

DEMOGRAPHY AND BREEDING ECOLOGY OF THE CRITICALLY ENDANGERED MONTSERRAT ORIOLE

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Abstract. The Montserrat Oriole (*Icterus oberi*) is a critically endangered species, confined to a small range in the hill forests of the volcanic island of Montserrat in the eastern Caribbean. From 1998 to 2005 we studied its breeding biology and survival of adults, finding that the Montserrat Oriole has a smaller clutch, more extended parental care, and higher adult survival than do orioles nesting in the North Temperate Zone. Adults' probabilities of survival varied by year from 0.60 to 0.76 but were similar for both sexes. Average clutch size was 2.6 eggs (± 0.04 SE), and post-fledging parental care was 40 ± 5 days. We found nest success of 29% ($n = 275$ nests), and 87% of nest failures were due to predation by either introduced rats (*Rattus* sp.) or the native Pearly-eyed Thrasher (*Margarops fuscatus*). Most pairs initiated several nesting attempts after both failed and successful first broods, leading to an overall annual productivity of 1.2 fledged chicks per pair. Despite being able to raise up to three broods per season, the Montserrat Oriole's annual productivity was lower than that of its temperate-zone congeners, and we recommend that conservation management focus on enhancing nesting success via rat control.

Key words: adult survival, breeding biology, Icteridae, *Icterus oberi*, Montserrat, tropical passerine.

Demografía y Ecología Reproductiva de *Icterus oberi*, una Especie en Peligro Crítico

Resumen. *Icterus oberi* es una especie en peligro crítico, restringida a un área de distribución pequeña en los bosques de las laderas de la isla volcánica de Montserrat en el este del Caribe. Desde 1998 a 2005 estudiamos su biología reproductiva y la supervivencia de los adultos, encontrando que *I. oberi* tiene un tamaño de nidada menor, un tiempo de cuidado parental mayor y una mayor supervivencia adulta que las especies congéneres de la Zona Templada del Norte. Las probabilidades de supervivencia de los adultos variaron entre años de 0.60 a 0.76, pero fueron similares para los dos sexos. El tamaño de la nidada fue de 2.6 huevos (± 0.04 EE) y el tiempo de cuidado parental posterior al emplumamiento fue de 40 ± 5 días. Encontramos un éxito de anidación de 29% ($n = 275$ nidos) y un 87% de los fracasos de los nidos se debieron a depredación por parte de ratas introducidas (*Rattus* sp.) o por una especie nativa (*Margarops fuscatus*). La mayoría de las parejas iniciaron varios intentos de anidación después de que los dos fallaran y después de una cría exitosa, resultando en una productividad anual total de 1.2 polluelos emplumados por pareja. A pesar de poder criar hasta tres crías por estación, la productividad anual de *I. oberi* fue menor que la de las especies congéneres de la zona templada. Recomendamos que el manejo para la conservación se enfoque en aumentar el éxito de anidación a través del control de las ratas.

INTRODUCTION

Nine species of the genus *Icterus* (orioles) breed on islands in the Caribbean, and four of these are endemic to single islands: the Bahama Oriole (*I. northropi*), St Lucia Oriole (*I. laudabilis*), Montserrat Oriole (*I. oberi*), and Martinique Oriole (*I. bonana*). Two of the single-island endemics, the Bahama and the Montserrat Oriole, have small populations and are considered threatened with extinction (Hilton et al. 2003, Garrido et al. 2005, Price and Hayes 2009).

The Montserrat Oriole, endemic to the Lesser Antillean island of Montserrat, suffered a rapid population decline between 1997 and 2003 (Arendt et al. 1999, Bowden et al. 2001, Hilton et al. 2003). Since July 1995, the Soufrière Hills volcano on Montserrat has erupted repeatedly (Aspinall et al. 1998, Wadge et al. 2010), and as a consequence almost 60% of the oriole's original habitat in semi-deciduous and evergreen moist forests on the island's main hill ranges has been destroyed (Arendt et al. 1999, Hilton et al. 2005). The Montserrat Oriole is now restricted to the Centre Hills (~11 km²)

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and a small (1–2 km²) rainforest remnant in the southern Soufrière Hills (Fig. 1). Following the initial volcanic destruction of habitat in 1996 and 1997, the population in the Centre Hills forest declined further until 2002 (Hilton et al. 2003, Dalsgaard et al. 2007). Because no information about the ecology of the species has been reported in the primary literature for over 70 years (Bond 1939), the causes of the population decline are poorly understood.

Potential causes for population declines besides the loss of habitat are the presence of invasive mammals, most notably rats (*Rattus rattus* and *R. norvegicus*) and cats (*Felis catus*), which have had devastating effects on many species endemic to islands around the world (Atkinson 1985, Towns et al. 2006, Hilton and Cuthbert 2010). In addition, the recent volcanism may have had negative effects on Montserrat Orioles even in forests that were not destroyed (Arendt et al. 1999, Hilton et al. 2003). Collapses of the volcanic dome on Montserrat frequently lead to large ash deposits over the whole island (Carn et al. 2004, Herd et al. 2005). The volcanic ash can lead to widespread defoliation and kill most forest invertebrates, thus effectively reducing the food available to birds like the Montserrat Oriole (Marske et al. 2007). Heavy ashfall

can also destroy nests or lead adults to abandon nests (Butcher 1981). Volcanic incidents may therefore suppress reproductive output and could also lead to higher mortality of adult birds if ash falls repeatedly and leads to longer periods of food scarcity (Dalsgaard et al. 2007). Because both the productivity and survival of adult Montserrat Orioles are currently unknown, information on these two basic demographic measures is urgently needed to set priorities for future conservation of the species.

Here we provide the first detailed descriptions of the breeding biology and estimates of survival of the Montserrat Oriole. We monitored nesting birds for six breeding seasons between 1998 and 2005 and banded both territorial adults and chicks with individual color-band combinations to document their movements and estimate survival probabilities. We assessed whether nest failures were mostly due to natural causes or to invasive predators. We use these data to infer what management options exist for improving the conservation status of the Montserrat Oriole.

METHODS

STUDY AREA

Montserrat (16° 45' N, 62° 12' W, 104 km²) is at the northern end of the Lesser Antilles in the eastern Caribbean Sea. The island has a dry season between January and June (mean dry-season precipitation 1999–2005 = 660 ± 85 mm SE) and a wet season from July to December (mean precipitation 1999–2005 = 1203 ± 113 mm). From the mid 17th century to the mid 19th century, the majority of the island's forest was cleared for agricultural plantations, but forest regenerated in the early 20th century when plantations became economically unviable. At any given time, some forest was likely always present on the island. Two natural events, Hurricane Hugo in 1989, and the continuing eruption of the Soufrière Hills volcano that started in 1995, have more recently destroyed or altered any existing forest. We conducted our study in the largest forest area remaining (~1100 ha), a contiguous but highly heterogeneous block of mostly secondary forest located in the Centre Hills (Fig. 1).

The Centre Hills area consists of a dormant volcanic cone (maximum elevation 737 m) dissected by steep-sided valleys. The natural vegetation is tropical dry semi-deciduous forest at lower elevations and transitions to tropical moist broadleaf forest above 200–300 m above sea level. Canopy heights of 15–25 m are typical, with small areas of elfin forest on exposed ridges at high elevations. Following the destruction caused by Hurricane Hugo in 1989, substantial areas are at an early successional stage and are dominated by tree saplings, tree-ferns, and *Heliconia caribaea* (see Arendt 1990). Montserrat Orioles inhabit moist forest and are absent from dry scrubby and open habitats (Jaramillo and Burke 1999, Raffaele et al. 2003). We therefore selected eight study sites within the forest (4–17 ha each, total area 71 ha, Fig. 1) that covered a range of

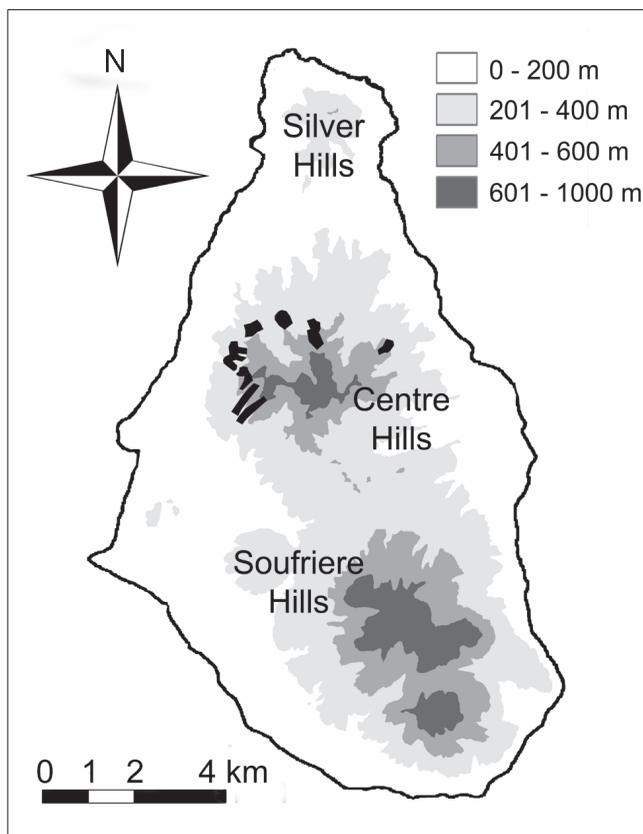


FIGURE 1. Map of the island of Montserrat, showing the main hill ranges and the location of Montserrat Oriole study sites (black polygons) in the Centre Hills.

aspects, elevations, and were accessible and conducive to the regular monitoring and study of Montserrat Orioles.

DESCRIPTION OF BREEDING BIOLOGY AND NEST MONITORING

We located all territorial pairs of Montserrat Orioles within each site during five breeding seasons (March–August 2001–2005) and obtained comparable data from a subset of sites in 1998. We monitored all nesting attempts from discovery through to fledgling independence/disappearance or nest failure. Territorial pairs and their nests were generally conspicuous and easy to locate (see below). We recorded the presence and nesting status of each territorial pair every 3–7 days. If we found a nest after the clutch was completed ($n = 182$), we inferred the date of nest initiation by subtracting the average incubation period from the date of hatching.

Once we located a nest, we recorded the plant species it was in, visually estimated the perpendicular height of the nest above ground, and inspected the contents. Montserrat Orioles typically build hanging basket-shaped nests that facilitate inspection of their contents (Bond 1939, Jaramillo and Burke 1999). Because most nests were hanging above eye level, we viewed nest contents by using an articulated mirror with a small flashlight attached to illuminate the contents. We noted evidence of failure (e.g., eggshells, feathers, predator signs etc.) when the status of a nest changed. Pairs were uniquely identifiable either because at least one of the adults was individually color-banded (83%) or because their location made confusion with neighboring pairs unlikely. Thus we were able to produce an accurate history of the entire breeding season for each pair (17–30 per year), including number of nesting attempts, nest-plant use, clutch sizes, nest-failure incidence, intervals between clutches, and number of chicks hatched and fledged. We report the average number of nesting attempts for each territorial pair, the average size of the clutch in nests found at the egg stage, and we describe the physical structure of nests and nest plants. We report observations of nesting behavior of territorial orioles and estimate the length of post-fledging care from the date of last detection of the last member of a brood in the natal territory. We report all metrics as mean \pm SE.

To identify nest predators we mounted custom-built nest cameras (Bolton et al. 2007) that recorded continuously for 3–4 weeks on 33 nests. After a nest failed, we inspected the photographs to identify the cause.

ESTIMATION OF REPRODUCTIVE PARAMETERS

Because of the Montserrat Oriole's conspicuous nesting behavior we were confident of finding almost all nests attempted, including those that failed prior to discovery. We defined a "nest attempt" as when a pair laid eggs into a nest, thus excluding nests that were constructed but never contained any eggs. "Hatching success" is the proportion of nests

that hatched at least one egg, "fledging success" the proportion of nests that hatched at least one egg to fledge at least one chick. "Nesting success" is the proportion of nests in which at least one egg survived from laying through to fledging, and we provide Mayfield estimates of nesting success to account for different exposure times of individual nests (Mayfield 1975). "Reproductive output" is the number of fledglings produced per territorial pair per year. "Chicks per successful nest" is the mean number of fledglings produced from nests where at least one chick fledged.

Nest failures were generally attributable to either natural causes (structural collapse of nest plant, nest covered by ash, nest abandonment) or nest predators, because the former were clearly observable and the latter left either dead chicks or eggshell fragments in the nest cup or immediate vicinity. We therefore calculated the proportion of nest failures caused by nest predators to determine the importance of predation on the Montserrat Oriole's reproductive output. Because the two most common nest predators are either native (Pearly-eyed Thrasher, *Margarops fuscatus*) or introduced (rats), identifying the most common predator was important from a conservation-management perspective. We used the records provided by nest cameras to estimate the proportion of robbed nests that were depredated by native and by introduced predators.

Renesting is an important factor in annual productivity (Grzybowski and Pease 2005). Because the probability of renesting varies with time over the breeding season and with the outcome of previous nesting attempts (Hatchwell et al. 2004, Kershner et al. 2004), for the Montserrat Oriole we estimated it in relation to the known outcomes of previous nests and the final day of the previous nesting attempt. We used a GLM with a binomial error distribution and present the mean model-predicted probability of renesting \pm SD.

BANDING AND ESTIMATION OF SURVIVAL PROBABILITIES

We banded nestlings ($n = 102$) with unique color combinations approximately 10 days after hatching. We caught free-flying (mostly adult) birds ($n = 119$) for color banding with a mist net, usually during a nesting attempt, but also opportunistically in the nonbreeding season. We used anodized aluminum color bands (AC Hughes, Ltd; <http://www.achughes.com/index.html>) to prevent orioles from removing plastic bands. We recorded the identity of banded adults and fledglings during regular visits to each site by noting the unique color-band combination. Because we were interested in probabilities of annual survival, we pooled resightings for observations obtained throughout an entire breeding season (March–August), and we considered each year as a separate encounter occasion. This analysis therefore had six mark/resighting occasions (2000–2005), and we estimated survival probabilities

for the five intervals between them. The intensive nest monitoring ensured that the effort at resighting banded orioles was high and constant across all years.

Rates of resighting of immature birds (birds in their second calendar year) were insufficient to estimate probabilities of juveniles' survival. We therefore estimated only probabilities of apparent adult survival and resighting by using Cormack–Jolly–Seber open-population live-recapture models in program MARK 5.1 (White and Burnham 1999) via the RMark interface version 1.9.6 (Laake and Rexstad 2008) in R 2.11.1 (R Development Core Team 2010). We included all birds in the analysis and specifically accounted for non-territory-holding adults that were seen only once by including a term for transience in survival models (Pradel et al. 1997). We compared four candidate models in which probabilities of survival and resighting were allowed to be either constant or to vary from year to year. In addition, we included two models including sex as a group and two models accounting for transients, leading to a total candidate set of eight models. We used second-order AIC corrected for small sample sizes (AIC_c) to rank models, and we present model-averaged mean probabilities of adult birds' survival and 95% confidence intervals (Burnham and Anderson 2002).

RESULTS

BREEDING BIOLOGY AND BEHAVIOR

Montserrat Orioles breed mostly between March and September (earliest and latest clutch-initiation dates 13 March and 31 August, respectively; $n = 272$ nests with known or estimated initiation dates). The median date of laying of first clutches was 19 April (± 30 days). We found a single active nest in January 1999 and observed recently fledged juveniles in December 2004, but intensive field work suggests that such unseasonal nesting is very rare. The Montserrat Oriole is multiple-brooded, laying a maximum of five clutches per season when some of these nests fail, and raising a maximum of three broods per year. Of 147 pairs observed for an entire season, 25% produced one clutch, 35% two clutches, 21% three clutches, 8% four clutches, and 4% five clutches. The initiation dates of last clutches ranged from 11 April to 31 August, with a median of 6 July ($n = 163$). We observed nine pairs (five in 1998, and four in 2001) that held territories through the breeding season but appeared not to produce a single clutch in that season. Some of these pairs started to build nests but apparently did not use them, nor did they nest in alternative nests.

Montserrat Oriole nests are a hanging basket structure sewn onto the underside of horizontal leaves or leaf clusters, as is typical for the genus (Jaramillo and Burke 1999). The nest is built entirely by the female. We observed males to indicate potential nest sites to their mates by hanging upside down from the underside of chosen leaves. The female began building the basket by shredding strands out of the leaf frond.

These formed the “ribs” of the structure, and the female oriole then weaved the basket around these ribs with fine strands of vegetation obtained from *Heliconia* and other forest plants. The nests were not conspicuously lined.

Most oriole nests were suspended from *Heliconia* leaves (83%, $n = 229$). A further 7% used the very similar leaves of banana (*Musa acuminata*). The remaining 10% of nests were suspended beneath the leaves of other broad-leaved trees such as *Cordia sulcata*, *Cecropia* spp., and *Coccoloba* spp. Nests' heights above ground averaged 4.5 m in *Heliconia* (range 1.5–10 m, $n = 191$) and 5.0 m in banana (range 3–9 m, $n = 15$). In other trees, nests were much higher above the ground, averaging 11 m (range 3–20 m, $n = 23$).

The interval between laying of each egg was approximately 24 hr, and full incubation did not appear to commence until the clutch was complete. Only the female incubated. The male remained generally within sight of the nest and responded aggressively to both intra- and inter-specific intrusion into the nest's vicinity throughout the incubation period. On the basis of nests for which we knew the dates of clutch completion and hatching, the mean length of incubation was 13.9 ± 0.2 days ($n = 70$ nests). For nests of known dates of hatching and fledging, the mean time from hatching to fledging was 13.1 ± 0.3 days ($n = 56$).

The mean length of post-fledging parental care for at least one member of a brood was 40 ± 5 days ($n = 35$ broods), and one brood was still being fed by parents 88 days after fledging. Parental care gradually diminished over time after fledging and was marginally shorter when the pair subsequently started a new nest in the same season than when it did not reneest ($b = -6.95$, $F_{1,33} = 4.83$, $P = 0.03$). In the first 15 days after fledging, 54% of detections of fledglings ($n = 128$) involved feeding by parents. Between 15 and 30 days after fledging, we observed 43% ($n = 90$) of fledglings being fed by parents, and after 30 days we observed 27% ($n = 163$) of fledglings being fed. In general, both parents fed the fledglings (52 out of 87 occasions among 21 pairs involved both parents feeding). Brood division was common in pairs that fed more than one fledgling, and each parent appeared to feed one of the fledglings preferentially. However, if only one fledgling was being fed, the female provided most of the care (24 of 47 solitary fledglings were fed solely by the female), and we never observed only males feeding fledglings.

Males sometimes chased their offspring that had been fledged for at least 55 days. Among eight broods detected on the natal territory >60 days after fledging, four were seen being chased by parents. On one occasion, a pair built a new nest 23 days after fledging its previous brood and started chasing offspring at that early time.

The mean interval to relaying following a successful nest was 34 ± 6 days between fledging and relaying, compared to 22 ± 3 days between failure and relaying following failure during incubation and 24 ± 4 days following failure during chick rearing ($F_{2, 143} = 7.61$, $P = 0.01$, Fig. 2). Of 44 successful first nests, 66% were succeeded by a second attempt

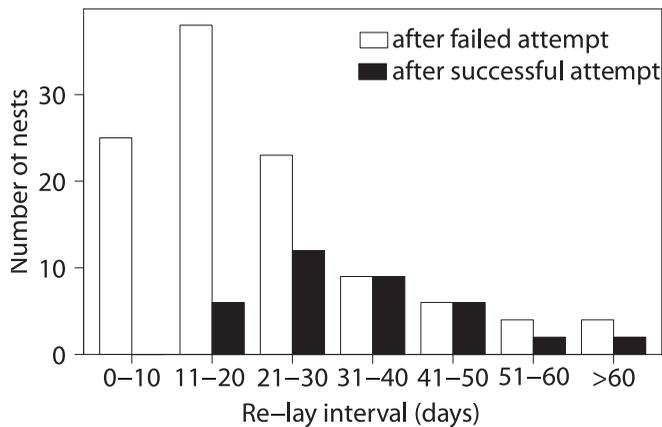


FIGURE 2. Number of nests of the Montserrat Oriole initiated after successful nesting attempts (black bars) and after failed nesting attempts (white bars) in relation to the time elapsed between the end of the first and the start of the subsequent nesting attempt (re-lay interval).

in the same season; similarly, 68% of 77 failed first attempts were followed by a subsequent attempt. Minimum observed intervals to laying of the next clutch were 3 days following failure during incubation, 5 days following failure during chick rearing, and 13 days after fledging of the brood. The average probability of re-nesting was lower after successful (0.48 ± 0.35) than after failed nesting attempts (0.56 ± 0.33 ; $b = -1.35$, $P = 0.006$) and declined significantly over the course of the season ($b = -0.06$, $P < 0.001$, Fig. 3).

MEASURES OF REPRODUCTION AND NESTING SUCCESS

Montserrat Oriole nests had a modal clutch size of three eggs (Table 1). Out of 213 nests of known clutch size, there were 12 clutches with a single egg and four clutches with four eggs. Average Mayfield nesting success across all years was 29%, ranging from 24% in 2001 ($n = 41$ nests) to 33% in 2003 ($n = 57$). Males in their second calendar year had Mayfield nesting success (16%, $n = 33$) lower than that of older males (31%, $n = 254$).

In nests where at least one fledgling left the nest, an average of 71% of eggs produced a fledgling (Table 1). Reproductive output averaged slightly over one chick pair⁻¹ year⁻¹ over the six years of the study (Table 1) but was unequally distributed among pairs. In each year, an average of 45% of all pairs did not produce any fledglings, while 18%, 17%, and 17% produced one, two, and three chicks, respectively. Only 8% of pairs managed two successful nests, and 3% of pairs produced four chicks in a single breeding season. One pair raised seven chicks from three successful broods in 2005.

Hatching success and fledging success were relatively constant from year to year (Table 1), whereas components of reproductive investment such as clutch size and number of clutches laid were more variable (Table 1). Nest failures were mostly a result of nest predation (87% out of $n = 192$ recorded nest

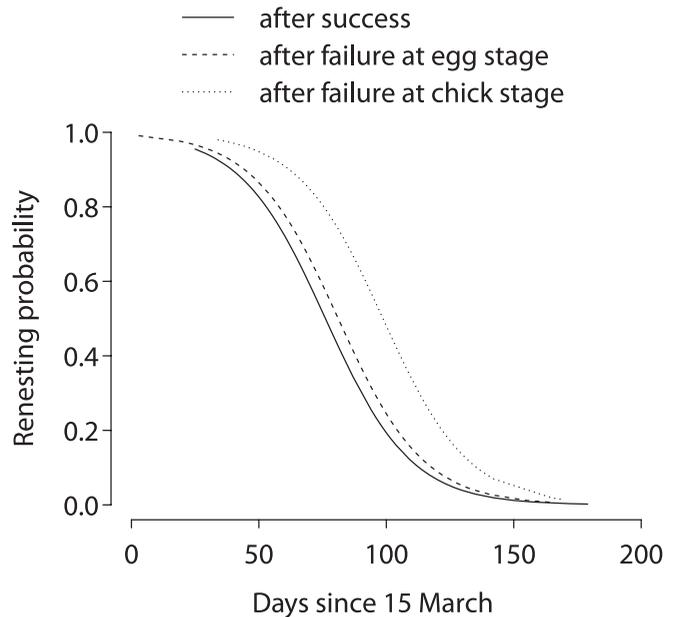


FIGURE 3. Probability of re-nesting of the Montserrat Oriole in relation to time over the breeding season and by fate of the preceding nesting attempt. The x-axis indicates the time of the year when the preceding nesting attempt ended.

failures), with smaller numbers of nests failing after falling ash covered nests ($n = 10$), structural collapse of the nest-supporting leaves ($n = 8$), human-induced nest loss ($n = 3$), or abandonment for unknown reasons ($n = 4$). Of 33 nests equipped with cameras, 13 (39%) fledged, 16 (49%) were depredated, three (9%) were abandoned, and one (3%) was lost because of leaf fall. Both rats ($n = 8$) and Pearly-eyed Thrashers ($n = 7$) were recorded in similar proportions as nest predators.

SURVIVAL, RECRUITMENT, AND SITE FIDELITY

Immatures appeared to have low philopatry to natal sites, and most individuals presumably dispersed outside the study area, which constituted only ~6% of the Centre Hills forest (Fig. 1). Only 9% of birds banded as chicks or fledglings were resighted as immatures, and only five birds (5%) recruited back into the breeding population at one of the study sites. Two males recruited at the age of one year, two males at the age of two years, and one female recruited at the age of three years. The majority (88%) of male territory holders were adult-plumaged birds, i.e., at least two years old. However, in all years except 1998, 5–21% of male territory holders were in immature plumage.

There was no evidence for significant lack of fit for the most general model describing the probability of adults' survival (goodness-of-fit test, $\chi^2_{10} = 9.33$, $P = 0.50$). A model accounting for annual variation in probabilities of survival and constant probability of resighting received the most support by the data (AIC_c weight $w_i = 0.33$), but there was considerable model-selection uncertainty with three models within 2 AIC_c units and

TABLE 1. Measures of Montserrat Oriole reproduction monitored over 6 years, 1998–2005. Size of fledged brood is the number of fledglings in nests where at least one bird fledged; reproductive output is the number of fledglings pair⁻¹ year⁻¹.

	<i>n</i>	Mean	SE
Clutches pair ⁻¹ year ⁻¹	147	2.09	0.10
Clutch size	213	2.55	0.04
Hatching success	287	51.41	1.26
Fledging success	153	58.18	0.03
Size of fledged brood	88	1.82	0.09
Reproductive output	141	1.19	0.11

all eight candidate models within 4 AIC_c units. Model-averaged survival probability was similar for males and females but varied by year from 0.60 ± 0.09 to 0.76 ± 0.11 (Table 2).

Adult orioles showed strong fidelity to the nesting territory in successive years. Of 83 occasions on which banded birds were known to have survived to the next breeding season, 67 (81%) used the same nesting territory in the subsequent year, and a further seven (8%) made moves of less than 100 m. Only one bird was recorded to move >1 km for the next breeding season.

Montserrat Orioles are socially monogamous. Of 24 instances of both members of a territorial pair being identifiable at the start of the breeding season and known to be alive at the start of the following breeding season, six (25%) entailed divorce and 18 (75%) entailed the pair remaining together. In five out of six divorces (83%), the female retained the original home range and the male relocated to a different home range.

DISCUSSION

The Montserrat Oriole is socially monogamous, territorial, and raises multiple broods within one breeding season. Only the female incubates, but care of chicks is biparental.

TABLE 2. Probabilities of apparent annual survival of adult Montserrat Orioles between 2000 and 2005, averaged across eight candidate models including variation by year and between sexes in survival and by year in probability of resighting.

Interval	Males		Females	
	Mean	SE	Mean	SE
2000–2001	0.76	0.11	0.76	0.11
2001–2002	0.60	0.09	0.61	0.10
2002–2003	0.74	0.10	0.74	0.10
2003–2004	0.64	0.08	0.64	0.08
2004–2005	0.68	0.11	0.68	0.11

These characteristics are consistent with the breeding biology of sister species (Orians 1985, Skutch 1996, Jaramillo and Burke 1999). The Montserrat Oriole's clutch size is smaller and its nestling period is longer than those of temperate-zone orioles (Rising and Flood 1998, Flood 2002), which seems to be a general pattern among the oriole species endemic to single Caribbean islands (Jaramillo and Burke 1999, Price et al. 2011). Clutches of many tropical South American birds are smaller than those of related North American species (Yom-Tov et al. 1994, Martin et al. 2000), and the pattern in the genus *Icterus* appears to conform to this general pattern (Table 3).

We found the probability of adult Montserrat Orioles' annual survival to be 60–76%, slightly lower than the 82% estimated for the endangered Yellow-shouldered Blackbird (*Agelaius xanthomus*), endemic to Puerto Rico (Post and Wiley 1977). In contrast to clutch size, the probability of adult Montserrat Orioles' survival therefore appears to be higher than for oriole species of temperate North America, in which adult survival estimated from >70 marked individuals averages 48%, and ranges from 39% to 59% (Searcy and Yasukawa 1981, DeSante and Saracco 2009). Our study therefore confirms the pattern that the probability of adults' annual survival appears to be higher for tropical species of some bird families (Johnston et al. 1997, McGregor et al. 2007, Ricklefs et al. 2011).

NESTING SUCCESS AND PRODUCTIVITY

The Montserrat Oriole's current rate of nesting success is relatively low because of predation. Native (Pearly-eyed Thrashers) and introduced (rats) nest predators appear to be universally abundant in all habitats (Dalsgaard et al. 2007, Young 2008) and were responsible for >85% of nest failures. The low (29%) rate of nest success that we found for the Montserrat Oriole is within the range of 71 Panamanian understory species (8–57%) but at the lower end of the range for an equivalent set of North American species (27–60%) (Robinson et al. 2000). Little is known about nest-success rates in other oriole species breeding in the West Indies, but Price et al. (2011) suggested that parasitism by the Shiny Cowbird (*Molothrus bonariensis*) might be more important than nest predation in reducing the Bahama Oriole's reproductive output. Cowbird parasitism affects several icterids and may require management to safeguard critically endangered species (Wiley et al. 1991, Jaramillo and Burke 1999, Post 2011, Price et al. 2011). Because cowbirds have not yet colonized Montserrat, parasitism does not currently affect the Montserrat Oriole.

The Montserrat Oriole's low nesting success does not necessarily lead to low reproductive output, as the species can lay up to five clutches and raise up to three broods per year. However, the probability of re-nesting declines markedly over the breeding season, and Montserrat Orioles fledged on average only 1.2 fledglings per pair and year, which is as low

TABLE 3. Comparison of measures of breeding of two endangered orioles of the West Indies (Bahama and Montserrat) and orioles of North America: clutch size (number of eggs), incubation period (days), broods raised year⁻¹, and reproductive output (fledglings pair⁻¹ year⁻¹). Ranges presented in parentheses.

Species	Breeding range	Clutch	Incubation	Broods	Reproductive output	Source
Montserrat Oriole <i>I. oberi</i>	Montserrat	3 (1–4)	14	2 (1–3)	1.2	this study
Bahama Oriole <i>I. northropi</i>	Andros, Bahamas	2–3	12–14	1.5 (1–4)	unknown	Price et al. 2011
Altamira Oriole <i>I. gularis</i>	eastern Middle America	4 (2–6)	14	1–2	unknown	Pleasants 1993
Orchard Oriole <i>I. spurius</i>	eastern USA and Mexico	5 (2–7)	12–14	1	unknown	Scharf and Kren 1996
Baltimore Oriole <i>I. galbula</i>	eastern USA and Canada	4–5 (2–6)	12 (11–14)	1	3.2	Rising and Flood 1998
Bullock's Oriole <i>I. bullockii</i>	northern Mexico, western USA	5 (3–7)	11–14	1	2.66	Rising and Williams 1999
Hooded Oriole <i>I. cucullatus</i>	southwestern USA, coastal Mexico	4 (2–5)	unknown	2	unknown	Pleasants and Albano 2001
Scott's Oriole <i>I. parisorum</i>	southern USA, Mexico	3 (1–5)	13 (11–15)	1 (1–3)	2.4	Flood 2002
Audubon's Oriole <i>I. graduacauda</i>	southern Texas, Mexico	3–5	unknown	2 (2–3?)	unknown	Flood et al. 2002

as in the declining and endangered Yellow-shouldered Blackbird (Wiley et al. 1991, López-Ortiz et al. 2002). Thus, despite its ability to raise more than one brood per year, the Montserrat Oriole's reproductive output is lower than that of single-brooded members of the genus elsewhere (Table 3) and may be the key factor limiting the species' population recovery (Hilton et al. 2003).

It is possible that prolonged parental care increases the probability of juveniles' survival, thus effectively compensating for a lower number of offspring produced (Martin 1995, Badyaev 1997, Badyaev and Ghalambor 2001). The Montserrat Oriole's post-fledging care averaged >5 weeks, as is characteristic of tropical and Southern Hemisphere songbirds (Russell 2000, Russell et al. 2004, Tarwater and Brawn 2010). Nonetheless, we did not detect Montserrat Orioles being recruited in or around the parental home range despite the long parental care, and our efforts at resighting therefore did not yield data sufficient for estimating the probability of juveniles surviving their first year. Further research will be necessary to distinguish between juveniles' mortality and permanent emigration.

Most Montserrat Oriole nests were built in a single early-successional plant—*Heliconia*. This degree of specialization contrasts with that of most orioles of Caribbean islands, which nest in a wide variety of plant species (Jaramillo and Burke 1999, Raffaele et al. 2003). Only the endangered Bahama Oriole is similarly stenotopic in nesting almost exclusively in coconut palms (Price et al. 2011). Because we observed some pairs to switch between nesting in *Heliconia* and nesting in broad-leaved trees within a breeding season, *Heliconia* nesting is unlikely to be a fixed trait of the Montserrat Oriole. Instead, this specialization could be a recent

phenomenon resulting from the natural devastation of other habitat types and the Montserrat Oriole's limited distribution in hill forests (Arendt and Arendt 1984). Arendt and Arendt (1984) did not report a strong specialization for nesting in *Heliconia* among the oriole population in the Southern Hills prior to Hurricane Hugo and the volcanic eruption. Hurricane Hugo caused massive tree-fall and defoliation in September 1989, presumably leading to an increase of early-successional habitat in subsequent years. *Heliconia* is a key feature of such early-succession areas on Montserrat, and it is possible that a greater availability of this plant has recently led to the apparent specialization we recorded.

IMPLICATIONS FOR CONSERVATION AND FUTURE RESEARCH

For a species with relatively high annual survival and low productivity, the population trend is rather sensitive to changes in survival probabilities (Woodworth et al. 1999, Sæther and Bakke 2000, Sibly and Hone 2002). Research to determine the factors driving the annual variation in adult survival is needed, as is information about juveniles' survival and recruitment probabilities. We found low productivity in the Montserrat Oriole, which may offer immediate possibilities for conservation intervention (Jones 2004). Parasitism by the Shiny Cowbird has not been detected on Montserrat, but the artificially open landscape of the lowlands of Montserrat may increase the probability of cowbird colonization. We recommend careful monitoring of the avifauna on Montserrat to detect any arrival of the Shiny Cowbird.

While the causes of the large annual variation in reproductive investment (clutch size and frequency of re-nesting) appear to be related to rainfall (Oppel and Allcorn, unpubl. data), management to reduce nest predation by introduced rats may yield

short-term benefits in increasing productivity (Lavers et al. 2010, Smith et al. 2010). Because of the Montserrat Oriole's limited range, we propose that rat control in areas the oriole inhabits as an option that may help to stabilize the population. In addition, all existing forests on Montserrat should be protected to avoid further loss of valuable habitat for the Montserrat Oriole.

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