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Long-term variation in the winter resident bird community of Guánica Forest, Puerto Rico: lessons for measuring and monitoring species richness

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ABSTRACT. Because the winter season is potentially limiting for migratory birds, understanding their nonbreeding distributional patterns is essential. At a given site, patterns of species occurrence and abundance may vary over time and, within a species, wintering strategies may vary with regard to the degree that individuals are site-faithful both within and between winters. We examined long-term patterns in the composition of a winter resident bird community to determine how long a site must be studied to understand the wintering community. Over a 34-yr period of constant-effort mist netting at a site in Guánica, Puerto Rico, we captured 21 species of winter resident birds, with mean total captures varying from 8.3 to 18.9 individuals per net line and 6–14 species captured per year. Species richness capture/recapture models generated numbers similar to actual capture rates. Capture and recapture data allowed us to categorize winter residents into three groups: sporadic winter residents (14 species), regular winter residents (four species captured nearly every year), and dominant winter residents (three species captured each year with high rates of recapture). Our results suggest that sampling for at least three consecutive winters is needed to accurately characterize the bird community at a site. However, sampling for 5 yr is better, and 10-yr samples generate patterns similar to those based on our entire 34-yr sample. A 1-yr sample provides minimal information about the composition and characteristics of a winter resident bird community.

SINOPSIS. **Variación a largo plazo de una comunidad de aves residentes de invierno del Bosque de Guánica, Puerto Rico: lecciones para medir y monitorear la riqueza de especies.**
Debido a que la temporada invernal es potencialmente limitante para aves migratorias, es esencial entender sus patrones de distribución durante la época no-reproductiva. En una localidad determinada, los patrones de presencia y abundancia de especies pueden variar a través del tiempo, y entre las especies, las estrategias invernales relacionadas al grado de fidelidad de sitio, pueden variar a lo largo de una temporada inviernal o entre varios inviernos. Para determinar cuánto tiempo se debe estudiar una localidad para poder caracterizar a la comunidad invernal, examinamos los patrones de largo plazo en la composición de una comunidad residente de invierno. A lo largo de 34 años de operación constante de varias líneas de redes en el Bosque de Guánica, Puerto Rico, hemos capturado 21 especies de aves residentes de invierno, con promedios de captura que varían entre 8.3 y 18.9 individuos por línea de redes y de 6-14 especies capturadas por año. Los modelos de riqueza de especies de captura/recaptura generan cantidades similares a las tasas de captura reales. Los datos de captura y recaptura nos permiten categorizar a las residentes invernales en tres grupos: residentes invernales esporádicas (14 especies), residentes invernales regulares (cuatro especies capturadas casi todos los años) y residentes invernales dominantes (tres especies capturadas todos los años con altas tasas de recaptura). Nuestros resultados sugieren que se deben hacer muestreos durante al menos tres años consecutivos para poder caracterizar con precisión la comunidad de aves de una localidad. Sin embargo, el muestreo por cinco años es mejor y muestras de 10 años generan patrones similares a los obtenidos en 34 años de muestreo. Un muestreo de un año provee información mínima sobre la composición y característica de una comunidad invernal residente de aves.

Key words: mist netting, Neotropical migrants, Puerto Rico, species richness, winter residents

The last 25 yr of research on the demographics of Neotropical migratory songbirds has led to the realization that populations can be limited on wintering grounds as well as their breeding grounds (Sillett and Holmes 2002, Sherry et al. 2005). However, management and conservation geared toward avoiding winter limitation of songbirds require knowledge of both winter ranges and the habitats resulting in the highest winter survival (Sherry and Holmes 1995, Latta and Faaborg 2001). For many species, our knowledge of winter ranges (Remsen 2001),

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survival, and possible effects of habitat preferences on survival is sparse. One exception at the habitat scale is the work on habitat selection by American Redstarts (*Setophaga ruticilla*), including fitness costs of intersexual dominance patterns and their effect on habitat use by different age and sex groups (Marra et al. 1998, Marra and Holmes 2001) in both native and agricultural habitats (Johnson et al. 2006). However, a similarly detailed study of all species in a coexisting wintering community is likely not feasible.

In many cases, investigators try to determine habitat preferences that reflect habitat quality and, ultimately, high winter survival for entire bird communities from presence/absence survey data. Unfortunately, documenting and describing habitat use without data on survival in these wintering habitats may tell us nothing about habitat quality (Faaborg 2002, Johnson et al. 2006). In addition, determining winter habitat use and species composition of Neotropical migrants in winter habitats can be difficult because wintering birds are generally silent during the nonbreeding season and difficult to survey.

For monitoring and conservation purposes, evaluating the whole community of winter residents using a site may be valuable. If so, methods that permit surveying as many species as possible are best, perhaps using both point-counts and some form of mist netting to record hard-to-observe species (Ralph et al. 2004). Single-year estimates and indices of abundance provide minimal information. In addition, to understand patterns of overwinter persistence, interannual site tenacity, and ultimately, survival, individual birds must be captured and marked. There are now a variety of survey techniques and modeling approaches that allow investigators to integrate detection probabilities and produce less biased estimates of the abundance and density of individual species (Williams et al. 2002), survival, species richness (White et al. 1978, Burnham and Overton 1979), and, most recently, occupancy dynamics (McKenzie et al. 2006). In addition to appropriate data collection protocols, investigators need appropriate analytical tools to generate estimates and test hypotheses concerning the use and quality of winter habitats by Neotropical migrants. Although such studies should clearly last for multiple years at the same location with standardized sampling protocols and modern modeling approaches, questions remain concerning how many years of sampling are needed.

We have used mist nets to monitor bird populations in a dry forest in southwestern Puerto Rico since 1972. At this site, point counts reveal few winter residents (0.01 detections per point); only netting over a period of several years has provided a complete sample of the winter resident community (Faaborg et al. 2004). At least one mist-net line has been operated annually since 1973, with multiple lines since 1989. Here we use the long-term data collected at this site to determine the number of years of monitoring needed to understand: (1) overall species richness, (2) the annual variation in species richness, and (3) the importance of Guánica Forest for each winter resident species. We used capture-recapture methods to estimate species richness and site quality was inferred from abundance, capture rates, and patterns of annual occurrence for each species.

METHODS

The 4015-ha Guánica Commonwealth Forest Reserve (17°55′N, 67°05′W) is located on the southwestern coast of Puerto Rico and comprises mature dry subtropical forest (Ewel and Whitmore 1973). Approximately half the reserve is second growth and the other half is relatively pristine. Vegetation is generally <10 m in height and is partially evergreen with many arborescent cacti. Terborgh and Faaborg (1973) provide a detailed description of the vegetation and bird communities. We attempted to distribute study sites across the range of vegetative types and topography available in the forest.

Guánica Forest is subject to regular droughts that affect populations and survival rates of both resident (Dugger et al. 2000) and winter resident (Dugger et al. 2004) birds. The forest was also damaged by Hurricane Georges in September 1998. Although the hurricane appeared to have little effect on populations or survival of winter resident birds (Dugger et al. 2004), we are still investigating its possible effects on resident birds.

We monitor bird populations in the Guánica Forest using a form of constant-effort mist netting (Terborgh and Faaborg 1973, Faaborg et al. 2004). Lines of 16, 12-m long mist nets with 30-mm mesh are placed end-to-end along a trail in as straight a line as possible during January or early February of each year. Each line is operated from dawn to dark for 3 consecutive days. Captured birds are counted only for the first capture of the sampling period.

Capture rates decline dramatically during this sample, thus obviating the need for a fourth day of netting. About 90% of winter residents are captured during the first two days of sampling. The decline in captures after 3 d suggests that the birds have largely settled onto home ranges and that the number of total captures over 3 d represents most of the individuals available for capture. Latta and Faaborg (2001), Wallace (1998), and Baltz (2000) monitored West Indian winter resident bird populations from October through March and also suggested that January and February were the best months for sampling winter residents.

We operated one net line annually from 1973 to 1988 (except 1977 and 1979), and the results of this work were summarized by Faaborg et al. (2000). We added six additional lines in 1989, an eighth line in 1990, and a ninth in 1991, and have operated the same nine lines from 1991 to 2006. Since 1991, our constant-effort monitoring procedures constituted 432 net-days or nearly 5000 net-hours annually in a variety of microhabitats in the Guánica Forest. In sum, we operate the equivalent of over 1.6 km of net line for a 3-d period. Here, we discuss capture patterns from 1973 to 2005. Data on diversity (richness) and survival were based on multiple samples taken from 1989 to 2006 and presented on a captures-per-net line basis to account for variance in effort during 1989–1990. Species richness was estimated for years when nine net lines were run (1991–2006).

All captured birds were banded with a uniquely numbered federal (USGS) aluminum band to ensure that individuals are counted only once each year and allow us to record recaptures both within and between years. All birds were also aged and sexed (Pyle 1997). We generated estimates of species richness across multiple net lines within years using a closed model capture-recapture approach that allows heterogeneous capture probabilities (White et al. 1978). This approach permits the robust estimation of species richness where detection probabilities are <1.0 and variable among species. We used the program SPECRICH2 (Nichols et al. 1998) to generate all estimates and standard errors. We generated estimates only for the period from 1991 to 2006 (when nine net lines were run) so that we could compare variation in species richness across years with consistent sample effort.

To better understand the number of years needed to obtain a reasonable estimate of the total species pool (i.e., total species richness on this site), we also generated estimates of species richness for 3-yr, 5-yr, and 10-yr blocks using temporal replicates of year. We compared these estimates to actual capture totals during similar time periods. Values are presented as mean $\pm$ 1 SE.

To better understand the importance of Guánica Forest to winter resident species, we categorized winter residents as sporadic, regular, or dominant based on frequency of occurrence, abundance, and site fidelity. "Sporadic winter residents" were those species rarely recorded in nets, "regular winter residents" were species captured every year, but typically in low numbers, and "dominant winter residents" were species captured every year with sufficient captures and recaptures to estimate annual apparent survival and population sizes using mark-recapture modeling techniques.

RESULTS

Over 34 yr, we captured 21 species that we consider winter residents (Table 1). Over 18 yr (7–9 net lines per year), the total mean number of captures of winter residents varied from 8.3 birds per net line in 2005 to 18.9 in 2001 (Table 1; Fig. 1). The number of species captured varied from 6 in 2003 to 14 in 2000 (Table 1; Fig. 2). Warblers dominated captures (>97%) and were the only winter residents captured during 4 yr. The proportion of previously marked birds (banded in a previous year) captured varied from 6.5% in 2001 to 37% in 2003, with a mean of 21.3 $\pm$ 9.7% (Table 1). Annual capture probabilities for the three dominant warbler species on our study area (American Redstarts, Black-and-white Warblers [*Mniotila varia*], and Ovenbirds [*Seiurus aurocapilla*]) varied by species, but were constant over time for Black-and-white Warblers, exhibited a decrease for Ovenbirds, and varied among years for American Redstarts (Dugger et al. 2004).

Our models suggested that the total species pool wintering in Guánica Forest during 1991–2006 was 21 $\pm$ 2.9. However, the estimated number of species captured each year from this available pool varied (Fig. 2). Annual estimates of species richness ranged from

Table 1. Distribution of capture frequencies of different species across seven net lines in 1989, eight net lines in 1990, and nine net lines from 1991 to 2006 in Guánica Forest, Puerto Rico.

Species	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Merlin	1	1							1	1		1		1				
Baltimore Oriole																		1
Bicknell's Thrush																	1	
Black-whiskered Vireo		1									1	1						
Blue-winged Warbler											1							
Northern Parula	4	3	7	8	7	4	7	1	2	22	15	17	15	10	1	6	5	7
Magnolia Warbler			1		1		1			1	2	2	2					
Cape May Warbler	2	1	9				3			1		1				3	2	
Prairie Warbler	2		4	12	4	10	5	2	6	21	19	16	13	10	12	13	8	7
Black-and-white Warbler	35	52	60	67	38	38	50	56	34	41	43	44	45	26	26	15	16	26
American Redstart	13	21	19	30	11	9	29	21	7	34	18	16	24	16	23	14	9	7
Prothonotary Warbler	2		1	1							1	3	6					
Worm-eating Warbler	4	2	6	5	2	3	8	7	10	3	7	5	5	1	3		5	6
Ovenbird	26	44	29	35	34	18	44	38	33	34	22	31	41	30	16	20	24	23
Northern Waterthrush		2	4	1				2			1							
Kentucky Warbler											1						1	
Hooded Warbler	7	10	8	4	1	2	3	2		2	2	2	5			2	3	
Black-throated Blue Warbler		2	2															
Swainson's Warbler		1		1	1								2			1		1
Indigo Bunting			1	1					5	1		1				1		
Rose-breasted Grosbeak							2			2		12	12			4	1	1
Total individuals captured	96	140	151	165	99	85	152	129	98	163	133	152	170	94	81	79	75	79
Mean captures per line	13.7	17.5	16.8	18.3	11.0	9.4	16.9	14.3	10.9	18.1	14.8	16.9	18.9	10.4	9.0	8.8	8.3	8.8
% Recaptured (banded in previous year)	2.1	2.1	15.0	13.2	15.2	33.3	25.9	20.4	24.8	33.7	17.2	18.8	10.5	6.5	31.9	37.0	16.5	6.7	30.3

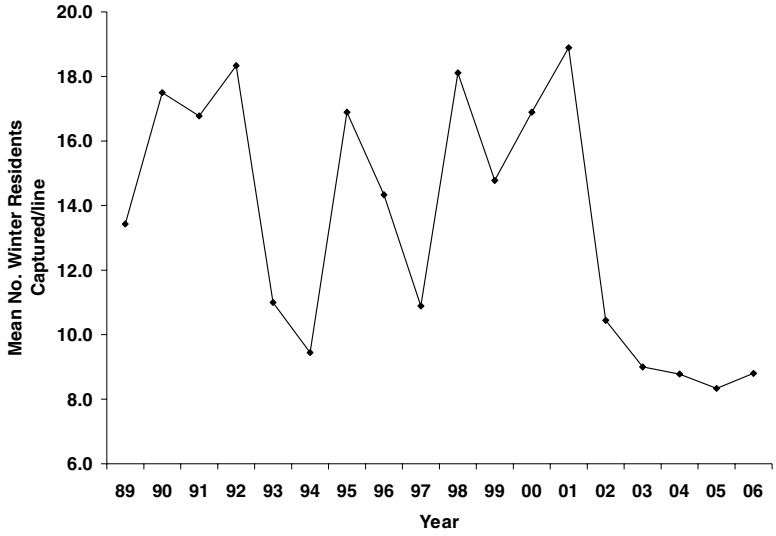

Fig. 1. Mean number of total winter resident individuals captured per line per year in Guánica Forest, Puerto Rico during 1989–2006.

6 in 1997, 2002, and 2003 to 15 in 1991 and 1999 (Fig. 2). Coefficients of variation ranged from 6% to 27%, but were typically around 20%. The number of species captured underestimated species richness in most years (Fig. 2).

Obviously, attempting to describe the winter resident community at Guánica with a single annual sample could provide dramatically different results depending on the sample year. Estimates generated using 3 yr of capture data provide

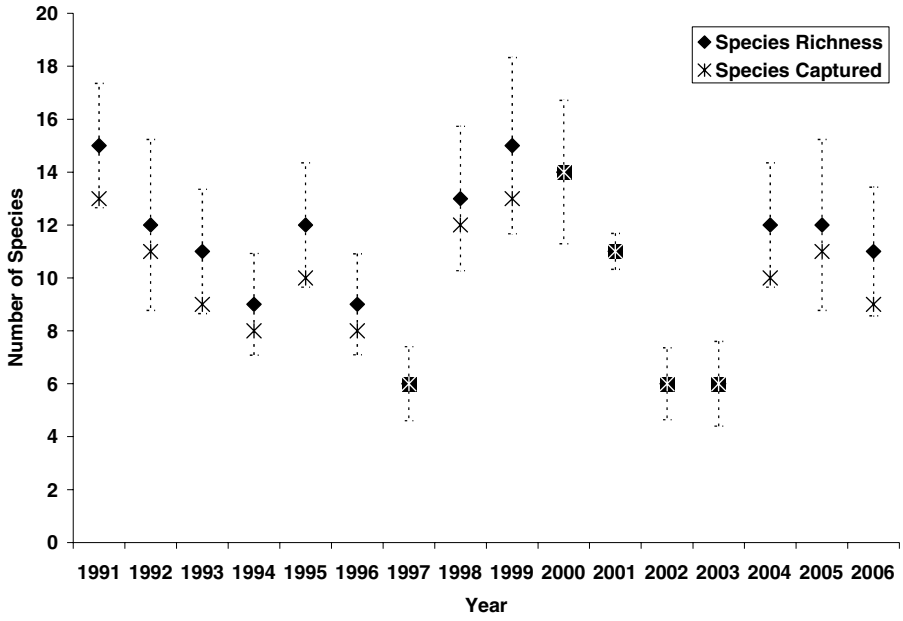

Fig. 2. Annual estimates with standard errors of species richness and actual number of species captured for years when nine net lines were monitored (1991–2006) during January in Guánica Forest, Puerto Rico.

much better estimates of the total species pool (Table 2) and, during the 3-yr period from 1997 to 1999, the estimate equaled the 16-yr estimate. Estimates over 5 yr were somewhat better than the 3-yr estimates, and 10-yr estimates were very good (Table 2). Clearly, both the number of years sampled and the specific years sampled are important sources of variation.

Presence/absence is only one measure of habitat use. We assume that annual return rates are a measure of habitat selection because they suggest that an individual chooses to return to a site. Because we have monitored capture totals and capture probabilities of individual birds over several decades, we can further categorize the 21 species (Table 1) we have captured into three groups defined above.

Table 2. Estimates of winter resident species richness and actual number of species captured for 1-yr, 3-yr, 5-yr, and 10-yr samples in Guánica Forest from 1991 to 2006.

	Year	Estimate (SE)	Number of species captured
Annual estimates			
	1991	15 (2.4)	13
	1992	12 (3.2)	11
	1993	11 (2.4)	9
	1994	9 (1.9)	8
	1995	12 (2.4)	10
	1996	9 (1.9)	8
	1997	6 (1.4)	6
	1998	13 (2.7)	12
	1999	15 (3.3)	13
	2000	14 (2.7)	14
	2001	11 (0.7)	11
	2002	6 (1.4)	6
	2003	6 (1.6)	6
	2004	12 (2.4)	10
	2005	12 (3.2)	11
	2006	11 (2.4)	9
3-yr estimates			
	1991–1993	15 (1.5)	14
	1994–1996	14 (2.6)	11
	1997–1999	21 (3.2)	17
	2000–2002	15 (2.2)	15
	2003–2005	13 (2.2)	13
5-yr estimates			
	1991–1995	16 (1.8)	15
	1996–2000	18 (1.8)	17
	2001–2005	20 (3.9)	16
10-yr estimates	1991–2000	21 (2.4)	19
	1997–2006	20 (2.8)	20

Sporadic winter residents. We categorize 14 species as sporadic winter residents in the Guánica Forest. The mesh size and placement of our mist nets are not appropriate for capturing Merlin (*Falco columbarius*), but they occur regularly in the area and have been captured in 6 yr. We recaptured one individual banded in the same location the previous year.

Black-whiskered Vireos (*Vireo altiloquus*) are intratropical migrants that breed in the Guánica Forest, but generally migrate to South America in winter (although some individuals are present year-round in several forest types in Puerto Rico). We have captured three individuals with no recaptures.

Individual Blue-winged (*Vermivora pinus*) and Kentucky (*Oporornis formosus*) warblers were captured in 1999, and a second Kentucky Warbler was caught in 2005. Single Bicknell's Thrushes (*Catharus bicknelli*) were caught in 1985 and 2005, respectively. A single Baltimore Oriole (*Icterus galbula*) was captured in 2006. Magnolia Warblers (*Dendroica magnolia*), Northern Waterthrushes (*Seiurus noveboracensis*), Black-throated Blue Warblers (*Dendroica caerulescens*), Swainson's Warblers (*Limnothlypis swainsonii*), and Indigo Buntings (*Passerina cyanea*) have been captured $\leq$11 times during our study. Rose-breasted Grosbeaks (*Pheucticus ludovicianus*) have been captured during 6 yr, with as many as 12 (1.3 birds/line) captured in 1 yr. Cape May Warblers (*Dendroica tigrina*) have been captured in about half of our samples, with as many as nine individuals captured (1 bird/line). Prothonotary Warblers (*Protonotaria citrea*) have been caught 19 times in 10 yr. Of the above species, only one Black-throated Blue Warbler, one Prothonotary Warbler, and one Swainson's Warbler were recaptured in subsequent years.

Regular winter residents. Four species of warblers were caught nearly every year, but sometimes in low numbers or not at all. Hooded Warblers (*Wilsonia citrina*) have been caught most years, with total captures ranging from 2 to 10 individuals. We have records of two individuals recaptured between years. Northern Parulas (*Parula americana*) were captured in 9 yr from 1973 to 1988 and annually since 1989, with the number varying from 1 to 22 (2.4/net line) and too few recaptures to compute survival rates. Similarly, Prairie Warblers (*Dendroica discolor*) were captured in most years, but were

only recaptured occasionally. Although Worm-eating Warblers (*Helmitheros vermivorum*) were captured every year from 1989 to 2003, sample sizes were always small and none was captured in 2004. Several individuals of this species have been recaptured over as long as a 6-yr period, and recapture rates of this relatively small number of individuals are marginal with regard to survival analysis.

Dominant winter residents. Ovenbirds, American Redstarts, and Black-and-white Warblers have always been present in reasonable numbers and exhibited relatively high site faithfulness between years. Although we have presented analyses of survival rates for these species (Dugger et al. 2004), high variability in recapture rates (with no captures in some years) makes modeling of the American Redstart problematic even though this species occurs regularly and some individuals have returned to a site for up to 8 yr.

In the Guánica Forest, more than 90% of captured Black-and-white Warblers and American Redstarts are female. Through 2006 we had never recaptured a male of either species between years, so survival estimates include females only (Dugger et al. 2004). Among other sexually dimorphic species, samples are also biased in favor of females. However, sample sizes are small, so it is unwise to draw conclusions about sex-related differences in habitat use for these species.

DISCUSSION

Any attempt to evaluate the importance of Guánica Forest as a wintering site and its importance for any species must take into account annual variability in total abundance and species diversity, and the traits of the species involved, particularly site faithfulness. Properly assessing both the total number of species using this forest and the traits of the component species requires monitoring over at least 3 yr, with many more years required to generate a true representation of the total species pool. A single year's assessment of the Guánica avifauna would identify about half the species possible (on average) and could underestimate the species pool by a factor of 2 or more. Of course, no information about which species or individuals return to this site from year to year could be gathered in 1 yr. Expanding the effort to three consecutive years adds an average of five species per 3-yr sample and decreases the negative bias associated with 1-yr estimates of total species richness. Five-year samples are better, and 10-yr samples provide the most accurate estimates of total species using Guánica Forest in a given year (Table 2). Samples collected over longer periods are more likely to provide the longitudinal data needed to generate the more sophisticated models used to estimate survival rates because samples will include more individuals and more recaptures over longer periods.

Because this is a single-site study, inferences regarding temporal variation in species richness and the conclusions we have reached regarding sampling effort must be made carefully because different patterns in survival, site fidelity, and abundance at other sites will result in changes in species richness patterns. The Guánica dry forest has distinct wet and dry periods, potentially resulting in large within- and between-season variation in habitat quality. Other tropical habitats with a more consistent resource base might not exhibit the kind of variation in species richness we observed and, therefore, fewer years of sampling might be required to reach the same levels of accuracy and precision we attained after 10 yr of netting.

Guánica Forest is clearly an important wintering site for Black-and-white Warblers and Ovenbirds, with relatively large populations present each year. Although recapture rates for both species were high and relatively consistent, Ovenbird recapture rates have exhibited a strong declining trend (BAWW: 0.29 ± 0.04, OVEN: 0.50 ± 0.12 in 1990 to 0.15 ± 0.07 in 2002; Dugger et al. 2004). American Redstarts exhibit much higher variation in capture rates and apparent survival rates (reflecting both true survival and site fidelity; Dugger et al. 2004), suggesting that Guánica Forest may be a secondary habitat for this species. However, individuals of all three species have been found to be site-faithful over long periods (6–8 yr) despite variation in habitat quality due to local rainfall patterns (Dugger et al. 2004), suggesting that this an important and predictable wintering site for these species.

For Northern Parulas, Prairie Warblers, and, perhaps, Hooded Warblers, Guánica Forest may provide adequate habitat to survive at least one season. However, low return rates suggest that birds go elsewhere in subsequent years, perhaps achieving higher dominance status and access

to better-quality wintering habitats (Marra and Holmes 2001). We have already suggested that part of the decline in numbers at our original Guánica net line (Faaborg and Arendt 1989, 1992) was due to Northern Parulas and Prairie Warblers leaving Guánica Forest for acacia (*Acacia* sp.) and mesquite (*Prosopis* sp.) trees in old pastures that became more abundant in the 1980s. At these sites, Prairie Warblers also show high return rates between years (Baltz 2000). In general, we believe that Guánica Forest is not the most preferred habitat for these species, but will be used either when population levels are high or alternative habitat availability or quality is low, as was the case when Hurricane Georges heavily damaged the trees in pastures.

For other species (besides Merlins that were not sampled adequately by our methodology), our data suggest that Guánica Forest is not high-quality wintering habitat. Although we have reported a relatively stable population of Worm-eating Warblers, they were confined to a small part of the area sampled and were absent in 2004. Possibly, these warblers have specific habitat requirements and only some parts of the forest are adequate. In addition, the occasional recapture of a Hooded or Prothonotary warbler from one year to the next may reflect an occasional high-quality wintering site discovered by a few individuals, but does not suggest high overall habitat quality for these species.

Although it may seem inappropriate to suggest that a habitat used only sporadically may be important for a species (such as Guánica Forest for Rose-breasted Grosbeaks that occur infrequently, but are sometimes abundant), we may need to reconsider the habitat requirements of species that seem to exhibit irruptive wintering behavior. For example, grosbeaks may winter in Guánica Forest because of unusually high fruit and seed availability in some years, or because more typical wintering locations may be lower in quality in some years and Guánica provides an important, although infrequently used, refuge. High recruitment after the summer breeding season may also be influencing grosbeak populations in Guánica Forest in some years, particularly because a large number of young produced the previous summer are generally captured in those years when capture totals for grosbeaks are high. Measuring the fitness consequences of habitat selection for such wide-ranging species will be a formidable task.

Although there appeared to be a general relationship between species richness and capture totals during the 1990s, this has not been the case since then because richness increased from 2004 to 2006 whereas captures have been unusually low since 2002. Given that most of our captures are of the three most common species, peaks in species richness like those in 1991 and 1999 suggest some sort of causative ecological phenomenon operating on multiple species. Many of the irregular winter residents, such as Worm-eating Warblers, Hooded Warblers, Prothonotary Warblers, and Prairie Warblers, breed in the southeastern United States where similar ecological factors might be at work affecting whether species winter in Puerto Rico in some years. Longer monitoring may help us better understand winter resident bird communities, but it will probably require more time than we have currently invested.

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