
Assessing Habitat Quality for a Migratory Songbird Wintering in Natural and Agricultural Habitats

MATTHEW D. JOHNSON,* THOMAS W. SHERRY,† RICHARD T. HOLMES,‡ AND PETER P. MARRA§

*Department of Wildlife, Humboldt State University, Arcata, CA 95521, U.S.A., email mdj6@humboldt.edu

†Department of Ecology & Evolutionary Biology, Tulane University, New Orleans, LA 70118, U.S.A.

‡Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, U.S.A.

§Smithsonian Migratory Bird Center, National Zoological Park, 30001 Connecticut Avenue, Washington, D.C. 20008, U.S.A.

Abstract: *As tropical forests are cleared, a greater proportion of migratory songbirds are forced to winter in agricultural and disturbed habitats, which, if poorer in quality than natural forests, could contribute to population declines. We compared demographic indicators of habitat quality for a focal species, the American Redstart (*Setophaga ruticilla*), wintering in Jamaican citrus orchards and shade coffee plantations with those in four natural habitats: mangrove, coastal scrub, coastal palm, and dry limestone forests. Demographic measures of habitat quality included density, age and sex ratio, apparent survival, and changes in body mass. Measures of habitat quality for redstarts in citrus and coffee habitats were generally intermediate between the highest (mangrove) and lowest (dry limestone) measurements from natural habitats. The decline in mean body mass over the winter period was a strong predictor of annual survival rate among habitats, and we suggest that measures of body condition coupled with survival data provide the best measures of habitat quality for nonbreeding songbirds. Density, which is far easier to estimate, was correlated with these more labor-intensive measures, particularly in the late winter when food is likely most limiting. Thus, local density may be useful as an approximation of habitat quality for wintering migrant warblers. Our findings bolster those of previous studies based on bird abundance that suggest arboreal agricultural habitats in the tropics can be useful for the conservation of generalist, insectivorous birds, including many migratory passerines such as redstarts.*

Keywords: American Redstart, body condition, body mass, coffee, density, Jamaica, Neotropical migrant, survival

Evaluación de la Calidad de Hábitat para Aves Canoras Invernantes en Hábitats Naturales y Agrícolas

Resumen: *A medida que los bosques tropicales son talados, una mayor proporción de aves canoras migratorias es obligada a invernar en hábitats agrícolas y perturbados, que, si tienen menor calidad que los bosques naturales, podrían contribuir a las declinaciones poblacionales. Comparamos indicadores demográficos de la calidad de hábitat para una especie focal que inverna en Jamaica, *Setophaga ruticilla*, en huertos de cítricos y plantaciones de café de sombra con los parámetros en cuatro hábitats naturales: manglar, matorral costero, palmar costero y bosques secos en suelos calizos. Las medidas demográficas de la calidad del hábitat incluyeron densidad, proporción de edades y sexos, supervivencia aparente y cambios en la masa corporal. La medidas de la calidad del hábitat para *Setophaga ruticilla* en huertos de cítricos y plantaciones de café generalmente fueron intermedias entre las medidas más altas (manglar) y más bajas (caliza seca) de los hábitats naturales. La declinación de la masa corporal promedio a lo largo del periodo invernal fue un pronosticador robusto de la tasa de supervivencia anual entre hábitats, y sugerimos que las medidas de la condición corporal aparejadas con datos de supervivencia proporcionan las mejores medidas de la calidad del hábitat para aves canoras no reproductivas. La densidad, que es más fácil de estimar, se correlacionó con estas medidas que requieren de mayor labor, particularmente al final del invierno cuando el alimento probablemente es más limitante. Por lo tanto, la densidad local puede ser útil como una aproximación a la calidad del hábitat para aves canoras migratorias invernales. Nuestros resultados refuerzan a los de estudios previos basados en la abundancia de*

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aves que sugieren que los hábitats agrícolas arbóreos en los trópicos pueden ser útiles para la conservación de aves insectívoras generalistas, incluyendo muchos paserinos migratorios como Setophaga ruticilla.

Palabras Clave: café, condición corporal, densidad, masa corporal, migratoria neotropical, *Setophaga ruticilla*, supervivencia

Introduction

As tropical forests are cleared, a greater proportion of migratory songbirds are forced to occupy agricultural and disturbed habitats in the nonbreeding (winter) season (Robbins et al. 1989; Petit et al. 1999; Hughes et al. 2002). If these habitats are lower in quality than natural forests, then tropical land conversion could reduce wintering populations of migrants and contribute to their decline (Rappole & McDonald 1994; Conway et al. 1995; Rappole et al. 2003a; but see Faaborg 2002). Evaluating this prospect empirically has been difficult in part due to uncertainty over how to assess habitat quality for wintering migrants. Measures of abundance (i.e., density) can be misleading indicators of habitat quality if parameters more important in driving population dynamics (e.g., survival and/or reproduction) vary inconsistently with density across habitat types (Van Horne 1983; Marra & Holmes 2001; Battin 2004). Bock and Jones (2004) found that density generally corresponds with habitat quality for breeding birds but cautioned that disconnects occur disproportionately in human-disturbed habitats. They urge that future studies focus on assessing habitat quality for nonbreeding birds and on investigating the relationship between survival and density, neither of which were examined enough to include in their analysis.

A thorough quantification of habitat quality for a population is the product of density and measures of individual fitness or per capita rate of population change (e.g., lifetime reproductive success; Stearns 1992; Franklin et al. 2000). In the nonbreeding season, survival is the parameter most clearly linked to lifetime reproductive success, so habitat-specific estimates of survival rates should yield the most relevant measures of winter habitat quality. But as a measure of habitat quality, survival is often impractical. Rigorous estimates of overwinter survival rate require a large amount of effort and large data sets, limiting their application for land managers charged with monitoring multiple sites. Even when overwinter survival estimates can be obtained, mortality caused by a poor wintering habitat may not manifest until spring migration, when survival is even more difficult to estimate (Silllett & Holmes 2002). Annual and between-winter survival include such delayed effects of winter habitat but are confounded by interseason emigration and the birds' varying breeding habitats (Wunderle & Latta 2000). In addition, although winter habitat can directly influence fitness by affecting survival, its influence on fitness may be masked until the

reproductive season via other effects that carry over to breeding birds (Webster et al. 2002; Norris 2005; Runge & Marra 2005). For example, isotope analyses reveal that a bird's winter habitat can influence its departure date from winter quarters (Marra et al. 1998), condition during migration (Bearhop et al. 2004), and subsequent date of arrival and condition on the breeding grounds (Marra et al. 1998), which in turn can affect reproductive success (Norris et al. 2004; Smith & Moore 2005).

These complications have prompted numerous researchers to examine sublethal effects of winter habitat on body condition of birds, including winter fat scores (Rogers 1991), body mass corrected for body size (Strong & Sherry 2001), overwinter change in body mass (Marra & Holmes 2001), pectoral muscle scores (Latta & Faaborg 2002), stress hormones (Marra & Holberton 1998), and feather growth rates (ptilochronology; e.g., Strong & Sherry 2000). These techniques are potentially more sensitive than survival to winter habitat quality, but their usefulness hinges on the poorly tested assumption that a bird's good physiological condition in winter translates into fitness benefits by enhancing its survival probability or subsequent reproductive output.

We examined multiple indices of habitat quality in six winter habitats used by American Redstarts (*Setophaga ruticilla*) in Jamaica, West Indies. Although processes undoubtedly vary among bird species, we focused on this species because it is a focal migrant bird species for Neotropical work and intensive work has revealed advances in understanding issues common to many migrant birds (e.g., Holmes et al. 1989; Sherry & Holmes 1996; Marra et al. 1998; Norris et al. 2004). We compared habitat quality in shade coffee plantations and citrus orchards to that in four natural forest types by examining eight indices of habitat quality independently. We then examined the congruence of these measures of habitat quality to determine which measures may be most reliable and useful for conservation and management. We also tested the assumption that a measure of body condition (biomass corrected for body size) reflects variation in survival among habitats.

Study Sites

We studied redstarts on 12 gridded, flagged study sites (5–10 ha) in 6 habitats in Jamaica (see Table 1) from 1987 to 2000. Four habitats were considered natural: (1)

Table 1. Study sites, years studied, and origin of data (1, Sherry & Holmes 1996; 2, current study).

Habitat and study site	Winter year												
	1987-1988	1988-1989	1989-1990	1990-1991	1991-1992	1992-1993	1993-1994	1994-1995	1995-1996	1996-1997	1997-1998	1998-1999	1999-2000
Coastal scrub forest	1	1	1	1	1	1	1	2					
Luana Point Scrub Site													
Coastal palm forest	1	1	1	1	1	1	1						
Paradise													
Dry limestone forest				1	1	1	1	2	2	2	2		
Portland Ridge Upper													
Dry limestone forest			1	1	1	1	1	2	2	2	2		
Portland Ridge Lower													
Black mangrove forest	1	1	1	1	1	1	1	2					
Luana Pt. Mangrove 1													
Black mangrove forest			1			1	1						
Luana Pt. Mangrove 2													
Black mangrove forest			1	1	1	1	1						
Luana Pt. Mangrove 3													
Shade coffee plantation									2	2	2	2	2
Baronhall Farms													
Shade coffee plantation									2				
James Hill													
Shade coffee plantation										2	2	2	2
Coleyville Farms													
Citrus orchard									2	2	2	2	
Kew Park													
Citrus orchard										2	2	2	
Comforthall Farms													

black mangrove forest, (2) coastal scrub forest, (3) coastal palm forest, and (4) dry limestone forest. Detailed site descriptions and locations for these habitats are available in Holmes et al. (1989), Sherry and Holmes (1996), and Marra and Holmes (2001). Partial redstart demographic data from some of these sites were published by Sherry and Holmes (1996). Black mangrove forest was represented by three sites near Luana Point on the S. coast and contained tall (5–15 m), close-canopied (60–100% cover) forests dominated by *Avicennia germinans* L. These sites were adjacent to the coastal scrub forest sites, which were dominated by short (4–10 m) *Haematoxylum campechianum* L. thickets (50–75% cover) interspersed with small grassy openings. Coastal palm forest was represented by a 30-ha patch of relatively tall (15–25 m), diverse wet forest (60–100% cover) near Savanna-La-Mar and was composed of species such as *Metopium brownii* Jacq., *Grias cauliflora* L., *Clusia* L. sp., *Eugenia* L. sp., and the palms *Roystonea princeps* Beccari and *Sabal jamaicensis* Beccari. Both dry limestone forest sites were located along Portland Ridge on the southernmost peninsula of the island. This extensive (> 100 ha), very arid undisturbed forest was relatively open (25–75% cover), ranged from 5 to 15 m in height with occasional emergents up to 25 m, and was dominated by drought-deciduous tree species such as *Bursera simaruba* L. and *M. brownii*. Saplings of these trees along with *Baubinia divaricata* L., *Canella winterana* Gaertn, and associates comprised much of the

dense (50–80% cover) subcanopy, which grew to 8 m. Although both the coastal scrub forest and coastal palm forest sites were somewhat disturbed by humans, they were composed almost entirely of wild-growing vegetation and were virtually unmanaged (except for light cattle grazing and charcoal cutting) and therefore contrasted markedly in “disturbance” to the agricultural sites.

We worked in five sites representing coffee and citrus agricultural habitats from 1995 to 2000. Locations and additional site descriptions for these agricultural habitats are provided by Johnson and Sherry (2001). Citrus sites contained orange (*Citrus sinensis* L.) and ortanique (*C. s. x C. reticulata* Blanco) trees, which were relatively old (30–45 years), and were managed minimally (Kew Park) to moderately (Comfort Hall), with pesticides applied regularly in the latter. Ethion, a miticide, was used generally three times a year, snail bait (Metaldehyde mixed with white lime) was “painted” on citrus trunks, and herbicides were occasionally used for weed control, especially in wet years. Small (<100-m diameter) patches of mixed woodland (10–20 m in height) grew in shallow depressions within the orchards, which varied from relatively isolated (surrounded by pasture; Kew Park) to one embedded within a citrus-dominated landscape (Comfort Hall).

The shade coffee sites were composed of coffee trees (*Coffea arabica* var. *typica* L.) planted in rows and pruned periodically to maximize fruit production. The coffee trees were shaded primarily by *Inga vera* (Willd.; 9–24 m;

Baronhall and Coleyville), but *Pseudalbizia berteriana* (Britton & Rose) was also present (James Hill). Shade trees were 30–40 years old, and the canopy ranged from 9–24 m in height (25–50% cover). The coffee-tree understory varied in density, based on frequency of pruning, from very dense (nearly 100% cover) to open (<25% cover) and was generally 1.8–2.5 m tall. Basudin and Thiodan, insecticides for the control of white coffee leaf miner (*Leucoptera coffeella*) and coffee berry borer (*Hypothenemus hampei*), respectively, were applied directly to infested coffee trees (roughly 75% of the plantation) with hand-held pump dispensers usually twice a year (April–May and June–July). A compatible fungicide (Bayleton) was applied simultaneously to combat coffee leaf rust, *Hemileia vastatrix*. All coffee sites were located in mixed agricultural landscapes (i.e., pastures and row crops with small patches of native forest).

Methods

We visited each site twice every winter corresponding to the early and late dry season (October to early December and February through late March, respectively), hereafter early winter and late winter. We chose these dates to avoid periods of migration, early phases of territory establishment, and territory abandonment/preparation for spring migration (Marra et al. 1998; R. Sutton, personal communication; R. T. H. & T. W. S., unpublished data). During each visit, we spent 2–9 days on a site, capturing, marking, censusing, and mapping movements of individual redstarts. We captured birds in mist nets either by luring birds with a combination vocalization playback and a decoy or by “blanketing” a study site with 6–18 nets, often within particular unbanded redstarts’ territories (Holmes et al. 1989). Playbacks do not pull wintering redstarts off their territories (Holmes et al. 1989; Sliwa & Sherry 1992), so use of playbacks did not affect density estimates, which were determined from mapped territories, not capture rates. Each captured redstart was marked with a unique combination of a numbered U.S. Fish & Wildlife Service aluminum band and two plastic colored leg bands. We aged and sexed most individuals based on skull ossification (early winter only) and plumage characteristics (Pyle 1997). Aged individuals were classified as yearlings (in their first winter) or adults (in at least their second winter).

We repeatedly traversed the study sites during each visit, recording and mapping locations and movements of all marked and unmarked birds on maps (Holmes et al. 1989). Study sites were gridded at 25-m intervals and area of a study site was thus measured on the ground to the nearest 0.0625 ha. Most individual birds (>80%) on a site were marked. Unmarked birds were occasionally identifiable by unique plumage patterns, particularly the

extent and pattern of black on the breast and flanks in adult males or the degree and patterning of black spotting in yearling males. All sightings of unmarked and indistinguishable birds of the same age or sex class within 25 m of each other over a period of at least 2 days were considered sightings of a single individual for mapping purposes. Individual mapping was done to determine redstart density and to assist in relocating birds rather than to determine strict territory boundaries or sizes. Therefore, we delineated minimal activity ranges by enclosing all observations of each individual on summary maps generated after each site visit (Holmes et al. 1989; Wunderle 1995).

We used eight indices to examine the consequences of habitat quality on birds: two measures of density (early and late winter), sex ratio, age ratio, body mass adjusted for body size, and overwinter, between-winter, and annual survival. Density was the total number of minimal activity ranges ($\geq 50\%$ within the study site boundaries) per 10 ha of study site at each visit, and sex and age ratios were the percentage of those that were male or adult, respectively (unbanded birds of unknown sex or age were excluded). Body mass was the weight of each bird at capture, measured to the nearest 0.1 g with an electronic scale (Ohaus, Pinebrook, New Jersey), and each bird’s unflattened wing chord was used as a covariate to adjust for body size in analyses (sensu Latta & Faaborg 2002). Most birds were lean, so we did not analyze fat scores. Mark-resighting data and Cormack-Jolly-Seber (CJS) open population models were used to estimate apparent survival (Lebreton et al. 1992).

Analyses

Before conducting between-habitat comparisons, we tested for differences in indices of habitat quality between years and between study sites within a habitat. In a total of 48 tests, few results were statistically significant. Redstart density varied between years in dry limestone forest, where it was relatively high in 1995–1996 and low in 1993–1994. Nevertheless, there was no overall effect of year across sites and habitats ($F_{9,43} = 0.7$, $p > 0.6$). Density was higher at the Baronhall coffee site than at the other coffee sites, but this effect was relatively weak and did not approach significance with Bonferroni adjustments. Survival analyses also showed little evidence for year effects (Survival Analyses below). Given these weak differences among years and sites within habitats, the large number of nonsignificant comparisons, and the fact that conservation decisions are usually made at the habitat level and seldom recognize small variations among sites within broad vegetation types, we did not include site or year as factors in analyses and instead treated “site years” as replicates. Although bird responses to various management practices among sites are interesting and potentially

important (e.g., Johnson 2000), our data did not yield sufficient statistical power to address them effectively.

We tested for habitat-specific differences in density and body mass with analysis of variance (ANOVA) and covariance (ANCOVA). Site years were used as replicates for analyses of density (*sensu* Holmes et al. 1989; Wunderle 1995; Sherry & Holmes 1996), with habitat (six types) and season (early and late winter) as factors in a two-way ANOVA. Birds were sample units in analyses of body mass. We recaptured too few birds within a winter (8.5%) to examine individuals' changes in body mass, so we used data on body mass from captures of birds in early- and late-winter samples independently in a four-way ANCOVA with sex, age (adult/yearling), habitat, and season as factors and wing chord as the covariate. Only the initial captures of recaptured birds were included for analysis. Data on body mass were unavailable for the palm forest habitat. We used chi-square tests of independence to examine habitat-related differences in sex and age ratios.

We evaluated the assumption that winter body condition influences survival by regressing overwinter, between-winter, and annual survival of redstarts against habitat-specific measures of the loss of body mass (average late-winter mass—average early-winter mass). We examined the congruence of all measures of habitat quality with a Pearson correlation matrix. All of the above analyses were conducted in SPSS 11.5 (SPSS, Chicago, Illinois) and an alpha level of 0.05 was treated as statistically significant. For correlation analyses, we used one-tailed tests because we hypothesized a priori that measures of habitat quality would be positively correlated (except loss of body mass, which should be negatively correlated with all other measures). Density was normalized by log transformation; all other data were normally distributed.

Survival Models

We estimated redstart apparent survival (φ) and detection (resight or recapture) probabilities (p) with CJS models in program MARK (White & Burnham 1999). We used an information theoretic approach and Akaike's information criterion adjusted for small sample size (AIC_c). Models in each candidate set were ranked by AIC_c differences (Δ_i ; Burnham & Anderson 2002), and relative likelihood of each model in a candidate set was estimated with AIC_c weights (w_i ; Burnham & Anderson 2002). We model-averaged top models with delta AIC_c values ≤ 2 to calculate survival estimates. Statistical support for group-related differences in φ and p was assessed by summing the w_i for all models in which a parameter of interest occurred (Anderson et al. 2000; Burnham & Anderson 2002; Sillett & Holmes 2002). The degree to which 95% confidence intervals for slope coefficients (β_i) overlapped zero was also used to evaluate the strength of evidence for model parameters (Dugger et al. 2004).

Mortality cannot be distinguished from permanent emigration with mark-recapture methods without additional information on individual dispersal. Nonetheless, high rates of emigration or mortality both indicate poor habitats, thus apparent survival serves as a useful measure of habitat quality. Moreover, redstarts on our study areas are both territorial and generally site faithful (Holmes et al. 1989; Holmes & Sherry 1992), making them ideal candidates for the use of CJS models to estimate apparent survival and detection probabilities.

The interpretation of a "year" effect in our linear modeling analysis would be difficult for this data set because the years for which data were collected varied by habitat type and study area (Table 1). We did test for year effects within study areas but found no significant annual variation within study areas (perhaps due to insufficient sample size); therefore, we excluded year as a variable in our subsequent linear models. Some sites were monitored too briefly (e.g., James Hill Coffee Farm) or intermittently (e.g., Luana Pt. Mangrove 2) to include in survival analyses. Monitoring stopped at some sites earlier than others (e.g., Luana Pt. Mangrove 3), requiring individuals from those sites to be "censored" from the data set after the last visits to those sites to account for the fact that we could no longer detect them. In addition, we did not study agricultural habitats over the same years as all the natural habitats, so we could not combine all the data into a single set (T. S. Sillett & J. Hines, personal communication), so we divided the data into natural and agricultural data sets (with 20 and 8 encounter occasions, respectively). We used profile likelihood 95% confidence intervals to compare parameter estimates (White & Burnham 1999).

For each data set, we developed a list of candidate models prior to data analysis based on our knowledge of redstart biology (Sherry & Holmes 1997; Burnham & Anderson 2002). We used resighting data from early and late winter at each study site; therefore, survival probabilities were calculated for overwinter (early to late winter) and between-winter (late winter to early next winter) intervals. The latter includes both spring and fall migrations. Annual survival is the product of the probabilities of these two survival intervals. To keep the number of candidate models relatively low, we started with a global model that included variables hypothesized to affect φ (age, sex, habitat, and interval type) and ran models variously parameterized for p until the best-fit model for p was selected. Keeping this parameterization for p , we then examined a priori candidate models for φ (Lebreton et al. 1992). We did not parameterize p for age or interval type because our resighting efforts were fairly consistent between seasons and because yearlings and adults were considered similarly conspicuous. We required all models to distinguish φ for overwinter and between-winter intervals because migration undoubtedly elevates mortality (Sillett & Holmes 2002). We emphasized additive models to minimize the number

of parameters. Sample sizes (number of birds) at some individual study sites were low, and we considered replicate sites of a habitat type part of the natural variation inherent in habitat. Therefore, we did not attempt to quantify site-related differences in ϕ and p . We verified the fit of the models with the program RELEASE goodness-of-fit procedure (Burnham et al. 1987) implemented within program MARK ($\chi^2 = 86$ and 46 , $df=173$ and 54 , $p > 0.95$ and 0.90 for natural and agricultural data sets, respectively).

Results

Density

Redstart density varied threefold among habitats (main effect of habitat: $F_{5,109} = 40.9$, $p < 0.001$; Fig. 1). Density did not differ significantly between seasons ($F_{1,109} = 1.3$, $p = 0.26$), and habitat-season interaction was not significant ($F_{5,109} = 1.6$, $p = 0.17$), although density increased from early to late winter only in coffee. The density of redstarts in citrus and coffee was intermediate between that in mangrove (highest) and dry limestone (lowest) and thus did not differ consistently from the four natural forest types. Density was at least 12 birds per 10 ha higher in mangrove forest, coffee, and coastal scrub forest than in the other three habitats, and it was significantly lower in dry limestone forest than in all other habitats except palm forest.

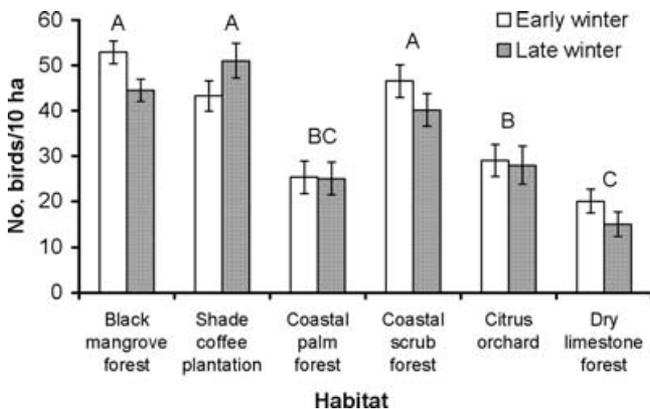


Figure 1. Density of American Redstarts in early and late winter in six habitats in Jamaica (mean \pm 1 SE). Habitats with different letters were significantly different from each other; there were no significant seasonal differences ($p < 0.05$, Tukey post hoc tests). Sample sizes are the combined number of years of data for each study site in a given habitat as follows (early/late winter): black mangrove forest 16/16, coastal scrub forest 8/8, shade coffee plantation 10/10, citrus orchard 7/7, coastal palm forest 7/7, and dry limestone forest 17/17.

Sex and Age Ratio

Sex and age ratio did not differ from early to late winter in any habitat, so we present data only on early-winter ratios, which have been more frequently presented in the literature. Sex ratio was male biased in mangrove forest (70% male; $\chi^2 = 21.1$, $df=1$, $p < 0.001$) and female biased in coastal scrub forest (40% male; $\chi^2 = 6.0$, $df=1$, $p = 0.01$), as described elsewhere (Marra et al. 1998). It did not differ from 1:1 in any other habitat. Sex ratio in citrus and coffee was close to 1:1 and, like density, was intermediate between high and low values in natural habitats. Age ratios differed significantly among habitats ($\chi^2 < 13.2$, $df=5$, $p < 0.03$), ranging from 58% (palm forest) to 38% (scrub) adult, with citrus and coffee values again intermediate (42 and 55% adult, respectively) between these extremes.

Body Mass

Body mass adjusted for wing chord (hereafter body mass) differed among sexes, ages, habitats, and seasons (Table 2). Variation was modest, with most birds (>95%) weighing between 6.5 and 8.0 g, so statistical differences stemmed from variation in fractions of a gram. For example, males averaged 0.12 g heavier than females, and yearlings were on average 0.06 g heavier than adults given their wing lengths. The age effect varied by habitat, however (age \times habitat interaction $p = 0.02$), with yearlings 0.07–0.20 g heavier than adults in citrus, scrub, and

Table 2. Analysis of covariance statistics of American Redstart body mass adjusted for wing-chord length analyzed among six habitats in Jamaica in early and late winter by age (adult and yearling) and sex.

Source and n ^a	df	Mean square	F	p
Model	39	0.84	6.07	<0.001
Intercept	1	5.56	40.11	<0.001
Wing chord (covariate)	1	4.46	32.16	<0.001
Age (adult 329, yearling 297)	1	0.59	4.26	0.039
Sex (female 282, male 344)	1	1.03	7.45	0.007
Habitat ^b	4	1.73	12.49	<0.001
Season (early 453, late 173)	1	4.17	30.03	<0.001
Age \times sex	1	0.48	3.48	0.062
Age \times habitat ^b	4	0.41	2.94	0.020
Sex \times habitat ^b	4	0.23	1.62	0.167
Age \times sex \times habitat ^b	4	0.22	1.60	0.172
Age \times season	1	0.68	4.88	0.028
Sex \times season	1	0.29	2.11	0.147
Age \times sex \times season	1	0.05	0.36	0.552
Habitat ^b \times season	4	0.26	1.85	0.118
Age \times habitat ^b \times season	4	0.04	0.31	0.873
Sex \times habitat ^b \times season	4	0.27	1.94	0.103
Age \times sex \times habitat ^b \times season	3	0.06	0.40	0.750
Error	586	0.14		
Total	626			

^aSample sizes for each main effect level are shown (total n = 626).

^bHabitats and sample sizes: citrus orchard 95, shade coffee plantation 171, dry limestone forest 128, black mangrove forest 73, and coastal scrub forest 159 (see Table 1).

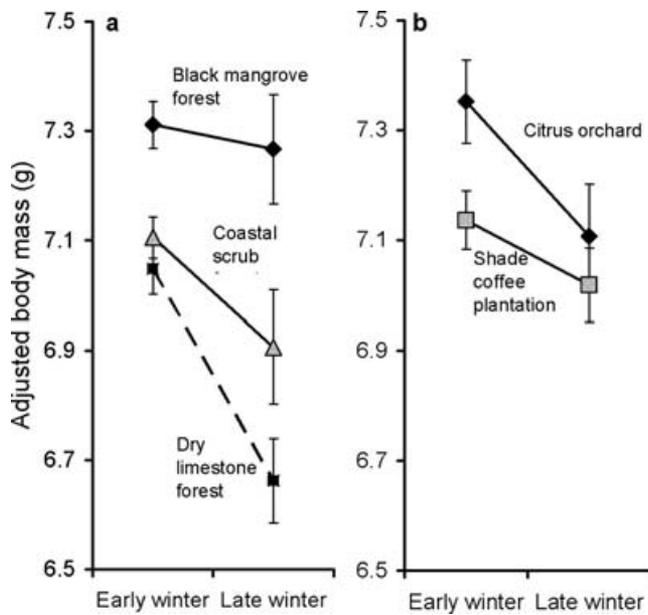


Figure 2. Body mass adjusted for wing length (evaluated at wing chord of 60.2 mm via analysis of covariance) for American Redstarts wintering in (a) three natural and (b) two agricultural habitats (right) in Jamaica (mean ± 1 SE). Samples sizes are (early/late winter): black mangrove forest 82/16, coastal scrub forest 187/25, dry limestone forest 100/35, citrus orchard 66/35, and shade coffee plantation 102/80.

mangrove and 0.05 and 0.08 g lighter than adults in coffee and dry limestone, respectively. On average, birds were 0.21 g lighter in late than early winter, representing about a 3% loss of body mass over the winter. This loss differed by age (adult 4% reduction, yearling 2% reduction; age × season interaction $p = 0.028$). Overall, birds were heaviest in citrus orchards and mangrove forest and lightest in dry limestone forest (Fig. 2). The seasonal loss of mass did not differ significantly by habitat (habitat × season interaction $p = 0.118$), but birds generally maintained mass best in mangrove forest and lost the most mass in dry limestone forest (Fig. 2).

Detection and Survival Probabilities

Among the natural forests, detection probability (p) varied by habitat (all top models in Table 3 parameterized for p_{habitat}). It was highest in palm forest and lowest in dry limestone forest (Table 4), but it was largely independent of sex. Detection probabilities were higher for males than for females among agricultural habitats, where AIC_c weights indicated that sex-specific p received 19.3 times more support than sex-independent p (Table 5).

Model selection (Tables 3 & 5) and estimates of survival and detection probabilities (Table 4) differed modestly among habitats. Based on AIC_c weights, habitat-specific survival received 1.6 times more support than habitat-

Table 3. Models of survival (ϕ) and recapture (p) probabilities for American Redstarts wintering in four natural habitats in Jamaica.^a

Model ^b	K	AIC_c	Δ_i	Deviance	w_i
$\phi_{\text{age+habitat+interval}}, p_{\text{habitat}}$	10	2269.51	0.00	1374.43	0.28
$\phi_{\text{age+interval}}, p_{\text{habitat}}$	7	2270.15	0.64	1374.43	0.20
$\phi_{\text{age*interval+habitat}}, p_{\text{habitat}}$	11	2271.54	2.03	1387.37	0.10
$\phi_{\text{age+sex+habitat+interval}}, p_{\text{habitat}}$	11	2271.55	2.04	1373.48	0.10
$\phi_{\text{age+sex+interval}}, p_{\text{habitat}}$	8	2271.55	2.05	1389.45	0.10
$\phi_{\text{age*interval}}, p_{\text{habitat}}$	8	2272.16	2.65	1371.61	0.07
$\phi_{\text{age+sex+habitat+interval}}, p_{\text{sex+habitat}}$	12	2272.63	3.12	1382.25	0.06
$\phi_{\text{age*sex+habitat+interval}}, p_{\text{habitat}}$	12	2272.92	3.41	1380.54	0.05
$\phi_{\text{habitat+interval}}, p_{\text{habitat}}$	9	2275.30	5.79	1381.17	0.02
$\phi_{\text{age+sex+habitat+interval}}, p_{\text{sex*habitat}}$	15	2276.91	7.40	1382.26	0.01
$\phi_{\text{sex+habitat+interval}}, p_{\text{habitat}}$	10	2277.32	7.81	1390.48	0.01
$\phi_{\text{interval}}, p_{\text{habitat}}$	6	2277.44	7.93	1390.48	0.01

^aKey: K, number of estimable parameters; AIC_c , second-order Akaike's information criterion values; Δ_i , AIC_c deviance; AIC_c weights (w_i).

^bSubscripts give parameterization for ϕ and p : no subscript, constant over group and time variables; age, two age classes (adult and yearling); sex, female and male; habitat, coastal scrub, coastal palm, black mangrove, and dry limestone forests; interval, overwinter survival (early winter to late winter) or between-winter survival (late winter to the following early winter). Subscripts joined by a plus (+) or an asterisk (*) indicate additive and factorial models, respectively. Only the top 12 models are shown, all others had $w_i < 0.01$. Early and late winter months were October–December and February–March, respectively.

independent survival in the natural data set and 2.4 times more support in the agricultural data set. Nevertheless, the 95% confidence intervals for the habitat-slope coefficients generally included zero ($\beta = 0.27$, 95% CI = -0.09–0.64 and $\beta = -0.51$, 95% CI = -1.07–0.05 for natural and agricultural data sets, respectively), indicating a relatively weak effect of habitat. In the natural habitat data set, only dry limestone forest had significantly lower apparent survival than the other habitats ($\beta = 0.39$, 95% CI = 0.07–0.71). Model-averaged estimates of habitat-specific survival ranged from about 70–97% for overwinter survival and 43–66% for between-winter survival (Table 4), which includes fall and spring migrations and the breeding period. Overwinter survival was especially high in coffee (97%), which had a comparatively low between-winter survival (52%), yielding an intermediate probability of annual survival (50%). Mangrove forest had a lower rate of overwinter survival (82%), but combined with high between-winter survival (66%) mangrove forest had the highest annual survival probability among habitats (54%). Overwinter survival in citrus orchards was similar to that in mangrove forest (83%), but between-winter survival

Table 4. Estimates of apparent survival (ϕ) and recapture (p) probabilities, sample sizes, unconditional standard errors, and profile likelihood 95% confidence intervals for American Redstarts wintering in Jamaica.^a

Age/sex/habitat (no. of birds)	$\phi \pm 1 SE$ (95% CI)		
	overwinter survival ^b	between-winter survival ^c	$p \pm 1 SE$ SE (95% CI)
Adult (311)	0.861 \pm 0.020 (0.816–0.896)	0.577 \pm 0.021 (0.536–0.617)	0.835 \pm 0.035 (0.756–0.892)
Yearling (323)	0.753 \pm 0.034 (0.680–0.814)	0.369 \pm 0.080 (0.230–0.534)	0.767 \pm 0.016 (0.735–0.796)
Male (329)	0.832 \pm 0.023 (0.781–0.873)	0.586 \pm 0.023 (0.533–0.637)	0.804 \pm 0.019 (0.765–0.838)
Female (305)	0.797 \pm 0.023 (0.748–0.839)	0.568 \pm 0.030 (0.508–0.627)	0.740 \pm 0.023 (0.639–0.783)
Black mangrove forest (135)	0.817 \pm 0.033 (0.745–0.873)	0.664 \pm 0.038 (0.585–0.734)	0.778 \pm 0.026 (0.722 \pm 0.825)
Coastal scrub forest (141)	0.772 \pm 0.042 (0.679–0.845)	0.539 \pm 0.046 (0.448–0.627)	0.720 \pm 0.036 (0.645–0.784)
Shade coffee plantation (134)	0.968 \pm 0.040 (0.694–0.997)	0.519 \pm 0.045 (0.431–0.606)	0.842 \pm 0.029 (0.775–0.891)
Citrus orchard (76)	0.829 \pm 0.074 (0.637–0.931)	0.434 \pm 0.072 (0.302–0.577)	0.821 \pm 0.056 (0.684–0.907)
Coastal palm forest (74)	0.852 \pm 0.038 (0.758–0.914)	0.591 \pm 0.046 (0.493–0.681)	0.844 \pm 0.031 (0.774–0.895)
Dry limestone forest (98)	0.699 \pm 0.042 (0.610–0.774)	0.467 \pm 0.066 (0.338–0.596)	0.622 \pm 0.044 (0.534–0.704)

^aTop models with AIC_c values ≤ 2 (from Tables 3 & 5) were model averaged to calculate parameter estimates. Annual survival (Fig. 3) is the product of the two survival probabilities shown.

^bApparent survival from early (October–December) to late (February–March) winter.

^cApparent survival from late (February–March) to the following early (October–December) winter.

was lower than in any other habitat (43%), yielding a relatively low annual survival probability (36%). Dry limestone forest had relatively low survival rates over both intervals (70% overwinter and 47% between winter); consequently, it had the lowest annual survival probability (33%).

Age-dependent survival received more support than age-independent survival in both natural and agricultural habitats (31.4 and 4.1 times more support, respectively; Tables 3 & 5). The 95% confidence intervals for the age-slope coefficients did not include zero ($\beta = 0.64$, 95% CI = 0.20–1.07 and $\beta = 0.82$, 95% CI = 0.01–1.62 for natural and agricultural data sets, respectively). Adults had appreciably higher survival rates than yearlings (Table 4). Additive models generally received more support via Akaike's weights than interactive models (Tables 3 & 5), suggesting that the effects of age (adult vs. yearling) and interval (between winter vs. overwinter) operated similarly among habitats. We found little evidence for sex-specific survival (sex-independent models received over twice as much support as did sex-specific models in both the natural and agricultural data sets).

Congruence of Habitat Quality Indices

The loss of mass over the winter was a significant predictor of annual survival ($F_{1,4} = 36.8$, $p < 0.01$, $r^2 = 0.93$; Fig. 3). The slope of this relationship indicated that

a loss of 0.1 g over the winter corresponded, on average, to a reduction in annual survival probability of 6.8%. The loss of mass over winter was also correlated with both between-winter and overwinter survival, although not significantly ($p = 0.12$ and 0.22 , $r^2 = 0.44$ and 0.66 , respectively). Considering all eight measures of habitat quality (Table 6), annual survival and the loss of body mass over the winter were the most consistently congruent with the other measures (Pearson's r range 0.62 to 0.96 and -0.35 to -0.93 , respectively). Overwinter and between-winter survival were moderately consistent with the other measures, although they were only weakly correlated with each other ($r = 0.17$). Density was reasonably well correlated with our most reliable measures of habitat quality, survival, and change in body mass, particularly in late winter ($r = 0.68$ – 0.92). Age and sex ratios were the least consistently congruent with other measures.

Discussion

Agricultural versus Natural Habitats

For American redstarts wintering in Jamaica, the quality of citrus orchards and shade coffee habitats fell within the range of variation among the natural habitats. In particular, in shade coffee, overwinter change in body mass and overwinter survival were comparable to the best natural

Table 5. Models of survival (ϕ) and recapture (p) probabilities for American Redstarts wintering in citrus and coffee habitats in Jamaica.^a

Model ^b	K	AIC _c	Δ_i	Deviance	w _i
$\phi_{\text{age+habitat+interval}}, p_{\text{sex}}$	6	618.45	0.00	263.63	0.24
$\phi_{\text{age+interval}}, p_{\text{sex}}$	5	619.50	1.06	263.54	0.14
$\phi_{\text{habitat+interval}}, p_{\text{sex}}$	5	620.32	1.87	268.88	0.09
$\phi_{\text{age*interval+habitat}}, p_{\text{sex}}$	7	620.39	1.95	264.15	0.09
$\phi_{\text{age+sex+habitat+interval}}, p_{\text{sex}}$	7	620.46	2.01	264.12	0.09
$\phi_{\text{age*interval}}, p_{\text{sex}}$	6	621.35	2.90	268.08	0.06
$\phi_{\text{age+sex+interval}}, p_{\text{sex}}$	6	621.56	3.12	267.18	0.05
$\phi_{\text{age+habitat+interval}}, p_{\text{sex}}$	5	621.98	3.54	264.22	0.04
$\phi_{\text{age+sex+habitat+interval}}, p_{\text{sex+habitat}}$	8	622.03	3.58	264.09	0.04
$\phi_{\text{sex+habitat+interval}}, p_{\text{sex}}$	6	622.31	3.86	267.33	0.03
$\phi_{\text{age*sex+habitat+interval}}, p_{\text{sex}}$	8	622.51	4.06	268.15	0.03
$\phi_{\text{interval}}, p_{\text{sex}}$	4	622.56	4.12	267.34	0.03

^aColumn headings are defined in footnote of Table 3.
^bSubscripts give parameterization for ϕ and p : no subscript, constant over group and time variables; age, two age classes (adult and yearling); sex, female and male; habitat, citrus orchard or shade coffee plantation; interval, overwinter survival (early winter to late winter); or between-winter survival (late winter to the following early winter). Subscripts joined by a plus (+) or an asterisk (*) indicate additive and factorial models, respectively. Only the top 12 models are shown, all others had w_i < 0.01. Early and late winter were October-December and February-March, respectively.

habitat we sampled, mangrove forest. These results support conclusions of previous studies based on bird abundance that arboreal agricultural habitats can be useful for the conservation of wintering redstarts and perhaps other foraging generalist species that occupy tree-dominated habitats (Perfecto et al. 1996; Greenberg et al. 1997a, 1997b; Wunderle & Latta 1998; 2000; Lindell et al. 2004).

Nevertheless, the conclusion that shade coffee is a valuable habitat for migrant conservation must be qualified by two caveats (see also Rappole et al. 2003b, 2003c). First, we lack data with which to compare the quality of coffee plantations to the habitats from which they were probably originally carved (midelevation wet forests). Although some agroecosystems may provide habitat for some species, they are not adequate replacements for natural forest and do not possess their complete suite of species or ecosystem functions. Indeed, coffee habitats themselves may be partially reliant on pollinators from surrounding intact, native forest (Ricketts et al. 2004). Second, our results stem from studies of a single species in a single region and must be extrapolated cautiously. The conversion of natural forest to agriculture can have dramatic negative impacts on many resident, nonmigratory bird species, some of which appear dependent on intact understories and are unable to use shade coffee or other agricultural habitats successfully (Tejada-Cruz & Sutherland 2004). Even some migratory songbirds (e.g., Scarlet Tanager [*Piranga olivacea*], Kentucky

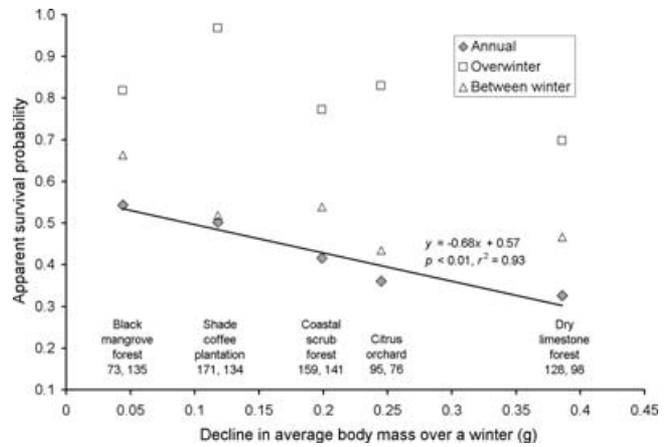


Figure 3. Relationship between the decline in average body mass of American Redstarts wintering in five different habitats and their apparent overwinter, between-winter, and annual survival rates in each. The line indicates the tight linear relationship between body condition and annual survival. Values beneath habitat names correspond to numbers of birds used in body mass and for survival estimates, respectively.

Warbler [*Oporornis formosus*], Swainson’s Warbler [*Limnothlypis swainsonii*], Golden-cheeked Warbler [*Dendroica chrysoparia*]) appear dependent on undisturbed forests (Mabey & Morton 1992; Strong & Sherry 2001; Rappole et al. 2003a, 2003c). Among forest-dwelling migratory songbirds, the redstart shows considerable habitat breadth (Sherry & Holmes 1997); other, more specialized species are likely less flexible in their use of evolutionarily novel habitats such as agricultural areas.

Link between Body Condition and Survival

The very tight correlation between overwinter change in mean adjusted body mass and annual survival (Fig. 3) has several important implications. First, it indicates that the decline in average redstart body mass over the course of a winter is a strong predictor of survival probability and hence habitat quality. Here, a simple habitat-specific measure of physical condition in the nonbreeding season predicted differences in survival, a parameter linked directly to fitness. This condition is a necessary assumption of the carry-over-effect hypothesis for habitat quality (Webster et al. 2002; Norris 2005; Runge & Marra 2005). That is, lethal effects of winter habitat may not manifest until after birds depart for spring migration. Second, it evinces the importance for birds to maintain body mass over the winter. From our data, a loss of 0.1 g over the winter corresponded to a reduction in annual survival probability of 6.8% (slope of line in Fig. 3). Similarly, Marra and Holmes (2001) found that birds in scrub forest in Jamaica lost an average of 0.3 g overwinter and had lower annual survival than birds in mangrove.

Table 6. Pearson's correlation matrix (*r*) for eight measures of habitat quality for American Redstarts wintering among six habitats in Jamaica (probability in one-tailed tests).^a

	Density (early winter)	Density (late winter)	Sex ratio	Age ratio	Loss of body mass	Overwinter survival ^b	Between-winter survival ^c	Annual survival
Density (early winter)	1	0.91*	0.36	-0.11	-0.93*	0.36	0.59	0.63**
Density (late winter)		1	0.19	0.06	-0.92*	0.69**	0.44	0.68**
Sex ratio			1	0.59	-0.59	0.04	0.85*	0.68**
Age ratio				1	-0.35	0.44	0.48	0.62**
Loss of mass					1	-0.66	-0.79	-0.96***
Overwinter survival						1	0.17	0.64**
Between-winter survival							1	0.86*
Annual survival								1

^aSignificance: * $p < 0.05$; ** $p < 0.10$; *** $p \leq 0.01$.

^bApparent survival from early (October–December) to late (February–March) winter.

^cApparent survival from late (February–March) to the following early (October–December) winter.

Maintenance of body mass, in turn, is probably linked to sufficient food supply. For redstarts, overwinter changes in food availability have been correlated with changes in body mass (Johnson & Sherry 2001), although a cause-effect relationship has not been established. Experimental reductions and additions of food supply for Ovenbirds (*Seiurus auricapilla*) in Jamaica led to corresponding changes in body mass and other indicators of body condition (D. Brown & T.W.S., unpublished data). Taken together, these studies suggest food supply in winter habitats may affect annual survival, which may limit migrant populations (Sherry et al. 2005).

Measuring Habitat Quality

In theory survival should be the parameter most clearly linked to lifetime reproductive success and fitness for animals in the nonbreeding season (Stearns 1992). Nevertheless, a winter habitat's influence on birds' preparation for migration and reproduction could be its biggest contribution to fitness (Marra et al. 1998; Norris et al. 2004), and simple overwinter survival misses these sublethal effects. Thus, estimates of annual survival are probably the most accurate and informative measures of habitat quality for this and perhaps other wintering migratory songbirds.

Unfortunately, annual survival analyses need data sets comprised of large numbers of individuals and spanning at least three encounter occasions (i.e., years). In our study, the strong correlation between adjusted body mass and annual survival (Fig. 3) substantiates the assumption that a bird's good physiological condition in winter translates into fitness benefits by enhancing annual survival for this species. Body condition measures can be obtained over far shorter time periods than can survival data (i.e., a single winter). Therefore, our results reinforce the idea that body condition is a useful indicator of nonbreeding habitat quality (Marra & Holberton 1998; Strong & Sherry 2000; Marra & Holmes 2001; Latta & Faaborg 2002).

Most measures of body condition, however, require birds to be captured at least once, which requires con-

siderable time and expertise, limiting the spatial and temporal extent of data collection. Measures of relative abundance (or density) are usually far easier to collect and can be reasonably good indicators of habitat quality (Bock & Jones 2004), except in cases where they are poorly connected with lifetime reproductive success.

In our study, density corresponded reasonably well with change in body mass and annual survival, our best measures of habitat quality. The correlations were especially high in late winter (Table 6), when food resources appear to be most limited (Strong & Sherry 2000; Sherry et al. 2005) and when warbler densities are spatially correlated with food availability (Johnson & Sherry 2001). Taken together, these results suggest that density can be a good indicator of habitat quality for wintering songbirds, especially when surveys (e.g., point counts) are conducted late in the winter. Nevertheless, redstart density was statistically indistinguishable between mangrove and coastal scrub forests in Jamaica (Marra & Holmes 2001), even though the former was clearly higher in quality based on physiological indices (Marra & Holberton 1998). Thus, density may potentially overlook subtle, but biologically important, differences among habitats.

Van Horne (1983) suggested several environmental and species characteristics (e.g., temporally unpredictable habitats, strong social dominance interactions) that may increase the probability that density is decoupled from habitat quality. For breeding birds, Bock and Jones (2004) found that these characteristics have relatively little influence, but density is a poor indicator of habitat quality more often in areas of human disturbance than in natural areas. They suggest this may be particularly pronounced in newly modified landscapes, where birds have not yet adapted to avoid poor but attractive habitats (i.e., ecological traps, Battin 2004). Our results are not consistent with this hypothesis. Our study involved heavily modified agricultural habitats, most of which were relatively young (<60 years), yet density was positively correlated with habitat quality. Generalist songbirds, such as redstarts, can track food resources in the nonbreeding season

(Johnson & Sherry 2001), and this may enable better detection and response to factors directly influencing the quality of novel habitats created by human or natural disturbances, thereby preserving the link between density and habitat quality.

Investigations of other wintering migratory songbird species have revealed sexual habitat segregation (Ornat & Greenberg 1990; Marra et al. 1998), and results of studies have indicated that, at least for redstarts, the best habitats are occupied disproportionately by males (Marra 2000; Marra & Holmes 2001). Nevertheless, our analyses here suggest caution when using sex ratio as a measure of habitat quality across a wide array of habitats. We found only a modest variation in sex ratio; only mangrove and scrub forest deviated significantly from 1:1. Although sexual segregation may be common in songbirds wintering in the tropics, it may be difficult to detect in many areas because it is manifested at smaller spatial scales than that of the habitat level, possibly occurring among vertical layers of vegetation within a single habitat (*sensu* Greenberg & Ortiz 1994; Johnson & Sherry 2001). Age ratio was only weakly correlated with the other measures, suggesting little promise as a measure of habitat quality.

We offer a tiered recommendation for land managers wishing to quantify habitat quality for wintering migrants: (1) survival estimates are best if feasible, (2) where survival estimates are not feasible, appropriate measures of body condition may provide a good surrogate for short-duration projects, and (3) measures of abundance provide rough indicators of quality, possibly depending on species, and especially late in the winter when their relationship with better measures (survival and body condition) may be strongest.

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