
Overwinter Survival of Neotropical Migratory Birds in Early-Successional and Mature Tropical Forests

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Abstract: *Many Neotropical migratory species inhabit both mature and early-successional forests on their wintering grounds, yet comparisons of survival rates between habitats are lacking. Consequently, the factors affecting habitat suitability for Neotropical migrants and the potential effects of tropical deforestation on migrants are not well understood. We estimated overwinter survival and capture probabilities of Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapillus*), Hooded Warbler (*Wilsonia citrina*), and Kentucky Warbler (*Oporornis formosus*) inhabiting two common tropical habitat types, mature and early-successional forest. Our results suggest that large differences (for example, ratio of survival rates (γ) ≤ 0.85) in overwinter survival between these habitats do not exist for any of these species. Age ratios did not differ between habitats, but males were more common in forest habitats and females more common in successional habitats for Hooded Warblers and Kentucky Warblers. Future research on overwinter survival should address the need for age- and sex-specific survival estimates before we can draw strong conclusions regarding winter habitat suitability. Our estimates of overwinter survival extrapolated to annual survival rates that were generally lower than previous estimates of annual survival of migratory birds. Capture probability differed between habitats for Kentucky Warblers, but our results provide strong evidence against large differences in capture probability between habitats for Wood Thrush, Hooded Warblers, and Ovenbirds. We found no temporal or among-site differences in survival or capture probability for any of the four species. Additional research is needed to examine the effects of winter habitat use on survival during migration and between-winter survival.*

Supervivencia de invernación de las aves migratorias Neotropicales en bosques tropicales de sucesión temprana y maduros

Resumen: *Numerosas especies Neotropicales migratorias habitan tanto bosques maduros como aquellos en estadios de sucesión temprana como sus áreas de invernación; sin embargo, existe una falta de estudios que comparen las tasas de supervivencia entre los distintos hábitats. Como consecuencia, no existe una buena comprensión de los factores que afectan el grado de adecuación del hábitat para las aves migratorias Neotropicales y los potenciales efectos que la deforestación de la selva tropical tiene sobre estos. Estimamos la supervivencia de invernación y la probabilidad de captura de *Hylocichla mustelina*, *Seiurus aurocapillus*, *Wilsonia citrina* y *Oporornis formosus* que habitan dos tipos de hábitats tropicales comunes: bosques de sucesión temprana y bosques maduros. Nuestros resultados sugieren que no existen grandes diferencias en la supervivencia de invernación (por ejemplo el cociente de tasas de supervivencia [γ] ≤ 0.85) entre estos hábitats para ninguna de estas especies. Las proporciones de edades no difirieron entre los hábitats, pero los machos fueron más comunes en los bosques maduros y las hembras lo fueron en los hábitats sucesionales para *Wilsonia citrina* y *Oporornis formosus*. La investigación futura sobre la supervivencia de invernación debe considerar la necesidad de estimaciones de supervivencia específicas por edad y sexo antes de llegar a conclusiones terminantes con respecto a la adecuación del hábitat invernal. Nuestras estimaciones de supervivencia invernal se tradujeron en tasas de supervivencia anual que fueron generalmente más bajas que estimaciones previas de*

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supervivencia anual de aves migratorias. La probabilidad de captura de Oporornis formosus difirió entre los hábitats, pero nuestros resultados proveen una evidencia sustancial en contra de grandes diferencias entre hábitats para la probabilidad de captura de Hylocichla mustelina, Seiurus aurocapillus y Wilsonia citrina. No encontramos diferencias temporales o entre sitios en la probabilidad de supervivencia y captura para ninguna de las 4 especies. Se necesita una investigación adicional para examinar los efectos del uso del hábitat invernal sobre la supervivencia durante la migración y la supervivencia entre inviernos.

Introduction

Many populations of Neotropical migratory birds have declined in recent years (Robbins et al. 1989; Askins et al. 1990), but, despite the obvious importance of understanding the proximate and ultimate causes of those population changes for effective conservation programs, few data are available to address alternative hypotheses. Declines in migratory bird populations are considered by many to be at least partially a result of habitat alteration on wintering grounds (Terborgh 1980, 1992; Morton & Greenberg 1989; Robbins et al. 1989). Numerous studies have addressed winter habitat suitability for migratory birds, but these have relied upon the assumption that abundance is related to habitat quality. Abundance indices are not the most appropriate measure of habitat suitability, however; survivorship is probably a better indicator of habitat value for wintering migratory birds (Martin 1992; Sherry & Holmes 1993).

Migratory bird populations may be limited principally by factors affecting winter survival (Fretwell 1972; Morse 1980; Morton 1992; Rappole et al. 1992), and survivorship has been suggested to be relatively low in early-successional habitats (Rappole et al. 1989; Winker et al. 1990; Blake & Loiselle 1992). Yet variation in winter fitness associated with different habitats has not been addressed (Petit et al. 1993; but see Greenberg 1992), and few estimates of annual survival are available for Neotropical migratory birds (Cox 1985; but see Holmes et al. 1989). Estimates of survival during different periods of the annual cycle are necessary for constructing life tables, for examining population ecology and evolution of life-history traits (Ricklefs 1992), and for implementing effective recovery plans for declining species. Also, the environmental factors affecting survival influence evolution, behavior, population dynamics, and conservation of populations.

Neotropical migratory birds spend two-thirds of the annual cycle on wintering grounds in Latin America (Keast 1980), and winter may be a stressful time for many migrants. Yet estimates of winter survival are rare (Holmes et al. 1989), especially in the context of determining those ecological factors, including habitat use, that affect survival during winter (Holmes et al. 1989; but see Rappole et al. 1989). Clearly, habitat suitabilities,

based upon estimated survival probabilities, are necessary to understanding the effects of tropical-forest alteration on migratory bird populations and to establishing land-based conservation priorities in the tropics (Lynch 1992; Petit et al. 1993; Sherry & Holmes 1993).

We examined the effect of tropical deforestation on migratory bird populations by testing the null hypothesis that winter survivorship of understory migratory birds is not different between mature and early-successional forest. We present results for four small Neotropical migratory bird species that overwinter in southern Belize: Wood Thrush (*Hylocichla mustelina*), Ovenbird (*Seiurus aurocapillus*), Hooded Warbler (*Wilsonia citrina*), and Kentucky Warbler (*Oporornis formosus*). Several studies have recorded declines for all four species (Robbins et al. 1989; Robbins et al. 1993; Roth & Johnson 1993), and all are commonly found in both habitat types (Lynch 1989; Kricher & Davis 1992; Petit et al. 1992, 1993). Mature and successional forest were chosen because both provide winter habitat for a variety of neotropical migratory birds and because early-successional forest (secondary growth) is a common byproduct of tropical deforestation in some parts of the neotropics.

Methods

Our study sites were within the coastal plain and piedmont of the Maya mountains, 0–340 meters elevation, in Toledo District, southern Belize. We established 11 study sites: six in mature, undisturbed forest and five in disturbed, early-successional forest. Mature forest sites had closed canopies at least 25 meters high. Early successional forests were naturally regenerating agricultural lands that had been fallow for 4–10 years and had canopies 3–10 meters high. Traditional plot-rotation agricultural methods are practiced by Mayan farmers on these sites without the use of mechanized farm equipment. Consequently, our successional forest sites rotate between active farmland for 1–3 years and then are left as fallow, successional land for 4–15 years before being re-used again. These areas are generally cleared with machetes, burned, and then planted with corn, rice, or beans. Plant composition and stem density varied greatly among our successional sites, undoubtedly depending

on rotation interval, time left fallow, and distance to seed sources.

We established six 12-ha sites in November 1991 (three in mature forest and three in successional forest) and an additional five 6-ha sites in November 1992 (three in mature forest and two in successional forest). At the 12-ha sites we placed 48 mist nets at 50-meter intervals in an evenly spaced grid system. At each site, we opened nets for 18–20 hours over a 2–3 day period during each of four sampling periods (November–December 1991, February 1992, March 1992, and March 1993). One of these 12-ha sites was not trapped in March 1993 due to disturbance. At the 6-ha sites we opened 24 nets for 18–20 hours during each of three sampling periods (November–December 1992, February 1993, and March 1993). Nets were left open throughout the day, and we netted in all weather, checked nets hourly, and released banded birds at the net of capture. Intervals between sampling periods averaged 73 days (November–December to February), 19 days (February to March), and 359 days (March to March). Distance between sites was similar for mature-forest sites ($\bar{x} = 23.0$ km, range 1.7–40.7 km) and early-successional forest sites ($\bar{x} = 19.9$ km, range 5.4–32.4 km), and we documented no movement of birds among sites.

We recorded age (hatch-year or after-hatch-year) and sex of all birds removed from nets whenever possible. We determined the sex of Hooded Warblers and Kentucky Warblers by examining plumage, but we could not determine the sex of Ovenbirds and Wood Thrushes because there are no techniques available for these two species. We determined age by examining skull pneumatization and plumage (Pyle et al. 1987).

We used chi-square analysis for contingency tables to test the hypothesis that sex and age ratios differ between habitats (Zar 1984). Estimation and testing of overwinter survival probabilities was accomplished using capture-recapture models developed specifically for our data and implemented using the computer program SURVIV (White 1983). Data from each species were modeled separately, but we did not attempt to analyze data by age class or sex because of limited sample sizes. The most general model ($\phi_{i,l}, p_{i,l}$) included survival (ϕ) and capture (p) probabilities specific to time (the three or four sampling periods, depending on location) and location (the 11 study sites). This model is thus equivalent to 11 separate Cormack-Jolly-Seber models (Cormack 1964; Jolly 1965; Seber 1965, 1982), one for each study site.

Because of our interest in developing parsimonious models (Pollock et al. 1990; Lebreton et al. 1992), we expressed the probability of an individual surviving from one sampling period to the next and not permanently emigrating from the study sites, $S_{i,l}$ (where i denotes sample period and l denotes location), as a function of monthly survival probability, $\phi_{i,b}$ and the time (in

months) between consecutive sampling periods at each location, $t_{i,l}$. Thus,

$$S_{i,l} = \phi_{i,l}^{t_{i,l}}$$

and the right-hand side of this expression was incorporated directly into our models. We defined capture probability in the standard manner as the conditional probability that a bird alive and in the population during the sampling period was captured.

In addition to the general model that incorporated both time and location ($\phi_{i,l}, p_{i,l}$), we fit a number of reduced-parameter models to the data (Table 1). In our notation for specifying models, the absence of subscript i denotes a parameter that is constant over all sampling periods. When subscript b replaces the subscript l , the parameter is assumed to differ by habitat type (mature versus successional forest) but not by location within habitat type. Absence of subscripts l and b denotes a parameter that is constant over all locations and habitats.

The most parsimonious model for each species was selected using Akaike's Information Criterion (AIC; Akaike 1973), as recommended by Burnham and Anderson (1992) and Lebreton et al. (1992). Goodness-of-fit of the models to the data was assessed with chi-square statistics, pooling cells with small expected values using the algorithm of SURVIV (White 1983).

Tests for differences between habitats in overwinter survival and capture probabilities were conducted using likelihood ratio tests between the AIC-selected model and the neighboring model that expressed a different hypothesis about habitat (if the model with the smallest AIC parameterized survival as a constant, ϕ , then the alternative-hypothesis model incorporated habitat-specific survival, ϕ_b).

Table 1. Model parameterization and explanation.

Model	Explanation
(ϕ, p)	Survival and capture probability constant over time and habitat
(ϕ, p_b)	Survival constant over time and habitat; capture probability constant over time but variable by habitat
(ϕ_b, p)	Survival probability constant over time but variable by habitat; capture probability constant over time and habitat
(ϕ_b, p_b)	Survival and capture probability constant over time but variable by habitat
$(\phi_b, p_{i,l})$	Survival probability constant over time but variable by habitat; capture probability variable by time and location
$(\phi_{i,jb}, p_{i,l})$	Survival probability variable by time and habitat; capture probability variable by time and location (different p for each study site)
$(\phi_{i,l}, p_{i,l})$	Survival and capture probability variable by both time and location

Table 2. Test of the null hypothesis of equal monthly survival probabilities for mature and successional habitats versus the alternative hypothesis of different survival probabilities by habitat.

Species	Models Tested (H_o vs. H_a)	Likelihood Ratio Test Statistic			Survival Estimates Under H_a			
		χ^2	df	p	Mature		Successional	
					$\hat{\phi}$	SÊ ($\hat{\phi}$)	$\hat{\phi}$	SÊ ($\hat{\phi}$)
Ovenbird	(ϕ, p) vs. (ϕ_b, p)	0.13	1	0.71	0.91	0.048	0.89	0.028
Wood Thrush	(ϕ, p) vs. (ϕ_b, p)	0.05	1	0.82	0.91	0.033	0.90	0.036
Kentucky Warbler	(ϕ, p_b) vs. (ϕ_b, p_b)	1.57	1	0.21	0.86	0.032	0.93	0.041
Hooded Warbler	(ϕ, p) vs. (ϕ_b, p)	0.39	1	0.53	0.94	0.041	0.91	0.039

Likelihood ratio tests were conducted for each species separately, and a composite statistic was computed over all four species by summing the four chi-square statistics and associated degrees of freedom. When our null hypothesis of no difference in survival and capture probabilities between habitats was not rejected, we approximated power (the probability of rejecting the null hypothesis when the null hypothesis was indeed false) in the manner suggested by Burnham et al. (1987) and Lebreton et al. (1992). Finally, we tested the null hypothesis of no difference in overwinter survival rates among the four species using the monthly estimates and their estimated variances (program CONTRAST; Hines & Sauer 1989; Sauer & Williams 1989).

Results

In 28,349 net hours (1 net hour = 1 net open for 1 hour), we recorded 543 captures of 387 Wood Thrushes, 440 captures of 312 Ovenbirds, 330 captures of 193 Kentucky Warblers, and 216 captures of 137 Hooded Warblers. Percentage of birds banded in November-December that were subsequently recaptured in February or March was 32%, 29%, 46%, and 32% for Wood Thrush, Ovenbird, Kentucky Warbler, and Hooded Warbler, respectively. Proportion of males was greater ($\chi^2 > 22.0$, $df = 1$, $p < 0.001$) in forest habitats compared to successional habitats for both Hooded Warblers (0.72 and 0.31, respectively) and Kentucky Warblers (0.59 and 0.22, respectively). We did not detect any differences ($\chi^2 < 0.90$, $df = 1$, $p > 0.39$) in the proportion of hatch-year birds between habitats for any of the four species. Capture-history information was summarized using zeros and ones to represent not captured and captured, respectively, during each sampling period (Appendix). For example, the capture history of an individual captured in period 1, not captured in period 2, and recaptured in period 3 would be summarized as 101.

We detected no differences in monthly survival probabilities of birds inhabiting mature versus successional forests for any of the four species (Table 2). Likewise, the composite statistic pooling all four species was non-significant ($\chi^2_4 = 2.14$, $p = 0.71$). Indeed, the estimates

for monthly overwinter survival under the alternative hypothesis models were very similar for the mature and successional habitats (Table 2).

We approximated the power of these tests at an α -level of 0.05 for several proportional differences (γ) that we wished to detect. For these approximations we assumed that the monthly survival probability for mature forest equaled the estimate from the AIC-selected model ($\phi_m = \hat{\phi}_{AIC}$) and that the survival rate for successional forest equaled γ times this value ($\phi_s = \gamma \hat{\phi}_{AIC}$). Power was poor for these individual tests for $\gamma > 0.85$ (Table 3). Power for $\gamma = 0.80$ was fair for Ovenbird, Wood Thrush, and Hooded Warbler, but poor for Kentucky Warbler. Power for the composite test statistic with all species pooled exceeded 0.90 for $\gamma = 0.85$ and 0.80 (Table 3).

We detected no differences in capture probability between the two habitats for three of the four species (Table 4). There was evidence of lower capture probability

Table 3. Approximate power of the test for variation in survival among habitats, assuming $\alpha = 0.05$, $\phi_m = \hat{\phi}_{AIC}$ and $\phi_s = \gamma \hat{\phi}_{AIC}$.*

Species	γ	ϕ_m	ϕ_s	Power
Ovenbird	0.95	0.89	0.85	0.12
	0.90	0.89	0.80	0.31
	0.85	0.89	0.76	0.53
	0.80	0.89	0.71	0.72
Wood Thrush	0.95	0.90	0.86	0.16
	0.90	0.90	0.81	0.41
	0.85	0.90	0.77	0.65
	0.80	0.90	0.72	0.81
Kentucky Warbler	0.95	0.89	0.85	0.10
	0.90	0.89	0.80	0.21
	0.85	0.89	0.76	0.32
	0.80	0.89	0.71	0.40
Hooded Warbler	0.95	0.93	0.88	0.13
	0.90	0.93	0.84	0.31
	0.85	0.93	0.79	0.51
	0.80	0.93	0.74	0.67
Composite Test over all four species	0.95			0.22
	0.90			0.64
	0.85			0.91
	0.80			0.98

* $\hat{\phi}_{AIC}$ is the survival estimate based on the model with the smallest AIC; ϕ_m and ϕ_s are the monthly survival probabilities for mature and successional habitats, respectively.

Table 4. Test of the null hypothesis of equal capture probabilities for mature and successional habitats versus the alternative of different capture probabilities by habitat.

Species	Models Tested (H_o vs. H_a)	Likelihood Ratio Test Statistic			Capture Probability Estimates Under H_a			
		χ^2	df	p	Mature		Successional	
					\hat{p}	SÊ (\hat{p})	\hat{p}	SÊ (\hat{p})
Ovenbird	(ϕ, p) vs. (ϕ, p_b)	0.32	1	0.57	0.19	0.047	0.22	0.037
Wood Thrush	(ϕ, p) vs. (ϕ, p_b)	0.65	1	0.42	0.21	0.033	0.25	0.047
Kentucky Warbler	(ϕ, p) vs. (ϕ, p_b)	3.74	1	0.05	0.45	0.058	0.30	0.065
Hooded Warbler	(ϕ, p) vs. (ϕ, p_b)	1.95	1	0.16	0.29	0.063	0.19	0.050

ties in successional forest than in mature forest for Kentucky Warblers. Nevertheless, the composite statistic with all four species pooled was not significant ($\chi^2_4 = 6.66, p = 0.16$).

We approximated the power of these likelihood ratio tests for the three species that showed no difference in capture probabilities between habitats. In these approximations, we set the capture probability for successional habitat equal to the estimate under the AIC-selected model ($p_s = \hat{p}_{AIC}$). We then determined capture probability for the mature forest as $p_m = \gamma \hat{p}_{AIC}$, where γ assumed values between 0.5 and 0.8, based on the premise that capture probability might be lower in mature forests. Power was generally poor for tests involving the individual species, although the composite test with these three species pooled exceeded 0.7 for $\gamma = 0.6$ and 0.5 (Table 5).

The two-parameter model (ϕ, p) had the lowest value of AIC for three species: Ovenbird, Wood Thrush, and Hooded Warbler (Table 6). Thus, the data for these species did not provide evidence of variation in survival or capture probability associated with either location or time.

Table 5. Approximate power of the test for variation in capture probability among habitats, assuming $\alpha = 0.05, p_s = \hat{p}_{AIC}$ and $p_m = \gamma \hat{p}_{AIC}$ *

Species	γ	p_m	p_s	Power
Ovenbird	0.8	0.17	0.21	0.13
	0.7	0.15	0.21	0.25
	0.6	0.13	0.21	0.43
	0.5	0.11	0.21	0.64
Wood Thrush	0.8	0.18	0.22	0.16
	0.7	0.15	0.22	0.32
	0.6	0.13	0.22	0.54
	0.5	0.11	0.22	0.76
Hooded Warbler	0.8	0.19	0.24	0.11
	0.7	0.17	0.24	0.20
	0.6	0.14	0.24	0.34
	0.5	0.12	0.24	0.51
Composite Test over all three species	0.8			0.21
	0.7			0.45
	0.6			0.75
	0.5			0.94

* \hat{p}_{AIC} is the capture probability estimate based on the model with the lowest AIC; p_m and p_s are the capture probabilities for mature and successional habitats, respectively.

For Kentucky Warbler, the three-parameter model (ϕ, p_b) was selected, indicating the need to incorporate habitat-specific capture probability into our survival models.

The monthly overwinter survival estimates for all species were approximately 0.90 (Table 6). Models incorporating time-specificity of survival were not selected using AIC, indicating the absence of evidence for differences between monthly survival during early versus late winter. The test for species-specific variation in monthly survival probabilities provided no evidence of such variation ($\chi^2_4 = 1.19, p = 0.76$). Estimates of capture probability were between 0.20 and 0.25 for Ovenbird, Wood Thrush, and Hooded Warbler (Table 6). Estimates were higher for Kentucky Warbler and depended on habitat. As with survival, probability of capture did not vary over time, so there was no evidence of a need to incorporate time-dependent capture-probability parameters into our models.

Discussion

We found no difference in overwinter survival between birds wintering in mature and successional tropical forest habitats. Our power computations provided confidence that large differences in survival between birds in the two habitats ($\gamma \leq 0.85$, where $\phi_s = \gamma \phi_m$; for example, survival differences at least as large as $\phi_m = 0.90$ and $\phi_s = 0.77$) did not exist. But because we may not have been able to detect differences in monthly survival of less than 10% with these tests, we cannot draw any strong inferences about small overwinter survival differences. Because even small differences in survival can have considerable demographic consequences (Karr 1990), additional data are necessary to test adequately for relatively small differences in overwinter survival probabilities of birds wintering in mature and successional forest. Additional or larger sites, more sampling periods, and higher capture probabilities would increase the power of statistical tests and allow us to test more effectively for smaller differences. However, no other estimates of habitat-specific survival rates are available for wintering Neotropical migratory birds. Indeed, estimates of winter and even annual survival rates are rare

Table 6. Estimated monthly survival and capture probabilities and goodness-of-fit statistics for the low-AIC models.

Species	Model	Survival Probability		Capture probability		Goodness-of-fit test		
		$\hat{\phi}$	SÊ ($\hat{\phi}$)	\hat{p}	SÊ (\hat{p})	χ^2	df	p
Ovenbird	(ϕ, p)	0.89	0.026	0.21	0.032	27.16	29	0.56
Wood Thrush	(ϕ, p)	0.90	0.027	0.22	0.031	30.45	29	0.39
Kentucky Warbler	(ϕ, p_b)	0.89	0.025	$\hat{p}_m = 0.45$	0.058	33.50	28	0.22
				$\hat{p}_s = 0.30$	0.065			
Hooded Warbler	(ϕ, p)	0.93	0.032	0.24	0.045	34.54	26	0.12

for small passerines (Cox 1985; but see Ricklefs 1973; Nichols et al. 1981; Skutch 1985; Rappole et al. 1989; Karr et al. 1990). Clearly, this is an area of extreme importance for conservation efforts (Petit et al. 1993).

Our overwinter survival estimates are for all sexes and age classes combined. Survivorship may differ among sexes and age classes. Although we did not estimate survival for sexes and age classes, the models we used tested for heterogeneity in survival among individuals. We banded a high proportion of first-year birds (C. J. Conway, unpublished data). First-year survivorship for small tropical migrants is commonly low (0.28–0.35) (Sæther 1989), and winter survivorship of some first-year migrants is lower than that of older birds (Holmes et al. 1989). Age ratios were similar, however, between habitats. Sex ratios differed between habitats, and, if survival probability differs between sexes, further studies directed at sex-specific survival need to be conducted before the question of winter habitat suitability can be adequately addressed. However, the results of our model goodness-of-fit tests provided no evidence of substantial heterogeneity in survival among banded birds.

When our monthly survival estimates were extrapolated to correspond to a 12-month period ($\hat{\phi}^{12}$), they yielded annual rates ranging from 0.25 to 0.42. Estimates of annual survival for Neotropical migrants of this size are typically higher than our estimates (Farner 1955; Ricklefs 1973; Nichols et al. 1981; but see Snow & Lill 1974). Indeed, Roth and Johnson (1993) reported a minimum annual survival rate of 0.58 for female Wood Thrush. Estimates of annual survival of Ovenbirds (0.54 and 0.84) are available (Hann 1948; Roberts 1971), but they were obtained before the availability of unbiased methods for estimating survival. Survivorship over a five-month winter period in Jamaica was 0.80 and 0.66 for aggressive, territorial American Redstarts (*Setophaga ruticilla*) and Black-throated Blue Warblers (*Dendroica caerulescens*), respectively (Holmes et al. 1989). Extrapolated to a 12-month period, these estimates would yield annual survival rates of 0.58 and 0.37, slightly higher than our estimates.

However, our overwinter survival estimates incorporate all birds regardless of territorial behavior. Because we included the entire population, rather than only individuals holding territories, it is not surprising that our

survival estimates were lower than those of Holmes et al. (1989). In addition, winter conditions may differentially affect the probability of survival in different species within different regions, and there may be wide variation in survival rates among populations and time periods (Roberts 1971). Indeed, extrapolation of daily winter survival rates (0.996) of territorial radio-marked Wood Thrush in Mexico (Rappole et al. 1989; Winker et al. 1990) yields an annual survival rate (0.23) similar to our estimates. Movement patterns and the proportion of individuals holding territories may differ among habitats, and these differences may affect habitat-specific survival. Consequently, interpretation of our overwinter survival estimates will be enhanced once more information about movement strategies, sex and age segregation, and degree of territoriality is collected.

If survival of migratory birds is lower during the winter season than during the breeding season, our estimates, when coupled with the reported higher breeding-season survival estimates, may yield annual survival estimates similar to those previously reported. Alternatively, if birds are less territorial in winter, permanent emigration from the study area (movement of birds to areas not exposed to sampling efforts) may contribute to lower survival estimates. We did not detect differences in survival probabilities over time within either habitat, indicating that mortality may be constant throughout the winter season in these habitats.

Our estimates of avian survival are low and should be of concern because survival is thought to be an important mechanism regulating winter populations of some migratory species (Holmes et al. 1989; Winker et al. 1990). Although we detected no habitat-specific variation in survival rates, use of successional or mature forests may not be the principal factor affecting winter survival. Winter survival may vary temporally and between sexes, age classes, and individuals with different degrees of territoriality (Holmes et al. 1989; Rappole et al. 1989). In addition, stressful environmental conditions on the wintering grounds may not manifest themselves until birds attempt their spring migration. Examination of the effects of winter habitat use on spring migratory survival would be a fruitful avenue of research. Effective conservation and management of migratory landbirds requires understanding of the environmental features affecting

winter survival, and further research on winter survival of migratory landbirds is warranted. We need to understand the ecological processes limiting migrant populations on both wintering and breeding grounds before we can adequately explain population trends.

Many survey methods require that capture or detection probability does not vary over time or between habitats, but these assumptions are rarely tested (Ekman 1981). Also, knowledge of different capture probabilities among habitats or groups of individuals may provide insight into behavior, population dynamics, and the effectiveness of other survey techniques (Ekman 1981), yet estimates of habitat-specific capture probability are lacking. We found no evidence of a large difference in capture probability between mature and successional forest habitats for Hooded Warblers, Ovenbirds, and Wood Thrush. We cannot draw strong inferences regarding small differences, but the smaller the difference in capture probabilities the smaller any problem the difference may cause to other analyses that do not explicitly account for such differences; our analyses did. Capture probability of Kentucky Warblers was higher in mature forest habitats, contrary to what might be expected. We considered possible differential capture probability in the models we used to estimate overwinter survival, but our results suggest that capture probability does not differ among habitats for some species that inhabit forest understory. But future studies using mist-net data to compare the habitat suitability of other species should examine habitat-specific capture probabilities.

Tropical forests are being altered to support a variety of land uses. The type of alteration largely determines the resultant habitat and its suitability for wintering migratory birds. Agricultural areas that have undergone more-intensive, mechanized cultivation are probably less likely to undergo natural regeneration even if they are left fallow. Some land uses undoubtedly offer more-optimal habitat to wintering migrants than others do. For example, cattle ranching is the major cause of tropical forest alteration (Buschbacher 1986), and cattle pasture has lower migrant diversity than does secondary forest in Belize (Saab & Petit 1992). Traditional plot-rotation agriculture, practiced by indigenous Mayans, results in a variety of successional habitats. The value of disturbed successional forest as migrant habitat has been a topic of recent controversy. Our results suggest that early-successional disturbed tropical forest may not be an inferior habitat for some Neotropical migratory birds that are often associated with more mature tropical habitats. But we did not examine all stages of successional tropical forests. Mature forest is often not immediately replaced by successional forest in many areas of the neotropics. Rather, forest is often removed in favor of pasture, a habitat type where Wood Thrush, Kentucky Warblers, Ovenbirds, and Hooded Warblers seldom overwinter.

Our results suggest that landscapes that have a mosaic of mature and successional forest habitats may be suitable to many forest-migrant species as opposed to areas where forest habitats have been replaced by pasture.

The successional forest habitats in which we worked are a result of the traditional agriculture system practiced by indigenous Maya in southern Belize. Consequently, traditional agricultural techniques appear compatible with migratory bird populations, making their conservation value great compared to pasture. Unfortunately, these techniques are rapidly disappearing throughout the neotropics and being replaced by cattle ranching and mechanized agriculture. Traditional agriculture should not be discouraged for the sake of conservation because wintering migrants, and perhaps resident species, may find the successional habitats that result from this system more suitable than habitats resulting from mechanized agriculture. The introduction of cattle and the conversion of traditional agricultural areas to pasture should be discouraged because of potentially negative effects on migrant populations.

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Appendix

Number of individual birds with common capture histories from 11 netting sites^a in southern Belize, November 1991–March 1993.

Capture History ^b	Wood Thrush					Ovenbird					Kentucky Warbler					Hooded Warbler				
	Site					Site					Site					Site				
	1	3	4	5	6	1	3	4	5	6	1	3	4	5	6	1	3	4	5	6
1000	22	5	3	6	12	14	23	19	0	19	18	10	1	9	2	9	15	6	3	3
0100	9	1	11	6	3	2	20	6	2	7	5	4	1	3	2	3	3	2	2	3
0010	12	4	3	8	16	2	6	7	0	15	0	4	2	0	2	0	3	0	0	4
0001	4	4	3	11	6	7	12	8	1	12	5	5	2	3	4	6	4	6	2	4
1100	4	1	0	0	2	3	2	4	0	2	7	2	2	3	1	2	1	1	1	1
1010	0	1	1	2	1	0	2	6 ^c	0	2	2	3	1	1	1	1	2	0	1	0
1001	2	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1
0110	2	0	0	0	2	2	3	1	0	4	2	0	0	0	1	0	2 ^c	0	0	0
0101	0	1	0	0	0	0	0	0	0	2	0	1	1	0	0	0	0	2	0	0
0011	0	1	0	2	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0
1110	0	0	0	0	0	0	0	3	0	1	5	0	1	1	0	0	0	0	0	0
1101	0	0	1	1	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0
1011	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
0111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0

	Site					Site					Site					Site								
	2	7	8	9	10	11	2	7	8	9	10	11	2	7	8	9	10	11	2	7	8	9	10	11
100	10	6	13	7	7	15	3	5	4	8	4	5	9	0	2	7	1	3	2	3	3	2	2	1
010	5	3	11	9	3	15	1	0	7	2	3	6	2	0	3	0	1	1	1	6	1	2	1	0
001	6	1	1	14	6	32	0	1	5	4	5	3	2	0	2	3	3	4	0	0	0	2	0	1
110	3	1	3	2	3	8	1	0	1 ^c	2	2	2	3	0	1	0	0	1	0	1	0	0	1	1
101	3	3	0	1	2	2	1	0	1	3	1	1	0	1	2	2	3	2	0	0	0	0	3	0
011	3	1	0	3	1	6	0	0	2	0	1	0	2	1	0	1	1	1	0	0	0	1	0	1
111	0	1	0	3	1	0	0	0	0	2	0	4	0	2	0	0	1	1 ^c	0	1	1	0	2	2

^a Mature forest sites = 1, 2, 5, 7, 8, 11 and successional forest sites = 3, 4, 6, 9, 10.^b Each of the four columns represents a capture period, and zero's and one's represent not captured and captured, respectively, during each period. First column = November-December 1991; second column = February 1992; third column = March 1992; fourth column = March 1993. For those with only three columns, first column = November-December 1992; second column = February 1993; third column = March 1993, except site 2, for which columns represent November-December 1991, February 1992, and March 1992, respectively.^c Includes one individual found dead in net on last capture.