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Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird

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Our understanding of when natural populations are regulated during their annual cycle is limited, particularly for migratory species. This information is needed for parametrizing models that can inform management and conservation. Here, we use 14 years of data on colour-marked birds to investigate how conspecific density and habitat quality during the tropical non-breeding period interact to affect body condition and apparent annual survival of a long-distance migratory songbird, the American redstart (*Setophaga ruticilla*). Body condition and survival of birds in high-quality mangrove habitat declined as density increased. By contrast, body condition improved and survival did not vary as density increased in adjacent, lower quality scrub habitat, although mean condition and survival were almost always lower than in mangrove. High rainfall enhanced body condition in scrub but not in mangrove, suggesting factors such as food availability outweighed consequences of crowding in lower quality habitat. Thus, survival of overwintering redstarts in mangrove habitat, disproportionately males, appears to be regulated by a crowding mechanism based on density-dependent resource competition. Survival of individuals in scrub, mostly females, appears to be limited by density-independent environmental factors but not regulated by crowding. The contrasting effects of density and food limitation on individuals overwintering in adjacent habitats illustrate the complexity of processes operating during the non-breeding period for migratory animals, and emphasize the need for long-term studies of animals in multiple habitats and throughout their annual cycles.

1. Introduction

Many factors limit animal populations [1,2], but the processes that regulate abundance are less understood [3–5]. Population regulation occurs when density-dependent mechanisms such as intraspecific competition for food or territory sites [6,7] or interspecific interactions with natural enemies [8,9] cause vital rates to covary negatively with population size. Research on population regulation has typically emphasized detecting density dependence. However, we have insufficient information about how and when during the annual cycle density affects demographic rates [7,10,11]. This knowledge is needed for effective management and conservation of wildlife populations [12].

Resource competition associated with crowding is the basis of density-dependence as described by Lack [13] and is perhaps the most ubiquitous regulatory mechanism for territorial animal populations. At high densities, resources become limited due to smaller territories, more time spent in costly

interactions, or both. Individuals suffer reduced fecundity or survival as density increases [14]. The effects of crowding are probably strongest where individuals exist at high densities in relatively homogeneous environments [6,15,16].

Empirical research on the strength and form of density dependence in birds has focused primarily on population studies during their breeding season. Much of this work has investigated the relationship between density and reproductive success [8,17]. Studies designed to examine density-dependent effects on adult or juvenile survival have typically been conducted with relatively sedentary, small or recovering populations [18–20]. Investigations of migratory birds have considered the effects of density-dependent annual survival in large-bodied species with relatively slow life histories, such as great cormorant (*Phalacrocorax carbo*) [21] and black-tailed godwit (*Limosa limosa*) [22]. In a recent breeding example with a small, long-distance migratory bird, the American redstart (*Setophaga ruticilla*), years of higher density were associated with fewer offspring fledged per female, a reduced mean population rate of fledging success and a lower relative contribution of extra-pair fertilizations to male fitness [23].

We know less about the effects of regulatory processes during the non-breeding period. Theoretical work suggests that density dependence outside the breeding season should be widespread and important to avian population dynamics [24,25] and is supported by some empirical evidence [22,26–28]. The form and strength of density-dependent survival in the Eurasian spoonbill (*Platalea leucorodia leucorodia*) varied with age and season [29]. In this case, annual survival of subadult and adult birds declined with increasing population size, and density dependence occurred in early winter for subadults and late winter for adults. However, no study of a long-distance migratory passerine, to our knowledge, has been designed to detect non-breeding period density dependence, or the mechanisms driving it.

Many species of migratory songbirds are declining [30], emphasizing the need to understand when and how their populations are limited and regulated. Anthropogenic habitat destruction is the primary factor responsible for these declines [31], but density-dependent processes are central to population dynamics. For example, if overwinter survival is regulated by conspecific density, loss of high-quality tropical habitats could shape the strength and form of density dependence [24]. Management of migratory bird populations requires population models that encompass the full annual cycle, parametrized with estimates of seasonal density dependence [32–34].

Here, we investigate how conspecific density and habitat quality during the tropical non-breeding period interact to affect body condition and apparent annual survival of a long-distance migratory songbird. We used 14 years of data from our long-term study of American redstarts (*S. ruticilla*) on their non-breeding grounds in Jamaica, West Indies to test: (i) if redstart density influences body condition and apparent annual survival of individual birds, and (ii) if the strength of density dependence varies between two habitats known to differ in quality and sex composition [35,36]. Both males and females hold and vigorously defend non-breeding territories [36]. In addition, territories are acquired and maintained via behavioural dominance, with older males typically securing sites in high-quality habitat and forcing females and many younger males to occupy sites in lower quality habitat [35]. These considerations provided a unique opportunity to assess how density dependence varies among demographic groups of a migratory animal during the non-breeding period. If density dependence operates during this season, we predicted that individual physical condition would decline over winter, and that annual survival would decline following years of high redstart density, regardless of sex or habitat type.

2. Material and methods

(a) Study species and sites

American redstarts are small (6–9 g) entirely insectivorous songbirds that occupy non-breeding habitats which vary in quality primarily owing to differences in arthropod availability [37,38]. Redstart habitat quality influences numerous measures of bird performance in both sexes. Individuals in high-quality habitats are typically in better physical condition [39,40] and depart earlier on spring migration [39,41] at the end of the non-breeding period than individuals in lower quality habitat. Annual survival probability is also related to overwinter habitat quality [36,42].

This research was conducted at the Font Hill Nature Preserve (18°02′ N, 77°57′ W, less than 5 m above sea level), about 13 km west of Black River, St Elizabeth Parish, Jamaica. This site experiences strong seasonality in precipitation typical of many tropical regions. Rainfall is highest from August to November, typically exceeding 150 mm per month, and then declines to less than 60 mm per month during the dry season from January to March (Jamaica Meteorological Service; http://www.metservice.gov.jm/).

We studied redstarts in two habitats: mangrove forest and adjacent second-growth scrub. Mangrove forest was dominated by black mangrove (*Avicennia germinans*) but also contained some white (*Laguncularia racemosa*) and red (*Rhizophora mangle*) mangrove. Mangrove stands typically were inundated by 0.5–1.0 m of standing brackish water in October and November during the rainy season, but water levels became progressively lower towards February and March. Little understory or ground-level vegetation was present except for mangrove pneumatophores. Black mangroves ranged in diameter at breast height (dbh) from 8 to 75 cm, were regularly dispersed at intervals of 10–15 m, and had dense and contiguous canopies averaging about 8 m in height. These trees retained the majority of their leaves through the dry season, keeping this habitat relatively moist and shady throughout the time of redstart occupancy. Second growth scrub habitat contained shrubs and small trees ranging from 2 to 8 cm in dbh and 2–8 m in height, forming a dense understory and ground layer of vegetation. Although this area is a nature preserve, cattle roamed freely in some years, and trees were often cut for charcoal and fence-posts, creating a mosaic of thickets, vine tangles and grassy patches. Scrub vegetation was dominated by logwood (*Haematoxylon campechianum*), a thorny small tree with a fluted trunk and many small leaves introduced into Jamaica. Less frequent tree species included *Bursera simaruba*, *Terminalia latifolia* and *Crescentia alata*. Unlike mangrove forest, trees and other vegetation in scrub habitat dropped most of their leaves facultatively during the spring dry season, especially in the driest years, and standing water was never present.

(b) Field methods

Redstarts were studied for 14 years from mid-January through to mid-April, 1994–1998 and 2000–2009 on four 5 ha study plots, two in mangrove and two in scrub. Plots were separated by 200–700 m and were gridded at 25 m intervals to facilitate locating redstarts and mapping territories. Redstarts were captured and recaptured in mist nets accompanied by vocalization broadcasts and a decoy. Each captured individual was marked with a unique combination of coloured leg bands, measured (unflattened wing chord and tarsus length), weighed to

±0.1 g, sexed and aged as either yearling (less than 1 year old) or adult (more than 1 year old) following criteria in [36].

We counted the number of redstarts of each age- and sex-class in each study plot by intensively mapping the activities of colour-marked and unmarked individuals on each study site over a one to four month period each year. Both males and females vocalize regularly during territory defence and exhibit stereotyped chase behaviours at territory boundaries, making them easy to detect and count. Territory mapping consisted of recording redstart movements for an average duration of 10 min and occasionally up to 1 h per day. Within each season, each redstart was observed for several hours to identify territory boundaries. We converted mapping observations to densities by summing the total number of territories per plot divided by its total monitored area.

We built annual encounter histories by resighting marked birds that had occupied territories during the previous year. When a bird was not resighted on the first visit, we revisited that territory a minimum of three times in a season, often using song playbacks, to confirm that an individual was not present. We also intensively searched habitat within 150 m of each study plot to detect individuals that shifted territory locations. Because redstarts show strong fidelity to winter territories between years [36], our intensive search efforts produced reliable data on individual presence and absence.

(c) Statistical analyses

Effects of crowding were examined using body condition in relation to conspecific density. This analysis was done with only 9 years (1995, 1996, 1997, 2002, 2003, 2004, 2005, 2007 and 2008) of data, because we did not intensively capture birds in all years. We analysed only birds captured in spring (15 March–15 April). Body condition at this time of year reflected environmental conditions across the non-breeding period [36,38]. We estimated body condition as the standardized residuals from a regression of body mass on tarsus and wing length.

Body condition data were analysed using a linear mixed model with random intercepts fitted for each bird, because some individuals were sampled in more than 1 year. The full model contained fixed effects of age, sex, habitat type, rainfall, conspecific density, and two- and three-way interactions for density × age, sex and habitat. We did not model interactions of age and sex × habitat because redstart body condition is similar for all demographic groups in both habitats [36,38]. Rainfall data were obtained from the Burnt-Savannah Meteorological Station located approximately 20 km from our study site (Jamaica Meteorological Service; http://www.metservice.gov.jm/) and was included in models as standardized total precipitation (mm) from January through to March annually. We assessed the significance of each variable by iteratively removing it from the full model and comparing the reduced to the full model with a likelihood ratio test with 1 d.f. Analyses were done with package lme4 [43] in program R [44].

Initial analyses suggested that a number of birds in mangrove forest could strongly influence parameter estimates as indicated by their large residual values and high leverage. We defined data points with high influence as those with Cook's distance values greater than $4/n$, where n is the total number of birds in mangrove forest. Rather than exclude these data points, we performed robust regression with iterated reweighted least squares to reduce their influence on parameter estimates. We calculated the absolute value of standardized residuals and used Huber weights to down-weight data points of high influence. Analyses were done with the rlm function in package MASS [45].

We fitted Cormack–Jolly–Seber models in program MARK [46] to estimate apparent annual survival and recapture probabilities. Model goodness-of-fit was examined using the median $\hat{c}$

procedure on the most parametrized model. We first modelled recapture probability (p) as a function of age, sex, habitat and study effort. Study effort was determined for each year based on whether fieldwork was a high effort four-month visit or a lower effort one-month visit. Fieldwork was not done in 1999, so we fixed the recapture rate to 0 for that year, resulting in a 2 year average survival estimate from 1998 to 2000.

The recapture model with the greatest support was used to examine factors affecting annual survival. We first modelled apparent survival (ϕ) probability as conditional on habitat, sex and age, and examined the influence of these three covariates as additive effects and two- and three-way interactions. A marking effect was included depending on whether birds were marked in their second year or after their second year. Time dependence was measured by allowing a separate survival estimate each year by including common and separate temporal patterns in each habitat. We also evaluated a constrained time model that fitted ϕ differently only for 1996 because of an insect outbreak that led to abnormally high arthropod abundance in both habitats [47]. The most supported model for ϕ containing the above variables was then used to test the effect of rainfall from January through to March and of habitat-specific density on apparent annual survival. We considered models where density altered apparent survival equally in both habitats, differently between habitats, and in one habitat but not the other. Density estimates were unavailable in 1998, 1999 and 2006, and we used the overall mean density for survival analyses in those years.

We ranked candidate models by second-order Akaike's information criterion (AIC$_c$) differences and estimated the relative likelihood of each model with AIC$_c$ weights (w_i). Models within two units of the top model were considered to have equal support, except in cases where they differed by only one parameter and the more parametrized model had a higher AIC$_c$ [48]. Apparent survival probabilities for each age- and sex-class by habitat type were obtained by model averaging. Most models had annually variable survival owing to covariate effects or time-dependence. Therefore, model averaging generated an annual mean estimate and standard error for each group. The average of these annual values is reported as the expected mean apparent survival probability for the group with standard errors obtained using the Delta Method [49] with package emdbook [50] in program R [44]. We did not model average the regression coefficients because of the presence of interaction terms for density. Instead, we report the effect size and confidence intervals for the coefficients and how they varied among top models.

3. Results

Redstart density varied between habitats. Mangrove densities ranged from 4.9–8.5 birds ha^{-1} (6.3 ha^{-1} ± 1.0 (median ± s.d.), interquartile range = 5.7–6.8, $n = 12$ years) versus scrub habitat with 2.5–6.1 birds ha^{-1} (4.0 ha^{-1} ± 1.0, interquartile range = 3.8–5.0, $n = 12$ years). Despite some overlap (figure 1), density in mangrove forest exceeded that in second-growth scrub annually by 20–130% and was 50% higher on average.

The relationship between redstart body condition and conspecific density differed between mangrove forest and second-growth scrub (habitat × density: $\chi_1^2 = 4.86$, $p = 0.028$; $n = 9$ years, $n = 283$ birds), a pattern that held regardless of age (age × habitat × density: $\chi_1^2 = 2.60$, $p = 0.107$) or sex (sex × habitat × density: $\chi_1^2 = 2.87$, $p = 0.090$). Habitat-specific analyses confirmed these patterns and revealed an effect of rainfall. For redstarts in mangrove, mean body condition in each year was negatively correlated with conspecific density ($\hat{\beta} = -0.203 \pm 0.081$ s.e.; $\chi_1^2 = 6.19$, $p = 0.013$), whereas the
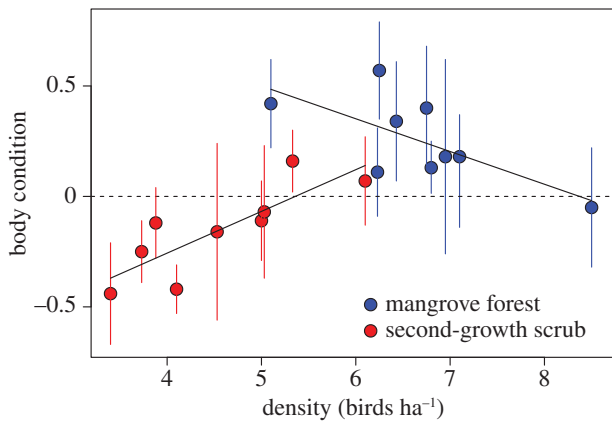
Figure 1. Influence of density on non-breeding season body condition of American redstarts in mangrove forest and second-growth scrub habitat at Font Hill Nature Preserve, Jamaica. Condition is measured as body mass corrected for overall size and is scaled to the average across both habitats. Error bars show ±1 s.e.

pattern was opposite in scrub habitat ($\hat{\beta} = 0.205 \pm 0.090$ s.e.; $\chi^2_1 = 5.14$, $p = 0.023$; figure 1). Birds in second-growth scrub had better body condition in rainy years, ($\hat{\beta} = 0.002 \pm 0.001$ s.e.; $\chi^2_1 = 5.17$, $p = 0.023$). Rainfall and body condition in mangrove were not correlated ($\hat{\beta} = -0.0001 \pm 0.0001$ s.e.; $\chi^2_1 = 0.002$, $p = 0.961$).

Nine data points in mangrove forest had large Cook's distance values, suggesting they could strongly influence the relationship between density and body condition in this habitat. These points represented the highest ($n = 6$) and lowest ($n = 3$) density years. When we down-weighted their influence through robust regression, the trend for lower body condition in high-density years remained ($t = -2.27$, $p = 0.025$).

Estimates of annual recapture probabilities varied between habitats and demographic classes ($n = 14$ years $n = 517$ birds; table 1). Recapture probability of birds in mangrove forest averaged 0.88 ± 0.04 s.e. in the 11 higher effort years and 0.71 ± 0.09 in the three lower effort years. In second-growth scrub, recapture probability was 0.93 ± 0.03 s.e. in higher effort years but only 0.42 ± 0.09 in years with lower effort. Recapture probability of males (0.94 ± 0.02) exceeded that of females (0.87 ± 0.04) but did not vary with age. In subsequent analyses, annual survival was modelled with recapture probability as a function of sex and an effort × habitat interaction. Goodness of fit tests with the median $\hat{c}$ procedure showed no evidence of over dispersion ($\hat{c} = 1.01$).

Annual survival of redstarts varied by sex, habitat and year. Annual survival probability was higher for males (0.51 ± 0.03) than females (0.44 ± 0.03) when averaged across habitats and age-classes. Adult birds (0.52 ± 0.02) also had higher survival than yearlings (0.44 ± 0.04). Habitat effects were more pronounced for males: apparent survival was 5–6% higher on average in mangrove compared to scrub. Female survival probability, by contrast, did not differ by habitat. When averaged across sex- and age-classes, apparent survival probability did not differ strongly between habitats (mangrove: 0.49 ± 0.03; scrub: 0.47 ± 0.03). Models of annual survival with full time dependence had little support; however, there was support for a separate survival estimate for the insect outbreak year of 1996 ($\Delta\text{AIC}_c = 1.26$; table 2). Models with a habitat × sex interaction plus an additive effect of age had the greatest support among two-way

Table 1. Apparent annual survival of American redstarts in relation to habitat, sex and age at Font Hill Nature Preserve, Jamaica. (Apparent survival was estimated by model averaging across the candidate set of models. n refers to the number of individual encounter histories for each group, but note that second year (SY) transition to after second year (ASY) after their first year and therefore the effective sample size is relatively larger for the ASY groups.)

habitat	sex	age	n	survival estimate (mean ± s.e.)
scrub	female	SY	80	0.40 ± 0.05
scrub	female	ASY	115	0.48 ± 0.05
scrub	male	SY	43	0.44 ± 0.06
scrub	male	ASY	34	0.52 ± 0.06
mangrove	female	SY	32	0.39 ± 0.06
mangrove	female	ASY	62	0.48 ± 0.06
mangrove	male	SY	97	0.50 ± 0.05
mangrove	male	ASY	108	0.59 ± 0.04

and three-way interactions of these three variables (table 2). This model structure was therefore retained to analyse the effect of density and rainfall on survival.

Models of density-dependent annual survival, with habitats pooled, had greater support based on AIC_c model weights, than those of density-independent survival (table 2). Annual survival probability in the top model was negatively correlated with density in mangrove ($\hat{\beta} = -0.29 \pm 0.13$; model 1 in table 2; figure 2a), but not in scrub ($\hat{\beta} = -0.04 \pm 0.13$; model 7 in table 2; figure 2b). Annual apparent survival of adult male redstarts in mangrove, the most abundant demographic group in this habitat, ranged from approximately 0.65–0.80 in low-density years to 0.45–0.60 in high-density years (figure 2a). By contrast, survival of adult females in scrub, the most common demographic class in this habitat, varied little over the range of densities observed (figure 2b). The addition of January–March precipitation as a habitat × rainfall interaction also improved model support (table 2). Apparent annual survival of mangrove redstarts varied little in relation to rainfall ($\hat{\beta} = 0.07 \pm 0.11$), but survival of scrub birds showed a negative relationship ($\hat{\beta} = -0.46 \pm 0.16$).

4. Discussion

Our results demonstrate that habitat during the non-breeding season mediated the strength of density-dependent body condition and apparent annual survival in redstarts. In high-quality mangrove forest, redstart body condition and annual survival decreased as conspecific density increased, but did not vary in response to rainfall. Body condition in second-growth scrub increased in response to rainfall and density. We observed no relationship between annual survival in scrub and conspecific density but a negative response to rainfall opposite to our expectation that rainfall would positively influence apparent survival in dry scrub habitat. These findings suggest that redstart populations are regulated, in part, by a crowding mechanism operating in high-quality habitat on the winter quarters. Furthermore, as

Table 2. Summary of model selection results for the annual survival of American redstarts at Font Hill Nature Preserve, Jamaica. (We compared 33 candidate models. The subset of models shown includes greater than 99% of model weight and represents key steps in the modelling process of our hypotheses about how density and rainfall affect apparent annual survival. Models with time dependence by habitat, constant survival and recapture are included for comparison. Model covariates include differences by sex, habitat (mangrove versus scrub) and age (SY versus ASY). Annual covariates include January–March precipitation in mm (rain) and the 1996 insect outbreak (96). Density is tested as a uniform response across both habitats (density), an effect only in mangrove ($m_{density}$), an effect only in scrub ($s_{density}$), or an effect in both habitats but with different slopes (density × hab). eff refers to high or low study effort years.)

| model	ΔAIC_c	w_i	k	deviance
{1} ϕ (sex × hab + age + 96 + $m_{density}$ + rain × hab) p (eff × hab + sex)	0.00	0.49	14	495.69
{2} ϕ (sex × hab + age + 96 + density × hab + rain × hab) p (eff × hab + sex)	1.71	0.21	15	495.34
{3} ϕ (sex × hab + age + 96 + density + rain × hab) p (eff × hab + sex)	2.11	0.17	14	497.82
{4} ϕ (sex × hab + age + 96 + rain × hab) p (eff × hab + sex)	4.60	0.05	13	502.36
{5} ϕ (sex × hab + age + 96 + $m_{density}$ + rain) p (eff × hab + sex)	5.94	0.02	13	503.69
{6} ϕ (sex × hab + age + 96 + density + rain) p (eff × hab + sex)	6.40	0.02	13	504.16
{7} ϕ (sex × hab + age + 96 + $s_{density}$ + rain × hab) p (eff × hab + sex)	6.65	0.02	14	502.35
{8} ϕ (sex × hab + age + 96 + density × hab + rain) p (eff × hab + sex)	7.09	0.01	14	502.79
{9} ϕ (sex × hab + age + 96 + rain) p (eff × hab + sex)	9.28	0.00	12	509.09
{10} ϕ (sex × hab + age + 96) p (eff × hab + sex)	10.59	0.00	11	512.46
{11} ϕ (sex × hab + age) p (eff × hab + sex)	11.85	0.00	10	515.76
{12} ϕ (sex × hab × age + 96) p (eff × hab + sex)	13.94	0.00	14	509.64
{13} ϕ (sex + hab + age) p (eff × hab + sex)	15.02	0.00	9	520.97
{14} ϕ (.) p (eff × hab + sex)	15.09	0.00	13	513.08
{15} ϕ (sex × hab + age + time × hab) p (eff × hab + sex)	18.62	0.00	38	463.56
{16} ϕ (.) p (.)	45.60	0.00	2	565.72

a consequence of sexual habitat segregation, males and females may be subject to different regulatory processes.

The decline in redstart body condition with increasing conspecific density in mangrove forest implies that birds frequently exceeded the carrying capacity of this habitat. Although we have not measured this threshold directly, carrying capacity is probably related to the availability of arthropod prey. We previously found that dry season rainfall predicted food availability in both mangrove and scrub habitat [38,41]. Our finding that conspecific density explained more variation in body condition than rainfall suggests that the potential benefits of elevated food were more often accompanied by intense competition for resources. Competition for territories in mangrove is strong, especially among adult males that comprise approximately 60% of birds in this habitat [36]. Experimental song playbacks accompanied by redstart decoys indicate that adult males respond more aggressively to one another than to other demographic groups [35]. The density-dependent decline in body condition in mangrove forest was probably owing to territory defence behaviours of adult males.

Consistent with patterns of body condition, apparent annual survival in mangrove forest was negatively correlated with density in the previous year. On average, apparent survival in mangrove habitat declined by about 10% for every additional redstart per hectare. Conspecific density is not strongly related to within-season survival [42]. This suggests that the density-dependent reduction in annual survival manifests itself as a seasonal interaction later on in the annual cycle. Redstarts in poor body condition depart non-breeding territories comparatively late on spring migration [39,40,51]. In high-density years, individuals departing later and in poorer condition

probably died either on migration or on breeding areas. An alternative explanation is that the density-dependent decline in body condition encouraged permanent emigration from study plots [52]. Redstarts exhibit strong site fidelity on the non-breeding grounds [36], but we cannot exclude the possibility that some birds recorded as dead permanently emigrated from the study area and became unavailable for detection. Even if birds emigrated from the study area, this was probably in response to density and was perhaps costly.

In contrast to redstarts in mangrove forest, birds in second-growth scrub improved body condition as both rainfall and density increased, but showed no change in apparent annual survival related to density. Critical to interpreting this pattern, however, is that mean body condition of redstarts in scrub habitat was nearly always lower than that of individuals in mangrove forest. Arthropod availability in drought-deciduous scrub is typically two to three times lower than in mangrove forest [41], but can increase for short durations owing to rapid leaf flushing following periods of high rainfall [38]. Indeed, experimental irrigation of scrub habitat demonstrated that higher food availability is linked to elevated primary productivity [53]. Irrigation on redstart territories resulted in greater leaf retention through the dry season, flushing of new leaves and shoots, and a possible, short-term increase in arthropod biomass. These patterns suggest that annual precipitation determines food availability in scrub habitat. However, food availability in this poor-quality habitat is probably low in most years, thereby maintaining redstart density below a level where resource competition could further reduce body condition and annual survival. Unlike the situation in high-quality mangrove forest where males may tend to overcrowd, density in drought-deciduous scrub might not
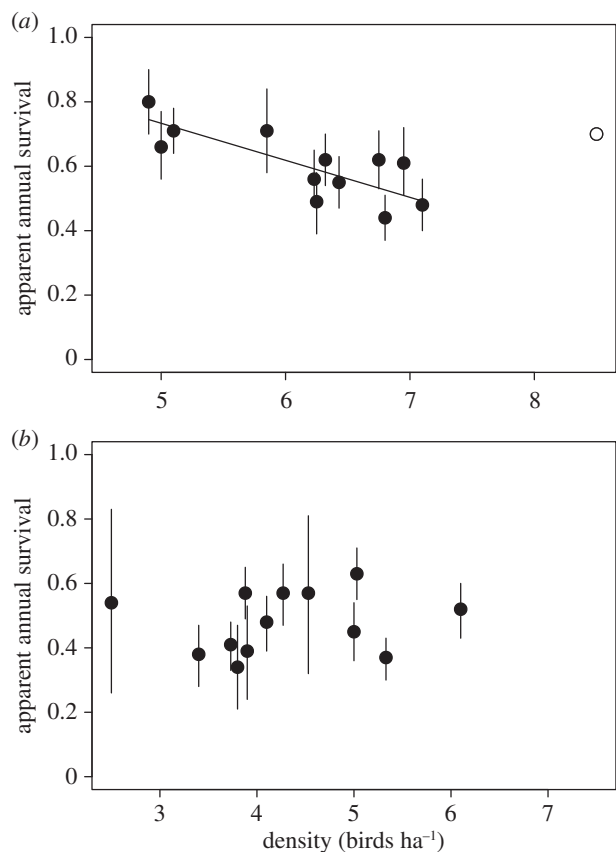
Figure 2. Habitat-specific effects of winter density on apparent annual survival of American redstarts at Font Hill Nature Preserve, Jamaica. Annual survival estimates were generated from a model allowing time dependence separately in each habitat (model 15 in table 2). Results are shown for (a) ASY males in mangrove forest and (b) ASY females in second-growth scrub habitat. The regression line in the top panel did not include data from 1996 during the insect outbreak (open circle). Years with poorly estimated survival between 1998 and 2001 were not included in the figures. Error bars show ± 1 s.e.

always be a reliable indicator of *per capita* resource abundance for an entire overwinter period [54,55].

We do not know what determines initial redstart densities on non-breeding grounds and have only a nascent understanding of how individuals produced on distinct breeding areas disperse across wintering sites [56]. Because adult redstarts exhibit high site fidelity between years [36,57], annual variation in density is probably driven by changes in the abundance of new yearling recruits [58]. Therefore, as migratory birds arrive and settle into tropical habitats in late August to late October, their densities are determined in part by reproductive success on breeding areas and the numbers of yearling redstarts surviving migration.

The carrying capacity of migratory passerine habitats in Jamaica in autumn is probably high because this is the rainy season, and arthropod abundance is limited by moisture [53]. Carrying capacity decreases in the late winter and early spring dry season when arthropod food resources become scarce [51]. However, mangrove and other moist evergreen habitats experience less drastic food declines [37]. Thus, the effects of precipitation and habitat type interact to determine both the magnitude of declines in food availability and decreases in redstart body condition [36,38]. The relationship between food and redstart body condition is also supported by the results of a food-reduction experiment in mangrove habitat: individuals on territories where food was reduced

via insecticide fogging lost pectoral mass and increased fat loads relative to controls [51].

The crowding effects we documented in mangrove habitat do not exclude the possibility of broader scale, density-dependent processes, such as buffer effects, in this system [6,22]. Buffer effects occur when annual changes in population size results in large changes in animal numbers in poor-quality sites but only small changes in good-quality sites. A greater proportion of birds tended to settle in scrub in years of higher total redstart abundance (P. P. Marra and T. W. Sherry 1994–2014, unpublished data). Two lines of additional evidence from our prior research suggest that buffer effects are operating on this population. First, the rate of replacement onto territories of experimentally removed redstarts was higher in mangrove compared with scrub [35]. Second, using stable isotope analyses, we determined that redstarts moving into vacant territories in mangrove originated from scrub habitat [40]. Taken together, these data and experiments support the hypothesis that multiple regulatory mechanisms affect redstart populations during the non-breeding season.

Our results also suggest that behavioural dominance and sexual habitat segregation [35] result in males and females being affected by different density-dependent processes during the non-breeding season. Adult males predominate in mangrove forest and therefore experience density-dependent annual survival via a crowding mechanism. Conversely, survival of females, which are largely relegated to second-growth scrub, is strongly limited by food availability, but might be regulated by density-dependent buffer effects. This complexity emphasizes the need to study migratory populations across a range of habitat quality on the non-breeding grounds.

Discovering the factors that regulate the abundance of migratory animals remains one of the great challenges for ecologists and conservation biologists. This is made especially urgent by the global declines of migratory species [30,59]. Although many obstacles remain, one of the largest is our limited understanding of migratory connectivity, how breeding populations of animals disperse onto non-breeding areas and vice-versa [60,61]. A better understanding of such patterns will improve our understanding of how factors that limit and regulate vital rates during one season interact with events in other seasons [24,25]. The work presented here represents one of the few long-term research efforts designed to quantify how density dependence operates during the non-breeding season to influence vital rates in a subsequent period of the annual cycle. Our results suggest that American redstart populations are regulated, in part, by a crowding mechanism acting in high-quality winter habitat. Population regulation of a migratory animal during any season of the year could affect population dynamics, but this response would be more pronounced if density also influences annual fecundity.

Recent evidence, as noted above, demonstrates that redstart reproductive success is negatively correlated with conspecific density on the breeding grounds [23]. An important next step will be to build two-sex population models parametrized with data from both breeding and non-breeding areas. Such an effort is needed to determine how and when in the annual cycle density-dependent fecundity and survival regulate abundance and sex ratios of migratory birds within the bounds that we see in nature. Research on migratory species continues to be largely focused on studying breeding season events despite growing evidence for the

critical role of events throughout the annual cycle in driving multiple aspects of the biology of migratory animals.

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