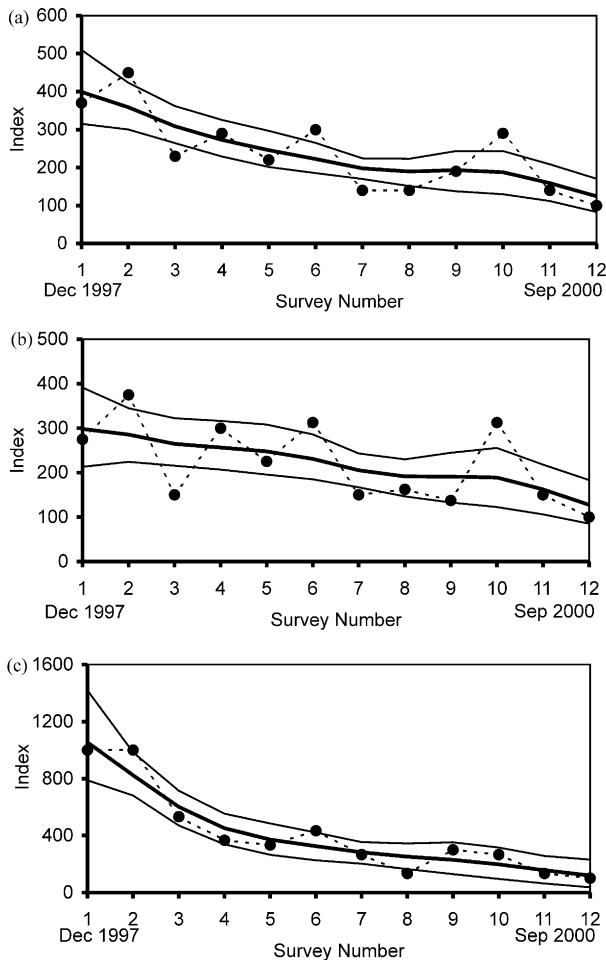


Fig. 2. Apparent decline in the Montserrat oriole population in the Centre Hills, 1997–2000. Dashed lines: Underhill indices for the twelve quarterly censuses. Values are scaled to equal 100 in September 2000. Thick solid line: General Additive Model (GAM) values for the Underhill indices. Thin solid lines: 95% confidence intervals, calculated by bootstrapping, for GAM values. (a) total oriole counts (silent period and tape-playback period combined); (b) oriole counts from the 10-min silent period only; (c) oriole counts from the tape-playback period only.

provide a simple test of the statistical significance of the temporal trend in oriole numbers revealed by the index, we used General Linear Models with ‘index of abundance’ as dependent variable, ‘census number’ as a covariate (December 1997 = 1, through to September 2000 = 12), and ‘season’ as a four-level factor (December, March, June, September). This tested for a significant linear trend over the course of the 12 censuses.

To reveal the underlying trend in the census data, the counts were smoothed using a General Additive Model with site and survey number as factors. The number of degrees of freedom associated with the survey number parameter determines the amount of smoothing. Varying the degree of smoothing may alter the interpretation of the overall trend, but for bird census work a figure of $0.3n$ degrees of freedom, where n is the number of degrees of freedom associated with the survey number

parameter, has been found to provide an acceptable degree of smoothing (Fewster et al., 2000; Atkinson and Rehfisch, 2000) and this protocol was followed here; 95% CIs for the smoothed abundance indices were estimated using 999 bootstraps.

The density and population size of Montserrat orioles in the Centre Hills were estimated using DISTANCE software (Laake et al., 1993) to analyse the distance-sampling census data for the two main censuses. The essence of estimating population density using distance-sampling observations is to fit a ‘detection function’ that describes the decline in bird detectability with distance from the observer. This allows the number of birds that were present but not detected to be estimated, and from this an estimate of population density can be made. The detection function is estimated using the observed decline in observations with distance from the observer. Following Buckland et al. (1993), four a priori detection functions were modelled, to find the best fitting curve for our data: half-normal with cosine adjustment, half-normal with polynomial adjustment, hazard-rate with cosine adjustment, and half-normal with hermite polynomial adjustment. The model giving the lowest Akaike’s Information Criterion (AIC, a measure of goodness of fit, adjusted for number of parameters) was selected.

Data from the 10-min silent period only were used in the DISTANCE analyses. The outer distance band of observations was set as 40–80 m. In the analysis, it is possible to record groups of birds as a single cluster—indicating that they are not independent samples for calculation of the detection function—or as a series of independent individual samples. Montserrat orioles are not a flocking species (maximum number of individuals recorded at a point = 6), so the method chosen made very little difference to the analysis outcomes. In the results presented here, each individual oriole was recorded as an independent separate cluster in the analysis. This avoids the need to make arbitrary decisions about assigning birds to clusters (it is often difficult to determine whether orioles are behaving as a single group, or simply in close proximity). Chi-squared goodness-of-fit tests and visual examination of the detection functions showed that the detection function fit was not improved by truncation (omitting data from the furthest or closest distance band). Since it is conceivable that detectability differed between the two surveys, we estimated population size in each census using separate best-fit detection functions. The duration of the sampling period represents a trade-off: longer sampling periods allow a higher proportion of the birds that are present to be sampled, and hence increase the statistical power of the census; however, the distance-sampling approach assumes that birds do not move into the area during a sampling period, and clearly, the longer the sampling-period, the greater the violation of this assumption. We examined the influence of sampling-period on the population estimates by

performing separate analyses on (1) data for birds detected during the first 5 min of a sampling period; (2) data for all birds detected during the 10-min sampling period.

The two main censuses were conducted in the non-breeding season (Montserrat orioles primarily breed between March and August, unpublished data, but see Arendt, 1990). We attempted to convert the census data into an approximate estimate of the number of pairs holding territory in the breeding season. Seven study plots, with a total area of 90.6 ha (ca. 6% of the area of the Centre Hills), were surveyed during the 1998 and 2000 breeding seasons. By assuming that oriole densities in the study plots are representative of those in the Centre Hills as a whole, one can extrapolate to the total number of territorial pairs in the Centre Hills:

Total population = pair density in study plots × area of Centre Hills

where total population is number of territorial pairs, pair density is pairs ha⁻¹, and area of Centre Hills is in ha.

Ideally, the plots would have been objectively stratified by forest type, but due to fieldwork constraints this was not possible. The sites were easily accessible areas with known oriole pairs, covering a wide geographical and altitudinal spread of the Centre Hills, and hence it is likely that their oriole densities were atypically high. Therefore, we calculated a corrected estimate of the number of breeding pairs, based on the relative numbers of orioles recorded at points lying within breeding season study sites and those recorded at points throughout the Centre Hills:

$$\begin{aligned} \text{Total population} &= \text{pair density in study plots} \\ &\times \frac{\text{birds point}^{-1} \text{ in all Centre Hills}}{\text{birds point}^{-1} \text{ within study plots}} \\ &\times \text{area of Centre Hills} \end{aligned}$$

3. Results

3.1. Population trends 1997–2000

When the analysis incorporated all birds recorded, including those detected during the tape-playback period, oriole numbers were significantly lower in the main census in December 1999 than in December 1997 ($n=137$ paired points, Wilcoxon Signed Ranks test, $Z=2.37$, $P=0.018$). The number of orioles recorded per point was 0.51 (95% CI calculated by bootstrapping 0.42–0.61) in December 1997, and 0.29 (0.19–0.35) in December 1999, giving an apparent decline in density of 43% over 2 years. However, a separate analysis performed on data gathered only during the 10-min. silent

period (prior to playing the tape of oriole calls) shows a smaller and non-significant 31% decline from 0.29 (0.22–0.36) to 0.20 (0.14–0.28) birds per point (Wilcoxon Signed Ranks, $Z=1.37$, $P=0.17$).

The quarterly monitoring data show a substantial decline between December 1997 and September 2000. The index of abundance for the overall counts (combining data from both the silent period and the tape-playback period) dropped by 69% over the three years (Fig. 2a). A General Linear Model showed that the decline over time was very highly significant ($F_{1,7}$ 'census number' = 27.8, $P=0.001$; $F_{3,7}$ 'season' = 14.3, $P=0.013$; interaction term *n.s.*; $r^2(\text{adj})=0.85$).

Using data from the 10-min silent period only, the decline in the index of abundance was slightly less severe, at 57% (Fig. 2b), though still highly significant ($F_{1,4}$ 'census number' = 43.9, $P=0.003$; $F_{3,4}$ 'season' = 8.11, $P=0.011$; interaction term $F_{3,4} = 8.34$, $P=0.034$; $r^2(\text{adj})=0.94$). The *season* × *time* interaction was significant because there was no decline in the June indices of abundance over the 3 years.

Using data from the tape-playback period only, the decline was 89% (Fig. 2c)—substantially greater than for the silent period ($F_{1,7}$ 'census number' = 21.3, $P=0.002$; $F_{3,7}$ 'season' = 1.21, *n.s.*; interaction term *n.s.*; $r^2(\text{adj})=0.72$).

3.2. Estimating the number of orioles from the main censuses

The population estimates given by DISTANCE software show large confidence intervals, and hence, although there is a decline of 55% in the population estimate between 1997 and 1999, this difference is not significant (there is considerable overlap in the 95% CIs of the two estimates) (Table 1).

Fig. 3 shows that the detection functions differed between the two censuses. In 1999, a smaller proportion of the birds was observed in the closest two distance bands and in the furthest distance bands, with a greater proportion in the intermediate distance categories. The best detection function for the 1999 census is a half-normal-hermite curve, whereas for 1997 it is a hazard-cosine function (Table 1). The effect of analysing data from the first 5 min of the sampling period only is to reduce the 1997 population estimate by 29%, and the 1999 estimate by 24%—though neither value differed significantly from that calculated for the 10-min period (Table 1).

3.3. Estimating the number of territorial pairs

Assuming that pair densities in the breeding season study plots are typical for the Centre Hills as a whole, population estimates derived by extrapolation from mapping of breeding season territorial pairs are lower

Table 1
Population estimates for the Centre Hills oriole population, based on distance-sampling^a

Year	Selected detection function	Model Goodness of Fit			Population density (birds ha ⁻¹) ^b	Population estimate for Centre Hills ^b (birds)
		χ^2	df	P		
10-min observation period						
1997	Hazard-cosine	0.11	1	0.75	2.63 (1.11–6.20)	3800 (1600–8900)
1999	Half-normal-hermite	1.76	3	0.62	1.16 (0.65–2.07)	1700 (930–3000)
5-min observation period						
197	Hazard-cosine	2.50	3	0.48	1.88 (0.76–4.64)	2700 (1100–6700)
1999	Half-normal-hermite	0.17	3	0.98	0.91 (0.48–1.73)	1300 (690–2500)

^a Estimates are based on DISTANCE software analysis of distance-sampling point counts ($n=137$ points) conducted during censuses in December 1997 and December 1999.

^b With 95% CI.

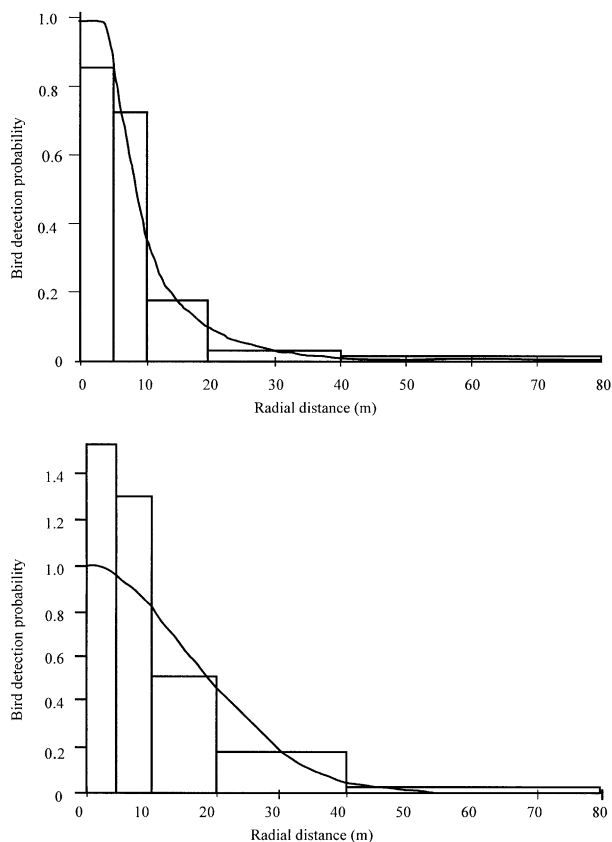


Fig. 3. Detection curves for Montserrat orioles during the 1997 and 1999 censuses. The models assume a detection probability of 1 at zero distance (all birds at distance = 0 m from the observer are detected). Blocks represent the observed density of birds detected in distance bands 0–5, 5–10, 10–20, 20–40 and 40–80 m. Curved lines represent the fitted decline in oriole detectability with distance from the observer. (a) 1997 census; best fit function is hazard-cosine; (b) 1999 census; best fit function is half-normal-hermite.

than those derived from December point-count censuses (Table 2).

However, the study plots have much higher oriole densities than is typical for the Centre Hills as a whole. This difference is significant for 1997 (negligible overlap

in 95% CIs calculated by bootstrapping), but not for 1999. Therefore, we adjusted the extrapolation of territory density to take into account the atypically high population densities within the study plots. The effect of this adjustment is to reduce the population estimate derived from territory mapping, and hence increase the discrepancy between territory mapping and point-count population estimates.

Surprisingly, the number of territorial pairs in the breeding season study plots remained rather constant between 1998 and 2000 (Table 2), despite the apparently large overall decline in the population.

4. Discussion

4.1. Conservation status of the Montserrat oriole

Following the initial massive reduction in range size when pyroclastic flows obliterated the forests in the southern hill ranges during 1995–1997, the Montserrat oriole appears to have suffered a further substantial decline during 1997–2000, within the Centre Hills range which comprises most of its remaining area of occupancy. The species has therefore been designated as globally critically threatened under both the ‘Rapid Decline’ and ‘Small Range, Fragmented and Declining’ criteria (BirdLife International, 2000).

The recent history of the Montserrat oriole provides striking support for the concept of including ‘Very Small Range’ as a criterion for threatened status, regardless of population trends or absolute numbers. Prior to 1995, the Montserrat oriole probably had a stable population, numbering perhaps several thousand birds, with no major anthropogenic threats. Despite this apparently positive conservation status, it did qualify as ‘Vulnerable’ under the ‘Very Small Range’ criterion following the establishment of Mace-Lande criteria (Mace and Lande, 1991), as it had an area of occupancy estimated at 30 km² (Arendt and Arendt, 1984). Out of

Table 2
Extrapolated number of territorial pairs, based on territory-mapping^a

Year ^a	Territorial pairs in study plots	Pair density in study plots (<i>pairs ha⁻¹</i>) ^b	Extrapolated no. of pairs in Centre Hills (<i>assuming uniform density</i>) ^c	Birds per counting station in study plots ^d (<i>n</i> = 17)	Birds per counting station in all Centre Hills ^e (<i>n</i> = 146)	Extrapolated no. of pairs in Centre Hills (<i>assuming non-uniform density</i>) ^f
1998	19	0.25 (0.17–0.35)	359 (244–503)	0.94 (0.59–1.35)	0.51 (0.42–0.61)	164 (94–312)
2000	16	0.21 (0.12–0.34)	302 (173–489)	0.59 (0.18–1.00)	0.23 (0.16–0.31)	99 (41–437)

The table shows extrapolations from breeding season territorial pair density in study plots of known size to the whole Centre Hills area. Extrapolations are based on (1) assuming that the study plots had pair densities that were typical of the Centre Hills as a whole; (2) adjustment of the extrapolation for the fact that the study plots appeared to have above average oriole density.

^a Point-count data are from the previous December, i.e. December 1997 and December 1999.

^b Median with 95% confidence intervals, calculated by bootstrapping values for each site.

^c Pair density in breeding season study plots, multiplied by the total area of the Centre Hills (= 1437.5 ha).

^d Median values (95% confidence intervals) from the main point-count censuses conducted in December 1997 and 1999 respectively, for counting stations that fall within the breeding season study plots.

^e Median values (95% confidence intervals) from the main point-count censuses conducted in December 1997 and 1999 respectively, for all counting stations.

^f Pair density in the study plots, multiplied by the total area of the Centre Hills, adjusting for the above average population density in the study plots.

1186 globally threatened bird species, 257 are designated under this criterion (BirdLife International, 2001), the rationale being that such populations are permanently vulnerable to extinction because their spatial restriction means that a single catastrophic event can impact the entire population. Clearly, such a designation was justified in the case of the Montserrat oriole.

In fact, however, the species was not officially designated as 'Vulnerable' prior to the eruption (see Collar et al., 1994). Arguably, the consequence of this mis-designation has been that there are now inadequate data on the species' biology with which to understand and manage the current crisis. Since the volcanic eruption began, a repeatable monitoring scheme has been established, two full censuses have been completed, and there have been investigations of reproductive output, diet and habitat use (Atkinson et al., unpublished data). However, attempts to elucidate the cause of the apparent decline in the Centre Hills are severely hampered by a lack of pre-eruption baseline data. This is perhaps in part due to the species being given a lower threat category than was merited.

4.2. Estimating the decline rate and population size

It is striking that, despite intensive monitoring and the use of several analytical methods, it has proved surprisingly difficult to estimate the magnitude of the decline. Different monitoring and analytical methods indicate a decline of 17–52% p.a., some statistically significant and some not (Table 3). For example, the quarterly monitoring data suggest a decline of >50% over 3 years. However, although there is a highly significant relationship between time and abundance index, wide confidence intervals mean that the magnitude of the decline

cannot be estimated with any precision. The comparison between the two main censuses (December 1997 and December 1999) indicates a population decline of ca. 30–55% over 2 years (Table 3). Such a decline rate would rapidly bring the species close to extinction: yet for the number of orioles per point recorded only during the silent period, the decline was not statistically significant. For distance-sampling population estimates, the very high variance of the density estimates that result from fitting a detection curve for a rather rare bird means that there is very little power to detect even large population changes. Confidence intervals for the estimates overlap greatly.

Furthermore, there are large discrepancies between the absolute population estimates derived by different methods: territory mapping indicates a much lower population than distance-sampling point counts (Table 3): 3800 birds were estimated in December 1997, but only 100–440 territorial pairs in April–July 1998. No data are available to assess whether non-territorial adults (floaters) or immature birds might make up the difference – again, the lack of baseline data on the species' ecology hampers interpretation of the data.

We suspect that territory mapping provides the most accurate picture, and that the oriole population probably lies in the range 100–400 pairs. The point-count data potentially violate some of the assumptions of the distance-sampling approach. Whereas theoretically the point-counts represent an instantaneous snapshot of birds present in the recording area (Buckland et al., 1993), in fact a 10-min recording period was employed in order to maximise the probability of detecting birds. The choice of sampling period is of course arbitrary, and represents a compromise between the need to detect the maximum number of birds, and the problem of birds

Table 3
Decline rates and population estimates calculated by different census and analysis techniques^a

Census	Analysis method		Decline rate (% p.a.)	First population estimate	Second population estimate
<i>Territorial pair mapping, 1998 and 2000</i>	Extrapolation using point-count data (adjusted for density variations within Centre Hills)		23%	164 pairs (= ca. 500 post-breeding birds, plus floaters)	99 pairs (= ca. 300 post-breeding birds plus floaters)
	Extrapolation using point-count data (not adjusted for density variations within Centre Hills)		8%	359 pairs	302 pairs
<i>Main point-count censuses, 1997 and 1999</i>	Paired Wilcoxon test on birds per counting station	Silent period	17%		
		All sampling-period	25%		
	DISTANCE sampling population estimate	First 5-mins of sampling-period	31%	2700 birds post-breeding	1300 birds post-breeding
		Whole 10-min sampling period	33%	3800 birds post-breeding	1700 birds post-breeding
<i>Quarterly point-count census, 1997 – 2000</i>	Underhill index of population trend	Silent period	25%		
		Tape playback	52%		
		All sampling-period	32%		

Decline rates in bold are statistically significant ($P < 0.05$), see Section 3.

^a A summary of the annual decline rates and population estimates derived from the different methods employed. Although the estimated decline is rapid in all cases, under some methods it is non-significant.

moving into the recording area during the period (Bibby et al., 1993). However, in distance-sampling point-counts of mobile species such as birds, particularly in habitats such as forests where detection is difficult, this arbitrary choice can have profound effects on population estimates. We conclude that using distance-sampling from point-counts to make absolute population estimates should be done with caution, and preferably corroborated with other forms of data.

Surprisingly, there were clear differences between the 1997 and 1999 main censuses in the detection functions for Montserrat oriole. In 1999, birds tended to be recorded at greater distances from the observer. The effect of this is to give a larger estimated decline than is given by comparisons of absolute numbers, because it is assumed that in 1999 a smaller proportion of the birds that were present went undetected. This pattern was repeated for other species recorded in the censuses (unpublished data). If this reflected a real difference between the censuses in the detectability of birds, then the distance-sampling approach would be invaluable in providing a more accurate estimate of real population change than simple counts. This might occur if, for example, lighter winds in 1999 made detection of distant calling birds more likely. Conversely, the difference might be an observer artefact. As with most forest bird censuses, the vast majority of registrations in these censuses were of calling birds. Even for experienced obser-

vers, subtle improvements in skill over time might increase detection and identification of distant birds that call briefly. This might be sufficient to change detection functions, and hence alter population estimates.

Finally, orioles sometimes appear to respond to human observers in their territory by approaching and calling. This violates the assumption that birds do not move in response to the observer, would inflate distance-derived density estimates, and suggests a mechanism whereby part of the decline may be an artefact of census technique. During the early part of the monitoring programme, the birds were less familiar with humans and tape-playback of oriole song, and may therefore have shown a stronger tendency to approach observers than was the case later on. This effect might cause an apparent decline. If so, one might predict:

1. That the oriole decline between the two main censuses would be greatest at those 47 points that are also part of the quarterly monitoring programme, since birds with territories along those routes would have received much greater exposure to humans. The bootstrapped average number of orioles per point at the 47 quarterly monitoring points during the December 1997 main census was 0.79 (95% C.I. 0.60–1.00). This declined by 49% to 0.40 (0.21–0.62) at the same points in the December 1999 main census. By

comparison, among the 99 points that were not monitored quarterly during the intervening 2 years, there was a 34% decline from 0.41 (0.30–0.53) to 0.27 (0.18–0.37). Although confidence intervals are large, there is a suggestion that the decline was more pronounced at regularly monitored sites.

2. There would be a greater decline in oriole detections during the tape-playing period than during the silent period. This is indeed the case. Taking the quarterly monitoring data, the decline in abundance index for birds recorded during the tape-playback period was ca. 90%, whereas the decline for birds recorded during the silent period was only ca. 60%. However, if this behavioural response is occurring, we would still expect to see some decline over time in silent-period observations. This is because, even during the silent-period, some registrations would have been of curious birds that had moved towards the human observers, and this effect would also have diminished over time.

Thus, there is evidence that this effect may have contributed to the apparent decline. However, the decline is most unlikely to be entirely artefactual: there is a high turnover of territorial pairs in the study plots. For example, 18 individuals from the 19 territorial pairs studied in 1998 were colour-ringed. Of these, only six apparently held territory in 2000, among 16 territorial pairs at the same sites. This suggests that familiarity with humans and their census routes is unlikely to develop over a long period. Furthermore, birds occupying territories away from the quarterly monitoring routes and study plots would have had minimal contact with humans between December 1997 and December 1999, yet still showed a considerable decline.

A further difficulty is the relatively constant number of territorial pairs in the breeding season study plots between 1998 and 2000. The explanation for this may be that the study plots hold exceptionally high oriole densities (Table 2), and may therefore provide optimal habitat that would continue to be occupied at high density even in a declining population. Between the 1997 and 1999 main censuses, there was only a 20% decline (95% CI of population change, calculated by bootstrapping = +80% to –120%) in the number of orioles recorded during the silent period at those recording stations ($n=17$) falling within the breeding season study plots. This compares with a 42% decline (95% CI of population change, calculated by bootstrapping +6% to –77%) at recording stations falling outside the study plots ($n=131$). Thus the census data provide some support for the idea that there was indeed rather little decline in the oriole population in these hotspots, compared to in the lower density population

in the rest of the Centre Hills, though the wide confidence intervals do make this conclusion very tentative.

In common with some other *Icterus* spp. (e.g. Enstrom 1992a,b, 1993), Montserrat orioles have deferred maturity: males retain juvenile (female-like) plumage as 1-year olds, and as 2-year olds have recognisably sub-adult plumage (unpublished data). In 1998, no 1-year old males ($n=21$ pairs) held territory in the study plots, whereas in 2001, four of 25 study females were paired to one-year old males. We suspect that in a healthy population, the habitat is likely to be saturated and survivorship of territorial adults is high. For instance, adult survivorship of 82.4% has been recorded in the yellow-shouldered blackbird (*Agelaius xanthomus*), another Caribbean island oriole (Post and Wiley, 1977). Therefore, there is likely to be a considerable population of non-territorial floaters and immature birds. As the population declines, opportunities for territory establishment will have increased; one-year old birds are increasingly able to establish territories, and the number of floaters has declined. As a result, there is likely to be a time-lag between the onset of population decline and a decline in the number of territorial pairs

4.3. Implications for research and monitoring of threatened species

This study demonstrates a surprising difficulty in effectively monitoring the status of a rare species, and illustrates a dilemma for conservation biologists. The precautionary principle dictates that conservation action would be taken if the balance of evidence suggests that a serious decline is occurring, rather than waiting for stronger confirmation. Clearly, in the case of the Montserrat oriole, conservation biologists would be failing in their duty if they did not act on the evidence presented here of a rare species that is apparently in rapid decline. However, this risks mistaken prioritisation of conservation effort—a serious problem in a world of finite conservation resources and >2000 Critically threatened species (Hilton-Taylor, 2000), and demonstrates the importance of careful power analysis in the design of monitoring schemes. Ideally, a target level of population change that will be statistically detectable should be pre-defined, and the monitoring scheme designed to have sufficient power to meet this target. The ability to detect population changes is a function of sample size (in our case, the number of points visited), and the frequency and variance of positive records. In the present study, difficulties arose because the apparent decline of the oriole during the course of the study greatly reduced the frequency of positive records, and hence the power, in the later stages, to detect population trends. The oriole is currently insufficiently rare and localised for complete censuses to be possible (particularly in view of the

extremely difficult terrain in the Centre Hills), but insufficiently common for a population-sampling programme to generate high power. We suspect that this applies to a large number of threatened species. In the case of the oriole point-count monitoring programme, increasing the number of counting stations is probably not an option, since this would result in the stations being so close together that they are non-independent. Repeat visits to counting stations, in order to reduce random variation, would improve the power of the census to detect population changes.

This study therefore highlights some potentially important problems for long-term monitoring of bird species. Changes in the response of the study species to observers can result in changes in detectability. This may be the decline in curiosity that we suspect has occurred in our study, or a loss of fear of humans that over time causes birds to become more easily detectable. Even subtle changes in observer skill may cause slight changes in rates of bird detection, that in turn generate spurious population trends. Generating statistical confidence, even in apparently major population changes, is difficult for dispersed birds in difficult terrain, and this hampers conservation decision making.

4.4. Causes of the oriole's decline

A major decrease in the oriole population resulted from the physical destruction of most of the southern forests. However, the decline within the Centre Hills during 1997–2000 occurred in intact forest, during a period of generally decreasing ash fall. A research project commencing in 2001 attempts to determine the cause of this decrease. Attention focuses on two hypotheses (which are not mutually exclusive): firstly, repeated ash falls may have reduced the insect food supply for orioles. Insects are known to be highly sensitive to ash damage, and leaf-gleaning insectivores were the most strongly affected avian foraging guild after the Mount St Helens volcanic eruption (Edwards and Schwartz, 1981; Foster and Myers, 1982). Secondly, the numbers of opportunist predators, notably rats (*Rattus* spp.) and pearly-eyed thrashers (*Margarops fuscatus*), may have increased as a result of forest disturbance, and the abandonment of small-scale cultivation and fruit harvesting. Increases in the number of omnivorous generalists have previously been observed in response to major hurricanes and fires (Lynch, 1991; Waide, 1991; Arendt, 2000). This in turn may have increased rates of predation on oriole nests. It is possible that the Centre Hills oriole population has always been a sink, maintained by source populations in the Soufriere and South Soufriere Hills.

Although the cause of the decline of the oriole within the surviving forest on Montserrat is currently unclear, it may be an indication that volcanic eruptions can have

impacts on avifauna that extend beyond direct habitat destruction. These impacts are poorly understood. Fifteen other globally threatened bird species are threatened by volcanic activity, and two bird species have their entire ranges on the slopes of currently active volcanoes (BirdLife International, 2000, 2001). The black-breasted puffleg (*Eriocnemis nigrivestris*) is known only from the sides of Mount Pichincha in Ecuador, which became active in 1999, and has deposited considerable ash-falls on the area. The Mount Karthala white-eye (*Zosterops mouroiensis*) occurs only on Mount Karthala in the Comoro Islands, where the volcano burnt a large area of montane vegetation in 1958. In both of these cases, as with the Montserrat oriole, anthropogenic habitat destruction has increased the species' vulnerability by reducing their range (BirdLife International, 2000). Further research into the links between the eruption and the population biology of the Montserrat oriole may help to identify practical measures that could be undertaken for this, and possibly other, threatened species.

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