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Improving our understanding of demographic monitoring: avian breeding productivity in a tropical dry forest

M. Edye Kornegay,[1] Amber N. M. Wiewel,[2] Jaime A. Collazo,[3,5] James F. Saracco,[4] and Stephen J. Dinsmore[2]

[1]*North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695, USA*
[2]*Department of Natural Resource Ecology and Management, 339 Science II, Iowa State University, Ames, Iowa 50011, USA*
[3]*U. S. Geological Survey, North Carolina Cooperative Fish and Wildlife Research Unit, Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina 27695, USA*
[4]*The Institute for Bird Populations, P. O. Box 1346, Pt. Reyes Station, California 94956, USA*

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ABSTRACT. The ratio of juvenile to adult birds in mist-net samples is used to monitor avian productivity, but whether it is a "true" estimate of per capita productivity or an index proportional to productivity depends on whether capture probability is not age-dependent (true estimate) or age difference in capture probability is consistent among years (index). Better understanding of the processes affecting age- and year-specific capture probabilities is needed to advance the application of constant-effort mist-netting for monitoring and conservation, particularly in many tropical settings where capture rates are often low. We ranked members of the avian community by capture frequencies, determined if temporary emigration influenced the availability of birds to be captured, and assessed the distribution of birds relative to mist-nets and the parity between capture-based productivity estimates and number of fledglings in nest plots in a tropical dry forest in Puerto Rico in 2009 and 2010. Few captures characterized the community of 25 resident species and, when estimable, capture probabilities were low, particularly for juveniles (typically < 0.1). Negative trends in capture probability, temporary emigration, and the distribution of birds suggest that avoidance of mist-nets influenced capture rates in our study. Increasing mist-net coverage or moving mist-nets between sampling periods could increase capture rates. The number of fledglings observed in nest plots (25 ha/plot) did not correlate well with capture-derived estimates (20 ha/net stations), suggesting the presence of immigrants or failure to find all nests. Our results suggest that indices of breeding productivity from mist-netting data may track temporal changes in productivity, but such data likely do not reflect "true" productivity in most cases unless age-specific differences in capture probability are incorporated into estimates. Pilot studies should be conducted to evaluate capture rates and the spatial extent sampled by mist-nets to improve sampling design and inferences before informing decisions.

RESUMEN. **Mejorando el entendimiento de monitoreo demográfico: productividad reproductiva en un bosque tropical seco**

La proporcion de juveniles a adultos atrapados en redes de niebla son usados para monitorear la productividad de aves, pero si el estimado es "verdadero" o es un índice proporcional a la productividad depende de que la probabilidad de captura no sea dependiente de la edad (estimado verdadero) o que la diferencia en captura por edad sea consistentemente proporcional entre años (índice). Se necesita un mejor entendimiento de los procesos que afectan probabilidades de captura por edad y año para adelantar la aplicación de esfuerzo-constante de redes de niebla para monitorear y conservación, particularmente en ambientes tropicales donde la tasas de captura son bajas. Nosotros ordenamos miembros de la comunidad de aves por frecuencia de capturas, determinamos si emigración temporal influenció la disponibilidad de aves a ser capturadas, y evaluamos la distribución de las aves relativo a las redes de niebla y la paridad entre estimados de productividad a base de capturas y numero de volantones en parcelas con nidos en un bosque tropical seco en Puerto Rico en 2009 y 2010. Pocas capturas caracterizó la comunidad de 25 especies de aves, y cuando se estimaron, la probabilidades de captura fueron bajas, particularmente para juveniles (típicamente < 0.01). Tendencias negativas en probabilidad de captura, emigración temporal, y la distribución de aves sugirió que las mismas eluden las redes de niebla influenciando las tasas de captura. Ampliar la cobertura o mover las redes de niebla entre periodos de muestreo puede aumentar tasas de captura. Los volantones observados en parcelas de anidamiento (25 ha/parcela) no correlacionaron bien con los estimados derivados de captura (20 ha/estación de redes), apuntando a la presencia de inmigrantes o fallo de encontrar todos los nidos. Nuestros hallazgos sugieren que los índices de productividad reproductiva de redes de nieblas pueden rastrear cambios temporales en productividad, pero esos datos probablemente no reflejan "verdadera" productividad en la mayoría de los casos a menos que las diferencias en probabilidad de captura por edad se usen para ajustar los estimados.

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Estudios pilotos deben llevarse a cabo para evaluar tasas de captura y el ámbito espacial muestreado por redes de niebla para mejorar el diseño de muestreo e inferencias antes de informar decisiones.

Key words: capture–recapture, MAPS, mist-nets, Puerto Rico, radio-telemetry, temporary emigration

Constant-effort mist-net sampling is commonly used to monitor avian demographic parameters (Nott et al. 2002, Ruiz-Gutierrez et al. 2016, Saracco et al. 2016). This sampling technique is appealing because of its relatively low cost and the results can be used to index or estimate a variety of demographic parameters, including local survival and breeding productivity rates, and population size (DeSante et al. 2004). These demographic parameters are invaluable for providing insights into underlying processes that sustain avian communities. Understanding these processes is of utmost importance in a conservation context in regions like the Caribbean where extensive human-modified habitats are commonplace relative to the small geographic extent of many islands (Lugo et al. 2012, Radeloff et al. 2015).

Several examples of the application of constant-effort mist-net sampling in the tropics have been reported in recent years. Ruiz-Gutierrez et al. (2012, 2016) used capture–recapture data to estimate annual survival and discern transitional periods of resident and Neotropical migrants in Central America. Saracco et al. (2016) used similar types of data to estimate annual survival rates, but also reported an index of breeding productivity in a remote tropical oceanic island on Saipan, Northern Mariana Islands. Ruiz-Gutierrez et al. (2012) summarized mist-net sampling studies in the tropics since 1990, but, except for a study by Saracco et al. (2016), emphasis to date has been on estimates of local annual survival rates and related site-persistence and residency metrics (Ruiz-Gutierrez et al. 2012, 2016).

Interest in breeding productivity is justified because it is a fitness parameter, useful in a wide array of conservation applications such as assessing population status and gauging responses of bird populations to environmental changes (DeSante et al. 2001, Saracco et al. 2016, 2018). The productivity metric derived from constant-effort mist-net sampling is also appealing because it reflects the cumulative outcome of an entire nesting cycle, including nest survival and early post-fledging survival. The few reports of breeding productivity derived from constant-effort mist-net sampling are likely due to stringent data requirements and model assumptions involved in its estimation. In its simplest form, if capture probability is not age-dependent, the age ratio stemming from capture data is an estimate of "true" per-capita productivity. However, this assumption is unlikely to ever be met, at least in temperate regions (Bart et al. 1999, DeSante et al. 2004), and the probable reason is the presence of transients in the population (Nott et al. 2002). In addition, adults have greater exposure to capture, i.e., resident adults are available for all sampling periods whereas HY birds are only available for some subset of periods between when they fledge and disperse (DeSante et al. 2001). Lastly, there is uncertainty about the spatial scale of sampling with mist-nets and its implications for inferences about local productivity (Dunn and Ralph 2004).

In practice, reliable insights about breeding productivity are gained when the age ratio is used as an index. The index is valid if age-specific capture probabilities are consistent among years or if temporal differences in age-specific capture probabilities can be accounted for by covariates (e.g., effort; Nott et al. 2002, Robinson et al. 2007, Saracco et al. 2016). In some cases, however, annual estimates of breeding productivity can be essential to advance avian conservation. This is exemplified by "species-at-risk" of endangerment or threatened and endangered species. In these cases, knowing how populations might rebound after, for example, a catastrophic event, informs decisions regarding the level of management required to recover a species' population or prevent its endangerment. These estimates would also be valuable when conducting demographic analyses (e.g., population viability analysis, or PVA) to project population persistence given a specified chance of recurrent catastrophic or management events and reproductive performance (Woodworth 1999, Beissinger et al. 2008).

The underlying processes that influence age-specific capture rates in the tropics are not well documented or understood.

[5]Corresponding author. Email: jcollazo@ncsu.edu

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Prominent among potential factors is the low capture rates of resident species, a phenomenon reported by MacArthur and MacArthur (1974) and Karr (1990). Because low capture rates can be pervasive, in either temperate or tropical regions, some researchers have suggested using only captures of juveniles to estimate breeding productivity (Nur et al. 1999, Robinson et al. 2007). This approach is appealing for its apparent simplicity, but relies on assumptions about the relationship between the number of adults and juveniles in a sampled area. Thus, if capture rates in the tropics are indeed low, focusing on juvenile capture rates alone does not make estimates immune to inferential problems.

We sampled the avian community of the Guanica State Forest, a dry forest in southern Puerto Rico, in 2009 and 2010 to gain a greater understanding of the processes that might influence capture probabilities in a tropical setting. In prior studies in this forest (Faaborg et al. 1984, 1997, 2013, Faaborg and Arendt 1995), investigators reported apparent estimates of annual survival and trends in capture rates derived from multi-year mist-net sampling data. We documented and ranked captures of birds in the resident community, and used data from three species with the highest capture rates to determine if data were adequate to estimate "true" annual estimates of breeding productivity (AHY $\cong$ HY) or support the use of an index of productivity. We also characterized patterns in the availability of individuals to be captured using three models of within-season temporary emigration advanced by Kendall et al. (1997). We complemented insights from capture models with radio-telemetry data to depict the spatial distribution of our focal species relative to mist-nets, and the probability that individuals of each species were present (occupancy) in the study area. Lastly, we searched four nest plots, each containing our mist-net stations, to evaluate the similarity between direct (or field) estimates of breeding productivity and those derived from mist-net efforts.

METHODS

Study area. The Guánica Dry Forest is a Biosphere Reserve on the southwest coast of Puerto Rico and represents a prime example of a subtropical dry forest (Fig. 1; Gould et al. 2007). Dominant plant communities include coastal scrub, semi-evergreen, and semi-deciduous forests (Lugo et al. 1978, Gould et al. 2007). The forest has an eastern tract (2915 ha) and a western tract (736 ha) that are 5 km apart. Average annual rainfall is ~860 mm, and average annual temperature is 25.1°C.

Focal species. Puerto Rican Bullfinches (*Loxigilla portoricensis*), Bananaquits (*Coereba flaveola*), and Adelaide's Warblers (*Setophaga adelaidae*) were among the most frequently captured species in our study (Table 1), and the only ones that yielded identifiable parameter estimates in the first year of our study (2009). Based on the latter results and interest in the reproductive biology of resident species (Wiewel et al. 2013), we augmented sampling efforts to include the western tract of the forest, searched four nest plots where mist-net stations were located, and radio-tracked individuals of each species to learn more about factors that might influence capture rates. Bananaquits are common throughout most of the Caribbean (Raffaele et al. 1998). Puerto Rican Bullfinches are a common endemic in forested habitats, and Adelaide's Warblers are also endemic and commonly found in moist limestone forests and thickets in dry forests such as Guánica.

Mist-net sampling. We operated four mist-net stations in the eastern tract of the forest in 2009 and 2010, and three stations in the western tract in 2010. We collected data employing commonly used schemes; namely, sampling one tract during one season (henceforth, single year-single tract or SYST), sampling multiple tracts in one year (single year-multiple tracts or SYMT), and sampling a tract multiple years (multiple years-single tract or MYST). Data collected in the western tract in 2010 corresponded to the SYST scheme. Data collected in 2010 at the eastern and western tracts represented the SYMT scheme. Data collected in 2009 and 2010 in the eastern tract represented the MYST scheme. Each station consisted of an array of 10 mist-nets (12-m long, 30-mm mesh) placed near habitat edges (e.g., trails) to enable mist-net operation and where capture rates tend to be higher as birds moved through forest breaks (DeSante et al. 2004). We positioned nets around core areas, defining a core area as 20 ha (DeSante et al.

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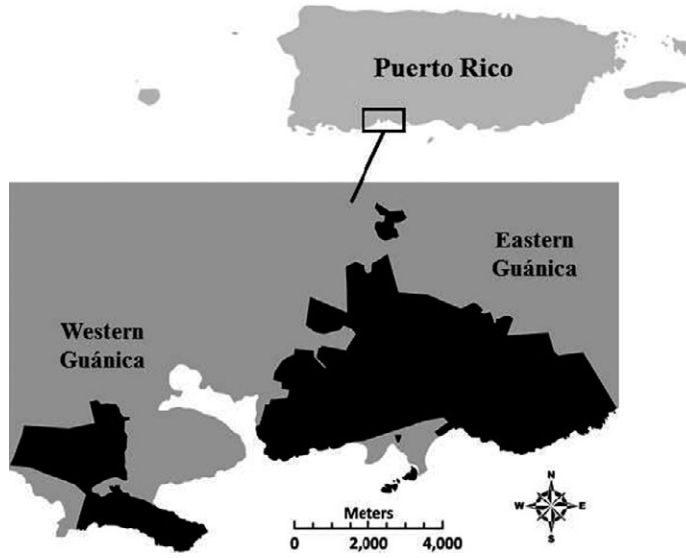

Fig. 1. Map of Puerto Rico and the Guánica Dry Forest showing the eastern and western tracts of the forest.

Table 1. Number of individuals of resident species of birds captured at the Guanica State Forest in Puerto Rico, 2009–2010.[a]

Species	Scientific name	East 2009	East 2010	West 2010	Total
Puerto Rican Bullfinch	*Loxigilla portoricensis*	119 (21)	61 (22)	139 (37)	319
Bananaquit	*Coereba flaveola*	86 (17)	71 (28)	154 (54)	311
Common Ground-dove	*Columbina passerina*	80 (9)	64 (10)	157 (17)	301
Puerto Rican Tody	*Todus mexicanus*	92 (44)	75 (38)	52 (25)	219
Adelaide's Warbler	*Setophaga adelaidae*	74 (25)	55 (28)	59 (20)	188
Caribbean Elaenia	*Elaenia martinica*	64 (12)	44 (11)	60 (21)	168
Black-faced Grassquit	*Tiaris bicolor*	36 (0)	28 (3)	47 (10)	111
Puerto Rican Flycatcher	*Myiarchus antillarum*	31 (7)	23 (5)	15 (9)	69
Pearly-eyed Thrasher	*Margarops fuscatus*	41 (4)	23 (2)	4 (0)	68
Red-legged Thrush	*Turdus plumbeus*	17 (2)	18 (6)	31 (6)	66
Puerto Rican Lizard Cuckoo	*Coccyzus vieilloti*	21 (6)	16 (6)	0 (0)	37
Puerto Rican Vireo	*Vireo latimeri*	10 (2)	9 (4)	10 (8)	29
Key West Quail-dove	*Geotrygon chrysia*	12 (1)	16 (2)	0 (0)	28
Black-whiskered Vireo	*Vireo altiloquus*	12 (1)	7 (1)	8 (4)	27
Mangrove Cuckoo	*Coccyzus minor*	12 (0)	6 (0)	9 (0)	27
Lesser Antillean Pewee	*Contopus latirostris*	10 (5)	5 (3)	0 (0)	15
Puerto Rican Spindalis	*Spindalis portoricensis*	3 (0)	1 (0)	11 (1)	15
Puerto Rican Woodpecker	*Melanerpes portoricensis*	8 (1)	6 (2)	0 (0)	14
Shiny Cowbird	*Molothrus bonariensis*	2 (0)	1 (0)	6 (0)	9
Venezuelan Troupial	*Icterus icterus*	0 (0)	0 (0)	7 (0)	7
Gray Kingbird	*Tyrannus dominicensis*	1 (0)	0 (0)	4 (0)	5
White-winged Dove	*Zenaida asiatica*	1 (0)	0 (0)	2 (0)	3
Antillean Euphonia	*Euphonia musica*	0 (0)	0 (0)	2 (0)	2
Northern Mockingbird	*Mimus polyglottos*	0 (0)	0 (0)	2 (0)	2
Zenaida Dove	*Zenaida aurita*	1 (0)	1 (0)	0 (0)	2

[a]Data are grouped by whether captures were in the eastern or western tract of the forest. The number of birds recaptured is shown in parentheses. Species are listed in descending order by total number of captures.

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2004). Stations remained in the same configuration and location during the study. Mist-net stations were operated from 4 March through 7 July each year, a period when juveniles and adults are available for capture based on available information on the breeding chronology of birds in dry forests in Puerto Rico (Staicer 1991, Wiewel et al. 2013). Nets were opened at local sunrise, operated for 6 h and then closed each day. Nets were not operated during periods of adverse weather conditions (e.g., rain, wind, and heat). All birds captured were banded with a United States Geological Survey aluminum band. Data on species, age, mass, and capture location were recorded. Birds captured in the same calendar year of hatching were aged as hatching-year (HY) and older birds were aged as after-hatching-year (AHY) based on the traditional calendar-based system (Pyle 1997).

Our sampling design and analyses followed Pollock's Robust Design (Pollock 1982), a framework that permits examination of potential factors influencing capture rates and temporary emigration. Under the Robust Design, we divided each breeding season into either 12 (western tract) or 13 (eastern tract) primary periods separated by intervals of 5.8–10.0 d each, weather conditions permitting. Sampling in the eastern and western tracts was alternated because simultaneous sampling in both tracts was not possible. Each primary sampling period included two consecutive days of mist-netting so it could be assumed that the population was closed to births, deaths, immigration, and emigration. Longer sampling periods were tried in 2009 (e.g., 3 d), but capture rates were too low to warrant the extra effort. The population was considered open to the aforementioned demographic events between sampling occasions. The Robust Design assumes that all animals have independent fates, no bands are lost, banding does not affect survival, and the animals marked are representative of the whole population (Kendall et al. 1995). Our telemetry and banding data indicated that no bands were lost, and banding did not affect survival. We also modeled within-year daily age-specific survival to avoid assuming all individuals had equal survival.

Modeling capture–recapture data. We modeled data focusing on estimating daily capture probability (P) and temporary emigration (G). Estimates were reported on a per daily basis, and refer to the core area or forest tract, or combination (SYMT). We tested for equal capture probability by age class (pHY = pAHY) within seasons (i.e., year), the underlying premise to estimate true breeding productivity. Depending on the data set, daily survival was modeled as constant (.), by year (YR), and by age (AHY, HY). Capture probability was modeled as constant (.), by age, by tract (east, west), and linear trend (T). We tested whether daily age-specific capture probabilities were consistent between years (YR) or whether potential differences could be accounted for by time (Age * YR). The linear trend fit is a reduced parameterization of an age * T model for capture rates. Recapture probability was only modeled as constant between ages because this was not a parameter needed to meet the objective of our study.

The potential for temporary emigration was investigated using three competing models: random and Markovian temporary emigration, and no movement (Kendall et al. 1997). These models have two parameters: gamma prime (G') and gamma double-prime (G''). The G' parameter represents the probability that a bird will remain unavailable during a sampling period i, given that the bird was not available during the previous sampling period i-1 and that it survives to period i. The G'' parameter represents the probability that a bird is unavailable for capture during a sampling period i, given that the bird was available for capture during the previous sampling period i-1 and that it survives to period i (Kendall et al. 1997). In the Markovian temporary emigration model, parameters are modeled separately (G', G'') so that the probability of transitioning between the available and unavailable states between primary periods depends on availability of a bird in the previous primary period. In other words, the probability of a bird being captured during the current mist-net session depends on whether the bird was available (or not) to be captured in the previous mist-net session. In the random or classic temporary emigration model, the probability of transitioning between the available and unavailable states between sessions does not depend on the availability of the bird in the previous session ($G' = G''$). Ecologically, this means that the

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probability of a bird being in the study area during the current mist-net session (primary sampling occasion) is the same for those previously in and those previously out of the study area during the previous mist-netting session (W. Kendall, pers. comm.). The null model for the two previous models is the no movement model, which assumes that unavailable birds remain unavailable and available birds remain available during all sampling periods ($G' = G'' = 0$). Data were insufficient to estimate age-specific temporary emigration rates, thus, our estimates refer to the availability (probability) of individuals of a species to be captured. We tested whether there was a linear trend (T) in temporary emigration throughout the season.

Models were run in program MARK (White and Burnham 1999) using the Robust Design and the Huggins closed captures data type options. We used Akaike's Information Criterion (AIC) to select the most parsimonious model. All of our global models fit the data (Goodness-of-fit Chi-square tests $P = 0.10–0.34$; Table S1). Models were ranked by corrected AIC (AIC_c), where the model with the lowest AIC_c was the model with the most support in the data. The difference in AIC_c units between the best supported model and any other model (ΔAIC_c) was used to calculate model weights (wt_i), which indicate the relative likelihood of the model given the data (Burnham and Anderson 2002). We report models with $\Delta AIC_c \leq 2$, but provide a list of all candidate models (Tables S2–S4). We considered an effect (i.e., β coefficient) as strongly supported if the 95% confidence interval did not overlap zero, otherwise it was considered as a weak effect or no effect. Parameter estimates $\pm$ SE are reported.

Radio-telemetry. We radio-tracked birds in the western tract of Guanica Dry Forest to determine the daily probability that birds were present in sampled areas during mist-net operations in 2010. Birds were radio-tagged between 19 March and 18 June 2010, corresponding to the 2nd to 12th primary sampling periods with mist-nets. These dates encompass the period when young were fledging (Wiewel 2011). We focused on the western tract because topography was more conducive to detecting radio signals.

Transmitters were attached using figure-eight harnesses (Rappole and Tipton 1991). We attached transmitters to 29 AHY Bananaquits (mean mass = 10 g), 31 AHY Puerto Rican Bullfinches (31 g), and 12 AHY Adelaide's Warblers (7 g). Six additional radio-tagged Bananaquits were juveniles (HY) to gain insights about age-dependent dispersal. Bananaquits, Adelaide's Warblers, and some Puerto Rican Bullfinches were equipped with transmitters (Model BD-2N; Holohil, Carp, ON, Canada) that weighed 0.5 g and had a nominal lifetime of 21 d. The remaining bullfinches were equipped with transmitters (Model BD-2; Holohil) that weighed 0.7 g and had a nominal lifetime of 28 d. We tracked birds from the time of release either to the end of the transmitter's lifetime or beyond if transmitters were still emitting signals. We tracked birds using receivers (R410 Scanning Receivers, Advanced Telemetry Systems, Isanti, MN) with three-element Yagi antennas twice daily, between 09:00–12:00 and again between 16:00–19:00. Bearings were taken from 23 permanent stations along a loop trail located in the study area, with two people starting at the north end of the trail and then moving south on each side of the trail, taking care to check signals simultaneously. Signals were checked on the ground at 18 stations and, at the remaining stations, from the top of 4.8-m-tall towers to increase the likelihood of detecting signals in uneven terrain. Bearings used for analysis were those of birds located at the same time of day (i.e., 09:00–12:00 and 16:00–19:00) to try to minimize the effect that bird movement might have on location estimates. We obtained estimated locations using a Maximum Likelihood Estimator (Lenth 1981) in program LOAS version 4.0.3.7 (Ecological Software Solutions, Urnasch, Switzerland). Intersections of bearings beyond 2 km were excluded because that was the maximum range of the transmitters. Weighted bivariate ellipses were calculated from the estimated locations of adult individuals to create a home range area where activity was concentrated (Samuel and Garton 1985). This method assumes that a bird's activity is concentrated in the center of the ellipse, which is a reasonable assumption for birds that might be breeding. Weighted bivariate ellipses also reduce the effect of

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extreme locations (i.e., outliers) on the size of home ranges.

Nest monitoring. Field-derived estimates of breeding productivity were obtained from a concurrent nest-monitoring study. Four 25-ha nest plots were established in each of two forest tracts, corresponding with the location of mist-net stations that sampled ~20 ha (DeSante et al. 2004). We searched for and monitored nests of the three focal species from April to July 2009 (east tract) and 2010 (east and west tracts) as described by Wiewel et al. (2013), effort that coincided with mist-net operation. We located nests by observing the breeding behavior of birds and by systematically searching in appropriate vegetation. Once a nest was found, flagging tape with directions to the nest was attached to vegetation at least 5 m from the nest. We monitored nests approximately every 3–5 d. Nests located higher than 2 m were checked by a small mirror mounted on a rod or a narrow plumbing snake camera (Ridgid micro-EXPLORER®, Ridge Tool Company, Elyria, OH). We considered nests failed if there were signs of predation or if nestlings disappeared before day 14, which was the expected day of fledging. A nest was considered successful if we observed fledglings near a nest or if a nest was observed with nestlings until potential fledging dates. Data were used as an empirical measure of breeding productivity to gauge the utility of the true estimate of breeding productivity derived from capture data. A strong, positive correlation between these two metrics is taken as an indication of its utility (DeSante et al. 2004, du Feu and McMeeking 2004, Saracco et al. 2006). Productivity from the nest-monitoring study was expressed as the number of fledglings per adult. We used the former metric to compare it to the true estimate of breeding productivity derived from mist-net data (DeSante et al. 1995). The latter metric was of interest because it has been advanced as an alternative metric to estimate breeding productivity, assuming that the number of juveniles captured in mist-nets is proportional to the population size in the study area (Nur et al. 1999).

Occupancy estimates. We estimated the daily probability that a bird would be present and detectable in the study area using a multi-season occupancy modeling approach where individual birds are viewed as "sites" (MacKenzie et al. 2006). The expected daily proportion of individuals with transmitters present in the area sampled by nets was obtained as: colonization probability/(colonization probability + extinction probability) (J. D. Nichols, pers. comm.). In our context, colonization refers to the daily probability that a bird with a transmitter is present in the study area at time t given that it was not present at time t-1. Conversely, extinction refers to the probability that a bird is not present at time t, given that it was present at time t-1. Note that this approach is equivalent to the Markovian temporary emigration model of Kendall et al. (1997; see Barbraud et al. 2003 for discussion of this equivalence). We also tested whether occupancy exhibited non-Markovian dynamics (i.e., occupancy at time t was independent of occupancy at time t–1 or eps = 1-gam). The study area was defined as the extent where birds would have a non-zero probability of being detected, i.e., within 2 km (maximum range of transmitters) of tracking trails. To account for possible seasonal differences in the time when birds were fit with transmitters, we divided the season into three periods based on observed breeding chronology, including early season ($\leq$ 23 April 2010), mid-season (24 April–30 May 2010), and late season ($\geq$ 31 May 2010). During all of these periods, young were fledging, albeit the peak was during the mid-season (Wiewel 2011). For Bananaquits, colonization and extinction rates were also modeled by season and age.

Model assumptions were: (i) the system was closed to changes in the occupancy status during 2-d mist-netting sessions, but open between different 2-d mist-netting sessions, and (ii) birds were not falsely detected. We believe that all assumptions were met because mist-netting sessions consisted of two consecutive days and detection of individuals was enhanced by radio-transmitters. Daily survival estimates of capture–recapture models lent support to the assumption of high survival during the period of study. Indeed, no mortalities of radio-marked individuals were recorded. We used AIC to evaluate support in the data for models in the candidate set and the strength of each covariate's effect on extinction and colonization rates (Burnham and Anderson 2002). Parameter estimates were derived from the model with the lowest

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AIC score for each species. The relationship of the probability of extinction and colonization with covariates was established using a logit link in program PRESENCE (Hines 2006). We considered an effect (i.e., covariate β coefficient) strongly supported if the 95% confidence interval did not overlap zero, and with a weak or no effect otherwise. Parameter estimates ± SE are reported.

RESULTS

Community capture summary Twenty-five species of resident birds were captured during our study (Table 1). In 2009, we captured 808 birds in the eastern tract, and 160 of those birds were recaptured in the same year. In 2010, mist-nets were operated in both tracts, with 632 birds captured in the western tract of the forest and 212 of those birds recaptured; 545 were captured in the eastern tract and 178 were recaptured. Puerto Rican Bullfinches, Bananaquits, and Adelaide's Warblers were among the most frequently captured species (Table 1), and served as focal species to examine factors influencing capture rates of resident birds.

Puerto Rican Bullfinches. We aged 303 of 319 Puerto Rican Bullfinches, including 85 AHY and 33 HY birds in 2009 and 163 AHY and 36 HY birds in 2010. A model featuring constant and equal survival between age classes, random temporary emigration ($G' = G''$), and equal capture probability between age classes with a linear trend over the season was the most strongly supported model for the SYST data ($wt_i = 0.26$; Table 2). The linear trend was strong and negative (Fig. 2A, $\hat{\beta}$ -0.24 ± 0.08). Capture probabilities ranged from 0.49 ± 0.36 early in the season to 0.06 ± 0.04 toward the end. The estimate of random emigration rates was 0.88 ± 0.06, indicating a high probability of a bird being unavailable for capture during a 2-d mist-netting session.

Four additional models were competitive ($\Delta AIC_c \leq 2$). The second-best model featured the same terms except that there was a linear trend in random temporary emigration and the trend was positive and strong ($\hat{\beta}$ 0.22 ± 0.08). The SYMS data set was best explained by a model with constant, equal survival between age classes, Markovian temporary emigration rates (G', G''), equal capture probabilities between age classes, and a location (east vs. west tracts) effect on capture probabilities ($wt_i = 0.26$; Table 2). The influence of tract on capture probabilities was not strong ($\hat{\beta} = -1.00 \pm 0.53$). Three additional models were competitive ($\Delta AIC_c \leq 2$). One of these featured age-specific daily survival rates and random emigration rates; the other two featured a negative linear trend in capture probabilities, albeit not strong ($\hat{\beta} = -0.08 \pm 0.07$).

The model with the highest support for the MYST data set featured constant, equal survival between age classes, random temporary emigration ($G' = G''$), and different age-specific capture probabilities ($wt_i = 0.18$; Table 2). Six additional models were competitive ($\Delta AIC_c \leq 2$), with five of six models featuring constant, equal survival between age classes, random emigration, and different age-specific capture probabilities. Daily probability of capture was 0.44 ± 0.09 for adults and 0.13 ± 0.08 for juveniles; random movement probability ($G' = G''$) was 0.95 ± 0.02. Among competing models, one featured year ($\hat{\beta} = 0.77 \pm 0.55$) and another year * age effects ($\beta = -0.97 \pm 1.52$), but their influence on capture probability was not strong. Overall, analyses of SYST and SYMT data sets provided support for use of the age ratio as a true (direct) estimate of breeding productivity. Age-differences in capture probability were detected in the MYST data set, but we found no year * age effects, suggesting that the age ratio should more generally be considered an index of productivity.

Weighted bivariate ellipses for all Puerto Rican Bullfinches were 9.00 ha (95% CI 8.03–10.15 ha), indicating that radio-tagged birds remained within the estimated mist-net sampling area of 20 ha (Fig. 3A). The expected proportion of Puerto Rican Bullfinches present in the study area on any given day was 0.32 (95% CI: 0.31–0.33) early in the season, 0.78 (95% CI: 0.75–0.89) during mid-season, and 0.61 (95% CI: 0.57–0.62) late in the season. Variation in capture rates for Puerto Rican Bullfinches was best explained by a model whose extinction probability was influenced by season (Table 3). Daily extinction probability was 0.11 ± 0.02, with a daily detection probability of 0.87 ± 0.01. Daily extinction probabilities were 0.23 ± 0.05 (early

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Table 2. Model selection tables for Puerto Rican Bullfinches, Bananaquits, and Adelaide's Warblers captured at Guánica State Forest in southwestern Puerto Rico, 2009–2010.

Model	AICc	ΔAIC_c	wt_i	*K*	Deviance
Puerto Rican Bullfinch (SYST)					
{S(.), G′(.) = G″(.), *P*(AHY = HY + T), c(AHY = HY)	483.89	0.00	0.26	5	176.91
{S(.), G″ = G″+T, *P*(AHY = HY), c(AHY = HY)}	483.95	0.06	0.25	5	176.97
{S(.), G(.) = G″(.), *P*(AHY ≠ HY + T), c(AHY = HY)}	484.17	0.28	0.22	5	175.06
{S(.), G″=G″ + T, *P*(AHY = HY + T), c(AHY = HY)}	485.21	1.32	0.13	5	176.10
{S(.), G′(.) = G″(.) = 0, *P*(AHY = HY + T), c(AHY = HY)}	485.54	1.65	0.11	4	180.66
Puerto Rican Bullfinch (SYMT)					
{S(.), G′(.), G″(.), *P*(AHY = HY + tract), c(AHY = HY)}	723.03	0.00	0.26	6	712.77
{S(AGE), G′(.) = G″(.), *P*(AHY = HY + tract), c(AHY = HY)	723.45	0.42	0.21	5	715.28
{S(.), G (.), G″(.), *P*(AHY = HY + tract + T), c(AHY = HY)}	723.89	0.86	0.17	7	711.53
{S(.), G′(.), G″(.), *P*(AHY ≠ HY + tract), c(AHY = HY)}	724.63	1.60	0.12	6	712.26
Puerto Rican Bullfinch (MYST)					
{S(.), G″(.) = G′(.), *P*(AHY ≠ HY), c(AHY = HY)}	588.52	0.00	0.18	5	578.23
{S(.), G″(.) = G′(.), *P*(AHY ≠ HY + YR), c(AHY = HY)}	588.67	0.16	0.14	6	576.26
{S(.), G″(.), G′(.), *P*(AHY ≠ HY), c(AHY = HY)}DS}	589.21	0.69	0.11	6	576.80
{S(.), G″(.) = G′(.), *P*(AHY ≠ HY + T), c(AHY = HY)}	589.47	0.95	0.10	6	577.06
{S(.), G″ = G′ + T, pAHY ≠ HY), c(AHY = HY)}	589.82	1.30	0.08	6	577.40
{S(YR), G″(.) = G′(.), *P*(AHY ≠ HY), c(AHY = HY)}	590.39	1.87	0.06	6	577.98
{S(.), G″(.) = G″(.), *P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	590.43	1.91	0.06	7	575.88
Bananaquit (SYST)					
{S(.), G″ = G′ + T, *P*(AHY ≠ HY + T), c(AHY = HY}	1033.93	0.00	0.32	7	975.15
{S(.), G (.) = G″(.), *P*(AHY ≠ HY), c(AHY = HY)}	1034.16	0.23	0.29	5	979.59
{S(.), G (.) = G″(.), *P*(AHY ≠ HY + T), c(AHY = HY)}	1035.07	1.14	0.18	6	978.40
{S(.), G (.), G″(.), *P*(AHY ≠ HY), c(AHY = HY)}	1035.74	1.81	0.13	6	979.08
Bananaquit (SYMT)					
{S(.), G′(.) = G″(.), *P*(AHY ≠ HY + tract), c(AHY = HY)}	1368.71	0.00	0.53	6	1356.47
{S(.), G (.), G″(.), *P*(AHY ≠ HY + tract), c(AHY = HY)	1370.56	1.85	0.21	7	1356.24
Bananaquit (MYST)					
{S(AGE), G″(.) = G′(.) = 0, *P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	739.47	0.00	0.35	7	724.91
{S(AGE + YR), G″(.) = G′(.) = 0, *P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	739.82	0.35	0.30	8	723.10
Adelaide's Warbler (MYST)					
{S(AGE), G″(.) = G′(.) = 0, *P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	733.59	0.00	0.20	7	718.97
{S(.), G″(.) = G′(.),*P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	733.88	0.30	0.17	6	721.43
{S(AGE), G″(.) = G′(.) = 0, *P*(AHY ≠ HY), c(AHY = HY)}	734.37	0.78	0.14	5	724.04
{S(AGE + YR), G″(.) = G′(.) = 0, *P*(AHY ≠ HY + YR + YR * AGE), c(AHY = HY)}	734.63	1.04	0.12	8	717.83
{S(AGE), G″(.) = G′(.) = 0, *P*(AHY ≠ HY + YR), c(AHY = HY)}	734.94	1.36	0.10	6	722.48

Models were ranked by the difference from the top model in AIC value corrected for small sample size (ΔAIC_c). Model parameters also include AIC_c weights (wt_i), deviance, and number of parameters (*K*). Only models with $\Delta AIC \leq 2$ are listed below. Model parameters were modeled according to the sampling schemed used to collect data: single year-single tract (SYST), single year-multiple tracts (SYMT), and multiple years-single tract (MYST). For SYST and SYMT, apparent daily survival (S) was modeled as the same (.) and by AGE (AHY, HY); for all data sets, temporary emigration (gammas, G) was modeled as random (G′ = G″), no movement (G′ = G″ = 0), and Markovian (G′ and G″ separately). For SYSS and SYMT, capture probability (*P*) was modeled as constant, equal and non-equal between age groups, and by tract. Tract = eastern or western forest tracts. For MYST, daily survival also modeled by YR, and captures by YR and YR * AGE. We also fit a linear trend term (T) on temporary emigration and capture rates.

season), 0.03 ± 0.01 (mid-season), and 0.07 ± 0.01 (late season). Extinction rates were strongly influenced by seasonal intervals ($\hat{\beta}_{mid} = -2.30$, 95% CI: -3.31 to -1.29; $\hat{\beta}_{late} = -1.39$, 95% CI: -2.31 to -0.47). Location data indicated that Puerto

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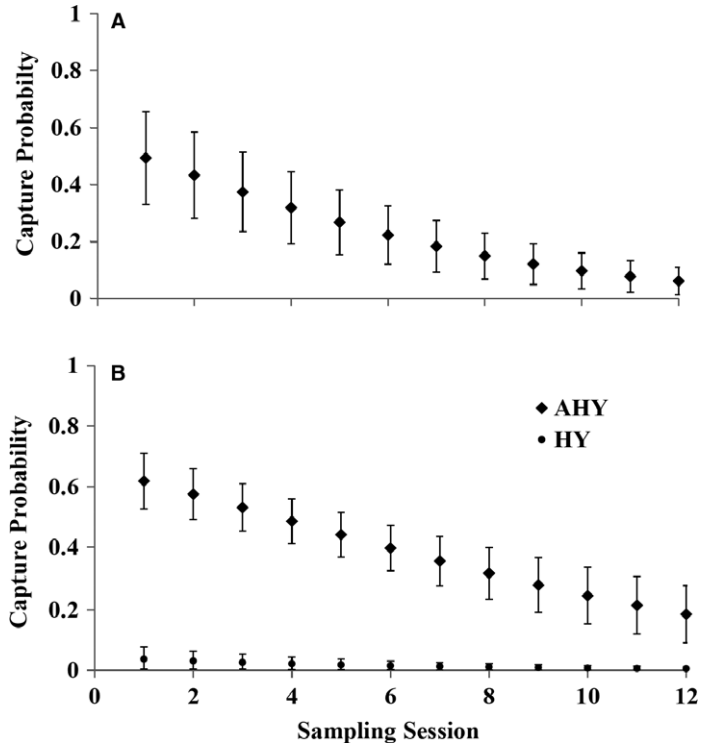

Fig. 2. Seasonal trend in capture probabilities (*P*) for (A) Puerto Rican Bullfinches (pHY = pAHY) and (B) Bananaquits (pHY ≠ pAHY) in the western tract of the Guanica Dry Forest in Puerto Rico, 2010.

Rican Bullfinches were present in the sampled area throughout the entire study period (Fig. 3A), but more often during middle and late seasons. Location data of selected individuals revealed that birds were located around the mist-net stations (Fig. 3B).

Bananaquits. We aged 290 of 311 Bananaquits captured during our study, including 68 AHY and 15 HY birds in 2009 and 178 AHY and 39 HY birds in 2010. A model with constant, equal survival between age groups, random temporary emigration ($G' = G''$) with a weak linear trend term (T), and unequal age-specific capture probabilities with a linear trend term (T) explained most of the variation for the SYST dataset ($wt_i = 0.32$; Table 2). On average, the probability of exhibiting random temporary emigration was 0.64 ± 0.06. The linear trend in capture probability was negative and strong ($\hat{\beta} = -0.18 \pm 0.07$, Fig. 2B). Daily probability of capturing an adult was 0.62 ± 0.05 early in the season and 0.18 ± 0.09 late in the season. The daily probability of capturing a juvenile ranged from 0.04 ± 0.03 early in the season to < 0.005 at the end. Of the three competing models ($\Delta AIC_c \leq 2$), one featured Markovian temporary emigration. Variation in daily capture probabilities in the SYMT dataset was best explained by a model with constant, equal survival between age groups, random movement ($G' = G''$), and unequal capture probabilities between ages and a tract effect on captures ($wt_i = 0.53$; Table 1). The probability of capture was 0.22 ± 0.06 for adults and 0.005 ± 0.005 for juveniles; random movement probability was 0.66 ± 0.05. Tract had a strong effect on capture probability ($\hat{\beta} = -1.14 \pm 0.36$), with a capture probability of 0.46 ± 0.07 in the western tract and 0.21 ± 0.06 in the eastern tract. A competing model ($\Delta AIC_c \leq 2$) featured Markovian temporary emigration with a movement probability of 0.67 ± 0.06 for G'' and 0.64 ± 0.08 for G'. Tract also had a strong effect in this model ($\hat{\beta} = -1.15 \pm 0.36$). For the MYST data set, variation in parameter estimates was best explained by a model with constant daily survival between age groups, no change in their availability status ($G' = G'' = 0$),

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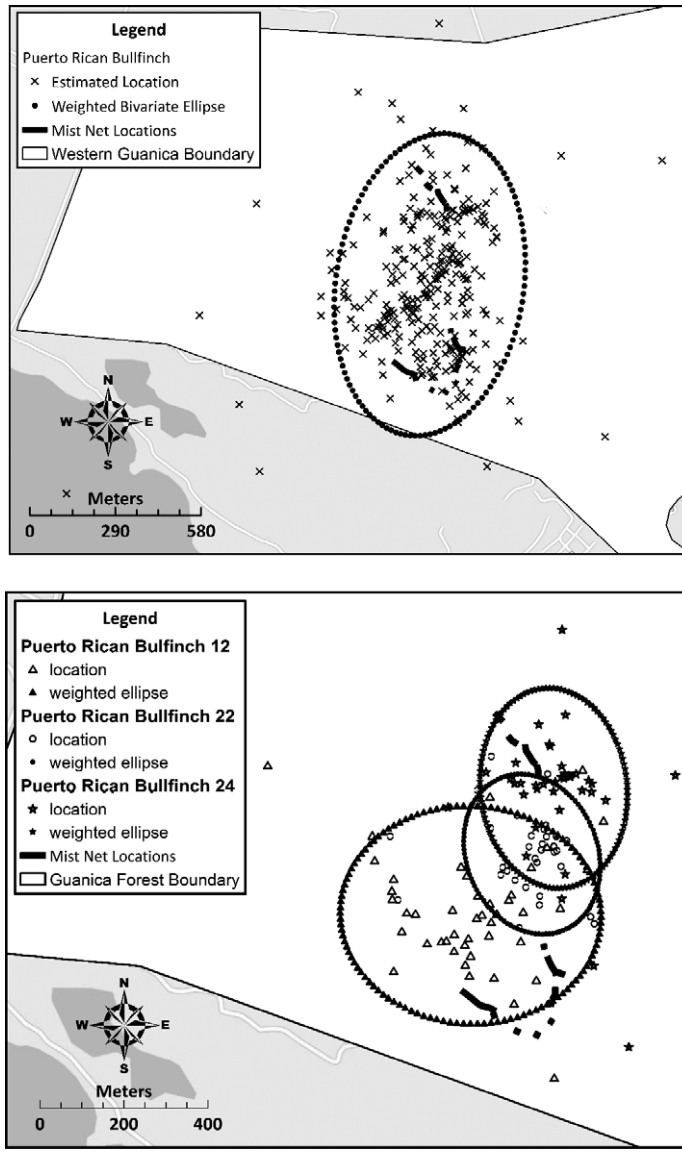

Fig. 3. Map showing estimated locations and the weighted bivariate ellipse for radio-tracked Puerto Rican Bullfinches in the western tract of the Guanica Dry Forest in Puerto Rico. Top panel depicts locations and the weighted bivariate ellipse for all radio-tracked bullfinches ($N = 31$); bottom panel depicts the same information for three bullfinches with the most estimated locations. Tracking was conducted for 21 d (life of battery) in April and May 2010. Mist-net locations where individuals were captured are highlighted in bold.

and unequal capture probabilities between ages (AHY = 0.04 ± 0.01; HY = 0.04 ± 0.01) ($wt_i = 0.35$; Table 2). The model included a strong and positive age * year effect ($\hat{\beta} = 0.77 \pm 0.32$). Overall, analyses suggested that there was no support for using the age ratio to estimate true productivity, or the use of the age ratio as an index of productivity.

Weighted bivariate ellipses for all individual Bananaquits were 17.41 ha (95% CI: 15.52–19.67 ha), suggesting that radio-tagged birds were within the estimated mist-net sampling

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Table 3. Model selection tables for occupancy probability for Bananaquits (BANA) and Puerto Rican Bullfinches (PRBU) in the western tract of the Guanica Dry Forest in Puerto Rico. Model parameters are initial occupancy (Psi), colonization (gam), extinction (eps), and detection probability (P).[a]

	ΔAIC	wt_i	K	Deviance
PRBU				
Psi, gam, eps(season), P	0	0.99	6	927.24
Psi, gam, eps, P	17.69	0.01	4	948.93
Psi, gam(season), eps, P	21.38	0	6	948.62
BANA				
Psi, gam, eps(season), P	0	0.98	6	996.02
Psi, gam, eps, P	9.94	0.01	4	1009.96
Psi, gam, eps(age), P	11.51	0.00	5	1009.53
Psi, gam(age), eps, P	11.82	0.00	5	1009.84
Psi, gam(season), eps, P	12.55	0.00	6	1008.57

[a]Models were ranked by the difference from the top model in AIC value, expressed as ΔAIC. AIC value was 1008.02 for Bananaquits and 939.24 for Puerto Rican Bullfinches. Model parameters also include AIC weights (wt_i), deviance, and number of parameters (K). Data were obtained using radio-telemetry in 2010. Age was either AHY or HY. Seasons were defined as early season (≤ 23 April 2010), mid-season (24 April–30 May 2010), and late season (≥ 31 May 2010).

area of 20 ha. The expected proportion of Bananaquits present in the study area on any given day was 0.52 (95% CI: 0.51–0.57) during early season, 0.91 (95% CI: 0.87–1.00) during mid-season, and 0.70 (95% CI: 0.67–0.80) during late season. Daily extinction probability was strongly influenced by season ($\hat{\beta}$ 0.11 ± 0.03), with a daily detection probability of 0.89 ± 0.01 (Table 3). Daily extinction probabilities were 0.10 ± 0.03 (early season), 0.01 ± 0.01 (mid-season), and 0.05 ± 0.02 (late season). Extinction rates were influenced by seasonal interval, strongly during mid-season ($\hat{\beta}_{mid} = -2.29$, 95% CI: −3.74 to −0.84). Locational data indicated that Bananaquits were present in the sampled area during the entire study period. The distribution of point locations of selected individuals indicated that birds were present around the mist-nets (Fig. S1).

Adelaide's Warblers. We aged 179 of 188 Adelaide's Warblers, including 58 AHY and 8 HY birds in 2009 and 102 AHY and 11 HY birds in 2010. A model with age-specific survival, no change in their availability status ($G' = G'' = 0$), and unequal capture probabilities between ages was the best supported model for the MYST dataset ($wt_i = 0.20$; Table 2). The daily probability of capture was 0.09 ± 0.02 for adults and 0.04 ± 0.01 for juveniles. The model featured year and year * age-specific terms, but neither had an influence on capture probability ($\hat{\beta}_{AHY} = 0.58 \pm 0.31$; $\hat{\beta}_{HY} = -0.03 \pm 0.36$). Five competing models ($\Delta AIC_c \leq 2$) featured similar model terms, but one included a random temporary term and another an additive year effect ($\hat{\beta} = 0.36 \pm 0.29$). These results indicated that the ratio of age classes could be used as an index of breeding productivity (Table 2). Encounter histories were insufficient to test the assumption of equal capture probabilities between age classes for the SYST and SYMT datasets. Similarly, telemetry data on the western tract were too sparse to run occupancy analyses. Location data, however, indicated that Adelaide's Warblers were present in the sampled area during the entire study period, and bird activity occurred around the mist-nets (Fig. S2). Weighted bivariate ellipses for all individual Adelaide's Warblers were 13.39 ha (95% CI: 10.80–17.10 ha), again suggesting that individuals were within the mist-net sampling area.

Nest monitoring. The total number of nests monitored and the number that successfully fledged at least one young were summarized according to our mist-net sampling schemes (Table 4). Average clutch sizes were 3.2 ± 0.44 ($N = 5$) for Adelaide's Warblers, 2.65 ± 0.48 ($N = 40$) for Bananaquits, and 2.93 ± 0.59 ($N = 15$) for Puerto Rican Bullfinches. The observed number of young fledged was lower than the number of HY birds captured in mist-nets for all three focal species (Fig. 4). For example, no fledgling Adelaide's Warblers were observed in nest-monitoring plots in either tract in 2010, whereas 11 HY birds were captured in mist-nets. We captured 41 HY Puerto Rican Bullfinches in the eastern

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Table 4. Total number and outcome of nests of Adelaide's Warblers, Bananaquits, and Puerto Rican Bullfinches monitored in four plots (25 ha each) in the eastern and western forest tracts of the Guanica State Forest in Puerto Rico.

Species/Tract/Year[a]	Number of nests	Successful	Failed	Unknown
Adelaide's Warbler				
East 2009–2010	11	1	10	0
West 2010	7	0	7	0
East–West 2010	10	0	10	0
Bananaquit				
East 2009–2010	19	3	16	0
West 2010	44	7	31	6
East–West 2010	53	8	39	6
Puerto Rican Bullfinch				
East 2009–2010	21	0	21	0
West 2010	30	2	24	4
East–West 2010	34	2	28	4

[a]Data summarized as SYST (West 2010), SYMT (East–West 2010), and MYST (East 2009–2010).

tract, but no young fledged from monitored nests. However, the number of fledglings per adult from monitored nests and the ratio of young to adult, also an estimate of "true" productivity, yielded similar results in most cases (Fig. 5).

DISCUSSION

We investigated multiple factors that could influence capture probability of birds in a resident community in a tropical dry forest and the implications for estimation of breeding productivity. At its most basic level, few captures and recaptures characterized the 25 species sampled at Guánica Dry Forest, a finding that paralleled previous studies in tropical settings (MacArthur and MacArthur 1974, Karr 1990, Ruiz-Gutierrez et al. 2012). This is worth noting because our focal species were among those with the most captures and we still either had problems running models (e.g., Adelaide's Warbler) or could not parameterize models to explore age-specific patterns (e.g., temporary emigration). Similarly, Ruiz-Gutierrez et al. (2012) were only able to model apparent survival for six of 136 resident species in Mexico. Sparse capture data likely limited our ability to discriminate among competing models, and thus make more definitive inferences about factors driving capture rates. This limitation was most notable for Puerto Rican Bullfinches, regardless of the data set.

One explanation for the low number of captures was the magnitude of random temporary emigration in competing models across most species. This finding suggested that the availability of birds to be captured was predominantly independent of the previous availability state. Becoming unavailable during any given primary period could occur if, for example, birds were tending nests and the activity spanned sampling occasions, or if they temporarily left in search of food during net operating hours. Multi-year results for Adelaide's Warblers also suggested that the availability status of a bird might not change across primary sampling occasions, underscoring the need for researchers to find ways to increase their capture probability.

Radio-telemetry data shed light on two important questions regarding the availability of birds to be captured. First, adult Bananaquits and Puerto Rican Bullfinches occupied the sampled area with seasonal average probabilities ranging from 0.56 to 0.71, respectively. In addition, locational data suggested that birds were located in and around nets. Second, juvenile Bananaquits were rather sedentary; none emigrated permanently from the sampled area over the lifetime of transmitters (21–28 d). These results suggest that low capture rates had a strong behavioral component, i.e., birds may have either avoided nets or remembered locations of capture (MacArthur and MacArthur 1974, Ruiz-

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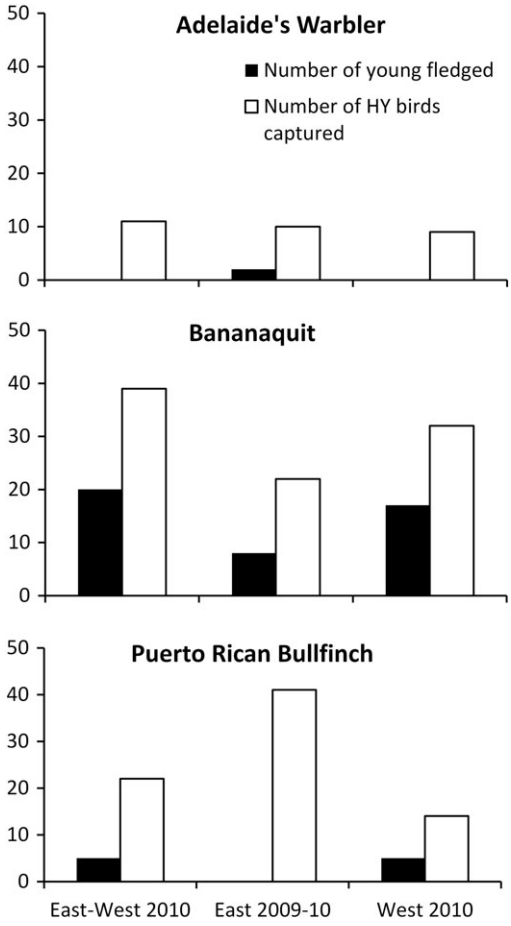

Fig. 4. Comparison of the number of young fledged recorded in four nest-monitoring plots (25 ha each) to the number of hatching year (HY) birds captured in mist-nets for Adelaide's Warblers, Bananaquits, and Puerto Rican Bullfinches in the eastern and western forest tracts of the Guanica State Forest in Puerto Rico. Data were summarized as SYST (West 2010), SYMT (East–West 2010), and MYST (East 2009–2010).

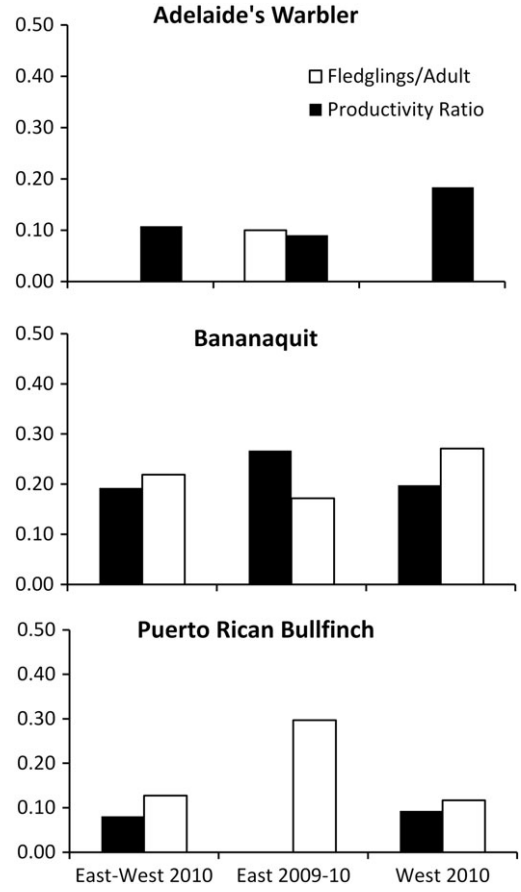

Fig. 5. Comparison of the number of young fledged per adult recorded in four nest-monitoring plots (25 ha each) and capture-based breeding productivity estimates (ratio HY/AHY) for Adelaide's Warblers, Bananaquits, and Puerto Rican Bullfinches in the eastern and western forest tracts of the Guanica State Forest in Puerto Rico. Data were summarized as SYST (West 2010), SYMT (East–West 2010), and MYST (East 2009–2010).

Gutierrez et al. 2012). The role of behavioral responses is supported by the negative trend in capture probability for Puerto Rican Bullfinches and Bananaquits in the western tract, whereas occupancy estimates in the same tract suggested that adults of the aforementioned species had an increasing daily probability of being present in the study area as the season progressed. These opposing trends underscore important differences between capture probabilities derived from radio-telemetry and those from mist-nets. Negative behavioral responses may not preclude modeling data, but may require more complex models and more data to populate models (Pradel 1993).

The utility of a true estimate of breeding productivity has traditionally been judged by comparing results to productivity estimates obtained from nest-monitoring plots containing the mist-net sampling stations (Nur et al. 1999). Although statistical analyses were not possible with our data, contrasting metrics of breeding productivity did not agree. For example, capture probabilities for Bananaquits were lower for juveniles than adults and decreased

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over time, ostensibly yielding biased low estimates of true productivity. However, the capture-derived estimate and the number of young fledged per adult were similar. In contrast, more juvenile Adelaide's Warblers were captured than the number of fledglings recorded in the nest-monitoring plots, suggesting that we may not have located all nests (Nichols et al. 1986). Discrepancies between metrics were not unlike those reported in similar studies in temperate regions (Saracco et al. 2006, Marra et al. 2017), where a possible explanation is that captured juveniles may have immigrated into the study area (Peach et al. 1996, DeSante et al. 2001). Although we cannot exclude this possibility, our data for juvenile Bananaquits suggested that discrepancies may not have all been attributed to immigrants. As noted above, none of the radio-tagged HY Bananaquits emigrated from the study area. Some researchers have proposed tallying only the number of juveniles captured in mist-nets to generate an index of productivity. This index is reliable if the density of breeding adults in the catchment area does not exhibit marked fluctuations (Nur et al. 1999). However, we caution potential users that captures of juveniles might also be adversely affected by availability (e.g., G′ or G″) and behavior and, thus, the underlying assumption that the number of juvenile captures and number of fledglings in the study area are correlated should be tested before making inferences about productivity.

We examined data collected using three common sampling schemes, all chosen to discern uses and limitations of capture data for estimating breeding productivity. Our results suggested that inferences from an index of productivity were better supported (two of three species) than the alternative (true estimates). Indices are meant to be an alternative to estimating parameters directly, and are useful in many situations over space and time (Williams et al. 2002). Indices of productivity have been informative in evaluating demographic trends (Robinson et al. 2007, Rockwell et al. 2017) and responses to changing environmental conditions (Nott et al. 2002, Eglington et al. 2015, Saracco et al. 2016). However, our results also suggest that researchers should be prepared to conduct mist-net sampling over multiple years to ensure parameters are estimable and reliable (Nott et al. 2002, Saracco et al. 2018). To put it in context, available recommendations to estimate apparent survival suggest that data should be collected for no fewer than 8 yr (DeSante et al. 2001), but, more recently, Ruiz-Gutierrez et al. (2012) suggested 10–30 yr would be more appropriate for studying the population dynamics of bird species in Neotropical systems. Puerto Rican Bullfinches came closest to meeting the assumption of equal capture probabilities between ages in our study (SYST and SYMT datasets), but uncertainty in model selection suggest caution against its untested and uncorrected application. Plausible explanations for differences in capture rates include annual variation in environmental factors (e.g., rainfall and fruiting phenology) that influence the timing of reproduction relative to sampling. For example, Faaborg et al. (1984) reported changes in breeding chronology during drought years, a possibility raised by Wiewel et al. (2013) during our study. There was also a negative seasonal trend in capture probabilities that suggest a behavioral component that might be exacerbated by inter-annual variation in environmental conditions.

We offer a few additional recommendations to enhance within- and between-season capture rates. First, increase the number of mist-nets in sampling areas. In our study, we had more recaptures (7%) at mist-net stations closer to each other (40 m), a proxy of net density, than those farther apart (400 m, 2%; Kornegay 2012). In addition to the spatial configuration used in our study, Ruiz-Gutierrez et al. (2012) provided examples of other spatial configurations to improve capture rates around core study areas through increased density of mist-nets. Second, moving mist-nets between sampling periods may reduce the likelihood that birds learn their location (Ruiz-Gutierrez et al. 2012). If this is done, particularly moving nets between primary sampling periods, researchers may want to be sure they are sampling roughly the same area to avoid sampling unique segments of the population. Finally, adopting an appropriate sampling scheme to meet predefined study objectives is essential. We agree with Ruiz-Gutierrez et al. (2012) that a robust design (Kendall et al. 1997) is better suited to understand factors influencing capture rates and generate reliable estimates of demographic rates (e.g., apparent survival and productivity) in tropical ecosystems. In this vein,

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pilot studies should be conducted to evaluate capture rates and the spatial extent sampled by mist-nets to adjust sampling effort and design before informing decisions.

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SUPPORTING INFORMATION

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Table S1. Goodness-of-fit tests for robust design models for Puerto Rican Bullfinches (*Loxigilla portoricensis*), Bananaquits (*Coereba flaveola*), and Adelaide's Warblers (*Setophaga adelaide*) captured at Guánica State Forest in southwestern Puerto Rico, 2009–2010.

Table S2. Model selection tables for Puerto Rican Bullfinches (*Loxigilla portoricensis*) captured at Guánica State Forest in southwestern Puerto Rico, 2009–2010.

Table S3. Model selection tables for Bananquits (*Coereba flaveola*) captured at Guánica State Forest in southwestern Puerto Rico, 2009–2010.

Table S4. Model selection tables for Adelaide's Warblers (*Setophaga adelaide*) captured at Guánica State Forest in southwestern Puerto Rico, 2009–2010.

Fig. S1. Map showing estimated locations and the weighted bivariate ellipse for radio-tracked Bananaquits (*Coereba flaveola*) in the western tract of the Guanica Dry Forest in Puerto Rico.

Fig. S2. Map showing estimated locations and the weighted bivariate ellipse for radio-tracked Adelaide's Warblers (*Setophaga adelaides*) in the western tract of the Guanica Dry Forest in Puerto Rico.

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