



The effects of rainfall on different components of seasonal fecundity in a tropical forest passerine

STEFFEN OPPEL,^{1*} GEOFF M. HILTON,^{1†} RICHARD ALLCORN,¹ CALVIN FENTON,² ADRIAN J. MATTHEWS³ & DAVID W. GIBBONS¹

¹Royal Society for the Protection of Birds, Sandy, Bedfordshire, UK

²Montserrat Department of the Environment, Brades, Montserrat, West Indies

³School of Environmental Sciences/School of Mathematics, University of East Anglia, Norwich, UK

Seasonal fecundity is a composite metric that is determined by component parameters such as clutch size, nest survival and re-nesting probability. Many of these component parameters are known to vary with environmental conditions, in particular rainfall prior to or during the breeding season. In some species, seasonal fecundity is positively related to rainfall, but little is known about which component parameters of seasonal fecundity respond most strongly to rainfall. We used intensive nest monitoring of a multi-brooded tropical forest passerine, the Montserrat Oriole *Icterus oberi*, to examine the effects of rainfall during the pre-breeding season on component parameters of annual fecundity. We monitored all nests of a total of 42 pairs over 5 years in which rainfall varied substantially. We then related clutch size, nest survival, onset and length of the breeding season, re-nesting probability and re-nesting interval to pre-breeding season rainfall using generalized linear mixed models that accounted for random variation across sites and individual pairs, and incorporated other variables known to affect the response. Higher pre-breeding season rainfall led to an increase in clutch size and a decrease in re-nesting interval, but nest survival, re-nesting probability and length of the breeding season were not affected by variation in rainfall. The onset of the breeding season was delayed in very dry years. We conclude that higher rainfall is likely to increase food availability and thus body condition of female Montserrat Orioles, leading to an increase in fecundity due to larger clutch sizes.

Keywords: clutch size, *Heliconia*, *Icterus oberi*, Montserrat Oriole, productivity, re-nesting.

Seasonal fecundity, defined as the number of offspring produced by a female bird over a single breeding season, is a key demographic parameter that affects the fitness of individuals and the status of populations (Roper *et al.* 2010, Etterson *et al.* 2011). Seasonal fecundity is determined by several distinct demographic processes acting in sequence over a breeding season: the timing of breeding, clutch size, the survival of eggs and chicks, re-nesting probability and interval, and the length of the

breeding season (Ricklefs & Bloom 1977). Many of these processes can respond to environmental variation, such as changes in temperature or rainfall, but the responses of different component parameters may vary considerably over a given environmental gradient (Mattsson & Cooper 2009). Thus, studies that relate variation in environmental conditions to variation in just a single fecundity parameter may not be sufficiently powerful to resolve the fitness implications of environmental variation (Mattsson & Cooper 2007, Etterson *et al.* 2011). Similarly, studies that demonstrate an effect of environmental variation only on overall fecundity are less informative than those that identify those components of the reproductive process that are most affected by environmental variation.

[†]Current address: Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK.

*Corresponding author.
Email: steffen.oppel@rspb.org.uk

Among the environmental variables known to affect component parameters of seasonal fecundity, rainfall in particular has received much attention (Grant *et al.* 2000, Morrison & Bolger 2002, Senapathi *et al.* 2011). However, the effect of rainfall upon fecundity varies between species and habitats. Rainfall and food abundance are often strongly correlated, especially in arid and tropical regions (Sinclair 1978, Polis *et al.* 1997), and an increase in food abundance can lead to larger clutch sizes and shorter re-nesting intervals (Illera & Diaz 2006, Preston & Rotenberry 2006b). Rainfall can reduce nest predation rates (Rotenberry & Wiens 1991, Preston & Rotenberry 2006a) or increase the length of the breeding season (Grant *et al.* 2000, Nagy & Holmes 2005). In some species, intermediate amounts of rainfall can lead to the highest nest survival (Mattsson & Cooper 2009), whereas in other species, increases in rainfall can reduce food availability and increase the mortality of eggs and chicks (Siikamäki 1996, Radford & Du Plessis 2003, Monadjem & Bamford 2009). A higher number of rainy days has also been found to delay the onset of the breeding season with negative consequences on fecundity (Senapathi *et al.* 2011). For those species in which variation in rainfall influences fecundity, it is often unclear whether these effects are a result of larger clutches and more frequent nesting attempts, or higher survival of eggs and chicks (but see Styrsky & Brawn 2011). Thus, understanding how rainfall influences all aspects of seasonal fecundity will elucidate possible mechanisms underlying the relationships.

Many songbird species are capable of raising more than one brood per breeding season. Because it is often logistically challenging to follow a single female over a whole breeding season, the observation of seasonal fecundity is particularly complicated for multi-brooded species (Grzybowski & Pease 2005, Roper 2005). To overcome the logistical challenges of observing seasonal fecundity in multi-brooded species, several models have been developed to estimate seasonal fecundity from component parameters (Farnsworth & Simons 2005, Mattsson & Cooper 2007, Etterson *et al.* 2009). However, none of these models allows a quantitative assessment of how component processes are affected by environmental variation. Intensive nest monitoring that provides empirical data on all component parameters of fecundity would facilitate such an evaluation, and thus shed

light on whether changes in fecundity are mostly driven by changes in clutch size and re-nesting probabilities or changes in survival probabilities of nests and chicks.

Here, we use data from five consecutive years of intensive nest monitoring of a multi-brooded tropical forest passerine, the Montserrat Oriole *Icterus oberi*, to examine the influence of pre-breeding season rainfall on seasonal fecundity and its component parameters. During the study period rainfall varied almost threefold, and we use this variation to demonstrate that seasonal fecundity in this species increased with the amount of rainfall during the 3 months prior to the breeding season. We then examine whether the amount of rainfall explained variation in clutch size, nest survival, re-nesting probability, re-nesting interval, and onset and length of the breeding season to assess which reproductive parameters have the greatest influence on increasing fecundity. Because the Montserrat Oriole is of great conservation concern, we use the relationship between rainfall and fecundity in conjunction with local precipitation trends over the past 110 years to assess implications for conservation.

METHODS

Study area and focal species

Montserrat (16°45'N, 62°12'W) is a small (104 km²) volcanic island at the northern end of the Lesser Antilles in the eastern Caribbean. Over the past three centuries, most of the island's forest has been cleared for agricultural plantations. Since 1995, the continuing eruption of the Soufrière Hills volcano has destroyed roughly two-thirds of the remaining forest, leaving only a *c.* 1100 ha block of forest located in the Centre Hills and a much smaller and inaccessible block (*c.* 250 ha) on the southern flank of the active volcano. The Centre Hills is a region of steep-sided valleys centred on a dormant volcano (maximum elevation 737 m asl). The natural vegetation is tropical dry semi-deciduous forest at lower altitudes, gradually giving way to tropical moist broadleaved forest at higher elevations. We studied Montserrat Orioles at eight study sites within the Centre Hills. These sites were 4–17 ha each, with a total area of 71 ha, ranged from 200 to 500 m in elevation, and were situated on the western, eastern and northern slopes of the Centre Hills (Allcorn *et al.* 2012).

The Montserrat Oriole is endemic to Montserrat and critically endangered due to recent population declines following a volcanic eruption and a hurricane (Arendt *et al.* 1999, Hilton *et al.* 2003, del Hoyo 2011). Montserrat Orioles are inquisitive birds that construct conspicuous hanging basket-shaped nests that are easily detected (Allcorn *et al.* 2012). The species is monogamous and territorial and its conspicuous behaviour allowed us to follow all nesting attempts of a given pair per season (Allcorn *et al.* 2012). Little is known about the diet of Montserrat Orioles, but they forage mostly on invertebrates, which they take from leaves, bark and flowers (A. Cassini, S. Oppel & C. Fenton pers. obs.). They also consume fruit, flowers and nectar, and forage frequently in floral bracts of *Heliconia* spp. (del Hoyo 2011).

Regional climate and rainfall measurements

Montserrat lies at the northern edge of the Inter-tropical Convergence Zone (ITCZ), and the rainfall season lasts from April to November, with a first peak in May and a larger, longer peak centred on September (Barclay *et al.* 2006). We obtained daily rainfall data for the years 1999–2012 from a meteorological station (Hope) adjacent to the western margin of the Centre Hills forest. We used these data to calculate total rainfall and the frequency distribution of rainfall (number of days with rainfall > 0 mm). However, the 13-year operation period of this local rain gauge may be insufficient to examine long-term trends in regional rainfall (Senapathi *et al.* 2011). We therefore obtained two additional sets of rainfall data that covered the years 1902–1963 and 1979–2011. Local rainfall data for 1902–1963 were obtained from the Montserrat Government (Walker 1965). These data were collected at two rain gauges (Olveston and Waterworks) within 1 km of the Hope station, on the same slope of the Centre Hills, thus minimizing differences that may be expected from local topographical variation. These data could thus be combined with the rainfall data from 1999 to 2012 to provide a time series of 110 years of local rainfall data. In addition, we obtained rainfall data from the Climate Prediction Center Merged Analysis of Precipitation (CMAP), which is a global gridded dataset derived from satellite measurements and validated against surface station precipitation measurements (Xie & Arkin 1997).

This dataset averaged precipitation over a $2.5^\circ \times 2.5^\circ$ grid cell centred on 61.25°W and 16.25°N , which is roughly 115 km southeast of our study area. Although these data have low spatial resolution, they offer the opportunity to examine trends in regional rainfall over the last 32 years (1979–2011).

For Montserrat Orioles, the breeding season usually starts in late March (Allcorn *et al.* 2012), coinciding roughly with the onset of the wet season (Barclay *et al.* 2006). In some birds, productivity has been linked to rainfall during a 1–3-month period prior to the nesting season (Patten & Rotenberry 1999, Rodriguez & Bustamante 2003). We therefore used the total rainfall amount during the 3 months prior to the onset of the breeding season (i.e. January–March) as an index of the rainfall intensity of a given year (hereafter: rainfall). Our results were robust to alternative approaches, and summing rainfall over half a year (January–June), or just the first half of the breeding season (March–May) did not alter our conclusions, mainly because pre-breeding season rainfall was strongly correlated with breeding season rainfall (rainfall amount: $r^2 = 0.86$, $P = 0.02$; number of rain days: $r^2 = 0.79$, $P = 0.03$, all $n = 5$).

We also assessed whether productivity was correlated with rainfall frequency, rather than just the amount of rainfall, because the number of rain days has been shown to affect breeding productivity in another tropical island endemic (Senapathi *et al.* 2011). For this analysis, we used two metrics of rainfall frequency and distribution: (1) the number of days with rain over the pre-breeding period (Senapathi *et al.* 2011), and (2) rainfall evenness. Rainfall evenness was calculated analogous to species evenness in community ecology (Magurran 1988), and reflected the proportional contribution of each day of the pre-breeding season to the total amount of rainfall. However, neither the number of rain days nor rainfall evenness explained variation in productivity as well as the amount of rainfall (likelihood-ratio tests, all $P > 0.5$). We therefore only present results from the analysis using the amount of rainfall as the predictor variable.

Nest monitoring

We conducted fieldwork from March to September every year in 2001–2005. Montserrat Oriole nests were located by actively searching the forest for nests and by following each pair to its nest.

We checked the status of each nesting attempt every 3–4 days by watching the adults' behaviour and inspecting nest contents with a pole-mounted mirror if adults were absent, or if they did not exhibit behaviours expected from a breeding pair such as food provisioning. We followed each pair over the entire breeding season, and recorded the outcome of every nest and the time that elapsed between the end of one nesting attempt and the initiation of the next. We defined the end of a nesting attempt as the day the nest failed or fledged. For nests that fledged, we counted the number of fledglings being fed by parents 3–6 days after fledging had occurred. Montserrat Orioles continue to provide care to fledglings up to 2 months after they leave the nest (Allcorn *et al.* 2012). Because we did not observe any fledglings being abandoned within the first 2 weeks of fledging, we are confident that our estimates of fledging success are accurate. Our measure of seasonal fecundity is the sum of all fledglings raised by a single pair over the entire breeding season in 1 year. This measure incorporates immediate post-fledging (< 3 days) mortality, but does not account for mortality of fledglings later during the post-fledging period (Mattsson & Cooper 2007, Ettersson *et al.* 2011).

Vegetation and habitat structure around the nest, and the density of predators, are well known to affect nest survival in many songbirds (Martin 1993, Stephens *et al.* 2004). To account for the effect of habitat characteristics on nest survival, we recorded the following vegetation and habitat characteristics at all nests: nest plant species, presence of open water, canopy cover, presence of big trees (> 15 m tall), presence of *Heliconia* plants, presence of banana (*Musa* spp.) plants, presence of a shrub layer, distance to cultivations, distance to habitat edge, distance to nearest fruiting tree and number of fruit available at nearest fruiting tree (details in Allcorn *et al.* 2012). Montserrat Oriole nests are vulnerable to predation by Ship Rats *Rattus rattus* and Pearly-eyed Thrashers *Margarops fuscatus*, and we estimated the relative abundance of these predators using tracking tunnels and performing point counts, respectively, at each site (Dalsgaard *et al.* 2007). Males were categorized as either first-year birds or older birds based on their plumage characteristics (del Hoyo 2011); female Orioles cannot be aged from their plumage. Lastly, we recorded whether > 5 mm of volcanic ash fall occurred during the time a nest

was active. Ash fall occurred after two major volcanic dome collapses on 29 July 2001 and on 12–13 July 2003 (Matthews *et al.* 2002, Herd *et al.* 2005) but because these incidents occurred late in the breeding season, they only affected a small number of nests.

Analysis

We used generalized linear mixed models (GLMM) to assess the effect of rainfall on fecundity and its component parameters. Because we conducted our study at eight different sites, with each site containing three to five pairs of Orioles, and each pair initiating one to six nests per breeding season, we accounted for spatial and serial autocorrelation at the pair and site levels by including them as random intercepts in each model (Bolker *et al.* 2009). We also included rainfall as a random slope to allow the response to rainfall to vary among different sites and pairs and thus induce the parameter estimate of the fixed effect to reflect more accurately the population mean response to rainfall (Schielzeth & Forstmeier 2009). We fitted all models using the Laplace approximation in R 2.13.1 (R Development Core Team 2010) with the packages 'lme4' and 'ordinal' (for clutch size) with the generic formula: $\text{lmer}(\text{response} \sim \text{rain} + (\text{rain}|\text{site}/\text{pair}))$.

For fecundity and each of its component parameters, we constructed two models: one containing rainfall as fixed effect and random slope, and a nested model without rainfall but with the same suite of random intercepts. To assess whether rainfall had an influence on our response variable, we compared the two models using a likelihood-ratio test (Lewis *et al.* 2011) and concluded that rainfall was a significant predictor if $P < 0.05$. In all analyses, we present mean parameter estimates and standard errors for the rainfall effect, and provide the estimated effect size of the response variable with 95% confidence intervals for a 100-mm increase in rainfall. The variation in rainfall experienced during this study was not large enough to yield hump-shaped relationships of reproductive parameters with rainfall. We initially explored models with quadratic relationships with rainfall, but none of them was supported, and we therefore present only monotonic relationships.

We first assessed the effect of rainfall on the number of fledglings raised by each pair of Montserrat Orioles during a season (fecundity) in a

GLMM with a Poisson distribution. To understand the process of increasing fecundity with rainfall, we then examined each component of fecundity and its relationship to rainfall.

Clutch size

Because clutch sizes are discrete, we treated clutch size as an ordinal response variable and used a proportional odds model (Cohen 1988, Guisan & Harrell 2000) implemented with the function 'clmm' in R package 'ordinal'. We report effect size as the expected ordered log-odds change for laying one more egg if rainfall increased by 100 mm.

Onset and length of breeding season, re-nesting probability and re-nesting interval

We used a normal distribution and an identity link function to relate the onset and the length of the nesting season to rainfall. The onset of a breeding season was defined as the first nest initiation date of a pair, and the length of the nesting season as the number of days between the initiation of the first and last nest in each of our study sites. We did not define nesting season length for each pair, as the end of the nesting season is dependent on the outcome of the last nest (Styrsky & Brawn 2011). Because the analyses of onset and length of the season were not at the individual level, we did not include pair as a random effect in these models.

In multi-brooded species, the probability of laying a further clutch is dependent on the time of season and the number and outcome of previous nesting attempts (Roper 2005, Etterson *et al.* 2009, Roper *et al.* 2010). Similarly, the interval between two successive nesting attempts is also dependent on the outcome of the first of these two nesting attempts. The re-nesting interval is generally shorter when nests fail early during incubation than when nests fail at the chick stage. In Montserrat Orioles, the re-nesting interval is longest if a nesting attempt is successful, because both parents continue to care for the fledglings for up to 2 months (Allcorn *et al.* 2012). To assess whether pre-breeding season rainfall affected the re-nesting probability and interval of Montserrat Orioles, we accounted for the time of season and the outcome of the previous nesting attempt. Subsequent nesting attempts could be attributed to individual females either because at least one of the pair was individually colour-ringed (83% of

pairs had at least one marked member) or because the location of the nest made it unlikely that it was in another pair's territory.

For each nest, we determined whether the female produced another clutch (re-nest) in the same season, and related that binary outcome to the date at which the nesting attempt ended and the fate of that nesting attempt (failed at egg stage, failed at chick stage, fledged). We included site and pair as random effects in a binomial model with a logit link function to estimate re-nesting probabilities, and examined whether pre-breeding season rainfall was associated with re-nesting probability.

To investigate the effect of pre-breeding season rainfall on the re-nesting interval, we used the re-nesting interval as response variable in a GLMM with a Poisson distribution and included the outcome of the nesting attempt as a fixed factor in both the rainfall and the null models. We present the change in re-nest intervals separately for nests that failed at the egg stage, nests that failed when chicks were > 4 days old and nests that fledged successfully.

Nest survival probability

We considered a nest successful if at least one egg survived from laying through to fledging, and we did not distinguish between egg and nestling survival, because a preliminary analysis indicated that predation risk was similar in these two stages (Allcorn *et al.* 2012). To assess whether rainfall affected nest survival probability, we first accounted for the influence of other variables on nest survival before exploring the influence of rainfall in a second step. In the first step, we identified habitat variables that influenced nest success using an algorithmic model. In the second step, we used a Mayfield logistic regression (Aebischer 1999) including the variables identified in the first step to evaluate the influence of rainfall on daily nest survival probabilities of Montserrat Orioles. Nests that failed during a given monitoring interval were assumed to have failed at the mid-point between the date on which the nest was found to have failed and the date of the previous visit to that nest (3–4 days earlier).

We identified important variables affecting nest success using a machine learning approach based on ensembles of regression trees (RANDOM FOREST). This approach was appropriate for our small dataset ($n = 213$ nests with environmental

covariates) with non-independent observations, and a large number (16, see 'Nest monitoring' above) of explanatory variables (Grömping 2009). We used the R package 'randomForest' and the extensions for variable selection provided by Murphy *et al.* (2010) to identify the most important habitat variables from those mentioned above and the following additional variables that were suspected to influence nest survival: elevation, site, year and nest initiation date. We averaged variable importance over 500 bootstrap replications, and considered all variables with an average relative importance value > 50% to be influential.

We then estimated mean daily nest survival using a logistic exposure model and the influential variables identified in the first step. We transformed daily nest survival estimates to a mean nest survival probability based on the assumption that each nest would have to survive 27 days to be successful (Allcorn *et al.* 2012) and present that mean estimate with 95% confidence intervals.

Rainfall trends on Montserrat

For our examination of fecundity relationships with rainfall, we used the data that coincided with our intensive bird monitoring from 2001 to 2005. To assess whether there were long-term trends in rainfall on Montserrat, we used a linear regression of pre-breeding season rainfall amounts from 1902 to 2012 (local rainfall data) and 1979–2011 (satellite-derived regional precipitation). The long-term trend analysis of local rainfall data was based on the assumption that there were no systematic differences in rainfall measurements between the historic stations and the station providing the most recent data, which is reasonable given their close spatial proximity.

RESULTS

We recorded a total of 287 nesting attempts by 42 pairs over the 5 years of study. In each year, we followed the fate of 20–29 pairs and observed between 41 and 75 nesting attempts, resulting in a total of 124 observations of pair-specific seasonal fecundity (Table 1). Rainfall was highly variable over the 5 years, with a relatively dry year in 2001, and very wet years in 2002 and 2004, the latter having nearly 300 mm (285%) more rainfall than 2001 (Table 1).

On average, the number of fledglings produced by a pair of Montserrat Orioles over the breeding season ranged from 0.71 ± 0.19 (se) in 2001 to 1.78 ± 0.30 in 2004 (Table 1), and between 45% (in 2001) and 67% (in 2002) of pairs managed to raise at least one offspring per year. Fecundity increased with rainfall ($\chi^2_5 = 15.0$, $P = 0.01$, Fig. 1), with an increase of 0.40 (95% confidence interval 0.05–2.07) fledglings produced per pair for each 100 mm increase in rainfall (slope parameter estimate $b = 0.003 \pm 0.001$). At the population level, rainfall proved to be an excellent predictor of annual productivity ($R^2 = 0.94$, Fig. 1).

Clutch size increased with increasing rainfall ($b = 0.004 \pm 0.001$), and the model including rainfall as a fixed effect was significantly better than the null model incorporating only variation at the site and pair levels ($\chi^2_1 = 14.1$, $P < 0.001$). For a 100 mm increase in rainfall, the expected ordered log-odds of laying one egg more increased by 0.004 ± 0.001 . The probability of laying one- or two-egg clutches decreased with increasing rainfall, whereas the probability of laying three- or four-egg clutches increased (Fig. 2).

Table 1. Average pre-breeding season rainfall (January–March) and fecundity parameters (\pm se) of Montserrat Orioles during 2001–2005 on the island of Montserrat.

Year	Rainfall (mm)	No. of pairs	No. of nests	Productivity (fledglings/pair)	Start of nesting season	Season length (days)	Clutch size (eggs)	Re-nesting probability
2001	166	20	41	0.71 ± 0.19	9 April	144	2.04 ± 0.08	0.43 ± 0.06
2002	413	21	54	1.41 ± 0.28	6 April	108	2.48 ± 0.09	0.60 ± 0.04
2003	311	29	57	1.04 ± 0.20	13 March	120	2.55 ± 0.07	0.45 ± 0.04
2004	478	25	60	1.78 ± 0.30	25 March	130	2.82 ± 0.07	0.61 ± 0.05
2005	359	29	75	1.39 ± 0.32	18 March	146	2.62 ± 0.07	0.57 ± 0.04

Nesting season length was defined as the difference between first and latest nest initiation dates for a given study site (see text for full details).

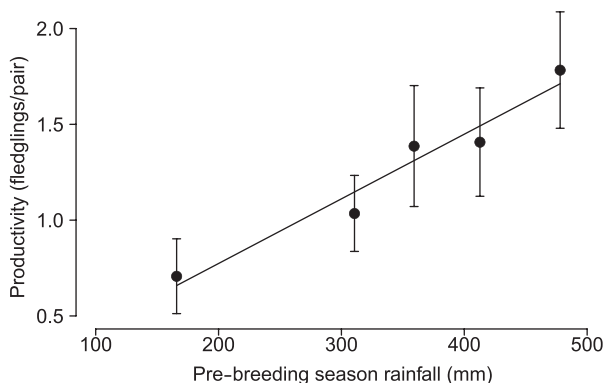


Figure 1. Relationship between pre-breeding season rainfall (January–March, in mm) and mean (± 1 se) seasonal fecundity (fledglings/pair) of Montserrat Orioles from 2001 to 2005 on the island of Montserrat.

The onset of the breeding season for each pair was slightly earlier in years with more rainfall ($b = -0.11 \pm 0.04$; $\chi^2_3 = 22.0$, $P < 0.001$). How-

ever, this relationship was driven by the driest year in our study, and was not apparent for rainfall amounts exceeding 300 mm. Although the length of the breeding season varied considerably over the 5 years of our study (Table 1), a model that included rainfall as a fixed effect did not explain any more of the variation in the length of the breeding season than a null model containing only site as a random effect ($\chi^2_3 = 0.78$, $P = 0.86$, Fig. 2). Re-nesting probability declined over the course of the season and depended on the outcome of the previous nesting attempt (all $P < 0.001$). There was no effect of rainfall when time of season and nest outcome were considered in the model ($\chi^2_5 = 0.73$, $P = 0.98$).

The interval between two subsequent nesting attempts within a season was shorter in years with higher rainfall ($b = -0.002 \pm 0.0005$, $\chi^2_5 = 303.99$, $P < 0.001$). On average, a 100-mm increase in rainfall reduced the re-nesting interval after a nest failed at the egg stage by 4.2 days

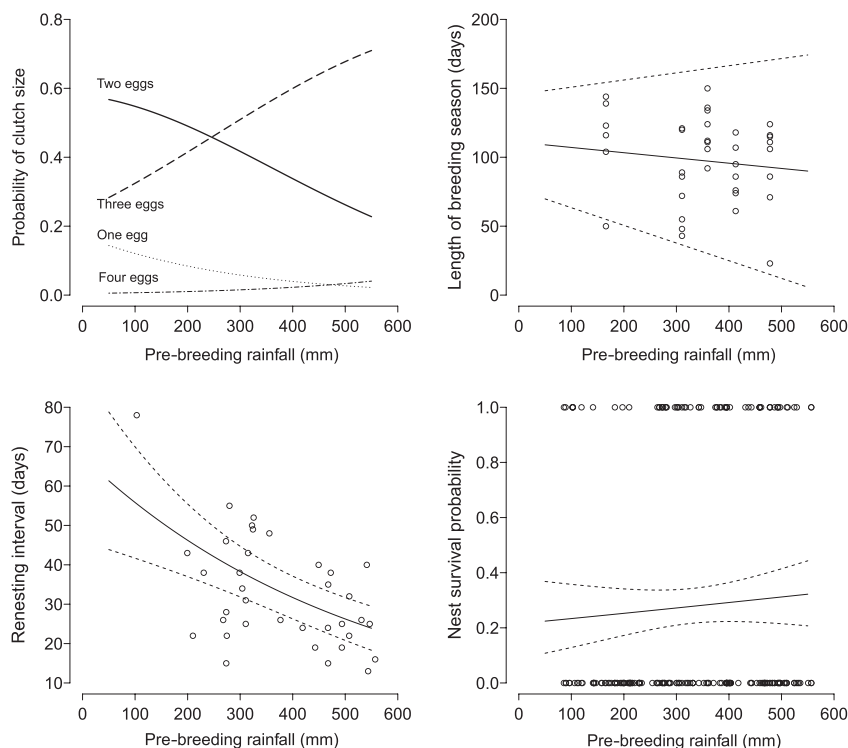


Figure 2. Predicted effects ($\pm 95\%$ confidence limits) of pre-breeding season rainfall on component parameters of fecundity (clutch size, length of breeding season, re-nesting interval and nest survival) of Montserrat Orioles over the range of pre-breeding season rainfall observed between 2001 and 2005 on the island of Montserrat. For clutch size, re-nesting interval and nest survival, the pre-breeding season rainfall was calculated as the sum of rainfall over the 3 months prior to the initiation of a nest. For the length of the nesting season, the pre-breeding season rainfall was the sum over the 3 months prior to the breeding season (i.e. January–March). Observed data are shown as open circles.

(95% confidence interval 2.9–4.6, Fig. 2). For nests that failed at the chick stage, the interval was reduced by 4.9 days (3.3–5.4), and for successful nests the interval was reduced by 6.0 days (4.0–6.6).

Of 16 environmental variables that were considered to affect nest survival, the random forest model consistently identified only nest initiation date and male age as important. We therefore included these two variables as fixed factors in models exploring the influence of rainfall on nest survival probability. The estimated nest survival probability of Montserrat Orioles averaged across the 5 years of the study was 0.27 (95% confidence interval 0.18–0.38) and rainfall did not have a measurable effect on nest survival ($b = 0.0005 \pm 0.0007$; $\chi^2_5 = 0.76$, $P = 0.98$, Fig. 2). Nest survival increased with male age ($b = 0.32 \pm 0.24$), and decreased for nests initiated later in the season ($b = -0.007 \pm 0.002$).

We found no significant trend in rainfall over the past 110 years (Fig. 3). Both local rainfall measurements on Montserrat between 1902 and 2012 ($b = 0.06 \pm 0.34$, $P = 0.85$) and mean average regional rainfall in the eastern Caribbean between 1979 and 2011 ($b = -0.68 \pm 0.35$, $P = 0.06$) were relatively stable.

DISCUSSION

The increase in seasonal fecundity of Montserrat Orioles in years with higher rainfall is likely to be the result of an increase in primary reproductive

investment. Higher rainfall was associated with larger clutch sizes and a reduced interval between subsequent nesting attempts, but we found no strong effect of rainfall on the length of the nesting season or the average nest survival probability. We also did not find an effect of rainfall on re-nesting probability, and because re-nesting probability and nest survival usually determine the number of fledged broods per year (Grzybowski & Pease 2005), there was no evidence for pairs having more successful nests in years with higher rainfall. The increase in seasonal fecundity therefore seems to be mainly a consequence of larger clutch sizes, and we conclude that rainfall affects the foraging efficiency of female Montserrat Orioles and enables them to lay more eggs. The strong response of clutch size may be valuable for future monitoring of potential demographic changes in response to climate change because the monitoring of clutch size is logistically easier to accomplish than the monitoring of seasonal fecundity.

The relationships we found were adequately described by linear models for the observed range of rainfall variation, but due to the humped relationship of many demographic parameters with environmental variables (Hamer 2010), fecundity may peak or asymptote at very high levels of rainfall. However, years in which rainfall is much higher than in our study period appear to be extremely rare (Fig. 3) and we are therefore confident that the linear relationships that we found in our study are valid for rainfall conditions generally

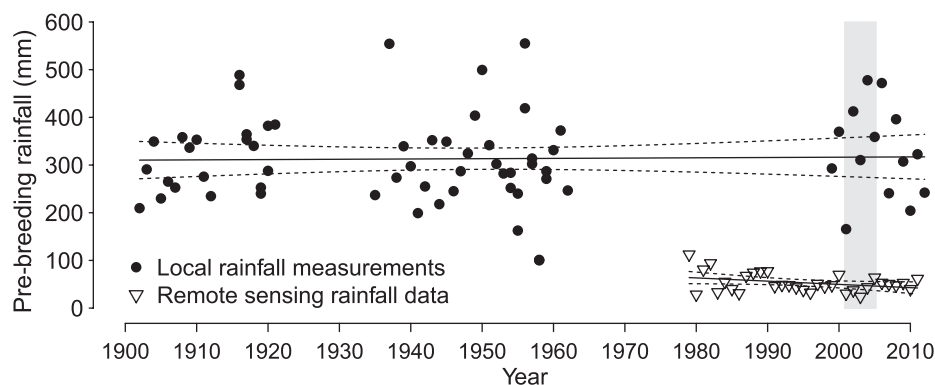


Figure 3. Pre-breeding season rainfall (January–March, in mm) between 1902 and 2012 from local rainfall measurements adjacent to the Centre Hills on Montserrat (filled circles), or derived from remote sensing data covering a 2.5° grid cell encompassing the island of Montserrat (open triangles). The grey box indicates the time period over which nest monitoring data were available for this study. Solid and broken lines represent linear regression fits and 95% confidence intervals for local rain gauge and remote sensing data, respectively. Note that average rainfall over a large region (remote sensing data) is naturally much lower than measured rainfall at a point location on a mountainous island where local topography enhances precipitation.

experienced in the forests on Montserrat (Bolger *et al.* 2005).

Potential mechanisms by which rainfall increases fecundity

Most studies in which rainfall, clutch size and seasonal fecundity were positively correlated were carried out in arid environments (Grant *et al.* 2000, Bolger *et al.* 2005, Illera & Diaz 2006). Our results indicate that increases in rainfall can lead to increases in fecundity even in a mesic tropical forest environment, where water is not as scarce as in arid environments. Food availability is generally higher after abundant rainfall in dry tropical habitats, presumably mediated by soil moisture rather than by rainfall per se (Grant & Boag 1980, Grant *et al.* 2000). Higher rainfall can also increase the availability of drinking water, which has been shown to increase clutch size in some species (Coe & Rotenberry 2003). Increased abundance of both food and drinking water presumably improved body condition in female Montserrat Orioles, which could result in larger clutch sizes and shorter re-nesting intervals (Brown & Sherry 2006). Montserrat Orioles may be able to regain the body condition required for nest initiation sooner after a previous nesting attempt if food and water are more abundant.

Montserrat Orioles nest and forage in *Heliconia* plants (Marske 2004, Allcorn *et al.* 2012), broad-leaved understorey plants up to 5 m tall that produce inflorescences consisting of brightly coloured, erect floral bracts which contain water to protect the developing flower and seeds from herbivores (Seifert 1982). The water attracts aquatic insects, and *Heliconia* floral bracts serve as food and water reservoirs for Montserrat Orioles (S. Oppel & C. Fenton pers. obs.). On Montserrat, the steep terrain and porous volcanic soils limit the availability of surface waters, hence the availability of drinking water in *Heliconia* floral bracts may be particularly important. Many plants respond to increasing water availability by increasing reproductive investment (Herrera 1991, Galen 2005), and because *Heliconia* plants actively maintain standing water within their floral bracts, it is possible that flower production is dependent on water availability. Thus, in years with higher rainfall, *Heliconia* plants may be able to increase their reproductive investment, leading to a larger number of *Heliconia* inflorescences in the forest. Because a larger num-

ber of these inflorescences may facilitate easier foraging and water uptake, Montserrat Orioles may be able to obtain improved body condition, leading to larger clutch sizes. Likewise, the widespread availability of *Heliconia* inflorescences as feeding and drinking stations may facilitate faster re-conditioning after a nesting attempt, leading to shorter re-nesting intervals.

In contrast to clutch size and re-nesting interval, we found no effect of rainfall on Montserrat Oriole nest survival. Because most nest failures were the result of predation (Allcorn *et al.* 2012), hypotheses linking rainfall to nest survival via thermoregulatory mechanisms (Morrison & Bolger 2002, Fletcher & Koford 2004) may not be relevant to our study system. Montserrat Orioles build basket-shaped nests which are usually suspended beneath the broad leaves of *Heliconia* plants (Allcorn *et al.* 2012). These broad leaves provide sufficient shelter from rainfall, which probably explains why even the most intense rainfall events are rarely accompanied by a rise in nest failures.

We found no evidence that the length of the breeding season was related to pre-breeding season rainfall, a result that is consistent with a similar study of Spotted Antbirds *Hylophylax naevioides* in Panama (Styrsky & Brawn 2011). However, there was some evidence that the amount of rainfall during the pre-breeding season affected the onset of the breeding season. In wetter years, birds initiated the first nests of the season earlier, and because nest initiation date was the most influential variable explaining nest survival, it is likely that wetter years have a higher proportion of successful nests simply because the birds initiate nests earlier in the season. A similar (but inverse) relationship was found for another tropical island endemic, the Mauritius Kestrel *Falco punctatus*, where years with more rain days delayed the onset of the breeding season and subsequently led to larger nest losses due to nest cavity flooding later in the breeding season (Senapathi *et al.* 2011). It is currently unknown what proximate cue triggers the cessation of reproductive activity in Montserrat Orioles, which occurs several weeks before the onset of the local dry season (Allcorn *et al.* 2012). Photoperiodic changes, although relatively small in the tropics, have been shown to affect gonadal growth rates in tropical forest birds (Hau *et al.* 1998), and it is possible that gradually shortening day lengths in August reduce the breeding activity of Montserrat Orioles. Alternatively, Montserrat

Orioles may stop initiating nests partly in response to the increase in storm frequency and a sharp increase in rainfall, which often occurs in September (Barclay *et al.* 2006). This pattern would be consistent with the hypothesized termination of the reproductive season of Spotted Antbirds (Styrsky & Brawn 2011). If the end of the breeding season is triggered by such environmental stimuli, then birds may not be able to extend the breeding season even in years with low pre-breeding season rainfall. However, more work will be required to understand the cues that determine the end of the breeding season.

In summary, we found that higher pre-breeding season rainfall was associated with larger clutches, shorter re-nesting intervals and earlier onset of the breeding season, which led to an overall higher annual fecundity in Montserrat Orioles. We suggest that this increase is because greater rainfall leads to a greater availability of *Heliconia* inflorescences, which in turn facilitate easier and more efficient foraging and drinking and lead to improved body condition among female Orioles. This improved body condition may in turn lead to larger clutch sizes and shorter re-nesting intervals. Our study indicates that variability in rainfall is more likely to affect reproductive investment than nest predation in a moist forest environment.

Implications for conservation

Our results suggest that a long-term decline in rainfall could reduce the annual reproductive output of Montserrat Orioles, which is of significant concern for a critically endangered species. However, neither the local rainfall data nor the satellite-derived precipitation data for the wider region show any evidence of a significant long-term change (Fig. 3). No reliable predictions of future rainfall exist for the Caribbean, and large-scale changes in rainfall are not amenable to conservation management. Hence, measures to protect the species must ensure that sufficient habitat is available. Because natural rain forest is important both as habitat for the Montserrat Oriole (Allcorn *et al.* 2012) and to maintain current rainfall regimes (Spracklen *et al.* 2012), the protection of all remaining forest habitats on Montserrat is the single most important conservation measure to preserve the endemic Montserrat Oriole. In addition, regular monitoring of clutch sizes needs

to be established to gauge whether reproductive investment exhibits a temporal trend. The control of invasive non-native nest predators (Allcorn *et al.* 2012), which is currently not a cost-effective solution for conservation, may become more important in the future if rainfall and reproductive investment of the Montserrat Oriole begin to decline.

We appreciate the support of the Montserrat Department of Environment in all aspects of the fieldwork on Montserrat. P. W. Atkinson, C. G. R. Bowden, M. Hulme, J. Madden, E. K. Mackley (all RSPB), J. Daley, G. Gray, L. Martin and J. Boatswain (all Montserrat Dept. of Environment) assisted with nest monitoring, capture and observations of birds. We thank the Montserrat Water Authority for sharing data from rainfall gauges, and B. Hemmings for digitizing and sharing the historical rainfall data. CMAP precipitation data were provided by the NOAA Earth Systems Research Laboratory Physical Sciences Division, Boulder, CO, USA, from their website at <http://www.esrl.noaa.gov/psd/>. J. Barclay provided valuable insights on rainfall measurements and patterns on Montserrat, and D. Senapathi shared valuable thoughts on the effect of rainfall metrics on fecundity. I. Stewart, M. Etterson, A. Cassini and several anonymous reviewers provided helpful comments on earlier drafts of the manuscript.

REFERENCES

- Aebischer, N.J.** 1999. Multi-way comparisons and generalized linear models of nest success: extensions of the Mayfield method. *Bird Study* **46**: S22–S31.
- 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. & Oppel, S.** 2012. Demography and breeding ecology of the critically endangered Montserrat Oriole. *Condor* **114**: 227–235.
- Arendt, W.J., Gibbons, D.W. & Gray, G.** 1999. Status of the volcanically threatened Montserrat Oriole *Icterus oberi* and other forest birds in Montserrat, West Indies. *Bird Conserv. Int.* **9**: 351–372.
- Barclay, J., Johnstone, J.E. & Matthews, A.J.** 2006. Meteorological monitoring of an active volcano: implications for eruption prediction. *J. Volcanol. Geotherm. Res.* **150**: 339–358.
- Bolger, D., Patten, M. & Bostock, D.** 2005. Avian reproductive failure in response to an extreme climatic event. *Oecologia* **142**: 398–406.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.-S.S.** 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* **24**: 127–135.
- Brown, D. & Sherry, T.** 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* **149**: 22–32.
- Coe, S.J. & Rotenberry, J.T.** 2003. Water availability affects clutch size in a desert sparrow. *Ecology* **84**: 3240–3249.

- Cohen, Y. 1988. Bayesian estimation of clutch size for scientific and management purposes. *J. Wildl. Manage.* **52**: 787–793.
- Dalsgaard, B., Hilton, G.M., Gray, G.A.L., Aymer, L., Boatswain, J., Daley, J., Fenton, C., Martin, J., Martin, L. & Murrain, P. 2007. Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles. *Ibis* **149**: 298–312.
- Ettersson, M.A., Bennett, R.S., Kershner, E.L. & Walk, J.W. 2009. Markov chain estimation of avian seasonal fecundity. *Ecol. Appl.* **19**: 622–630.
- Ettersson, M.A., Ellis-Felege, S.N., Evers, D., Gauthier, G., Grzybowski, J.A., Mattsson, B.J., Nagy, L.R., Olsen, B.J., Pease, C.M., van der Burg, M.P. & Potvien, A. 2011. Modeling fecundity in birds: conceptual overview, current models, and considerations for future developments. *Ecol. Model.* **222**: 2178–2190.
- Farnsworth, G.L. & Simons, T.R. 2005. Relationship between Mayfield nest-survival estimates and seasonal fecundity: a cautionary reply. *Auk* **122**: 1000–1001.
- Fletcher, R.J. & Koford, R.R. 2004. Consequences of rainfall variation for breeding wetland blackbirds. *Can. J. Zool.* **82**: 1316–1325.
- Galen, C. 2005. It never rains but then it pours: the diverse effects of water on flower integrity and function. In Reekie, E.G. & Bazzaz, F.A. (eds) *Reproductive Allocation in Plants*: 77–95. Burlington, MA: Academic Press.
- Grant, P.R. & Boag, P.T. 1980. Rainfall on the Galapagos and the demography of Darwin's finches. *Auk* **97**: 227–244.
- Grant, P.R., Grant, B.R., Keller, L.F. & Petren, K. 2000. Effects of El Niño events on Darwin's finch productivity. *Ecology* **81**: 2442–2457.
- Grömping, U. 2009. Variable importance assessment in regression: linear regression versus Random Forest. *Am. Stat.* **63**: 308–319.
- Grzybowski, J.A. & Pease, C.M. 2005. Renesting determines seasonal fecundity in songbirds: what do we know? What should we assume? *Auk* **122**: 280–292.
- Guisan, A. & Harrell, F.E. 2000. Ordinal response regression models in ecology. *J. Veg. Sci.* **11**: 617–626.
- Hamer, K.C. 2010. The search for winners and losers in a sea of climate change. *Ibis* **152**: 3–5.
- Hau, M., Wikelski, M. & Wingfield, J.C. 1998. A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proc. R. Soc. Lond. B* **265**: 89–95.
- Herd, R.A., Edmonds, M. & Bass, V.A. 2005. Catastrophic lava dome failure at Soufriere Hills Volcano, Montserrat, 12–13 July 2003. *J. Volcanol. Geotherm. Res.* **148**: 234–252.
- Herrera, C. M. 1991. Dissecting factors responsible for individual variation in plant fecundity. *Ecology* **72**: 1436–1448.
- Hilton, G., Atkinson, P., Gray, G., Arendt, W. & Gibbons, D. 2003. Rapid decline of the volcanically threatened Montserrat oriole. *Biol. Conserv.* **111**: 79–89.
- del Hoyo, J., Elliott, A. & Christie, D.A. (eds) 2011. *Handbook of the Birds of the World*, Vol. 16. Barcelona: Lynx Edicions.
- Illera, J.C. & Diaz, M. 2006. Reproduction in an endemic bird of a semiarid island: a food-mediated process. *J. Avian Biol.* **37**: 447–456.
- Lewis, F., Butler, A. & Gilbert, L. 2011. A unified approach to model selection using the likelihood ratio test. *Meth. Ecol. Evol.* **2**: 155–162.
- Magurran, A.E. 1988. *Ecological Diversity and its Measurement*. Princeton: Princeton University Press.
- Marske, K.A. 2004. *Effects of volcanic ash on the insect food of the Montserrat Oriole Icterus oberi Lawrence 1880*. M.Sc. Thesis, Montana State University.
- Martin, T.E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.* **141**: 897–913.
- Matthews, A.J., Barclay, J., Carn, S., Thompson, G., Alexander, J., Herd, R. & Williams, C. 2002. Rainfall-induced volcanic activity on Montserrat. *Geophys. Res. Lett.* **29**. doi: 10.1029/2002GL014863.
- Mattsson, B.J. & Cooper, R.J. 2007. Which life-history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush (*Seiurus motacilla*). *Auk* **124**: 1186–1200.
- Mattsson, B.J. & Cooper, R.J. 2009. Multiscale analysis of the effects of rainfall extremes on reproduction by an obligate riparian bird in urban and rural landscapes. *Auk* **126**: 64–76.
- Monadjem, A. & Bamford, A.J. 2009. Influence of rainfall on timing and success of reproduction in Marabou Storks *Leptoptilos crumeniferus*. *Ibis* **151**: 344–351.
- Morrison, S. & Bolger, D. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia* **133**: 315–324.
- Murphy, M.A., Evans, J.S. & Storfer, A. 2010. Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* **91**: 252–261.
- Nagy, L.R. & Holmes, R.T. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* **86**: 675–681.
- Patten, M.A. & Rotenberry, J.T. 1999. The proximate effects of rainfall on clutch size of the California Gnatcatcher. *Condor* **101**: 876–880.
- Polis, G.A., Hurd, S.D., Jackson, C.T. & Pinero, F.S. 1997. El Niño effects on the dynamics and control of an island ecosystem in the Gulf of California. *Ecology* **78**: 1884–1897.
- Preston, K.L. & Rotenberry, J.T. 2006a. Independent effects of food and predator-mediated processes on annual fecundity in a songbird. *Ecology* **87**: 160–168.
- Preston, K.L. & Rotenberry, J.T. 2006b. The role of food, nest predation, and climate in timing of Wrentit reproductive activities. *Condor* **108**: 832–841.
- R Development Core Team 2010. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Radford, A.N. & Du Plessis, M.A. 2003. The importance of rainfall to a cavity-nesting species. *Ibis* **145**: 692–694.
- Ricklefs, R.E. & Bloom, G. 1977. Components of avian breeding productivity. *Auk* **94**: 86–96.
- Rodriguez, C. & Bustamante, J. 2003. The effect of weather on lesser kestrel breeding success: can climate change explain historical population declines? *J. Anim. Ecol.* **72**: 793–810.
- Roper, J.J. 2005. Try and try again: nest predation favors persistence in a neotropical bird. *Ornitol. Neotrop.* **16**: 253–262.

- Roper, J.J., Sullivan, K.A. & Ricklefs, R.E.** 2010. Avoid nest predation when predation rates are low, and other lessons: testing the tropical-temperate nest predation paradigm. *Oikos* **119**: 719–729.
- Rotenberry, J.T. & Wiens, J.A.** 1991. Weather and reproductive variation in Shrubsteppe Sparrows – a hierarchical analysis. *Ecology* **72**: 1325–1335.
- Schiezeth, H. & Forstmeier, W.** 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behav. Ecol.* **20**: 416–420.
- Seifert, R.P.** 1982. Neotropical *Heliconia* insect communities. *Q. Rev. Biol.* **57**: 1–28.
- Senapathi, D., Nicoll, M.A.C., Teplitsky, C., Jones, C.G. & Norris, K.** 2011. Climate change and the risks associated with delayed breeding in a tropical wild bird population. *Proc. R. Soc. Lond. B* **278**: 3184–3190.
- Siikamäki, P.** 1996. Nestling growth and mortality of Pied Flycatchers *Ficedula hypoleuca* in relation to weather and breeding effort. *Ibis* **138**: 471–478.
- Sinclair, A.R.E.** 1978. Factors affecting the food supply and breeding season of resident birds and movements of palaeartic migrants in a tropical African savannah. *Ibis* **120**: 480–497.
- Spracklen, D.V., Arnold, S.R. & Taylor, C.M.** 2012. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* **489**: 282–285.
- Stephens, S.E., Koons, D.N., Rotella, J.J. & Willey, D.W.** 2004. Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biol. Conserv.* **115**: 101–110.
- Styrsky, J.N. & Brawn, J.D.** 2011. Annual fecundity of a Neotropical bird during years of high and low rainfall. *Condor* **113**: 194–199.
- Walker, S.H.** 1965. *Report on Water Resources of Montserrat*. Plymouth, Montserrat: Government of Montserrat.
- Xie, P. & Arkin, P.A.** 1997. Global precipitation: a 17-year monthly analysis based on gauge observations, satellite estimates, and numerical model outputs. *Bull. Am. Meteorol. Soc.* **78**: 2539–2558.

Received 2 December 2011;
 revision accepted 17 February 2013.
 Associate Editor: Ian Stewart.