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RESEARCH ARTICLE

Combining survey methods to estimate abundance and transience of migratory birds among tropical nonbreeding habitats

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ABSTRACT

Estimating population abundance for territorial species is challenging because individuals often differ in behavior (e.g., transience, multiterritoriality), and thus in detectability. How well prevailing methods detect and quantify individuals using multiple strategies is rarely addressed. In our effort to efficiently quantify avian abundance and transience among diverse nonbreeding habitats, we combined ‘unmarked’ (distance sampling) with traditional ‘marked’ (territory mapping) survey methods using a migratory passerine, the American Redstart (*Setophaga ruticilla*), wintering in 3 habitats in Jamaica from 2010 to 2012. We predicted that the ‘unmarked’ survey method would detect not only all known (marked) territorial individuals, but also individuals that were transient or nonterritorial in the same habitats. Comparisons of abundance estimates generated by our best distance sampling (unmarked) model with territory mapping data identified high proportions of transient individuals (up to 50%) in 2 habitats, coastal dry scrub and mangrove, and virtually none in the third habitat, higher-elevation wet limestone forest. Documenting so many nonterritorial individuals, disproportionately weighted toward females and yearlings, in some habitat–year combinations prompts questions of what conditions favor transience and what role these individuals play in population processes. Our results illustrate how unmarked and marked survey methods can be used jointly to establish the number and identity of transients from neighboring areas. The unmarked survey method was sufficient for estimating population size among different habitats, but marked survey methods were necessary to identify and quantify transient individuals. Combined, these methods provide a powerful tool for assessing the range and variation of space-use strategies deployed by nonbreeding individuals.

Keywords: density, distance sampling, mark–recapture, migratory species, nonbreeding season, survey methods, territory mapping, transients

Combinación de métodos de muestreo para estimar la abundancia y el tránsito de las aves migratorias en hábitats tropicales no reproductivos

RESUMEN

Estimar la abundancia poblacional de las especies terrestres es un desafío debido a que los individuos usualmente presentan diferentes comportamientos (e.g. en tránsito, territorialidad múltiple) y por ende su detectabilidad varía. Sin embargo, pocas veces se analiza que tan bien los métodos usados detectan y cuantifican los individuos que usan múltiples estrategias. En un esfuerzo por cuantificar eficientemente la abundancia de las aves y el tránsito de individuos en diversos hábitats no reproductivos, combinamos métodos de ‘no marcado’ (muestreo por distancia) con métodos tradicionales de ‘marcado’ usando una especie paserina migratoria, *Setophaga ruticilla*, invernando en tres hábitats de Jamaica desde 2010 a 2012. Predijimos que el método de no marcado detectaría no solo todos los territorios individuales conocidos (marcados), sino también los individuos en tránsito o no territoriales en estos mismos hábitats. La comparación de las estimaciones de abundancia generadas por nuestro mejor modelo de no marcado usando datos de territorios mapeados identificó una alta proporción de individuos en tránsito (hasta 50%) presentes en dos hábitats, matorral seco costero y manglares, y prácticamente ninguno en el tercer hábitat, bosque húmedo de caliza de elevaciones altas. El hallazgo de tantos individuos no territoriales, desproporcionalmente representados por hembras e individuos del año, en algunas combinaciones de hábitat–año induce preguntas sobre qué condiciones favorecen el tránsito y que rol juegan estos individuos en los procesos poblacionales. Nuestros resultados muestran cómo los métodos de no marcado y el mapeo de territorios pueden ser usados en conjunto para establecer el número y la identidad de los individuos en tránsito desde áreas vecinas. El método de no marcado es suficiente para estimar el tamaño poblacional entre diferentes hábitats, pero los métodos de marcado fueron necesarios para identificar y cuantificar los individuos en tránsito. De modo combinado, estos métodos brindan una herramienta poderosa para estimar el rango y la variación de las estrategias de uso del espacio desplegadas por los individuos no reproductivos.

Palabras clave: densidad, especies migratorias, estación no reproductiva, individuos en tránsito, marca-recaptura, mapeo de territorios, métodos de muestreo, muestreo por distancia

INTRODUCTION

Estimating the abundance of animal populations is fundamental to answering many ecological and conservation questions. Similarly, assessing population change requires estimates of total abundance repeated in time and/or space. Species with alternative reproductive or survival strategies typically contain multiple classes of individuals, such as territorial and transient, potentially differing in detectability, all of which must be included to estimate total population size (Brown and Long 2007, Penteriani et al. 2011, Gómez de Segura et al. 2012). Most methods for quantifying mobile animals, such as birds, take advantage of detecting territorial individuals, whose behaviors, e.g., singing and territory defense, make them relatively conspicuous. Transient individuals partially or entirely abandon this strategy, defending no territory and moving more often and over greater distances than territorial individuals (Brown and Long 2007). They can be classified as temporary visitors to a site with territories elsewhere or entirely nonterritorial. As such, these individuals may be less vocal and more mobile, which can reduce their detectability.

The question of bias in surveying and detecting transient individuals via marked or unmarked survey methods is rarely explored (Pollock et al. 2002, Schmidt et al. 2013). This is an important issue for unbiased estimation of abundance, and in turn for understanding patterns of distribution and abundance. We do not know how transients affect territorial individuals and broader demographic processes (Davies and Houston 1981, Brown and Long 2007). However, increases in the numbers of transient individuals in territorial species can reflect local or regional habitat loss and degradation, response to climate change, or increases in overall population size (Penteriani et al. 2005, 2011, Brown and Long 2007).

Transient behaviors have been documented in many Neotropical–Nearctic migratory birds (Winker 1998, Brown and Long 2007, Brown and Sherry 2008, Lenda et al. 2012, V. Ruiz-Gutierrez personal communication). Many of these species spend more than two-thirds of the annual cycle in nonbreeding (hereafter, winter) areas and in diverse habitats, and are thought to be primarily territorial on their wintering grounds (Greenberg and Salewski 2005, Salewski and Jones 2006). During winter, territorial and dominance relationships can occur among and within species (e.g., Marra 2000, Toms 2013). Individuals within a population can exhibit a variety of behavioral responses as a consequence of dominance. For example, in species such as the American Redstart

(*Setophaga ruticilla*), Black-throated Blue Warbler (*S. caerulescens*), and Prairie Warbler (*S. discolor*), social dominance hierarchies result in the exclusion of subordinate individuals from preferred habitats (Marra et al. 1993, Wunderle 1995, Marra 2000, Latta and Faaborg 2001). This leads some individuals to adopt alternative strategies, including multiple territories, larger home ranges, and transient behaviors (Greenberg and Salewski 2005, Brown and Long 2007, Townsend et al. 2012, Toms 2013). Birds may also adopt a transient strategy in low-resource years or habitats, when roaming allows better access to food sources over a larger area (Brown and Sherry 2008). Thus, multiple mechanisms, including the inherent mobility of birds as well as their social dominance structure, may lead to transient behaviors. Survey methods that are less biased with regard to the variety of behaviors exhibited by both transient and territorial individuals across multiple habitats are needed to better assess the presence and abundance of such individuals.

Marked survey methods such as territory mapping—capturing and marking individuals, then mapping their space use and movements—have been used to estimate territorial abundances (Wunderle 1995, Murphy 2001, Sillett et al. 2004, Johnson et al. 2006, McKellar et al. 2014). However, territory mapping may miss individuals with alternative behavioral strategies, such as transience, particularly those that remain unmarked and thus unidentifiable as individuals (Brown and Long 2007), thus biasing population estimates. Lin et al. (2011) found that territory mapping was problematic when estimating abundances of some tropical species due to the frequency of transient behaviors.

Unmarked survey methods encompass populations of individuals not previously captured or marked. Several unmarked survey methods are commonly used, including multiple observer (Kissling and Garton 2006), repeat count (Kéry et al. 2005, Dail and Madsen 2011), removal (Farnsworth et al. 2002, Chandler and King 2011, Reidy et al. 2011), and distance sampling (Buckland et al. 2001). Relatively unbiased estimates of abundance are possible with multiple methods, typically distance sampling done simultaneously with repeated counts, facilitating greater probability of detection and thus accuracy (Buckland et al. 2001, Farnsworth et al. 2002, Gale et al. 2009, Sillett et al. 2012). Many or most detections are typically made from call or song cues. Unmarked survey methods require relatively little field effort and time, and are thus cost-efficient for estimating the abundance of all individuals, territorial and transient alike. However, they are limited in their ability to quantify age, sex, and physiological or

territorial status, i.e. parameters often critical to population processes.

Current methods for identifying and estimating numbers of transient individuals are limited to radio-tracking, estimating movements via capture–mark–recapture (CMR) models (Pradel et al. 1997, Hines et al. 2003), or using multistate models to infer movements (Cam et al. 2004, Hénau et al. 2007, Schaub and von Hirschheydt 2009). Radio-tracking is expensive and time-intensive, and thus limits sample size. CMR and multistate models also require significant time and resources, and are typically used to estimate demographic parameters, such as the probability of survival, breeding, and permanent dispersal, rather than to quantify transients themselves. Recent advances in multistate open robust design models are promising in their ability to estimate the occurrence of transients in winter populations from CMR data (V. Ruiz-Gutierrez personal communication), but even these are limited in their ability to accurately distinguish transients from territorial individuals.

Here, we combine marked and unmarked survey methods to estimate population abundance, identify territorial and transient individuals, and compare the demographic structure of populations of territorial vs. transient wintering American Redstarts. We conducted repeated surveys in Jamaica, where individuals occur at varying densities among diverse habitats (Sliwa and Sherry 1992, Sherry and Holmes 1996, Johnson and Sherry 2001). Both marked and unmarked survey methods quantify differences in abundance among habitats. Using these 2 survey methods combined allowed us to test for demographic differences between territorial and transient population components potentially caused by behavioral dominance mechanisms. We tested 3 predictions about the unmarked survey method (distance sampling with repeated counts) compared with the marked survey method (territory mapping): that it would (1) quantify the total abundance of a migratory species among multiple nonbreeding habitats, (2) identify more individuals by also detecting mobile individuals (transients), and (3) potentially detect individuals of different age and sex classes.

METHODS

Focal Species

The American Redstart (*Setophaga ruticilla*; hereafter, redstart) is a widespread, long-distance Nearctic–Neotropical migrant passerine. Its winter range extends from southern Florida through the Caribbean Islands and into northern South America, but its highest abundances occur in the Greater Antilles (Arendt 1992, Sherry and Holmes 1997). Density, overwinter body condition, and annual survival of redstarts vary among diverse wintering habitats (Sherry and Holmes 1996, Marra and Holmes 2001,



FIGURE 1. Map of field site locations in Jamaica for estimating American Redstart abundance in 2010–2012. Coastal field sites (⊙) included mangrove and dry scrub; the wet limestone forest site (★) was located in the montane interior.

Johnson et al. 2006). Although they do not commonly sing in winter, redstarts are conspicuous in most habitats due to agonistic behaviors and fly-catching and active gleaning on most substrates, from the ground and foliage to tree trunks and branches (Sherry and Holmes 1997). Redstarts are often territorial in winter and segregated by sex among habitats (Marra et al. 1993, Parrish and Sherry 1994, Marra 2000). The intraspecific aggression contributing to habitat-use patterns is associated with frequent vocalizations of distinctive (species-specific) ‘chip’ or call notes, allowing reliable recognition by trained observers. Additionally, redstarts use variable social strategies in winter, from strongly site-faithful and territorial to transient (Lefebvre et al. 1992, 1994, Toms 2011, 2013).

Study Sites

To compare marked and unmarked survey methods, we chose 3 habitats in 2 regions of western Jamaica: mangrove swamp, xeric logwood scrub, and montane wet limestone forest. The mangrove and scrub sites were located in close proximity within the Font Hill Nature Preserve in Westmoreland Parish (UTM 18Q 189082, 1997416; 0–1 m elevation) and were within 2 km of the coastline (Figure 1). Hurricanes, woodcutting, and cattle grazing periodically disturb these coastal habitats. Mangrove habitats were dominated by black mangrove (*Avicennia germinans*) interspersed with red (*Rhizophora mangle*) and white (*Laguncularia racemosa*) mangrove. Dry logwood (*Hae-matoxylum campechianum*) scrub sites were adjacent to, and generally inland from, the mangrove forests. This scrub vegetation grew more densely than mangroves, and experienced greater leaf abscission in the dry season resulting in reduced canopy cover (Wilson et al. 2013). Our third research site, in the mountains of northernmost Westmoreland Parish (UTM 18Q 188786, 202045; 500 m elevation), was one of the few old-growth wet limestone forest fragments in the region (Figure 1). Disturbances here were limited to hurricanes, occasional cattle grazing, and selective logging. The tree community was diverse, including several palm species, blue mahoe (*Talipariti*

elatum), kapok (*Ceiba* sp.), African tulip (*Spathodea campanulata*), and mahogany (*Swietenia mahagoni*), with a mean canopy height of 20–25 m. Dense vine tangles resulting from hurricane damage and fallen trees resulted in a complex, vertically stratified habitat. Over the last 4 yr, this montane region received more than twice the monthly mean precipitation (220 mm) of our coastal sites (91 mm; Jamaica Meteorological Service, <http://www.metservice.gov.jm/>). All study plots were delineated into 50 × 50 m grids with flagging tape to facilitate the mapping of individual birds.

Survey Methods

Territory mapping methods. From 2009 to 2012, we conducted mist netting, color banding, resighting of banded individuals, and territory mapping of all individuals in the same habitats, research sites, and years (see Marra et al. 1993, Parrish and Sherry 1994, Sherry and Holmes 1996, Marra and Holmes 2001, and Studds and Marra 2005 for more details). Daily passive mist netting took place from sunrise to ~13:00 from mid-January to mid-February and again from mid-March to early April in long-term net lanes, distributed throughout research plots in mangrove, logwood, and wet limestone forest. We used target netting (intensive mist netting and call broadcast within a specific territory) to capture individuals observed during mapping or missed during passive netting. Captured birds were aged, sexed, and banded with a unique combination of 1 aluminum and 2 colored leg bands. Territory mapping (see below) took place from mid-January through early April. We followed a similar banding schedule in wet limestone forest habitat in January and February, and conducted periodic target netting from mid-February through early April, between unmarked survey intervals.

While mapping observations from early January to late March (ending more than a month prior to departure and migration), we recorded the locations and movements of both banded and unbanded birds on gridded sites (at 50 m intervals). Once located, a bird was followed from a distance (so as not to influence its behavior) and its movements were recorded, along with any aggressive interactions with other birds. For all birds, we noted age, sex, color bands (if applicable), and distinguishing plumage characteristics (if unbanded). All movements were mapped onto a study plot grid. Observers followed an individual bird for up to 30 min or until lost, mapping as much area used as possible. We attempted to acquire at least 10 separate observations per territorial bird on different days between January and April. With the accumulated observations of individuals we generated a 2-dimensional map for each habitat, from which the number of territorial birds ha^{-1} was estimated. Transient individuals were not included on these maps. We incorporated individuals

whose territories were estimated to overlap at least 25% with the edge of study plots in these calculations, because these edge birds were detectable by point-count surveys. Observers typically identified and mapped the remaining unbanded territorial individuals (10–30%) in a given site using unique plumage markers (black patches and brightness of orange pigment; Lemon et al. 1992, Sherry and Holmes 1992, Reudink et al. 2009) and territorial behaviors (calling within a consistent area). This allowed us to include these birds in territorial density estimates. However, 10–30% unbanded territorial individuals is a best estimate, because we were unable to distinguish all unbanded territorial individuals from transients. This uncertainty highlights the importance of the present study to gaining a more accurate estimate of how many unbanded individuals documented on territory maps are uncaptured residents vs. transients.

Quantifying transient individuals via territory mapping methods. We expanded on the methods of Latta and Faaborg (2001) to quantify the occurrence of transient birds. We cross-checked banded individuals with seasonal territory maps to determine whether the individual was recorded occupying a territory within the same or a neighboring study site. Individuals inhabiting no territory were classified as transient, i.e. nonterritorial within that site. These banding records also allowed us to compare the age and sex distributions of the territorial vs. transient components of the population.

In 2010, we had a larger field crew and mapped the locations of more birds on our plot grids. This allowed us to detect most of the transient birds present in the plots. We classified an individual as a banded transient if it was resighted at least once, but did not hold a territory. While we are not certain that these individuals did not hold territories outside our study plots, they could be classified as transients in our plots. The intensive mapping effort in 2010 allowed us to estimate numbers of these individuals directly, which we tallied for a given site from January to March and added to estimates of territorial birds (described above). This combined estimate accounted for all (territorial and transient) banded individuals present in our plots, thereby generating a best estimate of total redstart density to compare with the 2010 distance sampling (unmarked) survey estimates.

Unmarked survey methods. We distributed 20 point-count locations in mangrove and wet limestone sites, and 15 in logwood scrub sites, choosing locations that allowed 100 m between each survey point and at least 50 m from a habitat edge. We repeated distance sampling surveys (Buckland et al. 2001) at every point-count location, giving 2 periods per point, one each in mid and late winter (early–mid February and late March–early April; see also Kéry et al. 2005, Lyons et al. 2012). By January, territorial individuals have established territories and typically persist

TABLE 1. Basic distance sampling survey model results for combined sample data of American Redstarts collected in 3 habitats in Jamaica in 2010–2012. Environmental covariates are indicated by λ for abundance and σ for detection process. Models were ranked by the difference from the top model in Akaike's Information Criterion (Δ_i). K is the number of parameters in the model, Dev is the deviance, and w_i is the Akaike weight.

Model	K	Dev	Δ_i	w_i
$\lambda(\text{Habitat} + \text{Year}) \sigma(\text{Habitat} + \text{Year})^a$	11	2171	0.0 ^b	0.99
$\lambda(.) \sigma(\text{Year} + \text{Habitat})$	7	2187	9.1	<0.01
$\lambda(\text{Habitat} + \text{Year}) \sigma(\text{Habitat})$	9	2194	19.1	<0.01
$\lambda(\text{Habitat} + \text{Year}) \sigma(.)$	7	2202	24.2	<0.01
$\lambda(\text{Sample} + \text{Habitat}) \sigma(.)$	10	2200	26.8	<0.01
$\lambda(\text{Sample} + \text{Habitat} + \text{Year}) \sigma(.)$	12	2200	30.9	<0.01
$\lambda(\text{Habitat}) \sigma(\text{Habitat})$	7	2220	41.0	<0.01
$\lambda(.) \sigma(\text{Year})$	5	2226	42.9	<0.01
$\lambda(\text{Habitat}) \sigma(.)$	5	2229	46.1	<0.01
$\lambda(.) \sigma(\text{Habitat})$	5	2237	54.0	<0.01
$\lambda(\text{Year}) \sigma(.)$	5	2248	65.2	<0.01
$\lambda(\text{Sample}) \sigma(.)$	8	2244	67.8	<0.01
$\lambda(\text{Sample} + \text{Year}) \sigma(.)$	10	2244	71.8	<0.01
Hazard-rate: $\lambda(.) \sigma(.)$	3	2274	87.5	<0.01
Half-normal: $\lambda(.) \sigma(.)$	2	2285	96.3	<0.01

^aThe chi-square goodness-of-fit (GOF) P -value of this model = 0.86.

^bThe AIC value of the top model = 2193.

at these locations up to the time of northward migration (Marra et al. 1998, Marra 2000). One experienced observer (A. Peele) carried out these surveys in all years, along with one new observer each year trained by A. Peele to recognize species-specific winter vocalizations. Approximately 60% of detections were vocal, rather than visual.

We adapted distance sampling survey protocols from Buckland et al. (2001) by using a single observer per sampling point to record all redstarts detected, age and sex if possible, type of detection (seen vs. heard), and estimated distance (m) from the observer for each individual bird within a 10-min survey period. We classified birds detected at >50 m as outside the survey boundaries, due to the difficulty of redstart chip note identification beyond this range (A. Peele personal observation).

Statistical Methods

Distance sampling data analyses. To estimate densities via the unmarked survey method we used package unmarked in program R (R Development Core Team 2013), which incorporates the multinomial-Poisson mixture model of Royle (2004) and allows modeling of density and detection probabilities (Chandler 2011). We treated spatial variation in redstart number at each point count (N_i) as a Poisson random variable (λ_i) for the abundance distribution. We modeled the detection process using traditional distance sampling likelihoods for point count data (Buckland et al. 2001). We tested the fit of both the half-normal and hazard-rate detection functions, using model selection methods to choose the hazard-rate function (Table 1). This function assumes that detectability declines less precipitously initially than the half-normal function, allowing for similar detection

likelihoods in the closest (0.0 m, 12.5 m) detection distance intervals. We estimated distance as a continuous variable in the field, but, considering that most observations were based on auditory detections, we used larger distance intervals of roughly one-quarter of the maximum detection distance, or 12.5 m, in the models. Our distance sampling model integrated the hazard-rate detection function (σ) over each of these distance intervals to derive detection probabilities. The model used log-link functions to incorporate environmental covariates for abundance (λ_i) and detection (σ_j ; see Royle et al. 2004 and Sillett et al. 2012 for further details of models. Sample R code is provided in the Appendix).

Habitat, year, and sample (referring to timing of survey in mid or late winter) were considered as covariates for both abundance and detection in our candidate model set. We combined mid- and late-winter survey data in analyses, a common practice with repeated count distance sampling methods (Rosenstock et al. 2002), which allowed us to increase the numbers of birds detected (e.g., to improve fitting detection functions) without inflating the sample sizes used to estimate standard errors (calculated based on the numbers of points sampled, rather than birds detected). We used Akaike's Information criterion (AIC) to evaluate candidate models of redstart density. After identifying the top model, we used parametric bootstrapping and ran 150 simulations, testing the top model with a chi-square goodness-of-fit test (Chandler 2011). We compared predicted abundance for each habitat and year from the top model with density estimates from territory mapping. (Samples of data used in these models are available upon request from the lead author.)

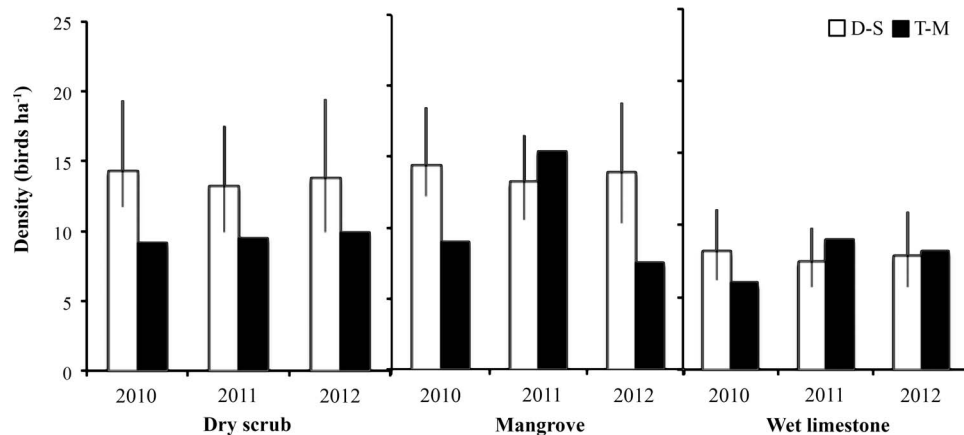


FIGURE 2. Comparison of predicted densities of American Redstarts in 3 habitats in Jamaica, 2010–2012, calculated via distance sampling (D-S) and territory mapping (T-M); the latter densities do not include transient individuals. Distance sampling densities were derived from the best model of the candidate set (Table 1). Error bars indicate 95% confidence intervals.

Age and sex analyses. To compare age and sex distributions between the territorial vs. transient components of the population, we used chi-square tests of the frequencies of males (M) vs. females (F), and separately of second-year (SY) vs. after-second-year (ASY) individuals. These frequencies were calculated from capture and territory mapping datasets.

RESULTS

Abundance Estimation via Unmarked and Marked Survey Methods

The best unmarked survey method (distance sampling = D-S) model included habitat and year effects on both density and the detection process (Table 1). Models containing sample period (mid- vs. late-winter) did not receive strong support, indicating that, given our data, redstart density did not change over the duration of winter. Parametric bootstrapping simulations and a chi-square goodness-of-fit test indicated that our top model provided a reasonable fit to the dataset ($P = 0.76$). Model outcomes indicated that the local population density of redstarts varied by both habitat and year. Mangrove habitat had the highest densities and greatest annual fluctuations, wet limestone had the lowest densities, and both wet limestone and dry scrub had the smallest annual changes (Figure 2, D-S estimates).

Estimated densities from the best-fit distance sampling model tended to be greater than densities estimated from territory mapping (T-M) across all habitats and years, except in mangrove habitat in 2011 and in wet limestone in 2011 and 2012 (up to 40% difference in estimates; Figure 2). Differences between point-count and mapping estimates were significant (T-M estimate outside 95% confidence interval of D-S estimate) in all 3 years in dry

scrub habitat, in 2 out of 3 years in mangrove habitat, and in 1 year in wet limestone. In all these cases the D-S estimate exceeded the T-M estimate, indicating that point counts either overestimated redstart density or detected individuals that territorial estimates missed. In 2011 (mangroves) and both 2011 and 2012 (wet limestone), the years with the highest overall redstart abundance, T-M densities increased to overlap D-S estimates.

Evidence for the Detection of Transient Individuals

The habitats in which point count densities differed most from those based on territory mapping of banded redstarts (dry scrub and mangrove; Figure 2) also had the highest occurrences of transient individuals (Figure 3). In the wet limestone habitat, where transient individuals were rare (8 individuals in 3 yr), distance sampling and territory mapping methods produced generally similar abundances. We identified 53 marked transient individuals in 2010 (26 in logwood, 27 in mangrove), calculated using banding and daily territory mapping data. Adding these individuals to the marked abundance estimates for their respective habitats resulted in densities that no longer differed significantly between the 2 methods (Figure 4).

Demographic Structure

Based on data from marked individuals, the age and sex composition of redstarts differed between the territorial and transient components of the population for all 3 habitats in some years. Transient populations tended to be composed of more females in both dry scrub and mangrove habitats (Table 2, Figures 5A, 5C). Proportionately more SY males were transient in mangrove habitats in 2010 and 2012 (Figures 5A, 5C). Territorial populations in mangroves were male-dominated, typically with a greater proportion of ASY individuals. In 2011, an unusually large

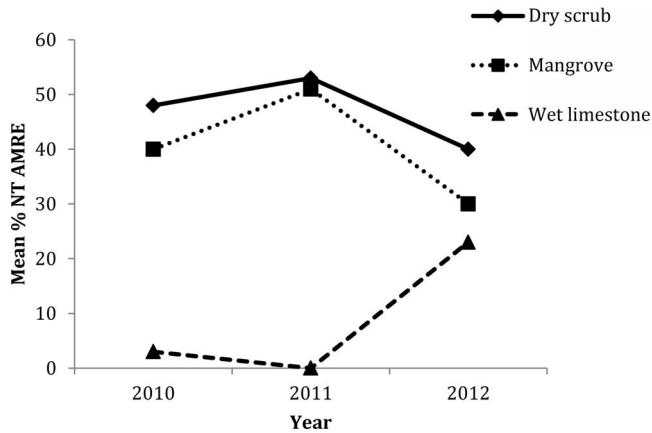


FIGURE 3. Percentages of captured American Redstarts (AMRE) that were nonterritorial transients (NT), i.e. captured within a habitat and not subsequently observed to hold a territory in that location, in 3 habitats in Jamaica, 2010–2012.

influx of young males caused a shift in age–sex ratios, resulting in more SY males than females in both transient and territorial populations in dry scrub and mangrove habitats (Figure 5B). Transient individuals, primarily females (7 of 8 such individuals), were present in the wet limestone habitat only in 2012. Territorial males (ASY and some SY) dominated this habitat, largely to the exclusion of females (Table 2, Figure 5C).

DISCUSSION

Both unmarked and marked survey methods can generate reliable estimates of abundance or density, depending on what portion of the population is of concern. The distance sampling method generated estimates of total population density and abundance that included transients and thus

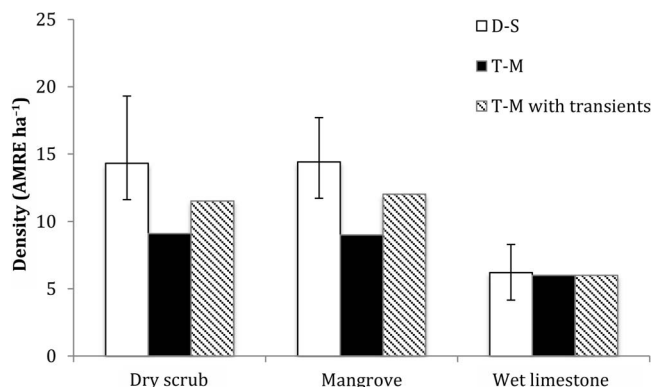


FIGURE 4. Comparison of 2010 density estimates of American Redstarts in 3 habitats in Jamaica from 3 methods: distance sampling (D-S); territory mapping (T-M); and T-M plus transient individuals, which produced a total density estimate that included nonterritorial birds detected during daily site mapping throughout the winter season.

TABLE 2. Age and sex distributions of territorial and transient American Redstarts within a given habitat–year combination in 3 habitats in Jamaica. Chi-square tests (all $df = 1$) were used to compare the frequencies of age and sex classes (adult and second-year birds, males and females). Significant results ($P < 0.05$) are indicated with an asterisk and highlighted in bold font.

Year	Habitat	χ^2 value	P
Age			
2010	Dry scrub	1.21	0.27
	Mangrove	0.18	0.67
2011	Dry scrub	1.40	0.24
	Mangrove	0.99	0.32
2012	Dry scrub	1.14	0.29
	Mangrove	0.20	0.65
	Wet limestone	0.33	0.93
Sex			
2010	Dry scrub	5.56	0.02 *
	Mangrove	2.51	0.11
2011	Dry scrub	1.22	0.27
	Mangrove	5.32	0.02 *
2012	Dry scrub	2.20	0.14
	Mangrove	0.00	0.98
	Wet limestone	3.11	0.08

individuals with multiple behavioral strategies. The territory mapping method distinguished between transient and territorial individuals, and provided demographic data showing that proportionally more subordinate (females and young, depending on habitat and year) and transient individuals were likely detected by distance sampling methods. Unmarked survey methods provided an estimate of total population size, independent of space-use strategy. Intensive marked survey methods provided an estimate of density for territorial individuals, as well as demographic information for all birds, transient and territorial alike. Each of these methods has limitations, but combining them provided better resolution of the distribution, abundance, and demography of the transient population component among diverse habitat types.

Unmarked survey methods do not generally provide demographic (e.g., age, sex) information or a means of distinguishing between territorial and transient individuals. Because these methods have been applied primarily during the breeding season and have relied on vocalizations for detections, they have been ill-suited to distinguishing sexes or territorial vs. transient individuals. Another problem has been inflated (biased) unmarked survey estimates compared with marked territorial survey estimates of breeding passerines due to long survey durations or small observation radii (Cimprich 2009, Reidy et al. 2011). For example, high song rates may increase detectability close to the observer (e.g., Staicer et al. 2006), biasing unmarked survey estimates high. We likely double-counted unmarked redstarts between point survey locations and among survey periods, but this is generally inconsequential within a distance sampling framework

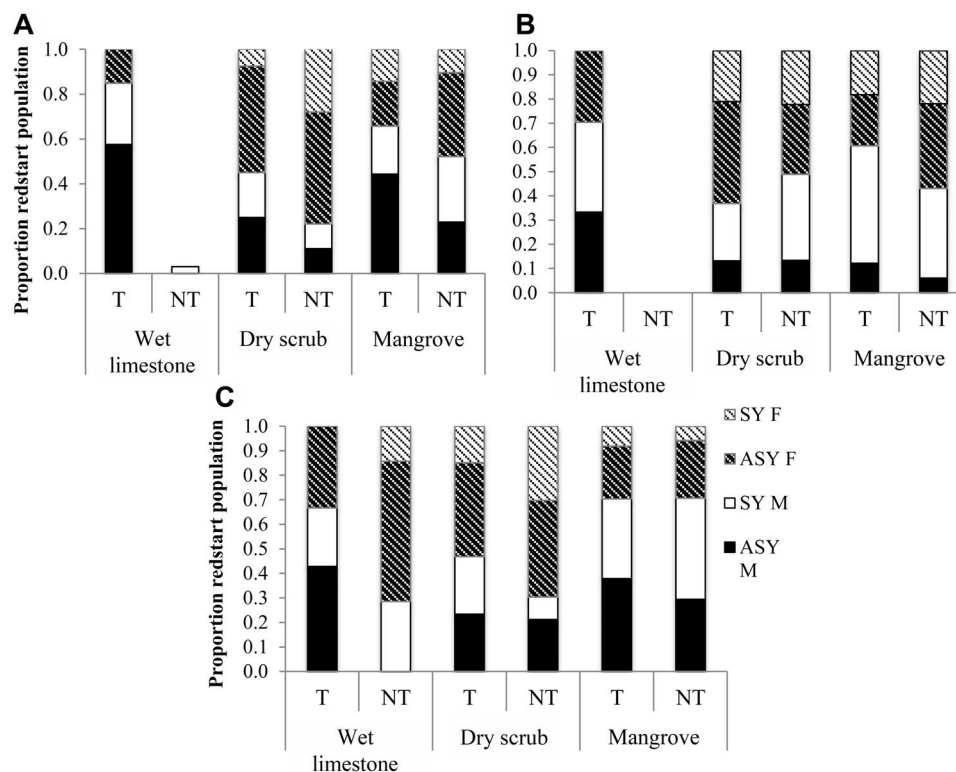


FIGURE 5. Comparisons of age and sex of captured territorial (T) and nonterritorial (NT) American Redstarts in 3 habitats in Jamaica in (A) 2010, (B) 2011, and (C) 2012. Age codes: SY = second year, ASY = after second year; sex codes: F = Female, M = Male.

(Buckland et al. 1993, Rosenstock et al. 2002). We detected no major shifts in the numbers of transients throughout the winter season.

Marked survey methods can provide information on territorial density and individual identity (e.g., age, sex), but are time- and resource-intensive. In our study system, banding and territory mapping efforts required >1,000 person-hours per season to generate the territory maps necessary for accurately estimating density and abundance in 2 habitats (~35 ha in total), whereas point counts required only ~150 person-hours per season. Additionally, identifying and counting transient individuals is possible with T-M methods alone (as illustrated by our 2010 data), but is even more difficult and time-intensive than just mapping marked territorial individuals, and thus is rarely done. Accurate estimation of the abundance of unmarked individuals during territory mapping operations is unreliable at best because of uncertainty about the numbers of such individuals. This highlights the importance of carefully considering the type of data needed, especially with regard to identifying territorial vs. transient individuals.

Although we operationally distinguished territorial and transient individuals in all of our study habitats, additional social strategies, from regular local movements (Smith et al. 2011) to complete transience (Wunderle 1995, Toms

2011, 2013), blur the line between these groups, suggesting more of a continuum of wintering space- (and resource-) use strategies. A small number of redstarts (<5%) was annually documented occupying multiple, spatially separated territories in our mangrove and scrub research plots, while other individuals vanished mid-season and returned in subsequent years (<5%). Redstarts elsewhere than Jamaica, and other migratory passerine species, indicate a similar range of space-use patterns during the nonbreeding season (Lefebvre et al. 1994, Lefebvre and Poulin 1996, Brown and Sherry 2008, Smith et al. 2011, Lenda et al. 2012). The agreement in abundances between our methods, once transients were added to marked individuals (Figure 4), suggests that unmarked survey methods are a more efficient and potentially less biased method for estimating total numbers of individuals. Point counts apparently missed few individuals present, regardless of their overwinter space-use strategy. However, population studies often require more detailed information on an individual bird's status, and we argue that point count and territory mapping approaches are complementary. Unmarked survey methods can be applied across a large spatial area and multiple habitats, while marked survey methods can sample detailed demographic data from a few key sites that can help to partition individuals into territorial vs. transient groups.

Our study also revealed differences in population density and demography among habitats. The results supported our expectation that most transient individuals would be young males and socially subordinate females (Marra 2000). Mangrove and scrub plots had similarly high occurrences of transient individuals and high densities of redstarts generally, but varied in their age–sex ratios. Wet limestone, in contrast, had few transient individuals in 2 of 3 years (<5%) and the lowest densities of redstarts overall, but also the greatest proportion of socially dominant (ASY male) individuals. This is consistent with previous findings (Johnson et al. 2006) that habitats differ qualitatively in terms of the size and social structure of the redstart populations present, and that these characteristics may be linked to behavioral mechanisms as well as environmental factors that fluctuate annually.

We defined ‘transient’ and ‘nonterritorial’ birds here as individuals that were observed in our research sites without holding a territory therein. This did not preclude the possibility of these individuals maintaining territories elsewhere, although the different age and sex composition suggested possibly different wintering strategies from territorial individuals. An important next step will be to track transient individuals across multiple nonbreeding habitats while monitoring extrinsic environmental changes like rainfall and food availability, to help understand the differences in the frequency of transient individuals among habitats, and possibly across seasons. Such tracking will provide clearer estimates of the specific overwintering strategies used by ‘transient’ individuals, and will improve abundance estimates. Another need is to compare characteristics such as body condition and survival of transient vs. territorial individuals, information that will help to explain variation in redstart habitat use and population limitation in nonbreeding landscapes.

Our understanding of wintering migrant populations and social systems will benefit from future analytical methods that combine information from disparate sources, including distance sampling of unmarked populations and intensive territory mapping of marked individuals. For example, we could not provide variance estimates for the proportions of transients within a plot and year. Integrating marked individuals into estimates of abundance will involve tradeoffs of effort. For example, V. Ruiz-Gutierrez et al. (<http://eco.confex.com/eco/2015/webprogram/Paper55022.html>) used CMR data to estimate movement and transience of multiple passerine species in winter. These methods estimated when and for how long a transient remained in a population. The approach that we used only provided a seasonal estimate of the number of transients in a given site. However, open population models based solely on CMR classify individuals as transient or resident based on the likelihood of recapture, rather than on behavioral data. Recapture probabilities of

residents are often low, so that relying exclusively on these histories could result in misclassifying individuals as transients when they are actually resident territory holders but not detected after first capture, e.g., because of holding a territory at the margin of a study area. In addition, resighting probabilities can be low when territory sizes are large; thus, careful consideration of possible biases is important for either method. The combination of unmarked and marked survey methods holds promise for increasing our knowledge of the demography, distribution, and role in population dynamics of transients.

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APPENDIX

Sample R code used in distance sampling data analyses of American Redstart densities in 3 habitats in Jamaica, 2010–2012, incorporating environmental and detection probability covariates.

```
##Upload point count data and covariates organized by individual point count ID. (Example dataset provided, which includes two years and habitats to illustrate data setup.)
allPC<-read.csv("RawSurveyData",header=TRUE)
allCovs<-read.csv("CovariateData",header=TRUE)

##Specify each point count with no detections or zeros (ID codes for our dataset shown to illustrate).
levels(allPC$PC)<-c(levels(allPC$PC),
"2M108","2L14","2L10","2L109","2L106",
"2L105","2W1","2W2","2W3","2W16","2W9","2W13",
"2W14","2W15","2W105","2W120","2W110","2W112",
"2W113","2W114","3W13","3W17","3W20","3W117")
```

```

##Format distance sampling data, specifying
detection distance intervals (dist.breaks).
allPCDat<-formatDistData (allPC,distCol=
"Distance",transectNameCol="PC",dist.
breaks=c (0,12.5,25,37.5,50))
allPCumf<unmarkedFrameDS(y=as.matrix(all
PCDat),siteCovs=allCovs,survey="point",dist.
breaks=c(0,12.5,25,37.5,50),unitsIn="m")

## Set fit list for later model organization.
allBest<-list()

##Create model set.

# Null model w/ half-normal detection curve:
allBest$half<-distsamp(~1~1,allPCumf)
# Null model w/ hazard-rate detection curve:
allBest$haz<-distsamp(~1 ~1,allPCumf,key
fun="hazard")

# Abundance effect models:
a l l B e s t $ Y e a r <- d i s t s a m p ( ~ 1
~Year,allPCumf,keyfun="hazard") *
a l l B e s t $ H a b i t a t <- d i s t s a m p ( ~ 1
~Habitat,allPCumf,keyfun="hazard")

# Detection effect model:
allBest$.habitat<-distsamp(~Habitat
~1,allPCumf,keyfun="hazard")
allBest$.year<-distsamp(~Year ~1, allP
Cumf,keyfun="hazard") *

# Combined models:

allBest$Hab.Hab<-distsamp(~Habitat
~Habitat,allPCumf,keyfun="hazard")
a l l B e s t $ Y e a r H a b <- d i s t s a m p ( ~ 1
~Habitat+Year,allPCumf,keyfun="hazard") *
allBest$YearHab.hab<-distsamp(~Habitat
~Habitat+Year,allPCumf,keyfun="hazard") *

## Generate model list and apply model selec-
tion.
fitsallBest<-fitList(fits=allBest)
(msallBest<-modSel(fitsallBest))

## Define fit statistic.
chisq<-function(fm) {
observed<-getY(fm@data)
expected<-fitted(fm)
sum((observed-expected)^2/expected)
}

##Estimate density (birds/hectare) and confi-
dence intervals from top model.
YrHab.habyear.level.density<-predict(all
Best$YearHab.habyr,type="state")$Predic-
ted
YrHab.hab.level.density

YrHab.habyear.level.lower<-predict(all
Best$YearHab.habyr,type="state")$lower
YrHab.habyear.level.lower

YrHab.habyear.level.upper<-predict(all
Best$YearHab.habyr,type="state")$upper
YrHab.habyear.level.upper

```