

## ABSTRACT

KORNEGAY, MARY EDYTHE. Abundance and Breeding Productivity of Resident Avian Species in Guánica State Forest. (Under the direction of Dr. Jaime A. Collazo.)

Effective conservation is possible only when sound demographic data are available with which to engage in conservation planning and assess the response of a system to management actions. I investigated the utility of a productivity index and analyzed factors affecting abundance estimates for avian species in Guánica State Forest, Puerto Rico in 2009-2010. The index of breeding productivity used by the Monitoring Avian Productivity and Survivorship (MAPS) program, derived from the ratio of juvenile to adult captures in mist-nets, assumes similar age-specific capture probabilities. I tested this assumption using a robust design framework and found equivocal support for equal age-specific capture probabilities for Puerto Rican Bullfinches (*Loxigilla portoricensis*), but no support for Bananaquits (*Coereba flaveola*) and Adelaide's Warblers (*Dendroica adelaiae*). Temporary emigration rates indicated that the majority of birds were unavailable or became unavailable for capture, whereas occupancy data from a concurrent telemetry study indicated that the majority of individuals were present in the study area. Net avoidance was prevalent, which was consistent with low recapture rates. Results suggested that annual estimates of productivity based on the ratio of captured juveniles to adults can be biased and species-specific. I suggest increasing net density and shifting net locations as possible ways to increase capture probabilities. Alternatively, adjusted estimates of population size could be used to index productivity if knowledge of the breeding chronology and dispersal patterns of focal species is available. I conducted time-of-detection point counts to obtain estimates of

avian abundance and determine factors affecting detection probabilities. LiDAR measurements of vegetation structure were significantly different between the two tracts of Guánica State Forest, which differ in their time since disturbance by at least 40 years. Avian species density was generally higher in the tract of the forest disturbed more recently. The prevalence of support for models with unequal probabilities of first and subsequent detections (Mb) in candidate sets could indicate a tendency of observers to anticipate calls made by birds that were already detected earlier in the survey period. The prevalence of support for models with heterogeneity in detection probabilities among individuals (Mh) could indicate variation in singing rates or distances from observer. Although LiDAR is a useful tool for landscape level studies for modeling species-habitat relationships, covariates derived from LiDAR did not account for as much variation in the data as did field measurements of vegetation structure and distance from observer.

Abundance and Breeding Productivity of Resident Avian Species in Guánica State Forest

by  
Mary Edythe Kornegay

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APPROVED BY:

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Dr. Jaime A. Collazo  
Committee Chair

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Dr. Theodore R. Simons

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Dr. James F. Gilliam

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Dr. Stephen J. Dinsmore

## DEDICATION

For Travis

## BIOGRAPHY

I was born and raised in Goldsboro, NC. I took a serious interest in birds in college when I started working in an ornithology lab where I completed an undergraduate thesis on stable isotope analysis of Adélie penguin eggshell to study diet. I graduated summa cum laude with honors from the University of North Carolina Wilmington in 2007 with a Bachelor of Science degree in Biology. After graduation I was lucky to land an internship with PRBO Conservation Science as a bird bander at the Palomarin Field Station in Bolinas, CA. My life became all about birds during my internship there, and that is where I discovered that I was truly a “bird nerd.” I feel very blessed that my graduate research project enabled me to further my passion by studying the birds of Puerto Rico, and hope that my career enables me to continue developing my love for these amazing creatures.

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Jaime Collazo has been a delightful advisor and friend to me during my time at North Carolina State University. In addition to helping me with planning and executing all aspects of my project, he also made sure to give me a warm introduction to the island where I conducted my research and the place that he calls home. His guidance and dedication to answering my many, many long distance emails was reassuring and very much appreciated. I am also grateful to my committee members, Dr. Ted Simons, Dr. Jim Gilliam, and Dr.

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My family is the reason why I am where I am today. My Mom and Dad have always supported me in what I wanted to do and they have always been there to celebrate my achievements with me. My husband Travis has provided unwavering support to me throughout my graduate career. Somehow he even survived helping me plan our wedding from a distance while I was conducting my research in Puerto Rico! His love, encouragement, and genuine interest in my project have helped me get through these three years. I cannot leave out our cat Penny who has been a loyal companion, despite me leaving her behind to do my field work every summer. She has been a great stress reliever for me, spending countless hours curled up beside me while I was typing away on my laptop for this manuscript.

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# Chapter 1

## Testing the utility of the breeding productivity index derived from the Monitoring Avian Productivity and Survivorship program

### **Abstract**

Estimates of seasonal breeding productivity from the Monitoring Avian Productivity and Survivorship (MAPS) protocol, calculated as the ratio of juvenile to adult captures in mist-nets, assume similar age-specific capture probabilities for juveniles and adults. I tested this assumption in 2009-2010 in Guánica State Forest, Puerto Rico using capture histories obtained from MAPS mist-netting stations in the eastern and western tracts of the forest. I also conducted a concurrent telemetry study in the western tract to study bird movement and gain insight into temporary emigration rates. There was equivocal support for equal age-specific capture probabilities for Puerto Rican Bullfinches (*Loxigilla portoricensis*), but no support for Bananaquits (*Coereba flaveola*) and Adelaide's Warblers (*Dendroica adelaidae*). Rates of temporary emigration suggested that the majority of birds were unavailable for capture or became unavailable (range 0.64 - 0.99). Telemetry results indicated that a large

percentage of individuals (58-75%) were present in the study area on any given day. Net avoidance was prevalent as indicated by low recapture rates. Estimates of productivity from a concurrent nest monitoring study did not correlate well with productivity indices. The comparison, though, might be spurious because nest-based productivity data assume perfect nest detection. Results suggested that estimates of productivity based on capture data can be biased and species-specific, possibly affecting their ability to estimate annual productivity. Low capture rates across species and unequal age-specific capture probability might hamper application of MAPS productivity index. I suggest increasing net density and shifting net locations as possible ways to increase capture probabilities to improve capture rates. Adjusted estimates of age-specific population size could be used to index productivity if knowledge of the breeding chronology and dispersal patterns of focal species is available.

## **Introduction**

Puerto Rico has been identified as part of a biodiversity hotspot in the Caribbean (Myers et al. 2000). The island supports 239 species of birds, of which 16 are endemic (Raffaele 1989). Except for endangered and game species, however, the status of most species is not known. Discerning the status of these “data deficient” species and formulating a strategic conservation plan for avifauna are priorities outlined in the Puerto Rico Comprehensive Wildlife Conservation Strategy (Garcia et al. 2005). The conservation strategy would be conceived and implemented under a structured decision making framework, where objectives, conservation actions, hypothesized linkages between

objectives and actions, and a monitoring program to gauge the response of the system are stipulated beforehand (Nichols and Williams 2006). In both instances monitoring plays a central role, placing a premium on selecting appropriate and statistically sound techniques.

Call-count surveys represent the only standardized avian monitoring program in place in Puerto Rico (Rivera-Milán 1990, 1992, 1993). The analytical framework supporting these surveys is distance sampling (Buckland et al. 2001). The program was designed to monitor columbids, but data on other species were collected (Rivera-Milán 1995). Data are used in Puerto Rico to generate estimates of population size and growth. Accuracy and precision of counts are affected by a number of factors (Buckland et al. 2001), including those impinging upon detectability (Simons et al. 2009). Arguably, distance sampling is not the most appropriate surveying technique for forest-dependent species nor was it designed to yield all parameters of interest or need. For example, attempts to characterize the status of species would have a stronger foundation if they include estimates of age-specific survival. Likewise, if the state-dependent variable of interest is breeding productivity (e.g., after implementing a cowbird control program) then another technique is required.

The Monitoring Avian Productivity and Survivorship program (MAPS) represents an approach that could meet some of the monitoring gaps not covered by call-count surveys, particularly in forested landscapes. MAPS is a standardized monitoring technique based on a capture-recapture framework, whose encounter histories are obtained using mist-nets (DeSante et al. 2004, 2011). Mist-netting studies have a long history in Puerto Rico, exemplified by work in Guánica State Forest. A winter mist-netting study has been conducted in the forest since 1972, reporting estimates of survival for migrant and resident

species, insights on population trends based on capture data, and population responses to environmental variables (Faaborg and Arendt 1995, Faaborg et al. 1997, Faaborg et al. 1984). However, because netting efforts are conducted in January-February and only for one period of 10-12 days, data cannot be used to derive estimates of breeding productivity and population size. Additionally, sampling is conducted only in the eastern tract of Guánica, limiting inferences due to lack of spatial replication. With 14 state forest reserves, representing nearly every forest plant community on the island (Gould et al. 2007), adopting a mist-net based approach could potentially provide a comprehensive and effective island-wide monitoring tool.

MAPS has been found to be proficient in generating dependable estimates of apparent survival for avian species, estimated as the probability that a bird banded in year  $t$  will survive and return to the same location where it was marked in year  $t+1$  (Saracco et al. 2010). However, the validity of the productivity estimates derived from MAPS, calculated as the ratio of hatching year (HY) or juvenile birds to after hatching year (AHY) or adult birds captured in mist-nets, has not been adequately assessed (DeSante 1999, Saracco et al. 2006). This index rests on the assumption that the numbers of juvenile and adult birds captured in mist nets are constant proportions of their actual population sizes within the sampling area (DeSante et al. 1995). Therefore, the index assumes that capture probabilities ( $p$ ) are similar for both juvenile and adult birds ( $p_{HY} \cong p_{AHY}$ ). Temporary emigration is also an important parameter because it helps determine the availability of birds for sampling. Estimates of population size are subject to bias if temporary emigration rates are high and may impinge on

the breeding productivity index if individuals of both age classes are not equally available for capture.

Nur et al. (1999) and DeSante et al. (1995) suggested that further assessment of underlying assumptions and demographic parameters derived from MAPS was needed, especially in tropical environments and over multiple sites. This study was designed with these objectives in mind. Specifically, I tested the assumption of equal capture probabilities between HY and AHY birds in Guánica State Forest in southwestern Puerto Rico during the breeding seasons of 2009-2010. I also assessed whether there was evidence in the data for temporary emigration. I tested these assumptions using encounter histories of Puerto Rican Bullfinches (*Loxigilla portoricensis*), Bananaquits (*Coereba flaveola*), and Adelaide's Warblers (*Dendroica adelaidae*) derived from operating mist-netting stations using MAPS protocol on seven study plots in the eastern and western tracts of the forest. I evaluated the assumption of equal capture probability using competing Robust Design models. Radio telemetry data were collected concurrently to determine whether or not juveniles and adults remained in the study area, providing insights into temporary emigration. Radio telemetry can supplement data from mist-netting studies to give additional insights into the movements of focal species (Rappole et al. 1989). Finally, a companion study established four 25-ha nest monitoring plots in each forest tract (Wiewel 2011). These plots encompassed mist-netting stations and the purported 20 ha area sampled by the MAPS stations (DeSante et al. 1995). This independent method of estimating breeding productivity provided an empirical estimate to compare against the index derived from capture-recapture data. I discuss results

in the context of using MAPS as a monitoring tool for avian conservation in forested landscapes in Puerto Rico and elsewhere in the tropics.

## Methods

### Study Area

Guánica State Forest is a 4,000 hectare Biosphere Reserve on the southwest coast of Puerto Rico that serves as a prime example of a subtropical dry forest. Guánica contains coastal scrub, semievergreen, and semideciduous forest types (Lugo et al. 1978). Average annual rainfall is approximately 860 mm and mean annual temperature is 25.1 degrees Celsius. Puerto Rico's Gap Analysis Program identified areas of high species richness that are not currently being conserved and managed. This project found that forested coastal hills, including both tracts of Guánica, were centers of high habitat heterogeneity and thus had an abundance of biodiversity (Gould 2009), reinforcing that the entire forest should be of high conservation priority on the island. Therefore, placing the study area in this location allows it to be used as a proxy to find the best monitoring techniques to implement throughout the island.

### Focal Species

I chose the Bananaquit, Puerto Rican Bullfinch, and Adelaide's Warbler as focal species for analyses. These species were commonly captured in mist-nets (Table 1.1) and of

an appropriate size for radio transmitter attachment for the concurrent telemetry study. A brief description of their life history follows.

The Bananaquit is the most abundant bird in Puerto Rico. Its high capture rates made it a good candidate for providing a large data set with which to test the statistical assumptions behind the MAPS productivity index. This species is widespread throughout the Caribbean islands and its range also extends into Mexico and parts of South America. Bananaquits can be found in most habitat types throughout the island and they forage at all levels of the forest on nectar, fruit, and insects (Oberle 2006, Raffaele et al. 2003). In Grenada, Bananaquits breed during a period from March through early August (Wunderle 1982), which also encompasses known breeding chronology for Puerto Rico (Gleffe et al. 2006), but more study is needed on the extent of their reproductive cycle which may have multiple peaks throughout the year. Males and females build themselves individual domed roosts, which are identical in appearance but separate from their nests, and defend a  $100\text{ m}^2$  area around them. Bananaquits have polyterritories because males will sing at their own roosting nest as well as their mate's nest (Wunderle 1984).

The Puerto Rican Bullfinch is endemic to Puerto Rico and is commonly found in forested parts of the island including Guánica State Forest. It forages mainly on seeds, fruits, and buds at all levels of the forest, but in dry forests such as Guánica it forages mainly in the canopy. Bullfinches also build domed nests with a side entrance (Oberle 2006). Cooperative breeding has been observed in this species, with juveniles assisting in nest building (Wiewel 2011). Breeding has been reported to occur from February through July (Collazo and Groom 2000).

The Adelaide's Warbler is another endemic to Puerto Rico and is found in moist limestone forests and thickets in dry forests such as Guánica. They forage on insects in the middle and upper levels of the forest. Adelaide's Warblers maintain all-purpose territories and monogamous pair bonds year-round (Staicer 1996), and they have an extended breeding season that lasts approximately from January through June (Staicer 1991). This species builds a cup nest in a tree or shrub 1-7 m above the ground (Oberle 2006).

## Sampling Protocol

### *Mist-Netting*

I established four MAPS stations within the eastern tract of the forest in 2009, and added three more in the western tract in 2010. Stations in the eastern tract were operated for two seasons in 2009 and 2010, but stations in the western tract were only operated in 2010. Each station consisted of an array of 10 mist-nets, which were 12 meters long with 30mm mesh. Nets were placed near habitat edges (e.g., trails) to enable capture of breeding adults as well as dispersing juveniles and adults. Net sites were established at each station and permanently remained in the same configuration during the study, complying with MAPS protocol (DeSante et al. 2011).

Mist-net operation occurred from March through July each year, encompassing the known breeding season of all focal species. Each season was divided into 12 periods which consisted of 10 days, and each array of mist-nets was operated for two consecutive days within each period. Nets were opened at local sunrise, operated for 6 hours, and then closed

each day. If it was not possible for nets to stay open for at least half of the 6 hours due to adverse conditions, the missing time was made up the following day. Nets were not left open in dangerous or adverse weather conditions (e.g., predators, rain, wind, and heat). All birds caught in the mist-nets were banded with a United States Geological Survey aluminum band containing a unique nine-digit number. Data on species, age, sex, status, breeding condition, molt, fat, wing chord, weight, and capture time and location were recorded for all newly captured and recaptured birds. Birds within the same calendar year of hatching were aged as HY and older birds were aged as AHY based on the traditional calendar-based system (Pyle 1997). This work was conducted under Institutional Animal Care and Use Committee permit number 09-040-O.

I used Pollock's Robust Design to analyze mist-netting data. This framework minimizes the effects of heterogeneity and trap response on capture probability, and thus on estimates of demographic parameters (Pollock 1982). In this design there are primary sampling periods and secondary sampling periods that lie within each primary sampling period (Figure 1.1). In this study, each 10-day period represented a primary sampling period and the two consecutive mist-netting days within each primary period represented the secondary sampling periods. Secondary sampling occasions are close together in time, so it can be assumed that the population is closed to births, deaths, immigration, and emigration between these periods. However, the population is considered open to these events between the primary sampling occasions because the time intervals between them are longer, making it more likely for these events to potentially occur. The Robust Design assumes that all animals have independent fates, survival probabilities are equal for all animals in a

population, no bands are lost, banding does not affect survival, and the animals marked are representative of the whole population (Kendall et al. 1995). Adopting the Robust Design allows the estimation of more parameters than the traditional Jolly-Seber model (Seber 1973). For example, population size can be estimated for all sampling periods, which is not possible with the traditional Jolly-Seber model (Pollock et al. 1990).

I evaluated the assumption of equal capture probability used to derive the MAPS productivity index by assessing support in the data for models where capture probabilities for HY and AHY birds were parameterized as being equal ( $p_{HY}=p_{AHY}$ ) and models where probabilities were not equal ( $p_{HY}\neq p_{AHY}$ ). Support in the data for the former parameterization would indicate that the index would be biologically meaningful or interpretable. Conversely, the latter parameterization would undermine the value of the index and suggest that the index is likely biased. Recapture probabilities ( $c$ ) were modeled as equal and not equal for the two age groups, consistent with the way capture probabilities were modeled. Capture and recapture probabilities were modeled as constant over time. Apparent survival ( $\phi$ ) was also estimated as constant over the season, and it was parameterized as equal and unequal for both age groups. Data were too sparse to model time-specific apparent survival, capture probabilities, or recapture probabilities.

I tested temporary emigration parameters using three competing models: random temporary emigration, Markovian temporary emigration, and no movement. In the random or classic temporary emigration model the probability of transitioning between the available and unavailable states between primary periods does not depend on the availability of the bird in the previous period. The parameter gamma ( $\gamma$ ) estimated in this model is the

probability that an individual was unavailable for capture during a primary sampling occasion. In the Markovian temporary emigration model the probability of transitioning between the available and unavailable states between primary periods depends on the availability of the bird in the previous primary period. This model has two different parameters: gamma prime ( $\gamma'$ ) and gamma double-prime ( $\gamma''$ ). The  $\gamma'$  parameter represents the probability of remaining 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  $\gamma''$  parameter represents the probability of being 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). 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 over all sampling periods. To obtain the random temporary emigration model I set  $\gamma' = \gamma''$ , to obtain the no movement model I set  $\gamma' = \gamma'' = 0$ , and to obtain the Markovian temporary emigration model I modeled  $\gamma'$  and  $\gamma''$  separately. Both parameters were modeled as constant over time.

I organized mist-netting data into three possible arrangements. The first arrangement represented data collected at one site over multiple seasons, which was the case in the eastern tract of Guánica in 2009 and 2010. The second arrangement represented data collected at two spatially replicated sites during only one season, which was the case in 2010 when data were collected in the eastern and western tracts of Guánica. The third and final arrangement represented data collected at one site for one season, which was the case for the western tract

of Guánica in 2010. I refer to each of these data arrangements as data structures to signify how they were treated and analyzed. These structures offered the opportunity to examine data stemming from different study designs or data sets exhibiting practical constraints (e.g., the ability to spatially replicate), but was also necessary to estimate state-dependent parameters annually (e.g., breeding productivity).

I assessed a candidate set of 24 competing models for all three data structures for each of the three focal species (Table 1.2). I also added one additional model into model sets to test for the effects of year or location (i.e., forest tract). Models that had convergence problems or yielded non-identifiable estimates were excluded from the model selection summary. Models were ran in program MARK (White and Burnham 1999) using the Robust Design with Huggins closed captures data type option. I used Akaike's Information Criterion (AIC) to select the most parsimonious model. 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 ( $\Delta AIC_c$ ) was used to calculate model weights ( $AIC_c$  weight), which indicate the relative likelihood of the model given the data (Burnham and Anderson 2002). Models with  $\Delta AIC_c \leq 2$  were considered as models with the highest support, but I focused on the top model to evaluate model parameters. I considered an effect (i.e., covariate  $\hat{\beta}$  coefficient) to be strongly supported if the 95% confidence interval did not overlap zero. Parameter estimates  $\pm$  SE and 95% confidence intervals are reported.

## *Radio Telemetry*

I conducted a radio telemetry study in the western tract of Guánica where the topography and density of vegetation were more conducive to the transmission of signals. I fitted transmitters to a number of captured birds of each focal species to independently assess if individual birds were present in the study area and available for capture in mist-nets. Radio transmitters were attached to birds that were captured in mist-nets using a figure eight harness, which fastens around the bird's legs and allows the transmitter to be positioned on the lower back and not interfere with normal movement (Rappole and Tipton 1991). I attached 35 radio transmitters to Bananaquits, 31 to Puerto Rican Bullfinches, and 12 to Adelaide's Warblers, including juveniles and adults if possible to observe whether or not dispersal differs based on age. I was able to attach six transmitters to juvenile Bananaquits, and the remaining transmitters were attached to adult birds. The Bananaquits, Adelaide's Warblers, and some of the Puerto Rican Bullfinches were equipped with Holohil's model BD-2N transmitters that weigh 0.51g and have a nominal lifetime of 21 days. The remaining bullfinches were equipped with Holohil's model BD-2 transmitters that weigh 0.75g and have a nominal lifetime of 28 days.

I tracked birds from the time of transmitter attachment until the end of the transmitter's lifetime or beyond if transmitters were still emitting signals. I acquired radio frequencies using Advanced Telemetry Systems R410 Scanning Receiver with a three-element Yagi antenna twice daily, once in the morning and once in the evening, for all birds with active transmitters. Bearings were taken from permanent stations along a loop trail

located in the study area, with two people starting simultaneously at the north end of the trail and then working their way southward on each side of the trail, taking care to check signals simultaneously. At every other station signals were checked on the ground and at the remaining stations signals were checked from the top of 4.8 m tall towers, which can greatly increase the range of reception (Kenward 1987). Bearings used for analysis were those that were taken on individual birds at the same time of day (i.e., morning or afternoon) to try to minimize the effect that bird movement might have on location estimates. I obtained estimated locations using a Maximum Likelihood Estimator (Lenth 1981) in program LOAS version 4.0.3.7 (Ecological Software Solutions). Intersections of bearings beyond 2 km were excluded because that was the maximum range of the transmitters used in this study. Weighted bivariate ellipses were calculated from the estimated locations to create a home range area where activity was concentrated (Samuel and Garton 1985). This method assumes that the bird's activity is concentrated in the center of the ellipse, which is a reasonable assumption for birds which may be tending a nest. Weighted bivariate ellipses also reduce the effect of extreme locations (i.e., outliers) on the size of the home range, so I chose this method for representing the home ranges of birds with transmitters.

I determined the percentage of birds that were present in the study area on days when nets were operated to gain insights about the availability of birds for capture. I also used a multi-season occupancy model to determine the daily probability that a bird would be present and detectable in the study area. Data permitted the estimation of these parameters because tracking was done twice daily (i.e., morning and afternoon) over the life of transmitters. The expected proportion of individuals with transmitters present in the study area on any day was

obtained as [colonization probability/(colonization probability + extinction probability)] (J. D. Nichols, Patuxent Wildlife Research Center, pers. comm.) In this case, colonization refers to the daily probability that a bird with a live 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  $t-1$ .

I focused on the Bananaquit and Puerto Rican Bullfinch for the occupancy analyses because they had the highest sample sizes. Study area was defined as the area where birds would have a non-zero probability of being detected, which was within 2 km of the trails used to track birds because that was the maximum range of transmitters. To account for possible seasonal differences in the time when birds were fitted with transmitters, I divided the season into three segments based on observed breeding chronology. These were early season ( $\leq$  23 April 2010), mid-season (24 April - 30 May 2010) and late season ( $\geq$  31 May 2010). Colonization and extinction rates were constrained by season and, in the case of Bananaquits, by age. Model assumptions are: 1) the system is closed to changes in the occupancy status during the secondary sampling period, but open between primary sampling periods, and 2) birds are not falsely detected. I believe that all assumptions were met as the time between intervals was short and detection of individuals was enhanced by radio transmitters. I used AIC<sub>c</sub> to evaluate the 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 AIC<sub>c</sub> 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). I

considered an effect (i.e., covariate  $\hat{\beta}$  coefficient) to be strongly supported if the 95% confidence interval did not overlap zero. Parameter estimates  $\pm$  SE are reported.

### *Nest Monitoring*

Field-derived estimates of breeding productivity were obtained from a concurrent nest monitoring study (Wiewel 2011). Four 25-ha nest plots were established in each of two forest tracts, corresponding with the location of mist-nets. Plots were intensively searched for nests, and when nests were encountered they were monitored until they either succeeded or failed (Martin and Geupel 1993). Plots were monitored for two breeding seasons in the eastern tract and for one season in the western tract, coinciding with mist-net operation. Estimates were used as an empirical measure of breeding productivity to gauge the utility of the breeding productivity index derived from MAPS. The goodness of the index was determined by whether it was similar or markedly different from the direct estimate obtained from nest monitoring.

Productivity from the nest monitoring study was expressed as the number of fledglings per adult and as the total number of fledglings produced per plot. I used the former metric to compare to the MAPS productivity index as proposed by DeSante et al. (1995). This expression of breeding productivity was calculated by dividing the number of fledglings by the number of nests monitored, and then dividing the resultant by two in order to express productivity in units of fledglings per adult. This estimate makes the assumption that there are two adults per nest, ignoring situations where there may be helpers (e.g.,

cooperative breeding in Puerto Rican Bullfinches, Wiewel 2011). Expressing productivity in these units makes it readily comparable to the MAPS productivity index. The latter metric was of interest because it has been advanced as an alternative measure of productivity seeing as it only assumes that the number of juveniles captured in mist-nets is proportional to their population size within the study area (Nur et al. 1999).

## Results

### Mist-Netting

#### *Capture Summary*

Thirty-five different species of resident and migratory birds were captured during the mist-netting study (Table 1.1). Two of these migratory species, the Connecticut Warbler (*Oporornis agilis*) and Blue-winged Warbler (*Vermivora cyanoptera*), were captured for the first time in Puerto Rico in my study. In 2009 there were a total of 775 birds captured in the eastern tract of Guánica State Forest, and only 163 of those birds were recaptured within the same year. In 2010, when mist-nets were operated in both tracts of the forest, more birds were captured in the western tract than in the eastern tract. In that year 795 birds were captured in the western tract of the forest, 212 of which were recaptured, and only 567 were captured in the eastern tract, 185 of which were recaptured. The Puerto Rican Bullfinch, Bananaquit, and Adelaide's Warbler were three of the five most commonly captured species in the study and were the focal species for data analysis (Table 1.1).

## *Bananaquit*

I captured a total of 311 individual Bananaquits during the study. Eighty-six individuals were captured in 2009, 17 of which were recaptured within the same year, and 225 individuals were captured in 2010, 82 of which were recaptured that year. More than twice the number of individuals was captured in the three mist-netting stations in the western tract (154) than in the four banding stations in the eastern tract of the forest (71) in 2010 (Table 1.1). There were several competing models accounting for variation in the data across all data structures ( $\Delta\text{AIC}_c \leq 2$ ). However, most variation in the data for the single site and single year data structure (i.e., western tract in 2010) was explained by a model where survival was equal for both age groups,  $\gamma'$  and  $\gamma''$  were equal (random temporary emigration), age-specific capture probabilities were unequal, and age-specific recapture probabilities were equal (Tables 1.3 and 1.4). For the single site and multiple years data structure (i.e., eastern tract in 2009-2010), most variation in the data was explained by a model with age-specific survival estimates,  $\gamma'$  and  $\gamma''$  that were fixed equal to zero (no movement), unequal age-specific capture probabilities, and equal age-specific recapture probabilities (Tables 1.5 and 1.6). Finally, most variation in the multiple sites and single year data structure (i.e., eastern and western tracts in 2010) was explained by a model where survival was equal for both age groups,  $\gamma'$  and  $\gamma''$  were equal (random temporary emigration), age-specific capture probabilities were unequal, and age-specific recapture probabilities were equal (Tables 1.7 and 1.8).

## *Puerto Rican Bullfinch*

I captured a total of 319 individual Puerto Rican Bullfinches in the study. One hundred nineteen individuals were captured in 2009, 21 of which were recaptured within the same year, and 200 individuals were captured in 2010, 59 of which were recaptured that year. More than twice the number of individuals was captured in the western tract (139) than in the eastern tract of the forest (61) in 2010 (Table 1.1). There were several competing models accounting for variation in the data across all data structures ( $\Delta AIC_c \leq 2$ ). Most variation in the data for the single site and single year data structure (i.e., western tract in 2010) was explained by a model featuring equal survival for both age groups, equal  $\gamma'$  and  $\gamma''$  (random temporary emigration), and equal age-specific capture and recapture probabilities (Tables 1.9 and 1.10). For the single site and multiple years data structure (i.e., eastern tract in 2009-2010), variation was best explained by a model with equal survival for both age groups, equal  $\gamma'$  and  $\gamma''$  (random temporary emigration), unequal age-specific capture probabilities, and equal age-specific recapture probabilities (Tables 1.11 and 1.12). Finally, most variation in the data collected at multiple sites in a single year (i.e., eastern and western tracts in 2010) was explained by a model with survival estimates that were equal for both age groups, unequal  $\gamma'$  and  $\gamma''$  (Markovian temporary emigration), and equal age-specific capture and recapture probabilities (Tables 1.13 and 1.14).

## *Adelaide's Warbler*

I captured a total of 188 individual Adelaide's Warblers in the mist-netting study. Seventy-four individuals were captured in 2009, 25 of which were recaptured within the same year, and 114 individuals were captured in 2010, 48 of which were recaptured that year. Approximately the same number of warblers were captured in the western (59) and eastern (55) tracts of the forest in 2010 (Table 1.1). Most variation in the data for the single site and multiple years data structure (i.e., eastern tract in 2009-2010) was explained by a model with age-specific survival estimates,  $\gamma'$  and  $\gamma''$  that were fixed as equal to zero (no movement), unequal age-specific capture probabilities, and equal age-specific recapture probabilities (Tables 1.15 and 1.16). Two other models were plausible alternatives ( $\Delta\text{AIC}_c \leq 2$ ). The second most supported model also supported unequal age-specific capture probabilities, but the third did not. Encounter histories were insufficient to test the hypothesis of equal age-specific capture probabilities for the single site and single year data structure (i.e., western tract in 2010) and the multiple sites and single year data structure (i.e., eastern and western tracts in 2010) for this species, yielding convergence problems or non-identifiable estimates.

## Radio Telemetry

Seventy percent of Bananaquits, 58% of Puerto Rican Bullfinches, and 75% of Adelaide's Warblers were detected within the study area on days that MAPS stations were operated. Individuals of all species tended to stay within the mist-net sampling area where they were originally captured. Weighted bivariate ellipses for all individual Bananaquits

(Figure 1.2; area = 17.41 ha, 95% CI: 15.52 to 19.67), Puerto Rican Bullfinches (Figure 1.3; area = 9.00 ha, 95% CI: 8.03 to 10.15), and Adelaide's Warblers (Figure 1.4; area = 13.39 ha, 95% CI: 10.80 to 17.10) showed that focal species remained within the mist-net sampling area. Weighted bivariate ellipses for the three individuals of each species with the most data also showed that most of these birds remained within the area of the mist-net where they were originally captured, with only one bird whose home range was slightly outside of the location where it was previously captured (Figures 1.5, 1.6 and 1.7).

Variation in colonization and extinction rate for Bananaquits and Puerto Rican Bullfinches was best explained by models whose extinction probability was influenced by season (Tables 1.17 and 1.18). Daily colonization probability was  $0.109 \pm 0.026$  for Bananaquits and  $0.106 \pm 0.023$  for Puerto Rican Bullfinches. Daily detection probability was  $0.895 \pm 0.011$  for Bananaquits and  $0.870 \pm 0.013$  for Puerto Rican Bullfinches. Daily extinction probabilities for Bananaquits were  $0.099 \pm 0.028$  (early season),  $0.011 \pm 0.006$  (mid-season), and  $0.046 \pm 0.016$  (late season). Extinction rates were negatively influenced by seasonal interval, strongly during mid-season ( $\beta_{\text{mid}} = -2.289$ , 95% CI: -3.737 to -0.841;  $\beta_{\text{late}} = -0.769$ , 95% CI: -1.704 to 0.166). Daily extinction probabilities for the Puerto Rican Bullfinches were  $0.230 \pm 0.054$  (early season),  $0.029 \pm 0.011$  (mid-season) and  $0.069 \pm 0.012$  (late season). Extinction rates were negatively and strongly influenced by seasonal intervals ( $\beta_{\text{mid}} = -2.301$ , 95% CI: -3.312 to -1.290;  $\beta_{\text{late}} = -1.389$ , 95% CI: -2.308 to -0.470). The expected proportion of Bananaquit individuals present in the study area on any given day was 0.524 (95% CI: 0.510 to 0.568) during early season, 0.908 (95% CI: 0.875 to 1.000) during mid-season, and 0.703 (95% CI: 0.674 to 0.799) during late season. The

expected proportion of Puerto Rican Bullfinch individuals present in the study area on any given day was 0.315 (95% CI: 0.310 to 0.329) early season, 0.785 (95% CI: 0.749 to 0.891) mid-season, and 0.606 (95% CI: 0.573 to 0.620) late season.

## Nest Monitoring

The number of young fledged in the nest searching study was substantially lower than the number of HY birds captured in the mist-nets for all three focal species (Figure 1.8). Nearly 40 HY Puerto Rican Bullfinches were captured in the eastern tract of the forest as compared to no fledglings observed during nest monitoring (Figure 1.8B). Likewise, there were no fledgling Adelaide's Warblers observed in nest monitoring plots in either tract of the forest in 2010, while there were 11 HY birds captured at MAPS stations (Figure 1.8C). The number of fledglings per adult from the nest monitoring study and the MAPS productivity index yielded relatively similar results in most cases, but for the Puerto Rican Bullfinch and Adelaide's Warbler there were still some data structures that yielded no fledglings while the productivity index yielded a substantial ratio of juveniles to adults in the mist-net catch (Figure 1.9).

## Discussion

The MAPS productivity index implicitly assumes that juveniles and adults are sampled in proportion to their true population sizes within a 20 ha sampling area (du Feu and McMeeking 2004, DeSante et al. 2011). For this to hold true there must be support in the

data for the assumption of equal age-specific capture probabilities. Failing to meet this assumption undermines the utility of the productivity index as a monitoring tool (Bart et al. 1999, DeSante et al. 2004). My results indicated that there was equivocal support for this assumption for the Puerto Rican Bullfinch and none at all for the Bananaquit and Adelaide's Warbler. Contrary to my expectations, capture probabilities were much lower for HY than for AHY in cases where the equal capture probability assumption was violated. This suggested that a productivity index derived from MAPS data would be biased low. Previous studies have reported this type of bias (Peach et al. 1996, DeSante et al. 2001), and Desante et al. (2001) speculated that this could be due to the fact that juveniles disperse from the local study area whereas adults are more sedentary, and thus available for capture. In contrast, but highlighting the same interpretational problems, Bart et al. (1999) reported that higher rates of capture for juvenile birds as compared to adults in Kirtland's Warblers resulted in an inflated estimate of productivity. Certainly, this body of work suggests that the potential utility of the productivity index is species-specific, and thus its use should be preceded by explicit tests of the equality of age-specific capture probabilities for the avian community of interest.

Overall probabilities of capture and recapture were low for all focal species in this study, so a possible way to increase capture rates would be to place a greater number of nets within the area of interest. In this project nets were at the highest density in the southern portion of the study area in the western tract of Guánica. Between northern and southern mist-net stations, which were separated by approximately 400 m, 2% of Bananaquits crossed over to be captured in both locations. In the two mist-netting stations in the southern portion

of the study plot, which were only separated by about 40 m, there was 7% cross over for Bananaquits. The latter possibility suggests that increasing net density may have an effect, although minimal, on increasing capture probability for some species. It is noteworthy that the prevalence of net avoidance behavior may be more pronounced in avian species in the tropics than in temperate regions (MacArthur and MacArthur 1974). This observation could be partly due to the fact that most birds captured in the tropics during the breeding season are year-round residents there and therefore may be better able to “learn” where nets are located, so moving nets between sampling occasions during the season should also be considered as a means to increase capture rates.

Differences between capture and recapture probabilities were substantial for all species and data structures, suggesting that birds were exhibiting a “trap shy” response. This response might influence other processes such as temporary emigration and undermine further inferences made from mist-net data. For example, most top-ranked models yielded elevated estimates of temporary emigration. Estimates of  $\gamma''$  suggested that a large proportion of birds became unavailable for capture between sampling occasions, and this might be due in part to a trap response. Models also yielded high estimates of  $\gamma'$ , suggesting that a large proportion of birds remained unavailable for capture from one sampling occasion to the next. Furthermore, some birds may not change their availability state between sampling periods ( $\gamma' = \gamma'' = 0$ ) as suggested for Bananaquits and Adelaide’s Warblers for the data obtained in the eastern tract of Guánica in 2009 and 2010. Possible explanations for these large temporary emigration rates is that birds may not be available for capture while

tending nests or that the distribution of food resources averts foraging ranges away from nets (e.g., Puerto Rican Bullfinch tracking fruit availability). These results underscore the difficulties of interpreting mist-net based productivity indices and the factors that might influence an estimate of population size, another parameter that can be derived from the MAPS sampling protocol (Kendall et al. 1997, DeSante et al. 2004).

The ratio of juvenile to adult birds captured during the time period when mist-nets were operated may not adequately represent annual reproductive success. It is possible that some resident avian species can breed at any time of year in Puerto Rico (e.g., Bananaquits), so if species lack a single definite peak in reproduction, the segment of the breeding season covered by our sampling period (i.e., March through July) might not adequately represent annual productivity. There were also difficulties assigning ages using the traditional calendar-based classification system, which ages birds based on the calendar year in which they hatched (Pyle 1997), due to the possibility of some species having breeding seasons that overlap January 1. A recently proposed solution to this dilemma is to use molt cycles and inserted plumages to place birds into age cohorts that estimate their ages in months (Wolfe et al. 2010). Certainly, more study is needed on molt for resident birds of Puerto Rico in order to make this method practical. These limitations highlight additional difficulties of applying MAPS protocol to study productivity of tropical avian species.

Radio telemetry offered valuable insights about the process of temporary emigration and the spatial extent sampled by mist-nets. Estimates of  $\gamma'$  and  $\gamma''$  from mist-netting data suggested that birds became unavailable or were unavailable for capture between sampling occasions. However, telemetry data suggested that birds were present and active within the

study area as indicated by their daily occupancy probability and home ranges. A plausible explanation to account for this apparent discrepancy is that the availability of birds for capture in mist-nets and their presence in the telemetry study area occurred at different spatial scales. DeSante (1995) offered general guidelines to establish net stations, describing net placement within an area of 8 ha to provide a basis for inferences to a larger 20 ha area. It is likely that telemetry surveyed a much larger area than did mist-netting since the maximum range of transmitters used was 2 km.

Seasonal estimates of the daily occupancy probability, when averaged over the length of the study (71.2% for Bananaquits, 56.9% for Puerto Rican Bullfinches), corresponded closely with the percent of birds that were detected with radio telemetry in the study area on days when nets were operated (70% of Bananaquits, 58% of Puerto Rican Bullfinches), reinforcing the validity of these estimates. The probability of being detected within the telemetry study area was lower early in the season for Bananaquits and Puerto Rican Bullfinches, but increased from mid- to late-season when I speculate birds had settled onto their breeding territories. This finding suggested that the MAPS productivity index should be most useful during the latter part of our field season when adults and fledglings are most available for capture, provided the equal age-specific capture probability assumption is met.

The utility of the MAPS productivity index has been traditionally judged by comparing results to productivity estimates obtained from associated nest monitoring plots. A strong, positive correlation between these two metrics is often taken as an indication of its utility (DeSante et al. 2004, Saracco et al. 2006, du Feu and McMeeking 2004). A tacit assumption in these assessments of utility is that the direct estimate of breeding productivity

from nest monitoring is accurate. This is a strong assumption because nest detection is likely imperfect (Nichols et al. 1986). In essence, most assessments of utility are made by comparing unadjusted nest-based estimates of productivity with productivity indices derived from mist-netting data without explicitly testing the assumption of equal age-specific capture probability. This makes productivity estimates and correlations difficult to interpret and perhaps spurious.

The interpretational difficulties that might arise when comparing these two estimates of productivity are exemplified by the Bananaquit and Adelaide's Warbler. Productivity indices from mist-nets reflect the cumulative effects of various phases and processes during the nesting cycle and post-fledging mortality, whereas nest monitoring studies are not able to capture all of these variables (Chase et al. 1997). Plots for the nest monitoring study were also larger than the reported sampling area of the mist-nets, so estimates of productivity from nest monitoring were expected to be higher than those from mist-netting, but my findings yielded opposite results. Model results for Bananaquits strongly suggested that capture probabilities were lower for juveniles than for adults, meaning that the MAPS productivity index would be biased low. However, the MAPS index and number of young fledged per adult were similar. In contrast, mist-net data from Adelaide's Warblers yielded more captures of juvenile birds than the number of fledglings observed in the nest monitoring study, implying that the probability of finding a nest was not perfect. This discrepancy was further emphasized in instances when no fledglings were recorded in nest plots, but there were a substantial number of juveniles captured in the corresponding mist-net stations. I cannot exclude the possibility that the juveniles captured in the nets had immigrated into the

study area, but this possibility was poorly supported by telemetry data. None of the HY Bananaquits outfitted with transmitters ( $N=6$ ) emigrated from the study area over the lifetime of their transmitters, and in fact most juveniles exhibited less movement than adults as illustrated by the relative size of their home range ellipses. I did not expect juveniles from neighboring areas to behave differently over the same period.

Nur et al. (1999) proposed tallying only the number of juveniles captured in nets as an index of productivity to avoid the assumption of equal capture rates required by the MAPS index. While the authors reported a correlation between the number of juvenile captures and number of fledglings in their study, captures of juveniles might also be adversely affected by availability (e.g.,  $\gamma'$ ,  $\gamma''$ ). Therefore, it is also possible that this simpler approach could misrepresent the strength of a reproductive year. As noted above, explicit tests about availability and capture rates should be performed prior to conducting a study. In principle, an index of productivity might also be derived from a ratio of juvenile and adult population size estimates. The robust design yields estimates of population size that are adjusted for capture-recapture probability and temporary emigration (Kendall et al. 1997), but two factors need to be considered before using these estimates to calculate a ratio. First, it requires knowledge of the life history and breeding phenology for each species to determine which pair of age-specific population size estimates should be used to calculate the index. Additionally, it is necessary to define the spatial extent over which inferences about population size derived from nets apply for juveniles and adults. In my opinion, this is still an area that needs further research as suggested by estimates of temporary emigration and home ranges.

Indices are meant to be an alternative to estimating parameters directly, and they are useful in many situations over space and time (Williams et al. 2002). Changes in the productivity index over time may reflect true population responses, such as those to changes in environmental conditions (e.g., the El Niño-Southern Oscillation, Nott et al. 2002), but the utility of an index is conditioned on understanding the functional relationship between the index and the parameter it tries to index (Williams et al. 2002). Few studies validate or try to establish this relationship between the index and the desired parameter. My study was an attempt to understand the merits of one of the variables in that relationship, the MAPS productivity index. My findings have shown that for some resident avian species in Puerto Rico the MAPS productivity index might be biased, thus making it more difficult to index the true parameter of interest.

A goal of the MAPS program is to monitor changes in productivity from year-to-year, but the ability to do so could be compromised by inadequate data to test its underlying assumption—equal age-specific capture probabilities. Many of the species captured in this study had insufficient data to test this assumption, even when examined over two years or over two spatial replicates, because encounter histories yielded convergence problems or non-identifiable estimates (e.g., Adelaide’s Warbler). It is possible that this is an artifact of resident tropical species that might tend to avoid nets (MacArthur and MacArthur 1974). Combining data over multiple years might be an option for studies aimed at discerning long-term trends if inferences made from an average capture probability are acceptable. However, discerning short-term responses (e.g., annual) should avoid pooling data in such a fashion as it averages inter-annual variation, negating the value of the annual index. For example,

annual estimates would be required in a structured decision making framework, where the state of the system (e.g. breeding productivity) needs to be assessed in that same time interval in order to gauge the response of the system to a management action (Nichols and Williams 2006). Although my capture-recapture data were collected over a relatively short period (i.e., two years), only one year of data are truly needed to calculate a productivity index. Thus, I do not expect that my conclusions will change in longer-term studies, which are built one year at a time. Increased spatial replication, increasing the density of net stations, and moving the nets between sampling occasions may yield higher capture rates to test the assumption of equal age-specific capture probability, and ultimately yield a suite of species for which inferences about annual breeding productivity can be made from mist-netting data.

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## APPENDIX

**Table 1.1** Table showing the number of individual captures per species for the east and west tracts of Guánica State Forest for each year that the mist-netting study was conducted. The number of those individuals that were recaptured is shown in parentheses. Species are listed in descending order by the total number of captures.

Species	East 2009	East 2010	West 2010	Total
Puerto Rican Bullfinch	119 (21)	61 (22)	139 (37)	319
Bananaquit	86 (17)	71 (28)	154 (54)	311
Common Ground-dove	80 (9)	64 (10)	157 (17)	301
Puerto Rican Tody	92 (44)	75 (38)	52 (25)	219
Adelaide's Warbler	74 (25)	55 (28)	59 (20)	188
Caribbean Elaenia	64 (12)	44 (11)	60 (21)	168
Black-faced Grassquit	36 (0)	28 (3)	47 (10)	111
Puerto Rican Flycatcher	31 (7)	23 (5)	15 (9)	69
Pearly-eyed Thrasher	41 (4)	23 (2)	4 (0)	68
Red-legged Thrush	17 (2)	18 (6)	31 (6)	66
Puerto Rican Lizard Cuckoo	21 (6)	16 (6)	0 (0)	37
Ovenbird	11 (3)	16 (7)	5 (0)	32
Puerto Rican Vireo	10 (2)	9 (4)	10 (8)	29
Key West Quail-dove	12 (1)	16 (2)	0 (0)	28
Black-whiskered Vireo	12 (1)	7 (1)	8 (4)	27
Mangrove Cuckoo	12 (0)	6 (0)	9 (0)	27
American Redstart	9 (2)	9 (2)	7 (0)	25
Black-and-white Warbler	8 (0)	7 (2)	1 (0)	16
Lesser Antillean Pewee	10 (5)	5 (3)	0 (0)	15
Puerto Rican Spindalis	3 (0)	1 (0)	11 (1)	15
Puerto Rican Woodpecker	8 (1)	6 (2)	0 (0)	14
Hooded Warbler	6 (1)	3 (3)	0 (0)	9
Shiny Cowbird	2 (0)	1 (0)	6 (0)	9
Venezuelan Troupial	0 (0)	0 (0)	7 (0)	7
Prairie Warbler	3 (0)	1 (0)	2 (0)	6
Gray Kingbird	1 (0)	0 (0)	4 (0)	5
White-winged Dove	1 (0)	0 (0)	2 (0)	3
Antillean Euphonia	0 (0)	0 (0)	2 (0)	2
Northern Mockingbird	0 (0)	0 (0)	2 (0)	2
Northern Parula	2 (0)	0 (0)	0 (0)	2
Worm-eating Warbler	1 (0)	1 (0)	0 (0)	2
Zenaida Dove	1 (0)	1 (0)	0 (0)	2
Blue-winged Warbler	1 (0)	0 (0)	0 (0)	1
Connecticut Warbler	1 (0)	0 (0)	0 (0)	1
White-eyed Vireo	0 (0)	0 (0)	1 (0)	1

**Table 1.2** Model structure for the candidate set of 24 models that were analyzed for three data structures for each of three focal species. Apparent survival ( $\phi$ ) was modeled as the same (.) or different (g) for age groups; gammas ( $\gamma'$  and  $\gamma''$ ) were modeled as equal for after hatching year (AHY) and hatching year (HY) birds (random temporary emigration), as not equal for those two age groups (Markovian temporary emigration), and as fixed to zero (no movement); and capture probability (p) and recapture probability (c) were modeled as equal between age groups and unequal between age groups.

$\phi(.)$ , $\gamma'=\gamma''$ , p(AHY=HY), c(AHY=HY)
$\phi(.)$ , $\gamma'$ , $\gamma''$ , p(AHY=HY), c(AHY=HY)
$\phi(.)$ , $\gamma'=\gamma''=0$ , p(AHY=HY), c(AHY=HY)
$\phi(.)$ , $\gamma'=\gamma''$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(.)$ , $\gamma'$ , $\gamma''$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(.)$ , $\gamma'=\gamma''=0$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(.)$ , $\gamma'=\gamma''$ , p(AHY=HY), c(AHY $\neq$ HY)
$\phi(.)$ , $\gamma'$ , $\gamma''$ , p(AHY=HY), c(AHY $\neq$ HY)
$\phi(.)$ , $\gamma'=\gamma''=0$ , p(AHY=HY), c(AHY $\neq$ HY)
$\phi(.)$ , $\gamma'=\gamma''$ , p(AHY $\neq$ HY), c(AHY $\neq$ HY)
$\phi(.)$ , $\gamma'$ , $\gamma''$ , p(AHY $\neq$ HY), c(AHY $\neq$ HY)
$\phi(.)$ , $\gamma'=\gamma''=0$ , p(AHY $\neq$ HY), c(AHY $\neq$ HY)
$\phi(g)$ , $\gamma'=\gamma''$ , p(AHY=HY), c(AHY=HY)
$\phi(g)$ , $\gamma'$ , $\gamma''$ , p(AHY=HY), c(AHY=HY)
$\phi(g)$ , $\gamma'=\gamma''=0$ , p(AHY=HY), c(AHY=HY)
$\phi(g)$ , $\gamma'=\gamma''$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(g)$ , $\gamma'$ , $\gamma''$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(g)$ , $\gamma'=\gamma''=0$ , p(AHY $\neq$ HY), c(AHY=HY)
$\phi(g)$ , $\gamma'=\gamma''$ , p(AHY=HY), c(AHY $\neq$ HY)
$\phi(g)$ , $\gamma'$ , $\gamma''$ , p(AHY=HY), c(AHY $\neq$ HY)
$\phi(g)$ , $\gamma'=\gamma''=0$ , p(AHY $\neq$ HY), c(AHY $\neq$ HY)

**Table 1.3** Robust design models for Bananaquit mist-netting data from the western tract of Guánica State Forest in 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(.), \gamma'(.)=\gamma''(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	1034.1568	0.0000	0.6858	1.0000	5	979.5876
* $\phi(.), \gamma'(.), \gamma''(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	1035.7399	1.5831	0.3108	0.4531	6	979.0769
$\phi(g), \gamma'(.)=\gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1044.8034	10.6466	0.0033	0.0049	5	990.2342
$\phi(g), \gamma'(.)=\gamma''(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1051.4970	17.3402	0.0001	0.0002	4	999.0058
$\phi(.), \gamma'(.)=\gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1060.7201	26.5633	0.0000	0.0000	4	1008.2288
$\phi(.), \gamma'(.)=\gamma''(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1067.7550	33.5982	0.0000	0.0000	3	1017.3256

**Table 1.4** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) from the top-ranked model for Bananaquit mist-netting data from the western tract of Guánica State Forest in 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY								
0.9754 (0.0038)		0.6436 (0.0611)		0.6436 (0.0611)		0.4469 (0.0780)		0.0154 (0.0159)	

**Table 1.5** Robust design models for Bananaquit mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(g), \gamma''(.)=\gamma'(.)=0, p(AHY\neq HY), c(AHY=HY)$	742.3211	0.0000	0.4933	1.0000	5	732.0240
* $\phi(g), \gamma''(.)=\gamma'(.)=0, p(AHY\neq HY), c(AHY=HY)\}, + \text{year}$	743.9577	1.6366	0.2176	0.4412	6	731.5398
$\phi(g), \gamma''(.)=\gamma'(.), p(AHY=HY), c(AHY=HY)$	744.6829	2.3618	0.1514	0.3070	5	734.3859
$\phi(.), \gamma''(.)=\gamma'(.), p(AHY\neq HY), c(AHY=HY)$	745.4914	3.1703	0.1011	0.2049	5	735.1943
$\phi(g), \gamma''(.)=\gamma'(.)=0, p(AHY=HY), c(AHY=HY)$	747.8186	5.4975	0.0316	0.0640	4	739.6216
$\phi(.), \gamma''(.)=\gamma'(.), p(AHY=HY), c(AHY=HY)$	752.4512	10.1301	0.0031	0.0063	4	744.2541
$\phi(.), \gamma''(.), \gamma'(.), p(AHY=HY), c(AHY=HY)$	754.2085	11.8874	0.0013	0.0026	5	743.9115
$\phi(.), \gamma''(.)=\gamma'(.)=0, p(AHY=HY), c(AHY=HY)$	755.7036	13.3825	0.0006	0.0012	3	749.5860

**Table 1.6** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Bananaquit mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY	AHY	HY	AHY	HY	AHY	HY	AHY	HY
0.9851 (0.0050)	0.8921 (0.0560)	0 (Fixed)		0 (Fixed)		0.0525 (0.0115)	0.0349 (0.0082)	0.0417 (0.0182)	

**Table 1.7** Robust design models for Bananaquit mist-netting data from the eastern and western tracts of Guánica State Forest in 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(.), \gamma'(.)=\gamma''(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	1374.9692	0.0000	0.7164	1.0000	5	1364.7983
$\phi(.), \gamma'(.), \gamma''(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	1376.9941	2.0249	0.2603	0.3633	6	1364.7541
$\phi(.), \gamma'(.)=\gamma''(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY}), + \text{tract}$	1382.7784	7.8092	0.0144	0.0201	5	1372.6075
$\phi(g), \gamma'(.)=\gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1384.5982	9.6290	0.0058	0.0081	5	1374.4273
$\phi(g), \gamma'(.), \gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1386.5727	11.6035	0.0022	0.0030	6	1374.3327
$\phi(.), \gamma'(.)=\gamma''(.)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	1388.1901	13.2209	0.0010	0.0013	4	1380.0765
$\phi(g), \gamma'(.)=\gamma''(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1396.9733	22.0041	0.0000	0.0000	4	1388.8597
$\phi(.), \gamma'(.)=\gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1404.0608	29.0916	0.0000	0.0000	4	1395.9472
$\phi(.), \gamma'(.), \gamma''(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1406.0614	31.0922	0.0000	0.0000	5	1395.8905
$\phi(.), \gamma'(.)=\gamma''(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	1416.8814	41.9122	0.0000	0.0000	3	1410.8134

**Table 1.8** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Bananaquit mist-netting data from the eastern and western tracts of Guánica State Forest in 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY	AHY	HY	AHY	HY	AHY	HY	AHY	HY
0.9756 (0.0034)		0.6989 (0.0471)		0.6989 (0.0471)		0.4406 (0.0672)	0.0147 (0.0151)	0.0744 (0.0179)	

**Table 1.9** Robust design models for Puerto Rican Bullfinch mist-netting data from the western tract of Guánica State Forest in 2010 ranked by their respective  $AIC_c$  values. Competing models ( $\Delta AIC_c \leq 2$ ) are indicated with an asterisk.

Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ Weight	Model Likelihood	Parameters	Deviance
* $\phi(.), \gamma'(.)=\gamma''(.), p(AHY=HY), c(AHY=HY)$	490.7299	0.0000	0.3955	1.0000	4	183.7473
* $\phi(g), \gamma'(.)=\gamma''(.), p(AHY=HY), c(AHY=HY)$	492.3695	1.6396	0.1742	0.4405	5	183.2571
* $\phi(.), \gamma'(.)=\gamma''(.), p(AHY \neq HY), c(AHY=HY)$	492.6627	1.9328	0.1505	0.3805	5	183.5502
$\phi(.), \gamma'(.)=\gamma''(.)=0, p(AHY=HY), c(AHY=HY)$	493.3188	2.5889	0.1084	0.2741	3	188.4390
$\phi(g), \gamma'(.)=\gamma''(.), p(AHY \neq HY), c(AHY=HY)$	494.3194	3.5895	0.0657	0.1662	6	183.0497
$\phi(g), \gamma'(.)=\gamma''(.)=0, p(AHY=HY), c(AHY=HY)$	495.0167	4.2868	0.0464	0.1173	4	188.0341
$\phi(g), \gamma'(.), \gamma''(.), p(AHY \neq HY), c(AHY=HY)$	495.1956	4.4657	0.0424	0.1072	7	181.7405
$\phi(g), \gamma'(.)=\gamma''(.)=0, p(AHY \neq HY), c(AHY=HY)$	497.0231	6.2932	0.0170	0.0430	5	187.9106

**Table 1.10** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Puerto Rican Bullfinch mist-netting data from the western tract of Guánica State Forest in 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY								
0.9920 (0.0095)		0.9895 (0.0049)		0.9895 (0.0049)		0.3114 (0.1120)		0.0538 (0.0234)	

**Table 1.11** Robust design models for Puerto Rican Bullfinch mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(.)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY≠HY), c(AHY=HY), + year	587.6350	0.0000	0.4699	1.0000	6	575.2232
* $\phi(.)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY≠HY), c(AHY=HY)	588.5193	0.8843	0.3020	0.6426	5	578.2266
$\phi(g)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY≠HY), c(AHY=HY)	591.9589	4.3239	0.0541	0.1151	6	579.5471
$\phi(.)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY=HY), c(AHY=HY)	592.5847	4.9497	0.0396	0.0842	4	584.3905
$\phi(g)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY≠HY), c(AHY=HY)	592.7572	5.1222	0.0363	0.0772	7	578.2055
$\phi(g)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY=HY), c(AHY=HY)	592.9277	5.2927	0.0333	0.0709	5	582.6350
$\phi(.)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY=HY), c(AHY=HY)	593.1911	5.5561	0.0292	0.0622	5	582.8984
$\phi(g)$ , $\gamma''(.)=\gamma'(.)$ , p(AHY=HY), c(AHY=HY)	593.7659	6.1309	0.0219	0.0466	6	581.3542
$\phi(g)$ , $\gamma''(.)=\gamma'(.)=0$ , p(AHY≠HY), c(AHY=HY)	595.4858	7.8508	0.0093	0.0197	5	585.1931
$\phi(.)$ , $\gamma''(.)=\gamma'(.)=0$ , p(AHY≠HY), c(AHY=HY)	598.8075	11.1725	0.0018	0.0037	4	590.6133
$\phi(.)$ , $\gamma''(.)=\gamma'(.)=0$ , p(AHY=HY), c(AHY=HY)	599.1394	11.5044	0.0015	0.0032	3	593.0234
$\phi(g)$ , $\gamma''(.)=\gamma'(.)=0$ , p(AHY=HY), c(AHY=HY)	599.4309	11.7959	0.0013	0.0027	4	591.2367

**Table 1.12** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Puerto Rican Bullfinch mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY	AHY	HY	AHY	HY	AHY	HY	AHY	HY
0.9943 (0.0045)		0.9942 (0.0020)		0.9942 (0.0020)		0.4851 (0.0978)	0.1583 (0.0982)	0.0092 (0.0093)	

**Table 1.13** Robust design models for Puerto Rican Bullfinch mist-netting data from the eastern and western tracts of Guánica State Forest in 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(\cdot), \gamma'(\cdot), \gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	726.7228	0.0000	0.2193	1.0000	5	716.4631
* $\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	727.0661	0.3433	0.1847	0.8423	4	718.8937
* $\phi(\cdot), \gamma'(\cdot), \gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY}), + \text{tract}$	727.3228	0.6000	0.1624	0.7408	4	719.1504
* $\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}\neq\text{HY})$	728.6852	1.9624	0.0822	0.3749	5	718.4255
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	729.0832	2.3604	0.0674	0.3072	5	718.8234
$\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	729.7781	3.0553	0.0476	0.2171	3	723.6751
$\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot), p(\text{AHY}\neq\text{HY}), c(\text{AHY}\neq\text{HY})$	730.1752	3.4524	0.0390	0.1780	6	717.8100
$\phi(g), \gamma'(\cdot), \gamma''(\cdot), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	730.2813	3.5585	0.0370	0.1688	7	715.7922
$\phi(g), \gamma'(\cdot), \gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}\neq\text{HY})$	730.4840	3.7612	0.0334	0.1525	7	715.9949
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot), p(\text{AHY}=\text{HY}), c(\text{AHY}\neq\text{HY})$	730.7204	3.9976	0.0297	0.1355	6	718.3552
$\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}\neq\text{HY})$	731.3793	4.6565	0.0214	0.0975	4	723.2069
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	731.7751	5.0523	0.0175	0.0800	4	723.6027
$\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	731.8075	5.0847	0.0173	0.0787	4	723.6351
$\phi(g), \gamma'(\cdot), \gamma''(\cdot), p(\text{AHY}\neq\text{HY}), c(\text{AHY}\neq\text{HY})$	731.9556	5.2328	0.0160	0.0731	8	715.3241
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}\neq\text{HY})$	733.3943	6.6715	0.0078	0.0356	5	723.1345
$\phi(\cdot), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}\neq\text{HY})$	733.4266	6.7038	0.0077	0.0350	5	723.1669
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	733.6834	6.9606	0.0068	0.0308	5	723.4236
$\phi(g), \gamma'(\cdot)=\gamma''(\cdot)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}\neq\text{HY})$	735.3206	8.5978	0.0030	0.0136	6	722.9554

**Table 1.14** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Puerto Rican Bullfinch mist-netting data from the eastern and western tracts of Guánica State Forest in 2010.

$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY								
1.0000 (0.0000)		0.9470 (0.0190)		0.8978 (0.0471)		0.2605 (0.0997)		0.0451 (0.0180)	

**Table 1.15** Robust design models for Adelaide's Warbler mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010 ranked by their respective AIC<sub>c</sub> values. Competing models ( $\Delta\text{AIC}_c \leq 2$ ) are indicated with an asterisk.

Model	AIC <sub>c</sub>	$\Delta\text{AIC}_c$	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
* $\phi(g), \gamma''(.)=\gamma'(.)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	734.3668	0.0000	0.3866	1.0000	5	724.0407
* $\phi(g), \gamma''(.)=\gamma'(.)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY}) + \text{year}$	734.9757	0.6089	0.2851	0.7375	6	722.5167
* $\phi(.), \gamma''(.)=\gamma'(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	736.1074	1.7406	0.1619	0.4188	4	727.8912
$\phi(.), \gamma''(.), \gamma'(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	737.9995	3.6327	0.0629	0.1626	5	727.6734
$\phi(.), \gamma''(.)=\gamma'(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	738.1354	3.7686	0.0587	0.1519	5	727.8093
$\phi(g), \gamma''(.), \gamma'(.), p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	738.9395	4.5727	0.0393	0.1016	6	726.4805
$\phi(.), \gamma''(.)=\gamma'(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	744.5257	10.1589	0.0024	0.0062	3	738.3967
$\phi(g), \gamma''(.)=\gamma'(.)=0, p(\text{AHY}=\text{HY}), c(\text{AHY}=\text{HY})$	745.4028	11.0360	0.0016	0.0040	4	737.1866
$\phi(.), \gamma''(.)=\gamma'(.)=0, p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	745.7021	11.3353	0.0013	0.0035	4	737.4859
$\phi(.), \gamma''(.), \gamma'(.), p(\text{AHY}\neq\text{HY}), c(\text{AHY}=\text{HY})$	749.8620	15.4952	0.0002	0.0004	6	737.4029

**Table 1.16** Estimates of apparent survival ( $\phi$ ), temporary emigration rates ( $\gamma'$  and  $\gamma''$ ), capture probability (p), and recapture probability (c) for the top-ranked model for Adelaide's Warbler mist-netting data from the eastern tract of Guánica State Forest in 2009 and 2010.

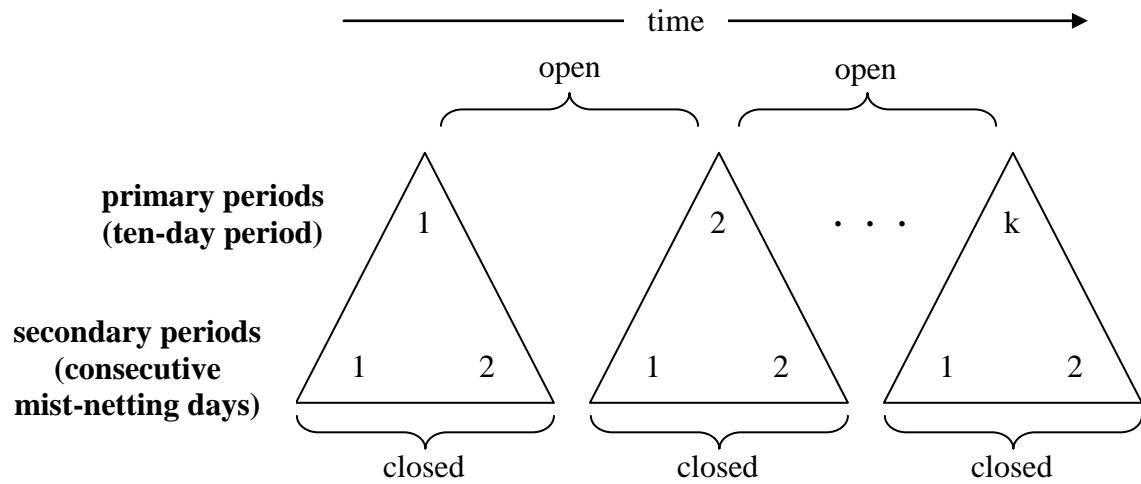
$\phi$ (SE)		$\gamma'$ (SE)		$\gamma''$ (SE)		p (SE)		c (SE)	
AHY	HY	AHY	HY	AHY	HY	AHY	HY	AHY	HY
0.9886 (0.0044)	0.9441 (0.0544)	0 (Fixed)		0 (Fixed)		0.0751 (0.0143)	0.0433 (0.0093)	0.0603 (0.0221)	

**Table 1.17** Model selection for Bananaquit probability of occurrence in the study area based on telemetry data for the western unit of Guánica State Forest during the 2010 breeding season. Parameter estimates of interest are colonization probability (gamma) and extinction probability (epsilon). Other parameters are initial occupancy probability (Psi) and detection probability (p).

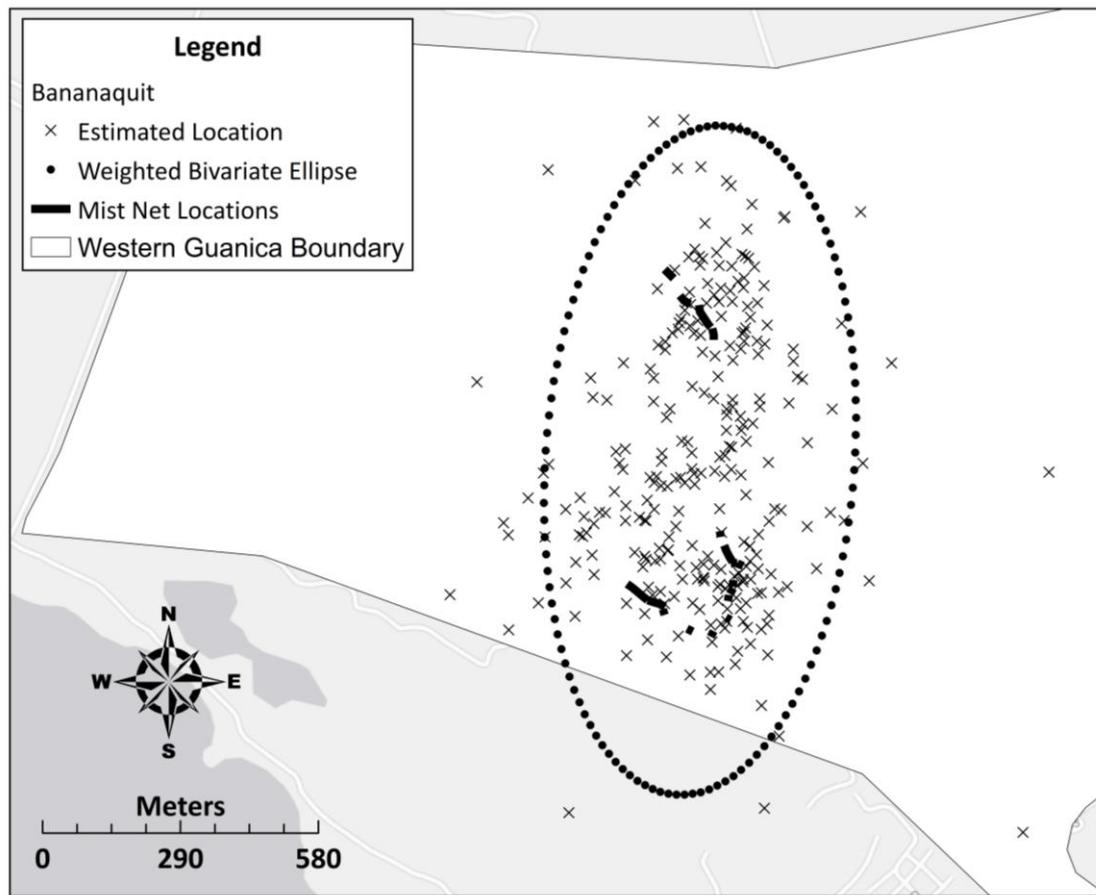
Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
Psi, gamma, epsilon(mid+late), p	1008.02	0	0.9855	1	6	996.02
Psi, gamma, epsilon, p	1017.96	9.94	0.0068	0.0069	4	1009.96
Psi, gamma, epsilon(age), p	1019.53	11.51	0.0031	0.0032	5	1009.53
Psi, gamma(age), epsilon, p	1019.84	11.82	0.0027	0.0027	5	1009.84
Psi, gamma(mid+late), epsilon, p	1020.57	12.55	0.0019	0.0019	6	1008.57

**Table 1.18** Model selection for Puerto Rican Bullfinch probability of occurrence in the study area based on telemetry data for the western unit of Guánica State Forest during the 2010 breeding season. Parameter estimates of interest are colonization probability (gamma) and extinction probability (epsilon). Other parameters are initial occupancy probability (Psi) and detection probability (p).

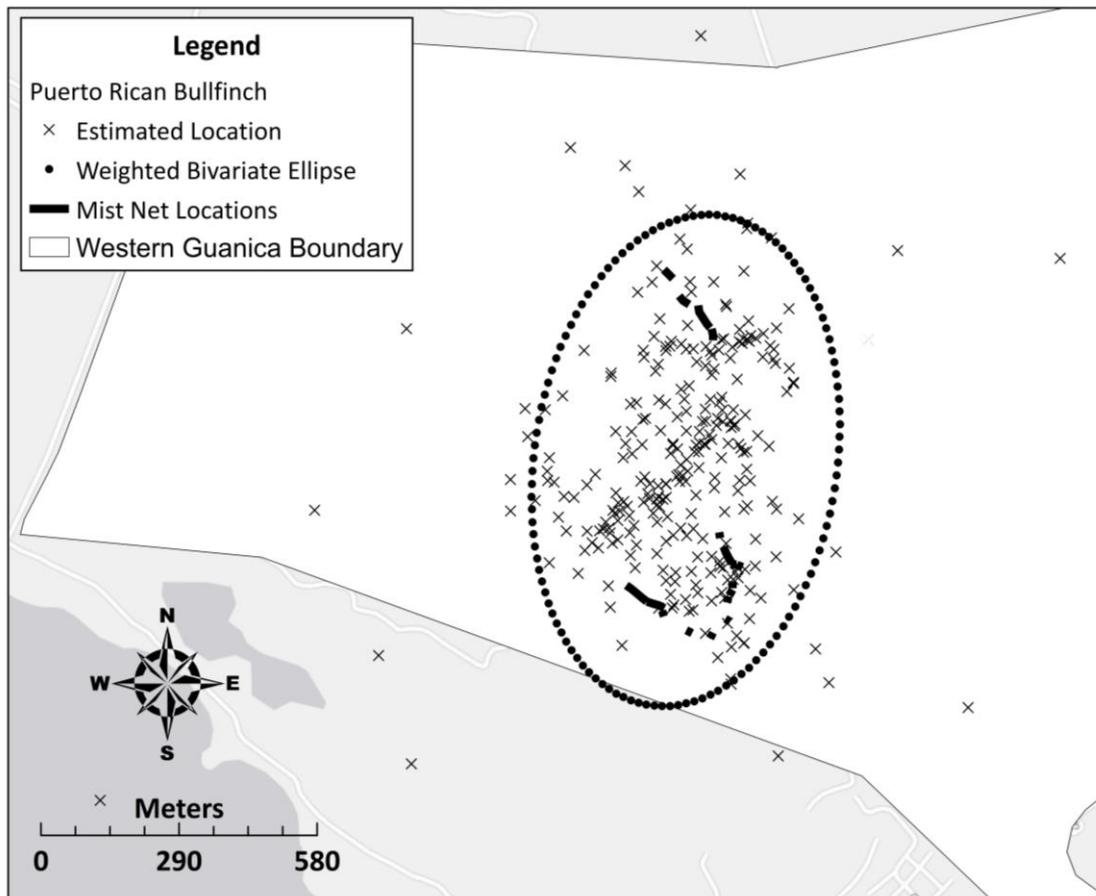
Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
Psi, gamma, epsilon(mid+late), p	939.24	0	0.9998	1	6	927.24
Psi, gamma, epsilon, p	956.93	17.69	0.0001	0.0001	4	948.93
Psi, gamma(mid+late), epsilon, p	960.62	21.38	0	0	6	948.62



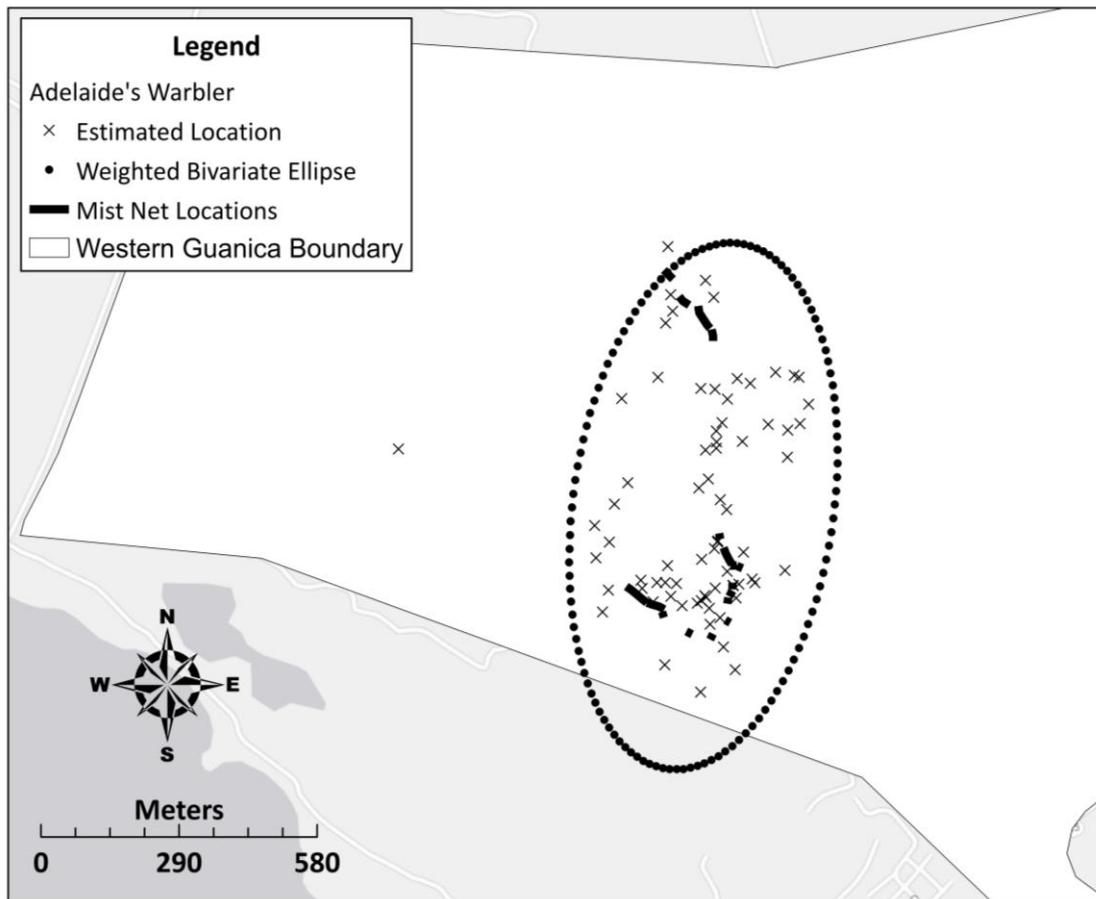
**Figure 1.1** Diagram showing  $k$  open primary sampling periods and two closed secondary sampling periods in Pollock's Robust Design (Pollock et al. 1990). It is assumed that the population is closed to births, deaths, immigration, and emigration between secondary periods, but the population is considered open to these events between the primary periods.



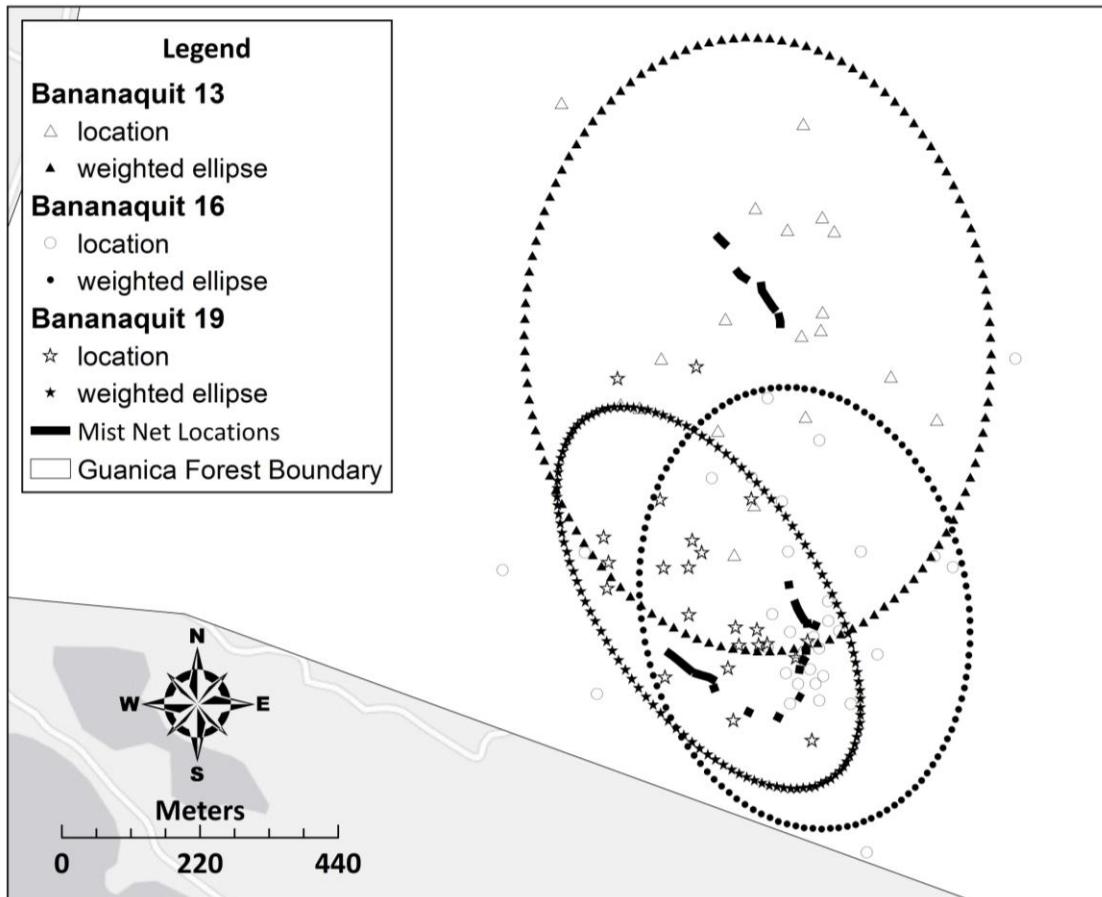
**Figure 1.2** Map showing all estimated locations for all individual Bananaquits in the telemetry study and the weighted bivariate ellipse which was calculated from those estimated locations. The ellipse encompasses all mist-net locations where birds were originally captured.



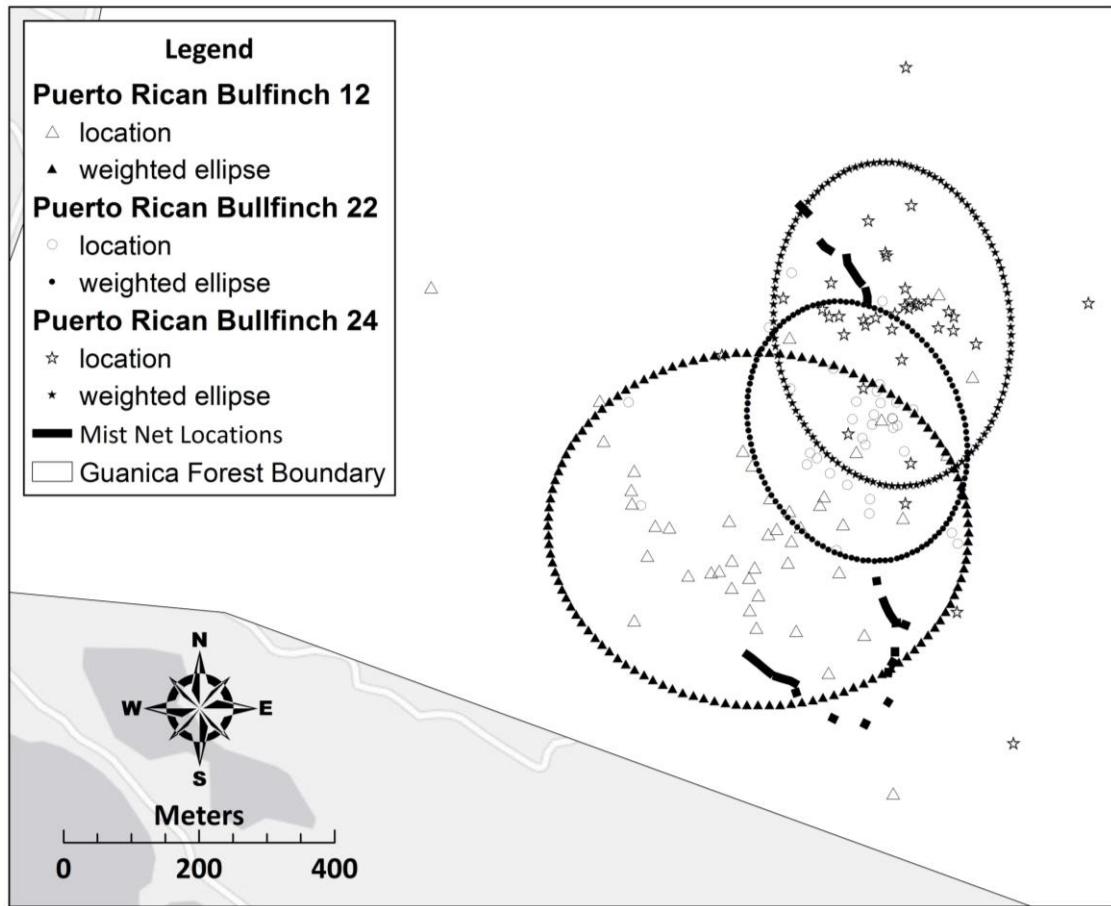
**Figure 1.3** Map showing all estimated locations for all individual Puerto Rican Bullfinches in the telemetry study and the weighted bivariate ellipse which was calculated from all of those estimated locations. The ellipse encompasses all mist-net locations where birds were originally captured.



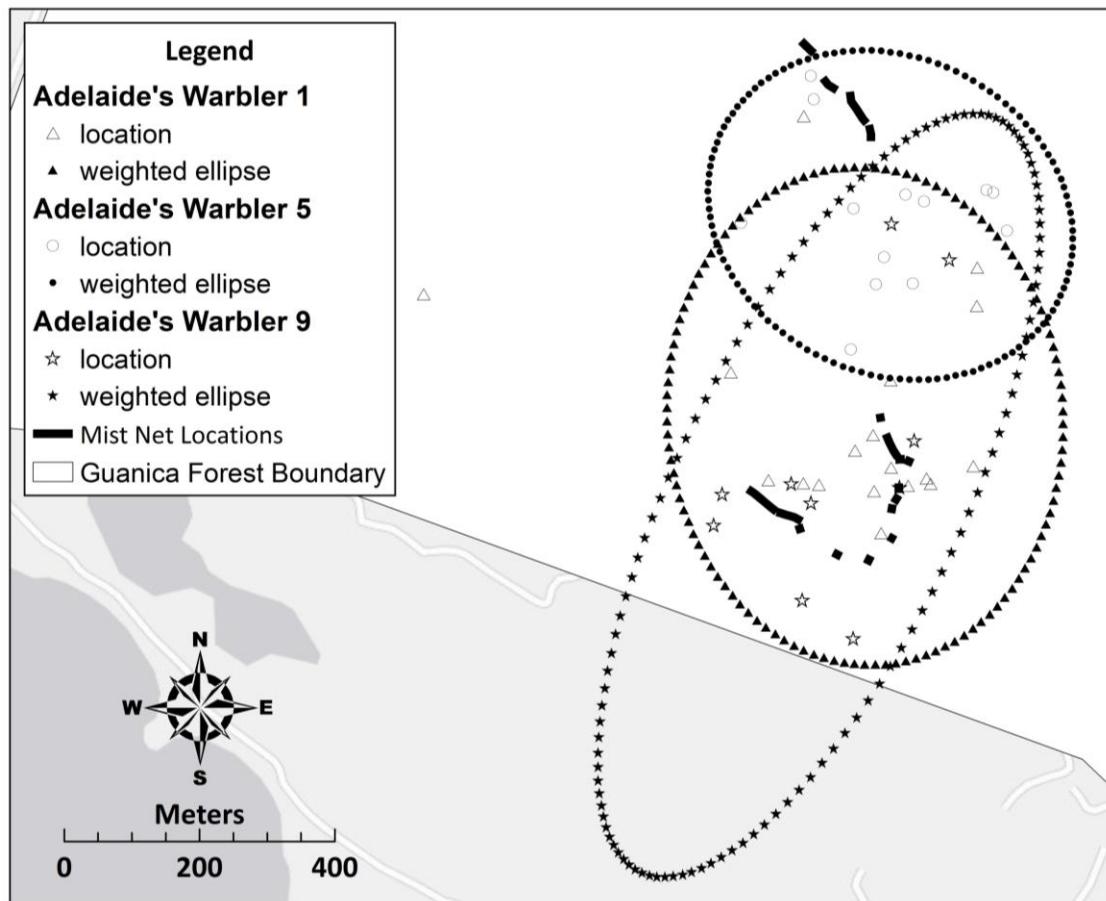
**Figure 1.4** Map showing all estimated locations for all individual Adelaide's Warblers in the telemetry study and the weighted bivariate ellipse which was calculated from all of those estimated locations. The ellipse encompasses all mist-net locations where birds were originally captured.



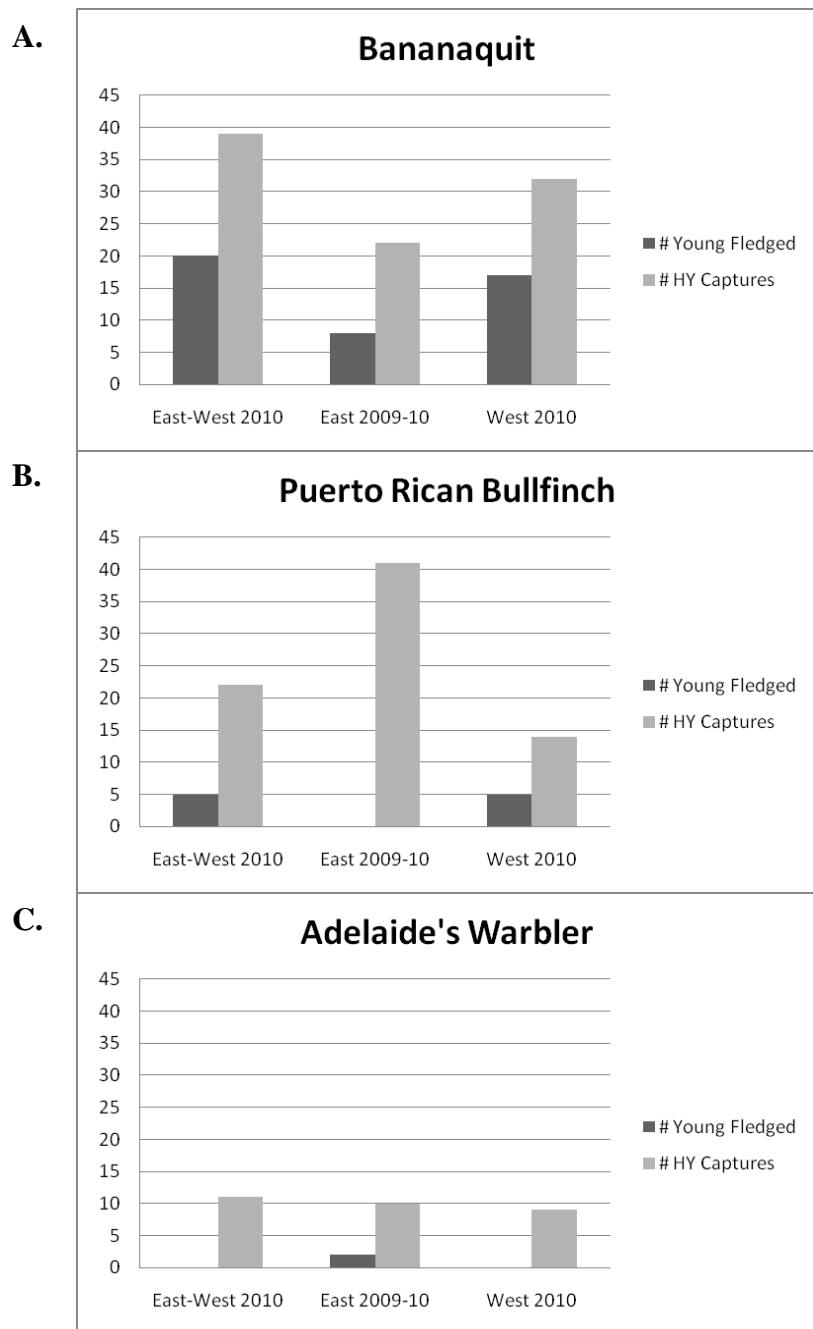
**Figure 1.5** Map showing all estimated locations for the three individual Bananaquits with the most telemetry data and the weighted bivariate ellipses which were calculated from those estimated locations. Ellipses for all three individuals encompass the location of the mist-net where that bird was originally captured.



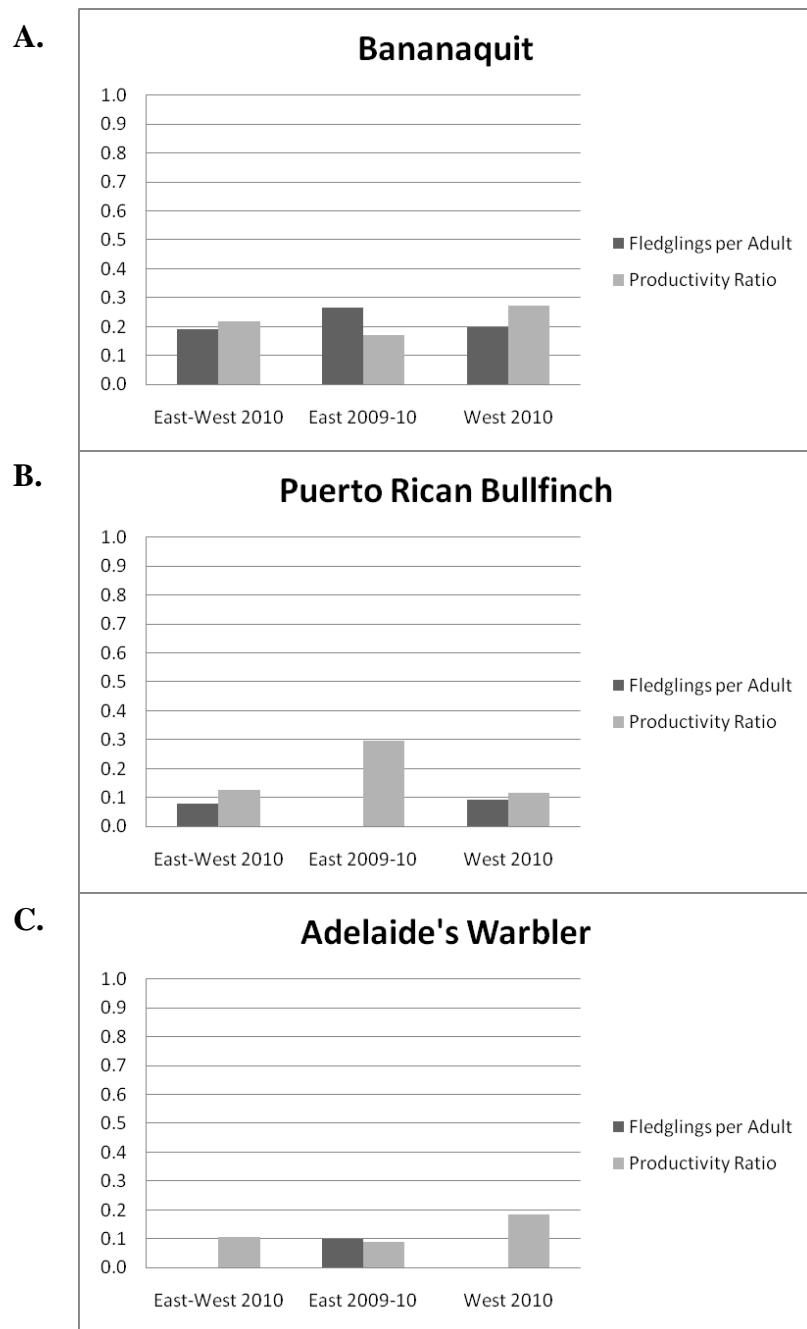
**Figure 1.6** Map showing all estimated locations for the three individual Puerto Rican Bullfinches with the most telemetry data and the weighted bivariate ellipses which were calculated from those estimated locations. Ellipses for two of the three individuals encompass the location of the mist-net where birds were originally captured.



**Figure 1.7** Map showing all estimated locations for the three individual Adelaide's Warblers with the most telemetry data and the weighted bivariate ellipses which were calculated from those estimated locations. Ellipses for all three individuals encompass the location of the mist-net where that bird was originally captured.



**Figure 1.8** Comparison of the number of young fledged observed in the nest monitoring study to the number of hatching year (HY) birds captured in the mist-nets for Bananaquits (A), Puerto Rican Bullfinches (B), and Adelaide's Warblers (C) across three data structures. The number of HY birds captured has been suggested by Nur et al. (1999) as an alternative measure of productivity because it makes fewer assumptions than the MAPS productivity index.



**Figure 1.9** Comparison of the number of young fledged per adult in the nest monitoring study, calculated as the number of fledglings per nest divided by two, to the MAPS productivity index, calculated as the number of HY captured divided by the number of AHY captured in mist-nets, for Bananaquits (A), Puerto Rican Bullfinches (B), and Adelaide's Warblers (C) across three data structures. These indices have no measure of precision.

## Chapter 2

# Factors affecting detection probability of resident avian species in a subtropical dry forest

### **Abstract**

Avian abundance is a commonly estimated parameter used to inform conservation and management decisions. I conducted time-of-detection point counts in the eastern and western tracts of Guánica State Forest to obtain estimates of avian abundance and determine factors affecting detection probabilities. LiDAR measurements of vegetation structure were significantly different between the two tracts, which differ in their time since disturbance by at least 40 years. Avian species density was higher in the western tract for all focal species except for the Pearly-Eyed Thrasher (*Margarops fuscatus*), which was nearly absent in that tract. Structural differences in vegetation and predation by thrashers on Bananaquits (*Coereba flaveola*), Puerto Rican Vireos (*Vireo latimeri*), and Puerto Rican Bullfinches (*Loxigilla portoricensis*) could be factors contributing to differences in density between tracts. The prevalence of support for models with unequal probabilities of first and subsequent detections (Mb) in candidate sets could indicate a tendency of observers to

anticipate calls made by birds that were already detected earlier in the survey period. The prevalence of support for models with heterogeneity in detection probabilities among individuals within a species ( $M_h$ ) could indicate variation in singing rates or distance from observer. Although LiDAR is a useful tool for landscape level studies for modeling species-habitat relationships, covariates derived from LiDAR did not account for as much variation in the data as did field measurements of vegetation structure and distance from observer.

## **Introduction**

Effective conservation is possible only when sound demographic data are available with which to engage in conservation planning and assess the response of a system to management actions (Nichols and Williams 2006). Avian abundance is one of those parameters, which is commonly estimated using point counts surveys. In this technique counts are made from a fixed point at which the observer records all birds detected through sight or sound within a limited or unlimited distance from that point. It is assumed that birds detected in this type of survey represent a constant proportion of the total population in the area, but this is not always the case (Thompson 2002). To correct for possible bias, estimates of abundance need to be adjusted for detection probability (Farnsworth et al. 2002, Alldredge 2004).

Farnsworth et al. (2002) proposed a time-of-removal model to account for availability and detection probability in count data. In this framework the survey period is split up into intervals and observers record the interval in which individual birds are first detected. This

model was generalized by adjusting for variation in singing rates of birds, which has a considerable effect on detection probabilities (Alldredge 2004, Alldredge et al. 2007a). The time-of-detection model considers bias due to availability of birds by modeling the probability of singing during the point count and it considers detection bias by modeling the probability that the bird is detected by the observer if it does sing. Closed population capture-recapture models can then be used to estimate abundance from the point count data. The time-of-detection method assumes that the population within the sampling area is closed, that individual birds are accurately tracked, and that birds are accurately assigned within the radius if a limited radius is used (Alldredge et al. 2007a).

Detection probabilities are influenced by factors such as species, observer, singing rate, distance from observer (Alldredge et al. 2007b), weather (Mayfield 1981), season (Best 1981), and ambient noise (Simons et al. 2007). Habitat type and structure also have been shown to influence detection probabilities (Pacifici et al. 2008, McShea and Rappole 1997). Traditionally, measurements of habitat structure are estimated by observers in the field (Martin and Geupel 1993, Conway and Martin 1999). However, in recent years Light Detecting and Ranging (LiDAR) remote sensing technology has emerged as a new technology that can be used to quantify the three-dimensional structure of landscapes across a broad area (Vierling et al. 2008). This form of remote sensing can be used to obtain information on many habitat characteristics such as canopy height, percent canopy cover, stand density and age, subcanopy height and density, and patch and edge characteristics (Martinuzzi et al. 2009b). LiDAR can be used to gather this information faster, more efficiently, and on a broader scale than traditional field methods. LiDAR data on canopy

height and heterogeneity have recently started to be used in conjunction with point count data to understand avian species-habitat associations (Seavy et al. 2009) and to characterize forest structure characteristics that are important to wildlife (Martinuzzi et al. 2009a).

Estimates of abundance are lacking for most avian species in Puerto Rico, with the exception of endangered and game species (Garcia et al. 2005). Estimates of this parameter are needed to assess the status of “data deficient” species, prioritize habitat for conservation, and assess system responses to management actions (Garcia et al. 2005, Nichols and Williams 2006). This study was designed to compare avian abundance between the two tracts of Guánica State Forest in southwestern Puerto Rico in 2009 and 2010. Impetus for this work stemmed from interest in monitoring populations of the Puerto Rican Vireo, whose population is being affected by brood parasitism from Shiny Cowbirds (*Molothrus bonariensis*) and predation from Pearly-eyed Thrashers (*Margarops fuscatus*) (Woodworth 1997), and on developing baseline data for the western unit of the forest, acquired in 1980. In addressing these basic objectives, I was interested in assessing factors that influenced detection probability. In particular, I was interested in the influence of forest structure on detection given that the two units differed in time since last disturbance by about 40 years. I considered measurements of vegetation structure obtained by observers in the field as well as measurements of topographic features and vegetation structure derived from LiDAR. I used these covariates in a time-of-detection modeling framework to address two questions: 1) was detection probability, and hence abundance estimates, influenced by habitat structure, and 2) did bird abundance differ between forest units, and were habitat structural differences (e.g., indexing time since disturbance) a contributor if differences existed? I discuss results in the

context of habitat structure associated with preferred habitat of focal avian species, and the application of time-of-detection point counts as a monitoring tool for birds in Guánica and elsewhere in Puerto Rico.

## Methods

### Study Area

Guánica State Forest is split up into eastern and western reserves that differ in disturbance and successional stage. I conducted this study in both of these tracts of Guánica State Forest, which are separated by a bay and suburban areas (Figure 2.1). The eastern tract of Guánica is 2,915 ha in size, whereas the western tract is only 736 ha. Some of the land that is now included in the eastern tract of the forest reserve was used in the past for housing, farmland, and charcoal pits (Colon and Lugo 2006). Deforestation hit a high in the 1940's (Birdsey and Weaver 1987), but parts of the eastern tract of the forest have now been protected for approximately 60 years and are in a late successional stage (Murphy and Lugo 1986). Ewel and Whitmore (1973) called the undisturbed parts of the forest "perhaps the best example of natural vegetation in subtropical dry forest anywhere in the world." The western tract of the forest has been disturbed more recently by livestock and removal of lumber for charcoal production, but that land was acquired by Puerto Rico's Department of Natural and Environmental Resources and has now been allowed to recover since the 1980's (Miguel Canals, PRDNER Guánica Forest Administrator, pers. comm.). Differences in

successional stages, and therefore vegetation structure, could have an influence on avian species densities in these two forest tracts.

## Focal Species

I chose five focal species for point count surveys that represented specific management interests at Guánica State Forest and that covered a wide range of life history characteristics. These were the Bananaquit (*Coereba flaveola*), Pearly-eyed Thrasher (*Margarops fuscatus*), Puerto Rican Bullfinch (*Loxigilla portoricensis*), Adelaide's Warbler (*Dendroica adelaidae*), and Puerto Rican Vireo (*Vireo latimeri*). All of these species are residents in Puerto Rico and the last three are endemic to the island.

The Bananaquit is the most abundant bird in Puerto Rico and it sings throughout the day (Oberle 2006). As such it would yield a large data set with which to address the objectives of this study. Bananaquits can be found in most habitat types throughout the island and they forage at all levels of the forest on nectar, fruit, and insects (Oberle 2006, Raffaele et al. 2003). Males will sing at their own roosting nest as well as their mate's nest (Wunderle 1984).

The Pearly-eyed Thrasher is a common species, with a patchy distribution across Puerto Rico. It is a classic example of an avian “supertramp” because of its ability to disperse and adopt generalized nesting and foraging strategies (Arendt 2006). They are opportunistic feeders on resources at lower and middle strata of the forest. Their song consists of two or three soft melodic phrases and they have an assortment of call notes

(Oberle 2006). The thrasher is a threat to many avian species, especially the endangered Puerto Rican Parrot (*Amazona vittata*), because it is a predator to their eggs and nestlings (Arendt 2000). Interest in the thrasher was prompted because Guánica was among the sites considered for reintroduction of the parrot, a major initiative in the species' recovery program (USFWS 2009, White and Llerandi-Roman 2010).

The Puerto Rican Bullfinch is an endemic, commonly found in forested parts of the island including Guánica State Forest. It forages mainly on seeds, fruits, and buds at all levels of the forest, but in dry forests such as Guánica it forages mainly in the canopy. Bullfinches have a loud, distinctive song that consists of whistled notes followed by a trill. They can be heard singing at any time of day from treetops, but they are less likely to be seen because they are often hidden by vegetation in the canopy (Oberle 2006).

The Adelaide's Warbler is an endemic found in moist limestone forests and thickets in dry forests such as Guánica. It is a small warbler that forages on insects in the middle and upper strata of the forest. Adelaide's Warblers maintain all-purpose territories and monogamous pair bonds year-round (Staicer 1996b). Adelaide's warblers have two categories of song, one that is thought to be more aggressive for communication between males and one that may be specialized for advertising to females (Staicer 1996a). They are often heard singing later in the morning than most other species and at all times of the year (Oberle 2006).

The Puerto Rican Vireo is an endemic that inhabits mountain forests, karst landscapes, and areas with dense thorn and vine tangles such as Guánica. It forages on insects in the middle and lower strata of the forest. It is often hard to locate because of its

preference for foraging in thick vegetation, but its loud song makes it easier to detect aurally (Oberle 2006). This species is one of the main hosts of the Shiny Cowbird, a brood parasite native to South America (Pérez-Rivera 1986, Woodworth 1997), and its nests are heavily predated by Pearly-eyed Thrashers (Woodworth 1997). Data on density are needed to help assess the status of the species and could be used to assess the response of the population to a cowbird control program.

## Point Counts

I randomly placed 79 point count stations throughout the eastern tract of the forest, and 50 stations in the western tract due to its smaller size (Figure 2.2). All points were at least 200 meters apart to reduce the chance of double counting individual birds. I conducted point counts at stations in the eastern tract of Guánica in 2009 and 2010, and at stations in the western tract in 2010 only. Each station was visited once per year in a random order from April through May. Upon reaching a station, I waited 2 minutes before counting to allow birds to settle and increase detection probability (Rosenstock et al. 2002). Each point count had a 10-minute duration and was split up into four 2.5-minute intervals. All point counts were conducted between sunrise and 0930, when birds are more likely to be singing (Robbins 1981). Birds detected within a 50 m radius of the point were recorded in each interval in which they were detected. Each bird detected was placed into one of seven distance bins bounded at 5, 10, 15, 20, 30, 40, and 50 m that approximated its distance from the observer at first detection (DFD). The use of distance bins tends to increase the accuracy and

consistency of detections among observers and sampling occasions (Buckland et al. 1993). At each point, canopy cover (CC) was assigned a score from 0 through 4 based on a visual estimation of the percentage of cover above the center of the station and understory cover (UC) was assigned a similar score based on a visual estimation of the percentage of cover 360 degrees around the center of the station.

The airborne LiDAR data used in this study covered Puerto Rico and the US Virgin Islands and were collected by 3001 Inc. and the US government during January and February of 2004. First, last, and intermediate return height values were recorded with varied low-density post spacing, and then converted to uniform 6 m post spacing. The reported mean vertical error was 9.27 cm. Only returns from within our 50 m radius point count stations were used in our analysis. LiDAR measurements including maximum height of vegetation (HMAX), mean height of vegetation (HMEAN), variance of vegetation height (HVAR), percent of canopy cover (DENSITY), and the percent of vegetation in the lower (STRATUM1), middle (STRATUM2), and upper strata (STRATUM3) were used to compare the structure of the eastern and western tracts of Guánica, which differ in their time since disturbance by at least 40 years. Means of these variables for each tract were compared using t-tests. I used the following LiDAR covariates in analyses of point count survey encounter histories: HMAX, STRATUM1, STRATUM2, and STRATUM3. LiDAR data were also available on elevation (ELEV), slope (SLP), aspect (ASP), and land cover type (SEMIDE, SEMIEV, or SCRUB) for the eastern tract of the forest, so they were included as covariates when analyzing data from the eastern tract of Guánica in 2009 and 2010 (Table 2.1, Martinuzzi 2010).

Four main types of models were considered when analyzing variation in detection probability, which is the likelihood that a bird was available and was detected by the observer through sight or sound during a point count survey (Alldredge et al. 2007a): Mo, Mt, Mb, and Mh models. The Mo model is one that assumes detection probabilities ( $p$ ) are equal for all individuals and constant over all intervals of the survey. This model is based on unrealistic assumptions, so it is mainly useful in its ability to serve as a null against which to test for sources of variation. The Mt model allows detection probabilities to vary among intervals, but still assumes that all individuals have an equal probability of being detected within each interval. The Mb model allows detection probabilities to vary by a behavioral effect. This model assumes that the probabilities of first and subsequent detections are unequal. The Mh model allows for heterogeneity in detection probabilities among individuals within a species. The Mh model we used was a two mixture model which allowed us to determine if there were two heterogeneous groups of birds within a species that had different detection rates (Otis et al. 1978). I also considered all two-way combinations of models for analyses (i.e., Mhb, Mth, Mtb) for a total of seven basic model structures.

Data for focal species were analyzed separately, and for each species I partitioned point count data into two different data structures: (1) a single site and multi-year data structure that included data collected from the eastern tract of Guánica in 2009 and 2010, and (2) a multi-site and single year data structure that included data collected in the western and eastern tracts of in 2010. These data structures were used to make the most use of data per site (i.e., 2 years of data in eastern tract), but also to gain insights into how data groupings (i.e., by year or tract) may influence variation in detection probability. We assessed the

candidate model set with and without groups (i.e., years or tracts) for a total of 14 models. We created additional models by including covariates of forest structure from LiDAR and field measurements in the top-ranked model to test for their effects on detection probability (Franklin et al. 2004). Models that yielded convergence problems or non-identifiable estimates were excluded from the model selection summary. Models were evaluated in program MARK (White and Burnham 1999) using the Huggins closed capture data type option (Huggins 1989). I used Akaike's Information Criterion (AIC) to evaluate the support in the data for models in the candidate set and the strength of each covariate's effect on detection probability (Burnham and Anderson 2002). 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 ( $\Delta AIC_c$ ) was used to calculate model weights ( $AIC_c$  weight), which indicate the relative likelihood of the model given the data (Burnham and Anderson 2002). Models with  $\Delta AIC_c \leq 2$  were considered to have substantial support in the data, but I focused on and discussed model results from only the top model. I considered an effect (i.e., covariate  $\hat{\beta}$  coefficient) to be strongly supported if the 95% confidence interval did not overlap zero. Abundance estimates from MARK output were converted to average densities by dividing estimates of population size by the size of the area covered by point count stations in the corresponding tract (i.e. 62 ha for the eastern tract and 39 ha for the western tract). Parameter estimates and 95% confidence intervals are reported.

## Results

### Forest Structure

There were significant differences in vegetation structure based on LiDAR measurements between the eastern and western tracts of Guánica State Forest (Table 2.2). STRATUM1 was higher in western Guánica ( $t_{(127)} = 6.964$ ,  $p < 0.001$ ), whereas STRATUM2 and STRATUM3 were higher in eastern Guánica ( $t_{(127)} = -6.727$ ,  $p < 0.001$ ;  $t_{(127)} = -3.358$ ,  $p < 0.001$ ). Measurements of the height of vegetation, including HMAX, HMEAN, and HVAR, were all significantly higher in eastern Guánica ( $t_{(127)} = -5.517$ ,  $p < 0.001$ ;  $t_{(127)} = -6.504$ ,  $p < 0.001$ ;  $t_{(127)} = -4.113$ ,  $p < 0.001$ ). DENSITY was also significantly higher in the eastern tract of Guánica ( $t_{(127)} = -6.668$ ,  $p < 0.001$ ).

### Point Count Models

#### *Bananaquit*

Variation in data for the Bananaquit from the eastern tract in 2009 and 2010 was best explained by a Mhb model, which allowed for detection probabilities to vary among individuals and between first and subsequent detections (Table 2.8). Detection was influenced by ELEV, STRATUM3, and SCRUB covariates. Scrub land cover type and elevation both had a strong negative influence on detection probability (beta = -2.988, 95% CI: -4.030 to -1.946; beta = -0.005, 95% CI: -0.010 to -0.001). The percent of vegetation in the upper stratum had a strong positive influence (beta = 0.045, 95% CI: 0.016 to 0.075). The mean number of Bananaquits detected per point count station in the eastern unit of

Guánica was slightly higher in 2009 than in 2010, but the difference was not significant (Tables 2.3 and 2.4). Adjusted estimates of population size and density for Bananaquits based on the model with highest support were higher in 2009 than in 2010, but the differences were not statistically significant (Tables 2.9 and 2.6).

Variation in the Bananaquit data from the eastern and western tracts in 2010 was best explained by a gMh model, which grouped data by site and allowed for detection probabilities to vary among individuals (Table 2.10). Competing models ( $\Delta AIC_c \leq 2$ ) featured DFD and CC or both as covariates. For the model with highest support, DFD had a weak negative influence on detection ( $\beta = -0.025$ , 95% CI: -0.055 to 0.004), whereas CC had a weak positive influence ( $\beta = 0.227$ , 95% CI: -0.022 to 0.475). The mean number of Bananaquits detected per point count station in 2010 was slightly higher in the eastern tract of Guánica than in the western tract, but the difference was not significant (Tables 2.4 and 2.5). Adjusted estimates of population size for Bananaquits based on the model with highest support were also higher in the eastern tract than in the western tract (Table 2.11), but after dividing estimates by the size of the sampled area, population density was slightly but not significantly higher in the western tract than the eastern tract (Table 2.7).

### *Puerto Rican Bullfinch*

Variation in the data for the Puerto Rican Bullfinch from the eastern tract in 2009 and 2010 was best explained by a gMhb model, which grouped data by year, allowed for different detection probabilities among individuals, and allowed for different detection

probabilities among first and subsequent detections (Table 2.12). For the model with highest support, UC had a strong positive influence on detection ( $\text{beta} = 0.962$ , 95% CI: 0.521 to 1.402). A competing model ( $\Delta\text{AIC}_c \leq 2$ ) also featured SEMIDE as a covariate. The mean number of Puerto Rican Bullfinches detected per point count station in the eastern unit of Guánica was significantly higher in 2009 than in 2010 (Tables 2.3 and 2.4). Adjusted estimates of population size and density for bullfinches based on the model with highest support were also higher in 2009 than in 2010, but the differences were not statistically significant (Tables 2.13 and 2.6).

Variation in the Puerto Rican Bullfinch data from the eastern and western tracts in 2010 was best explained by a gMth model, which grouped data by site and allowed for detection probabilities to vary over time and among individuals (Table 2.14). For the model with highest support, UC again had a strong positive effect on detection probability ( $\text{beta} = 0.402$ , 95% CI: 0.043 to 0.760). A competing model ( $\Delta\text{AIC}_c \leq 2$ ) also featured STRATUM1 as a covariate. The mean number of Puerto Rican Bullfinches detected per point count station in the 2010 was significantly higher in the eastern tract of Guánica than in the western tract (Tables 2.4 and 2.5). Adjusted estimates of population size for Puerto Rican Bullfinches based on the model with highest support were also higher in the eastern tract than in the western tract (Table 2.15). After dividing estimates by the size of the sampled area in each tract, population density was higher in the western tract of Guánica than in the eastern tract, although the difference was not significant (Table 2.7).

### *Adelaide's Warbler*

Variation in point count data for the Adelaide's Warbler from the eastern tract in 2009 and 2010 was best explained by a gMth model, which grouped data by year and allowed for detection probabilities to vary over time and among individuals (Table 2.16). For the model with highest support, DFD had a strong negative influence on detection probability ( $\text{beta} = -0.019$ , 95% CI: -0.033 to -0.005). A competing model ( $\Delta\text{AIC}_c \leq 2$ ) also featured UC as a covariate. The mean number of Adelaide's Warblers detected per point count station in the eastern unit of Guánica was significantly higher in 2009 than in 2010 (Tables 2.3 and 2.4). Adjusted estimates of population size and density for warblers based on the model with highest support were also significantly higher in 2009 than in 2010 (Tables 2.17 and 2.6).

Variation in the Adelaide's Warbler data from the eastern and western tracts of Guánica in 2010 was also best explained by a gMth model, which grouped data by site and allowed for detection probabilities to vary over time and among individuals (Table 2.18). For the model with highest support, DFD had a weak negative influence on detection probability ( $\text{beta} = -0.013$ , 95% CI: -0.031 to 0.004), whereas UC had a strong positive influence ( $\text{beta} = 0.484$ , 95% CI: 0.146 to 0.823). Two other models were plausible alternatives ( $\Delta\text{AIC}_c \leq 2$ ). One model featured an additional covariate, STRATUM1, and the other featured UC as a single covariate. The mean number of Adelaide's Warblers detected per point count station in the 2010 was slightly higher in the eastern tract of Guánica than in the western tract, but the difference was not significant (Tables 2.4 and 2.5). Adjusted

estimates of population size for Adelaide's Warblers based on the model with highest support were also higher in the eastern tract than in the western tract (Table 2.19), but after dividing estimates by the size of the sampled area in the corresponding tract, population density was not significantly different in the eastern and western tracts of Guánica (Table 2.7).

### *Puerto Rican Vireo*

Variation in the Puerto Rican Vireo data from the eastern tract in 2009 and 2010 was best explained by a gMb model, which grouped data by year and allowed detection probabilities to differ between first and subsequent detections (Table 2.20). For the model with highest support, ELEV had a strong positive influence on detection probability (beta = 0.016, 95% CI: 0.003 to 0.028). Two other models were plausible alternatives ( $\Delta AIC_c \leq 2$ ). One model featured STRATUM2 and the other featured STRATUM1 as covariates. The mean number of Puerto Rican Vireos detected per point count station in the eastern unit of Guánica was slightly higher in 2010 than in 2009, but the difference was not significant (Tables 2.3 and 2.4). Adjusted estimates of population size and density for vireos based on the model with highest support were also slightly larger in 2010 than in 2009, but the differences were not significant (Tables 2.21 and 2.6).

Variation in the vireo data from the eastern and western tracts of Guánica in 2010 was best explained by a Mth model, which allowed for detection probabilities to vary over time and among individuals (Table 2.22). DFD had a strong positive influence on detection probability (beta = 0.062, 95% CI: 0.010 to 0.115). The mean number of Puerto Rican

Vireos detected per point count station in the 2010 was slightly higher in the eastern tract of Guánica than in the western tract, but the difference was not significant (Tables 2.4 and 2.5). Adjusted estimates of population size for Puerto Rican Vireos based on the model with highest support were higher in the western tract than in the eastern tract (Table 2.23), and after dividing estimates by the size of the sampled area in each tract, population density was also higher in the western tract of Guánica than in the eastern tract, but not significantly so (Table 2.7).

### *Pearly-eyed Thrasher*

Variation in the Pearly-eyed Thrasher data from the eastern tract in 2009 and 2010 was best explained by a gMh model, which grouped data by year and allowed for detection probabilities to vary among individuals (Table 2.24). SEMIDE had a strong positive influence on detection probability ( $\beta = 3.857$ , 95% CI: 1.986 to 5.727). STRATUM1 ( $\beta = -0.031$ , 95% CI: -0.131 to 0.069) and STRATUM2 ( $\beta = -0.079$ , 95% CI: -0.194 to 0.035) both had a weak negative influence on detection probability. The mean number of thrashers detected per point count station in the eastern unit of Guánica was slightly higher in 2009 than in 2010, but the difference was not significant (Tables 2.3 and 2.4). Adjusted estimates of population size and density for thrashers based on the model with highest support were higher in 2010 than in 2009, but the differences were not statistically significant (Tables 2.25 and 2.6). The mean number of thrashers detected per point count station in the 2010 was significantly higher in the western tract of Guánica than in the eastern tract (Tables

2.4 and 2.5). However, there was insufficient data to model variation in the data between the eastern and western tracts of Guánica in 2010 because there was such a small amount of data on thrashers in the western tract (i.e., only one thrasher was detected in the western tract as opposed to 36 detected in the eastern tract in 2010).

## Discussion

Differences in vegetation structure between the eastern and western tracts of Guánica were as expected given the 40 years difference in time since disturbance. The higher values of the STRAT1 metric in the western tract of Guánica corresponded to shrubby plant communities, consistent with a more recently disturbed community. Conversely, the higher values of the STRAT2 and STRAT3 metrics in the eastern tract of Guánica were likely associated with a more mature community. The higher values of DENSITY and measures related to vegetation height (i.e. HMAX, HMEAN, and HVAR) in the eastern tract were also consistent with an older growth plant community.

As noted above, structural characteristics derived from LiDAR differed between forest tracts, but these measurements did not always explain most of the variation in detection probability. Instead, field measurements of canopy cover, understory cover, and distance at first detection had higher support in the data for explaining variation in detection probability. Large footprint LiDAR has been shown to be sensitive to differences in vertical canopy structure in forests (Drake et al. 2002); however, it is possible that visual estimation of canopy and understory cover might be more useful in explaining differences in detection

probability because measurements captured elements of observer perception that remote sensing is unable to capture. Notwithstanding, if a project is designed to assess species-habitat relationships over a large geographic extent, LiDAR still provides an effective and standardized tool to collect data on habitat structure over a broad area (Vierling et al 2008). Support for the DFD covariate was evident in several models exerting a negative influence on detection probability of Adelaide's Warblers and Bananaquits. However, DFD also influenced detection for Puerto Rican Vireos for data collected in eastern and western units in 2010, but its influence was positive. This is noteworthy because a decrease in detectability with increasing distance from the observer is consistent with tenets underlying distance sampling methods (Buckland et al. 2001). A possible explanation for the positive influence on detection was that vireos were less likely to sing when in close proximity to an observer (McShea and Rappole 1997).

Habitat structural features associated with the preferred foraging habitat of most focal species did not have a strong influence on detection probabilities. For example, the percent of vegetation in the lower and middle strata had a negative relationship with detection probability of Pearly-eyed Thrashers. This was unexpected because reported preferences for foraging habitat are in those layers. A plausible explanation for this finding is that thrashers are most vocal early in the morning, and then forage close to or on the ground during late morning hours and remain mostly silent (W. J. Arendt, IITF-USDA, pers. comm.). Likewise, it is possible that cross-over between preferred foraging layers and layer where most singing occurs also accounted for this pattern with Puerto Rican Vireos. Detection was positively associated with percent of vegetation in the upper stratum for vireos, but their preferred

habitat preferences are at the mid to lower levels of the forest. Measurements of vegetation structure that had a positive influence on detection probability of Bananaquits included the STRATUM3 and CC covariates, which both describe the amount of vegetation in the canopy. This suggests that Bananaquits may dwell on upper layers of the canopy when calling. The negative influence of the scrub land cover type on Bananaquit detection further supports this habitat preference. In view of the fact that coastal scrub habitat does not have any tall, mature trees to create a thick canopy, Bananaquits would be less likely to be detected in that habitat type. Although Bananaquits are also reported to be present at all elevations, there was a strong negative influence of elevation on detection probability for this species, indicating that within Guánica State Forest Bananaquits may make greater use of lower elevation microhabitats.

Densities of focal species were generally higher in the western tract of Guánica as compared to the eastern tract, with the exception of the Pearly-eyed Thrasher. Only one thrasher was detected in the western tract of the forest, indicating that thrasher abundance was lower in that tract than in the eastern tract where 36 thrashers were detected. This pattern was consistent with captures of thrashers in mist-nets during a concurrent study I conducted in Guánica where 23 individuals were captured in the eastern tract as compared to only 4 in the western tract in 2010 (Chapter 1). Thrashers are known predators of eggs, nestlings, and even adult birds of a variety of species (Arendt 2006). Specifically, they have been documented to prey on Bananaquits, Puerto Rican Vireos, and Puerto Rican Bullfinches in Puerto Rico and elsewhere in the Lesser Antilles (Netherlands Antilles National Park Foundation 1975, Vilella 1995, Woodworth 1997, Arendt 2006). In a concurrent study,

Wiewel (2011) reported that thrashers were the main nest predator in both tracts of Guánica, and suggested that the lower density of thrashers in the western unit may have contributed to higher Puerto Rican Bullfinch nest success in that tract. Woodworth (1997) reported that predation was the main cause of nest loss for Puerto Rican Vireos in the eastern tract of Guánica, with thrashers as the primary predator. Predation was followed by high rates of brood parasitism by Shiny Cowbirds as the main causes of nest failures (Woodworth 1997). Thus, it is possible that the higher density of thrashers in the eastern unit may be a contributing factor explaining lower abundance of Bananaquits, Puerto Rican Vireos, and Puerto Rican Bullfinches in that forest tract. Higher densities of other focal species in the western tract might also have a habitat component. Recently disturbed habitats or edges may support higher species richness and abundance than mature or less disturbed habitats (Van Horne 1983). Unlike cases where these habitats draw high numbers of species that might be detrimental to the community (e.g., brood parasites, nest predators, Van Horne 1983), it appeared that this was not the case in the western tract (Wiewel 2011).

This is the first study to investigate factors affecting detection probability of avian species in Puerto Rico. Failing to adjust for detection probability can lead to spurious inferences about abundance and species-habitat relationships (Rosenstock et al. 2002). The time-of-detection method is an appealing survey framework because it adjusts for availability and detection given availability (Alldredge et al. 2007a), but it also has practical limitations. The number of species and individuals singing during a count can affect the information that is available to observers (Simons et al. 2007), possibly affecting their ability to track multiple birds simultaneously. In traditional capture-recapture models, Mb models suggest a trap

response by the animal being surveyed. However, the prevalence of Mb models in the time-of-detection point count data is likely due to a tendency on the part of the observer to anticipate calls made by individual birds that were already detected earlier in the survey period (Riddle et al. 2010). Redetection probability was generally higher than initial detection probability, which is analogous to a “trap happy” response and could cause abundance estimates to be biased low if unaccounted for. An assumption of the time-of-detection method is that the observer can keep track of individuals without error, so recording detections of a subset of species that move little during a point count could help to decrease localization errors (Stanislav et al. 2010). Heterogeneity in detection probabilities existed among individuals in this study as exhibited by the prevalence of Mh models. Heterogeneity is commonly found in point count data due to factors such as differences in singing rate among individuals (Brewster 2007) and distance from observer (Buckland et al. 2001). Heterogeneity in detection probabilities can cause problems with identifiability (Link 2003), but using covariates when modeling the detection probabilities can help solve this problem (Huggins 1989). I found that the distance from observer covariate explained most of the variation in the data for many selected Mh models. It is also possible that there was heterogeneity in singing rates among individuals in this study, which can cause the time-of-detection method to underestimate population size, even in models allowing heterogeneity in detection probabilities (Alldredge et al. 2007c).

Approaches like the time-of-detection method hold promise to address questions regarding the status of “data deficient” species on the island and help frame strategic habitat conservation strategies (Garcia et al. 2005). Locally, this study was the first to generate

abundance estimates for resident species in Guánica State Forest. However, I confronted a limitation worth noting in the context of species-habitat relationships, and applications such as updating Puerto Rico Gap Analysis models (Gould et al. 2007). In building such models, station-level estimates of population size are commonly used as the response variable (Thogmartin and Knutson 2007). Further, and as shown in this study, adjusting estimates of abundance for detection probability requires large data sets of encounter histories, which in my study meant using all available data. The end result is that the estimate of density represents an adjusted, but average estimate per station. The parameter of interest, abundance per station, is “latent” or unknown, and its estimation requires other approaches that adjust for spatial correlation (Lichstein et al. 2002, Webster et al. 2008). Attempts to obtain this latent parameter were made, but the proximity of stations (i.e.,  $\geq 200$  m) and the number of stations (i.e., 129 total) proved too close (spatially correlated) and too few to yield estimates per station (M. Krachey, NCSU, pers. comm.). Restricting models to within relatively small reserves, which characterizes most reserves in Puerto Rico (Gould et al. 2007), represents a practical consideration for study design. I recommend that studies emphasize spatial replication by using multiple reserves or patches as their primary sampling unit, which should more easily accommodate sample size requirements for detection estimates, but also a hierarchical modeling framework where some samples are spatially correlated while others are independent.

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## APPENDIX

**Table 2.1** Abbreviations and definitions of LiDAR derived measurements of canopy structure, topographic variables, and land cover categories that were used as covariates in data analysis and/or to compare structure of forest tracts (Martinuzzi 2010).

ABBREVIATION	DESCRIPTION
<b>Canopy structure variables</b>	
DENSITY	percent canopy cover (measured at 1.5m - chest height)
HMAX*	maximum height of vegetation
STRATUM1*	percent of the vegetation in the lower strata (i.e. between .3m and 3m)
STRATUM2*	percent of the vegetation in the middle strata (i.e. between 3m and 8m)
STRATUM3*	percent of the vegetation in the upper strata (i.e. 8m and above)
HMEAN	mean height of vegetation
HVAR	variance of vegetation height
<b>Topographic variables</b>	
ELEV*	elevation
SLP*	slope
ASP*	aspect
<b>Land cover categories</b>	
SEMIIDE*	semideciduous
SEMIEV*	semievergreen
SCRUB*	scrub

\* included as covariate in closed capture models

**Table 2.2** Comparison of the mean  $\pm$  SE of LiDAR metrics of vegetation structure for point count stations in the eastern and western tracts of Guánica State Forest.

LiDAR metric	Eastern Guánica			Western Guánica		
STRATUM1	43.1034	$\pm$	2.2355	66.5854	$\pm$	2.3405
STRATUM2	53.0072	$\pm$	1.9390	32.7586	$\pm$	2.2191
STRATUM3	3.8894	$\pm$	0.7566	0.6550	$\pm$	0.1801
HMAX	9.5604	$\pm$	0.3270	6.9638	$\pm$	0.2877
HMEAN	3.6678	$\pm$	0.1224	2.5650	$\pm$	0.0892
HVAR	3.5068	$\pm$	0.2722	1.9848	$\pm$	0.1761
DENSITY	74.9005	$\pm$	1.5000	58.2108	$\pm$	2.0702

\* p < 0.0001

\*\* p < 0.001

**Table 2.3** The number of individuals per species detected at each point count station in the eastern tract of Guánica State Forest in 2009. Mean (SE) number of birds detected over all stations is presented for each species.

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
1E	2	2	2	1	0
2E	2	3	0	0	0
3E	4	1	4	0	0
4E	3	1	5	1	1
5E	3	2	5	0	0
6E	4	1	2	0	2
7E	5	3	3	0	2
8E	6	2	2	0	0
9E	5	3	1	0	0
10E	6	0	2	0	0
11E	2	1	3	1	0
12E	4	1	4	0	0
13E	4	0	4	2	0
14E	4	3	5	0	1
16E	4	1	5	0	1
17E	3	3	5	0	2
18E	5	1	5	0	2
19E	4	2	2	0	1
20E	3	0	6	0	0
22E	4	1	4	0	0
23E	4	1	3	0	0
24E	4	0	2	1	0
25E	4	1	4	0	1
26E	4	0	2	2	0
27E	5	4	4	2	0
28E	6	3	4	0	0
30E	6	3	4	1	0
31E	2	0	4	0	1
33E	7	1	3	1	1
34E	6	3	3	0	2
35E	4	1	4	0	2
37E	6	4	8	0	0
38E	6	4	7	0	0
39E	7	1	3	0	0
40E	6	0	0	0	1
41E	6	0	4	0	0
42E	5	2	3	1	0
43E	4	2	3	0	0
44E	4	2	3	0	0
45E	3	3	2	0	1
46E	3	0	0	1	0
47E	2	0	1	0	2

**Table 2.3** (continued)

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
49E	2	2	0	0	3
50E	3	2	5	0	0
51E	3	2	4	1	0
52E	3	3	3	0	0
53E	3	1	4	0	2
55E	4	2	6	0	0
56E	5	1	4	0	5
57E	3	4	3	1	0
58E	6	1	2	0	2
59E	4	1	3	0	2
70E	2	3	1	0	1
71E	5	3	1	0	1
73E	3	3	1	0	1
74E	4	1	2	0	0
75E	3	2	2	0	0
76E	3	0	0	0	1
77E	3	0	0	0	0
78E	3	2	2	0	0
79E	4	2	0	0	0
80E	4	0	0	0	1
81E	5	1	1	0	0
82E	5	2	0	0	1
83E	5	1	3	0	0
84E	4	1	1	0	0
85E	4	1	3	0	0
86E	5	2	3	1	0
87E	3	3	2	0	0
88E	4	2	1	0	0
89E	4	1	1	0	0
90E	4	3	3	1	0
91E	3	1	3	1	0
92E	5	1	3	0	0
93E	5	2	1	0	0
95E	3	1	1	0	0
97E	3	0	2	0	2
98E	3	3	4	0	0
99E	4	2	3	0	1
Mean (SE)	4.05 (0.14)	1.62 (0.13)	2.76 (0.20)	0.24 (0.06)	0.58 (0.10)

**Table 2.4** The number of individuals per species detected at each point count station in the eastern tract of Guánica State Forest in 2010. Mean (SE) of birds detected over all stations is presented for each species.

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
1E	3	1	1	0	0
2E	4	1	0	0	0
3E	3	2	1	0	2
4E	3	1	1	1	1
5E	4	0	1	0	1
6E	3	1	1	0	1
7E	6	1	3	2	0
8E	2	2	2	0	0
9E	4	3	2	1	0
10E	4	5	1	1	0
11E	3	1	3	0	1
12E	2	1	3	0	0
13E	4	3	0	0	0
14E	2	1	2	0	1
16E	3	1	3	0	1
17E	2	2	2	0	1
18E	2	1	3	0	0
19E	4	2	2	1	1
20E	5	1	2	0	1
22E	3	1	3	1	2
23E	3	1	4	1	1
24E	4	2	2	0	2
25E	3	0	1	0	0
26E	1	3	2	1	0
27E	4	0	1	0	0
28E	3	2	2	0	0
30E	5	1	3	1	0
31E	2	0	1	0	1
33E	4	1	4	1	0
34E	3	0	2	1	0
35E	2	1	2	0	0
37E	2	1	1	0	0
38E	4	1	1	0	1
39E	3	0	1	0	1
40E	4	1	0	0	2
41E	5	3	2	0	2
42E	3	2	0	0	0
43E	3	0	0	0	0
44E	3	0	1	0	0
45E	3	1	0	0	0
46E	2	0	1	0	0
47E	3	0	0	0	1

**Table 2.4** (continued)

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
49E	2	0	1	0	0
50E	4	0	2	0	0
51E	4	0	1	0	0
52E	3	1	1	0	0
53E	7	1	2	0	0
55E	3	2	4	0	0
56E	2	2	1	2	2
57E	3	4	2	1	0
58E	3	3	1	0	2
59E	1	2	1	0	0
70E	4	1	2	0	0
71E	2	1	1	0	1
73E	3	3	1	0	0
74E	4	1	0	0	0
75E	3	1	2	2	1
76E	3	0	1	0	0
77E	3	1	2	3	0
78E	3	2	2	1	0
79E	3	0	0	0	0
80E	4	2	1	0	0
81E	4	1	2	0	0
82E	3	2	2	0	0
83E	4	2	2	0	0
84E	3	1	2	0	0
85E	2	3	4	0	0
86E	3	0	3	0	0
87E	3	3	0	1	0
88E	3	3	1	0	1
89E	4	3	0	0	0
90E	2	3	2	0	1
91E	2	2	1	0	0
92E	2	1	1	0	0
93E	3	2	2	1	0
95E	4	2	1	0	1
97E	3	1	1	0	1
98E	3	1	2	0	0
99E	3	1	1	0	2
Mean (SE)	3.16 (0.11)	1.38 (0.12)	1.54 (0.12)	0.29 (0.07)	0.46 (0.08)

**Table 2.5** The number of individuals per species detected at each point count station in the western tract of Guánica State Forest in 2010. Mean (SE) of birds detected over all stations is presented for each species.

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
2W	3	0	3	1	0
3W	4	1	1	0	0
4W	3	3	2	0	0
5W	3	2	3	0	0
6W	6	0	2	1	0
7W	2	3	3	0	0
8W	3	2	3	2	0
11W	3	0	2	0	0
12W	2	1	2	1	0
13W	2	3	2	0	0
14W	4	2	3	0	0
17W	4	2	4	2	0
18W	4	2	3	2	0
20W	4	2	2	0	0
21W	4	1	4	1	0
22W	4	2	3	0	0
23W	3	5	6	0	0
26W	4	1	4	3	0
28W	3	3	3	0	0
29W	3	2	3	1	0
30W	5	0	3	0	0
31W	3	0	3	1	0
32W	3	1	2	1	0
33W	2	1	3	0	0
34W	3	2	4	2	0
36W	5	4	4	0	0
37W	4	1	3	0	0
38W	3	2	2	1	0
39W	4	2	3	0	0
41W	3	3	4	1	0
42W	4	1	1	0	0
43W	4	1	1	0	0
44W	4	2	2	0	0
45W	3	3	4	0	0

**Table 2.5** (continued)

Station ID	Adelaide's Warbler	Bananaquit	Puerto Rican Bullfinch	Puerto Rican Vireo	Pearly-eyed Thrasher
46W	5	3	3	0	0
47W	3	2	2	1	1
48W	2	3	1	0	0
49W	2	2	4	0	0
52W	3	2	2	1	0
53W	3	2	2	0	0
54W	3	3	3	1	0
57W	3	2	2	0	0
58W	3	3	0	0	0
59W	3	1	1	0	0
67W	3	2	2	0	0
68W	3	1	2	2	0
70W	2	2	3	0	0
71W	4	2	1	0	0
74W	3	1	5	0	0
76W	4	2	3	0	0
Mean (SE)	3.34 (0.12)	1.86 (0.15)	2.66 (0.16)	0.50 (0.11)	0.02 (0.02)

**Table 2.6** Average density estimates and 95% confidence interval for five focal species in 2009 and 2010 in the eastern tract of Guánica State Forest. Average density was calculated by dividing the abundance estimate from MARK output by the size of the area covered by point count stations. The best supported model that was used to obtain abundance estimates, as well as any covariates included in that model, are also listed.

Species	2009 Density (birds/ha)	2010 Density (birds/ha)	Model	Covariates
Bananaquit	3.0414 (CI: 2.5718, 3.9445)	2.6599 (CI: 2.2194, 3.5199)	Mhb	ELEV, SCRUB, STRATUM3
Puerto Rican Bullfinch	6.0476 (CI: 4.6969, 8.9401)	3.9662 (CI: 2.9254, 6.1364)	gMhb	UC
Adelaide's Warbler	5.2816 (CI: 5.2101, 5.4503)	4.4337 (CI: 4.2433, 4.7933)	gMth	DFD
Puerto Rican Vireo	0.3632 (CI: 0.3161, 0.6363)	0.4780 (CI: 0.3897, 0.9774)	gMb	ELEV
Pearly-eyed Thrasher	2.3025 (CI: 1.2480, 5.5518)	5.7737 (CI: 1.8733, 21.4390)	gMh	SEMIDE, STRATUM1, STRATUM2

**Table 2.7** Average density estimates and 95% confidence interval for four focal species in the eastern and western tracts of Guánica State Forest in 2010. Average density was calculated by dividing the abundance estimate from MARK output by the size of the area covered by point count stations. The best supported model that was used to obtain abundance estimates, as well as any covariates included in that model, are also listed.

Species	East Density (birds/ha)	West Density (birds/ha)	Model	Covariates
Bananaquit	2.0740 (CI: 1.8830, 2.5539)	2.4500 (CI: 2.3916, 2.6548)	gMh	CC, DFD
Puerto Rican Bullfinch	3.4304 (CI: 2.5429, 5.6838)	3.7171 (CI: 3.5156, 4.2337)	gMth	UC
Adelaide's Warbler	4.5048 (CI: 4.2775, 4.9403)	4.5801 (CI: 4.3782, 5.1066)	gMth	UC, DFD
Puerto Rican Vireo	1.0266 (CI: 0.4919, 3.9204)	1.9826 (CI: 0.8953, 7.6396)	Mth	DFD

**Table 2.8** Closed capture models for Bananaquit point count data from the eastern unit of Guánica in 2009-10 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{Mhb+ELEV+SCRUB+STRATUM3}	1188.2640	0.0000	0.9425	1.0000	7	1174.1449
{Mhb+ELEV}	1195.0514	6.7874	0.0317	0.0336	5	1184.9877
{Mhb+SCRUB}	1198.5429	10.2789	0.0055	0.0059	5	1188.4792
{Mhb+STRATUM3}	1198.7772	10.5132	0.0049	0.0052	5	1188.7135
{Mhb+all land cover}	1199.0477	10.7837	0.0043	0.0046	6	1186.9584
{Mhb+HMAX}	1199.2733	11.0093	0.0038	0.0041	5	1189.2096
{Mhb+SEMIEV}	1202.2055	13.9415	0.0009	0.0009	5	1192.1418
{Mhb+aspect}	1202.3044	14.0404	0.0008	0.0009	5	1192.2407
{Mhb+DFD}	1202.4125	14.1485	0.0008	0.0008	5	1192.3488
{Mhb+STRATUM1}	1202.7183	14.4543	0.0007	0.0007	5	1192.6546
{Mhb}	1202.8668	14.6028	0.0006	0.0007	4	1194.8244
{Mhb+SLP}	1203.0003	14.7363	0.0006	0.0006	5	1192.9366
{Mh}	1203.0331	14.7691	0.0006	0.0006	3	1197.0077
{Mhb+UC}	1203.3094	15.0454	0.0005	0.0005	5	1193.2457
{Mhb+STRATUM2}	1203.7529	15.4889	0.0004	0.0004	5	1193.6892
{gMh}	1204.0611	15.7971	0.0004	0.0004	5	1193.9974
{gMhb}	1204.2147	15.9507	0.0003	0.0003	7	1190.0956
{Mhb+CC}	1204.5520	16.2880	0.0003	0.0003	5	1194.4883
{Mhb+SEMIDE}	1204.6217	16.3577	0.0003	0.0003	5	1194.5580
{gMth}	1206.0729	17.8089	0.0001	0.0001	11	1183.7908
{Mth}	1208.3338	20.0698	0.0000	0.0000	6	1196.2445
{gMb}	1254.4939	66.2299	0.0000	0.0000	4	1246.4515
{Mb}	1263.3413	75.0773	0.0000	0.0000	2	1259.3286
{Mtb}	1264.4250	76.1610	0.0000	0.0000	4	1256.3826
{Mo}	1267.6506	79.3866	0.0000	0.0000	1	1265.6464
{gMo}	1267.6506	79.3866	0.0000	0.0000	1	1265.6464
{gMt}	1271.5311	83.2671	0.0000	0.0000	8	1255.3777
{Mt}	1273.0539	84.7899	0.0000	0.0000	4	1265.0115

**Table 2.9** Estimates of model parameters for the top-ranked model for Bananaquit point count data from the eastern unit of Guánica in 2009-10.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.1812	0.0305	0.1288	0.2488736
p (mix1)	0.9826	0.0100	0.9474	0.9943637
p (mix1)	0.9826	0.0100	0.9474	0.9943637
p (mix1)	0.9826	0.0100	0.9474	0.9943637
p (mix1)	0.9826	0.0100	0.9474	0.9943637
p	0.2803	0.0431	0.2040	0.3718362
p	0.2803	0.0431	0.2040	0.3718362
p	0.2803	0.0431	0.2040	0.3718362
p	0.2803	0.0431	0.2040	0.3718362
c (mix1)	0.9872	0.0067	0.9647	0.9954153
c (mix1)	0.9872	0.0067	0.9647	0.9954153
c (mix1)	0.9872	0.0067	0.9647	0.9954153
c	0.3473	0.0301	0.2909	0.4083824
c	0.3473	0.0301	0.2909	0.4083824
c	0.3473	0.0301	0.2909	0.4083824
N hat (2009)	188.7106	20.8291	159.5725	244.7403
N hat (2010)	165.0369	19.6973	137.7036	218.3984

**Table 2.10** Closed capture models for Bananaquit point count data from the eastern and western units of Guánica in 2010 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMh+CC+DFD}	1057.2730	0.0000	0.3028	1.0000	7	1043.1330
{gMh+CC}	1058.3976	1.1246	0.1726	0.5699	6	1046.2927
{gMh+DFD}	1058.5133	1.2403	0.1629	0.5379	6	1046.4084
{gMh}	1059.6475	2.3745	0.0924	0.3051	5	1049.5727
{gMh+UC}	1060.7811	3.5081	0.0524	0.1731	6	1048.6762
{gMh+STRATUM3}	1060.8525	3.5795	0.0506	0.1670	6	1048.7476
{gMh+HMAX}	1060.9369	3.6639	0.0485	0.1601	6	1048.8320
{gMh+STRATUM2}	1061.5769	4.3039	0.0352	0.1163	6	1049.4720
{gMh+STRATUM1}	1061.6624	4.3894	0.0337	0.1114	6	1049.5575
{gMhb}	1061.9662	4.6932	0.0290	0.0957	7	1047.8262
{Mh}	1064.2004	6.9274	0.0095	0.0313	3	1058.1705
{Mhb}	1065.2291	7.9561	0.0057	0.0187	4	1057.1793
{gMth}	1066.1813	8.9083	0.0035	0.0116	11	1043.8496
{Mth}	1068.3141	11.0411	0.0012	0.0040	6	1056.2092
{gMb}	1074.5030	17.2300	0.0001	0.0002	4	1066.4532
{Mo}	1078.6697	21.3967	0.0000	0.0000	1	1076.6647
{gMo}	1078.6697	21.3967	0.0000	0.0000	1	1076.6647
{gMt}	1079.5350	22.2620	0.0000	0.0000	8	1063.3548
{Mb}	1079.9265	22.6535	0.0000	0.0000	2	1075.9116
{gMtb}	1081.2945	24.0215	0.0000	0.0000	10	1061.0185
{Mtb}	1081.3345	24.0615	0.0000	0.0000	4	1073.2847
{Mt}	1082.9310	25.6580	0.0000	0.0000	4	1074.8812

**Table 2.11** Estimates of model parameters for the top-ranked model for Bananaquit point count data from the eastern and western units of Guánica in 2010.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.2601	0.1219	0.0922	0.5488
p (East, mix1)	0.8593	0.0942	0.5700	0.9657
p (East, mix1)	0.8593	0.0942	0.5700	0.9657
p (East, mix1)	0.8593	0.0942	0.5700	0.9657
p (East, mix1)	0.8593	0.0942	0.5700	0.9657
p (East)	0.3481	0.0848	0.2042	0.5263
p (East)	0.3481	0.0848	0.2042	0.5263
p (East)	0.3481	0.0848	0.2042	0.5263
p (East)	0.3481	0.0848	0.2042	0.5263
p (West, mix2)	0.8230	0.1141	0.5006	0.9557
p (West, mix2)	0.8230	0.1141	0.5006	0.9557
p (West, mix2)	0.8230	0.1141	0.5006	0.9557
p (West, mix2)	0.8230	0.1141	0.5006	0.9557
p (West)	0.5502	0.0492	0.4530	0.6437
p (West)	0.5502	0.0492	0.4530	0.6437
p (West)	0.5502	0.0492	0.4530	0.6437
c (East, mix1)	0.8593	0.0942	0.5700	0.9657
c (East, mix1)	0.8593	0.0942	0.5700	0.9657
c (East, mix1)	0.8593	0.0942	0.5700	0.9657
c (East)	0.3481	0.0848	0.2042	0.5263
c (East)	0.3481	0.0848	0.2042	0.5263
c (East)	0.3481	0.0848	0.2042	0.5263
c (West, mix2)	0.8230	0.1141	0.5006	0.9557
c (West, mix2)	0.8230	0.1141	0.5006	0.9557
c (West, mix2)	0.8230	0.1141	0.5006	0.9557
c (West)	0.5502	0.0492	0.4530	0.6437
c (West)	0.5502	0.0492	0.4530	0.6437
c (West)	0.5502	0.0492	0.4530	0.6437
N hat (East)	128.6846	9.7889	116.8340	158.4617
N hat (West)	96.2108	2.2839	93.9161	104.2536

**Table 2.12** Closed capture models for Puerto Rican Bullfinch point count data from eastern unit of Guánica in 2009-10 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMhb+UC}	1694.3083	0.0000	0.5780	1.0000	8	1678.2017
{gMhb+UC+SEMIDE}	1695.9817	1.6734	0.2503	0.4331	9	1677.8484
{gMhb+STRATUM1}	1699.0953	4.7870	0.0528	0.0913	8	1682.9887
{gMhb+STRATUM2}	1699.6200	5.3117	0.0406	0.0702	8	1683.5134
{gMhb+aspect}	1701.1408	6.8325	0.0190	0.0328	8	1685.0342
{gMhb+HMAX}	1701.6158	7.3075	0.0150	0.0259	8	1685.5092
{gMhb+SEMIDE}	1702.0707	7.7624	0.0119	0.0206	8	1685.9641
{gMhb+ELEV}	1703.8743	9.5660	0.0048	0.0084	8	1687.7677
{gMhb+all land cover}	1703.8947	9.5864	0.0048	0.0083	9	1685.7614
{gMhb+CC}	1704.2004	9.8921	0.0041	0.0071	8	1688.0938
{gMhb+STRATUM3}	1704.2043	9.8960	0.0041	0.0071	8	1688.0977
{gMhb+DFD}	1704.3261	10.0178	0.0039	0.0067	8	1688.2195
{gMhb+SLP}	1704.5855	10.2772	0.0034	0.0059	8	1688.4789
{gMhb}	1704.7020	10.3937	0.0032	0.0055	7	1690.6192
{gMhb+SEMIEV}	1705.0661	10.7578	0.0027	0.0046	8	1688.9595
{gMhb+SCRUB}	1706.6145	12.3062	0.0012	0.0021	8	1690.5079
{gMth}	1709.6598	15.3515	0.0003	0.0005	11	1687.4640
{gMh}	1720.0181	25.7098	0.0000	0.0000	5	1709.9738
{Mhb}	1729.8156	35.5073	0.0000	0.0000	4	1721.7861
{Mh}	1733.2208	38.9125	0.0000	0.0000	3	1727.2031
{Mth}	1737.6480	43.3397	0.0000	0.0000	6	1725.5859
{gMtb}	1758.0701	63.7618	0.0000	0.0000	10	1737.9070
{gMb}	1764.0609	69.7526	0.0000	0.0000	4	1756.0314
{gMt}	1784.4033	90.0950	0.0000	0.0000	8	1768.2967
{Mtb}	1812.8359	118.5276	0.0000	0.0000	4	1804.8064
{Mb}	1813.2621	118.9538	0.0000	0.0000	2	1809.2533
{Mo}	1817.1551	122.8468	0.0000	0.0000	1	1815.1522
{gMo}	1817.1551	122.8468	0.0000	0.0000	1	1815.1522
{Mt}	1821.8147	127.5064	0.0000	0.0000	4	1813.7852

**Table 2.13** Estimates of model parameters for the top-ranked model for Puerto Rican Bullfinch point count data from the eastern unit of Guánica in 2009-10.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.2991	0.0511	0.2092	0.4077
p (2009, mix1)	0.8165	0.0488	0.7015	0.8939
p (2009, mix1)	0.8165	0.0488	0.7015	0.8939
p (2009, mix1)	0.8165	0.0488	0.7015	0.8939
p (2009, mix1)	0.8165	0.0488	0.7015	0.8939
p (2009)	0.1399	0.0439	0.0738	0.2495
p (2009)	0.1399	0.0439	0.0738	0.2495
p (2009)	0.1399	0.0439	0.0738	0.2495
p (2009)	0.1399	0.0439	0.0738	0.2495
p (2009)	0.1399	0.0439	0.0738	0.2495
p (2010, mix2)	0.7690	0.0515	0.6535	0.8547
p (2010, mix2)	0.7690	0.0515	0.6535	0.8547
p (2010, mix2)	0.7690	0.0515	0.6535	0.8547
p (2010, mix2)	0.7690	0.0515	0.6535	0.8547
p (2010)	0.0737	0.0290	0.0334	0.1546
p (2010)	0.0737	0.0290	0.0334	0.1546
p (2010)	0.0737	0.0290	0.0334	0.1546
c (2009, mix1)	0.9286	0.0189	0.8814	0.9579
c (2009, mix1)	0.9286	0.0189	0.8814	0.9579
c (2009, mix1)	0.9286	0.0189	0.8814	0.9579
c (2009)	0.3222	0.0530	0.2281	0.4333
c (2009)	0.3222	0.0530	0.2281	0.4333
c (2009)	0.3222	0.0530	0.2281	0.4333
c (2010, mix2)	0.6543	0.0464	0.5588	0.7388
c (2010, mix2)	0.6543	0.0464	0.5588	0.7388
c (2010, mix2)	0.6543	0.0464	0.5588	0.7388
c (2010)	0.0433	0.0182	0.0188	0.0966
c (2010)	0.0433	0.0182	0.0188	0.0966
c (2010)	0.0433	0.0182	0.0188	0.0966
N hat (2009)	375.2325	63.4649	291.4243	554.7015
N hat (2010)	246.0904	48.2063	181.5127	380.7422

**Table 2.14** Closed capture models for Puerto Rican Bullfinch point count data from the eastern and western units of Guánica in 2010 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMth+UC}	1318.9806	0.0000	0.4686	1.0000	12	1294.6708
{gMth+UC+STRATUM1}	1320.9451	1.9645	0.1755	0.3745	13	1294.5833
{gMth}	1322.1033	3.1227	0.0983	0.2099	11	1299.8414
{gMth+STRATUM1}	1322.1205	3.1399	0.0975	0.2081	12	1297.8107
{gMth+STRATUM3}	1322.5132	3.5326	0.0801	0.1710	12	1298.2034
{gMth+DFD}	1323.2028	4.2222	0.0568	0.1211	12	1298.8930
{gMhb}	1325.7105	6.7299	0.0162	0.0346	7	1311.5998
{gMh}	1327.6142	8.6336	0.0063	0.0133	5	1317.5550
{Mth}	1332.2187	13.2381	0.0006	0.0013	6	1320.1358
{Mhb}	1335.7478	16.7672	0.0001	0.0002	4	1327.7084
{Mh}	1339.3112	20.3306	0.0000	0.0000	3	1333.2876
{gMtb}	1349.3266	30.3460	0.0000	0.0000	10	1329.1086
{gMt}	1350.5666	31.5860	0.0000	0.0000	8	1334.4242
{gMb}	1352.8712	33.8906	0.0000	0.0000	4	1344.8318
{Mtb}	1367.1531	48.1725	0.0000	0.0000	4	1359.1137
{Mt}	1367.4907	48.5101	0.0000	0.0000	4	1359.4513
{Mb}	1371.9332	52.9526	0.0000	0.0000	2	1367.9214
{Mo}	1373.1382	54.1576	0.0000	0.0000	1	1371.1343
{gMo}	1373.1382	54.1576	0.0000	0.0000	1	1371.1343

**Table 2.15** Estimates of model parameters for the top-ranked model for Puerto Rican Bullfinch point count data from the eastern and western units of Guánica in 2010.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.6290	0.0818	0.4602	0.7713
p (East, mix1, t1)	0.1549	0.0667	0.0632	0.3323
p (East, mix1, t2)	0.0691	0.0333	0.0261	0.1701
p (East, mix1, t3)	0.0995	0.0460	0.0388	0.2321
p (East, mix1, t4)	0.0792	0.0377	0.0303	0.1915
p (East, t1)	0.7857	0.0467	0.6803	0.8633
p (East, t2)	0.5975	0.0625	0.4715	0.7118
p (East, t3)	0.6885	0.0573	0.5669	0.7887
p (East, t4)	0.6325	0.0610	0.5072	0.7421
p (West, mix2, t1)	0.7925	0.0517	0.6733	0.8762
p (West, mix2, t2)	0.7740	0.0543	0.6508	0.8630
p (West, mix2, t3)	0.7547	0.0567	0.6279	0.8488
p (West, mix2, t4)	0.6921	0.0628	0.5580	0.8002
p (West, t1)	0.3473	0.0889	0.1979	0.5344
p (West, t2)	0.3230	0.0856	0.1813	0.5069
p (West, t3)	0.3001	0.0822	0.1661	0.4800
p (West, t4)	0.2385	0.0712	0.1268	0.4031
c (East, mix1, t2)	0.0691	0.0333	0.0261	0.1701
c (East, mix1, t3)	0.0995	0.0460	0.0388	0.2321
c (East, mix1, t4)	0.0792	0.0377	0.0303	0.1915
c (East, t2)	0.5975	0.0625	0.4715	0.7118
c (East, t3)	0.6885	0.0573	0.5669	0.7887
c (East, t4)	0.6325	0.0610	0.5072	0.7421
c (West, mix2, t2)	0.7740	0.0543	0.6508	0.8630
c (West, mix2, t3)	0.7547	0.0567	0.6279	0.8488
c (West, mix2, t4)	0.6921	0.0628	0.5580	0.8002
c (West, t2)	0.3230	0.0856	0.1813	0.5069
c (West, t3)	0.3001	0.0822	0.1661	0.4800
c (West, t4)	0.2385	0.0712	0.1268	0.4031
N hat (East)	212.8471	45.7467	157.7809	352.6593
N hat (West)	145.9704	6.6081	138.0588	166.2556

**Table 2.16** Closed capture models for Adelaide's Warbler point count data from the eastern unit of Guánica in 2009-10 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMth+DFD}	2556.3159	0.0000	0.4232	1.0000	12	2532.1783
{gMth+UC}	2556.5883	0.2724	0.3693	0.8727	12	2532.4507
{gMth}	2561.3467	5.0308	0.0342	0.0808	11	2539.2303
{gMth+SLP}	2562.2966	5.9807	0.0213	0.0503	12	2538.1590
{gMth+SEMIEV}	2562.4500	6.1341	0.0197	0.0466	12	2538.3124
{gMth+CC}	2562.5942	6.2783	0.0183	0.0433	12	2538.4566
{gMth+STRATUM2}	2563.0569	6.7410	0.0145	0.0344	12	2538.9193
{gMth+SCRUB}	2563.1171	6.8012	0.0141	0.0333	12	2538.9795
{gMth+SEMIDE}	2563.2226	6.9067	0.0134	0.0316	12	2539.0850
{gMth+STRATUM1}	2563.2362	6.9203	0.0133	0.0314	12	2539.0986
{gMth+STRATUM3}	2563.2582	6.9423	0.0132	0.0311	12	2539.1206
{gMth+aspect}	2563.3405	7.0246	0.0126	0.0298	12	2539.2029
{gMth+HMAX}	2563.3567	7.0408	0.0125	0.0296	12	2539.2191
{gMth+ELEV}	2563.3662	7.0503	0.0125	0.0294	12	2539.2286
{gMth+all land cover}	2564.2655	7.9496	0.0080	0.0188	13	2538.1049
{gMhb}	2576.3215	20.0056	0.0000	0.0000	7	2562.2722
{gMh}	2645.7799	89.4640	0.0000	0.0000	5	2635.7535
{Mth}	2655.0279	98.7120	0.0000	0.0000	6	2642.9909
{Mhb}	2662.1735	105.8576	0.0000	0.0000	4	2654.1559
{Mh}	2667.6255	111.3096	0.0000	0.0000	3	2661.6150
{gMtb}	2679.5223	123.2064	0.0000	0.0000	10	2659.4253
{gMb}	2716.5300	160.2141	0.0000	0.0000	4	2708.5124
{gMt}	2719.6938	163.3779	0.0000	0.0000	8	2703.6304
{Mtb}	2805.2052	248.8893	0.0000	0.0000	4	2797.1876
{Mt}	2826.2591	269.9432	0.0000	0.0000	4	2818.2415
{Mo}	2835.4106	279.0947	0.0000	0.0000	1	2833.4088
{gMo}	2835.4106	279.0947	0.0000	0.0000	1	2833.4088
{Mb}	2836.9783	280.6624	0.0000	0.0000	2	2832.9730

**Table 2.17** Estimates of model parameters for the top-ranked model for Adelaide's Warbler point count data from the eastern unit of Guánica in 2009-10.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.3602	0.0459	0.2760	0.4540
p (2009, mix1, t1)	0.9792	0.0311	0.7032	0.9989
p (2009, mix1, t2)	0.9870	0.0195	0.7925	0.9993
p (2009, mix1, t3)	0.9851	0.0223	0.7691	0.9992
p (2009, mix1, t4)	0.9892	0.0164	0.8208	0.9995
p (2009, t1)	0.4745	0.0458	0.3865	0.5642
p (2009, t2)	0.5934	0.0442	0.5047	0.6763
p (2009, t3)	0.5599	0.0450	0.4708	0.6453
p (2009, t4)	0.6365	0.0429	0.5490	0.7159
p (2010, mix2, t1)	0.9733	0.0111	0.9405	0.9883
p (2010, mix2, t2)	0.9236	0.0295	0.8421	0.9648
p (2010, mix2, t3)	0.8874	0.0414	0.7776	0.9467
p (2010, mix2, t4)	0.8599	0.0494	0.7333	0.9319
p (2010, t1)	0.6335	0.0526	0.5258	0.7294
p (2010, t2)	0.3642	0.0489	0.2747	0.4642
p (2010, t3)	0.2719	0.0434	0.1955	0.3645
p (2010, t4)	0.2253	0.0392	0.1577	0.3111
c (2009, mix1, t2)	0.9870	0.0195	0.7925	0.9993
c (2009, mix1, t3)	0.9851	0.0223	0.7691	0.9992
c (2009, mix1, t4)	0.9892	0.0164	0.8208	0.9995
c (2009, t2)	0.5934	0.0442	0.5047	0.6763
c (2009, t3)	0.5599	0.0450	0.4708	0.6453
c (2009, t4)	0.6365	0.0429	0.5490	0.7159
c (2010, mix2, t2)	0.9236	0.0295	0.8421	0.9648
c (2010, mix2, t3)	0.8874	0.0414	0.7776	0.9467
c (2010, mix2, t4)	0.8599	0.0494	0.7333	0.9319
c (2010, t2)	0.3642	0.0489	0.2747	0.4642
c (2010, t3)	0.2719	0.0434	0.1955	0.3645
c (2010, t4)	0.2253	0.0392	0.1577	0.3111
N hat (2009)	327.7061	3.5414	323.2676	338.1735
N hat (2010)	275.0945	8.3635	263.2837	297.4064

**Table 2.18** Closed capture models for Adelaide's Warbler point count data from the eastern and western units of Guánica in 2010 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMth+UC+DFD}	1994.9050	0.0000	0.3332	1.0000	13	1968.6849
{gMth+UC+DFD+STRATUM1}	1994.9462	0.0412	0.3264	0.9796	14	1966.6921
{gMth+UC}	1995.0102	0.1052	0.3161	0.9487	12	1970.8217
{gMth+DFD}	2002.3727	7.4677	0.0080	0.0239	12	1978.1842
{gMth+STRATUM1}	2003.6832	8.7782	0.0041	0.0124	12	1979.4947
{gMth+STRATUM2}	2003.9117	9.0067	0.0037	0.0111	12	1979.7232
{gMth+CC}	2004.7771	9.8721	0.0024	0.0072	12	1980.5886
{gMth}	2004.9237	10.0187	0.0022	0.0067	11	1982.7643
{gMth+HMAX}	2004.9381	10.0331	0.0022	0.0066	12	1980.7496
{gMth+STRATUM3}	2006.7810	11.8760	0.0009	0.0026	12	1982.5925
{Mth}	2006.8525	11.9475	0.0009	0.0026	6	1994.8019
{gMhb}	2030.9811	36.0761	0.0000	0.0000	7	2016.9136
{Mhb}	2032.8909	37.9859	0.0000	0.0000	4	2024.8668
{Mh}	2095.5763	100.6713	0.0000	0.0000	3	2089.5619
{gMh}	2096.1869	101.2819	0.0000	0.0000	5	2086.1508
{gMtb}	2110.1494	115.2444	0.0000	0.0000	10	2090.0166
{gMt}	2113.3972	118.4922	0.0000	0.0000	8	2097.3104
{Mt}	2115.2065	120.3015	0.0000	0.0000	4	2107.1824
{Mtb}	2115.5108	120.6058	0.0000	0.0000	5	2105.4747
{gMb}	2143.2554	148.3504	0.0000	0.0000	4	2135.2313
{Mb}	2146.5062	151.6012	0.0000	0.0000	2	2142.4990
{Mo}	2190.5886	195.6836	0.0000	0.0000	1	2188.5862
{gMo}	2190.5886	195.6836	0.0000	0.0000	1	2188.5862

**Table 2.19** Estimates of model parameters for the top-ranked model for Adelaide's Warbler point count data from the eastern and western units of Guánica in 2010.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.3678	0.0513	0.2740	0.4728
p (East, mix1, t1)	0.9713	0.0111	0.9395	0.9866
p (East, mix1, t2)	0.9178	0.0293	0.8392	0.9598
p (East, mix1, t3)	0.8788	0.0409	0.7736	0.9390
p (East, mix1, t4)	0.8495	0.0483	0.7291	0.9221
p (East, t1)	0.6312	0.0551	0.5182	0.7313
p (East, t2)	0.3607	0.0516	0.2668	0.4665
p (East, t3)	0.2681	0.0454	0.1889	0.3656
p (East, t4)	0.2219	0.0407	0.1523	0.3117
p (West, mix2, t1)	0.9187	0.0272	0.8471	0.9584
p (West, mix2, t2)	0.8765	0.0381	0.7808	0.9339
p (West, mix2, t3)	0.8019	0.0540	0.6753	0.8873
p (West, mix2, t4)	0.8366	0.0471	0.7227	0.9096
p (West, t1)	0.5540	0.0769	0.4030	0.6957
p (West, t2)	0.4383	0.0749	0.3006	0.5861
p (West, t3)	0.3080	0.0662	0.1948	0.4501
p (West, t4)	0.3603	0.0707	0.2359	0.5067
c (East, mix1, t2)	0.9178	0.0293	0.8392	0.9598
c (East, mix1, t3)	0.8788	0.0409	0.7736	0.9390
c (East, mix1, t4)	0.8495	0.0483	0.7291	0.9221
c (East, t2)	0.3607	0.0516	0.2668	0.4665
c (East, t3)	0.2681	0.0454	0.1889	0.3656
c (East, t4)	0.2219	0.0407	0.1523	0.3117
c (West, mix2, t2)	0.8765	0.0381	0.7808	0.9339
c (West, mix2, t3)	0.8019	0.0540	0.6753	0.8873
c (West, mix2, t4)	0.8366	0.0471	0.7227	0.9096
c (West, t2)	0.4383	0.0749	0.3006	0.5861
c (West, t3)	0.3080	0.0662	0.1948	0.4501
c (West, t4)	0.3603	0.0707	0.2359	0.5067
N hat (East)	279.5096	10.0622	265.4049	306.5287
N hat (West)	179.8585	6.6842	171.9305	200.5348

**Table 2.20** Closed capture models for Puerto Rican Vireo point count data from the eastern unit of Guánica in 2009-10 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMb+ELEV}	191.7162	0.0000	0.3308	1.0000	5	181.3458
{gMb+STRATUM2}	192.3263	0.6101	0.2438	0.7371	5	181.9559
{gMb+STRATUM1}	193.0228	1.3066	0.1721	0.5203	5	182.6524
{gMb+UC}	195.5458	3.8296	0.0487	0.1474	5	185.1754
{gMb+aspect}	196.4561	4.7399	0.0309	0.0935	5	186.0857
{gMb}	196.7299	5.0137	0.0270	0.0815	4	188.4845
{gMb+SLP}	196.9992	5.2830	0.0236	0.0713	5	186.6288
{gMb+SCRUB}	197.3398	5.6236	0.0199	0.0601	5	186.9694
{gMb+SEMIEV}	197.3427	5.6265	0.0199	0.0600	5	186.9723
{gMb+HMAX}	197.6611	5.9449	0.0169	0.0512	5	187.2907
{gMb+all land cover}	198.1319	6.4157	0.0134	0.0405	6	185.6101
{gMb+DFD}	198.3645	6.6483	0.0119	0.0360	5	187.9942
{gMb+STRATUM3}	198.3832	6.6670	0.0118	0.0357	5	188.0128
{gMb+CC}	198.7231	7.0069	0.0100	0.0301	5	188.3527
{gMb+SEMIDE}	198.7953	7.0791	0.0096	0.0290	5	188.4249
{gMhb}	199.3983	7.6821	0.0071	0.0215	7	184.6983
{Mb}	202.5334	10.8172	0.0015	0.0045	2	198.4607
{Mhb}	203.1096	11.3934	0.0011	0.0034	4	194.8642
{Mtb}	207.6668	15.9506	0.0001	0.0003	4	199.4214
{Mth}	210.0148	18.2986	0.0000	0.0001	6	197.4931
{gMth}	210.6400	18.9238	0.0000	0.0001	11	186.9477
{gMh}	215.5591	23.8429	0.0000	0.0000	5	205.1887
{gMt}	215.6943	23.9781	0.0000	0.0000	8	198.7886
{Mt}	216.7289	25.0127	0.0000	0.0000	4	208.4835
{Mo}	217.2840	25.5678	0.0000	0.0000	1	215.2599
{gMo}	217.2840	25.5678	0.0000	0.0000	1	215.2599

**Table 2.21** Estimates of model parameters for the top-ranked model for Puerto Rican Vireo point count data from the eastern unit of Guánica in 2009-10.

Parameter	Estimate	SE	Lower CI	Upper CI
p (2009)	0.4697	0.1245	0.2496	0.7023
p (2010)	0.3755	0.1263	0.1730	0.6334
c (2009)	0.9114	0.0492	0.7569	0.9714
c (2010)	0.6490	0.0715	0.4998	0.7738
N hat (2009)	22.5346	3.9255	19.6100	39.4821
N hat (2010)	29.6576	7.2445	24.1775	60.6415

**Table 2.22** Closed capture models for Puerto Rican Vireo point count data from the eastern and western units of Guánica in 2010 ranked by their respective AIC<sub>c</sub> values.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{Mth+DFD}	232.6122	0.0000	0.4690	1.0000	7	218.0035
{Mth+STRATUM3}	235.8438	3.2316	0.0932	0.1987	7	221.2352
{Mth}	235.9397	3.3275	0.0889	0.1894	6	223.4856
{Mth+DFD+STRATUM3}	236.3232	3.7110	0.0733	0.1564	8	219.5363
{gMth}	236.9369	4.3247	0.0540	0.1150	11	213.4703
{Mth+UC}	237.4571	4.8449	0.0416	0.0887	7	222.8484
{Mh}	237.4657	4.8535	0.0414	0.0883	3	231.3380
{Mth+HMAX}	237.9384	5.3262	0.0327	0.0697	7	223.3297
{Mth+STRATUM1}	238.0854	5.4732	0.0304	0.0648	7	223.4767
{Mth+STRATUM2}	238.6225	6.0103	0.0232	0.0495	7	224.0138
{gMhb}	238.8565	6.2443	0.0207	0.0441	7	224.2478
{Mhb}	239.0519	6.4397	0.0187	0.0400	4	230.8380
{gMh}	239.8093	7.1971	0.0128	0.0274	5	229.4867
{Mtb}	254.1857	21.5735	0.0000	0.0000	4	245.9718
{Mo}	257.1947	24.5825	0.0000	0.0000	1	255.1736
{gMo}	257.1947	24.5825	0.0000	0.0000	1	255.1736
{Mt}	257.5821	24.9699	0.0000	0.0000	4	249.3682
{Mb}	258.8806	26.2684	0.0000	0.0000	2	254.8171
{gMb}	259.1828	26.5706	0.0000	0.0000	4	250.9689
{gMt}	261.3075	28.6953	0.0000	0.0000	8	244.5206

**Table 2.23** Estimates of model parameters for the top-ranked model for Puerto Rican Vireo point count data from the eastern and western units of Guánica in 2010.

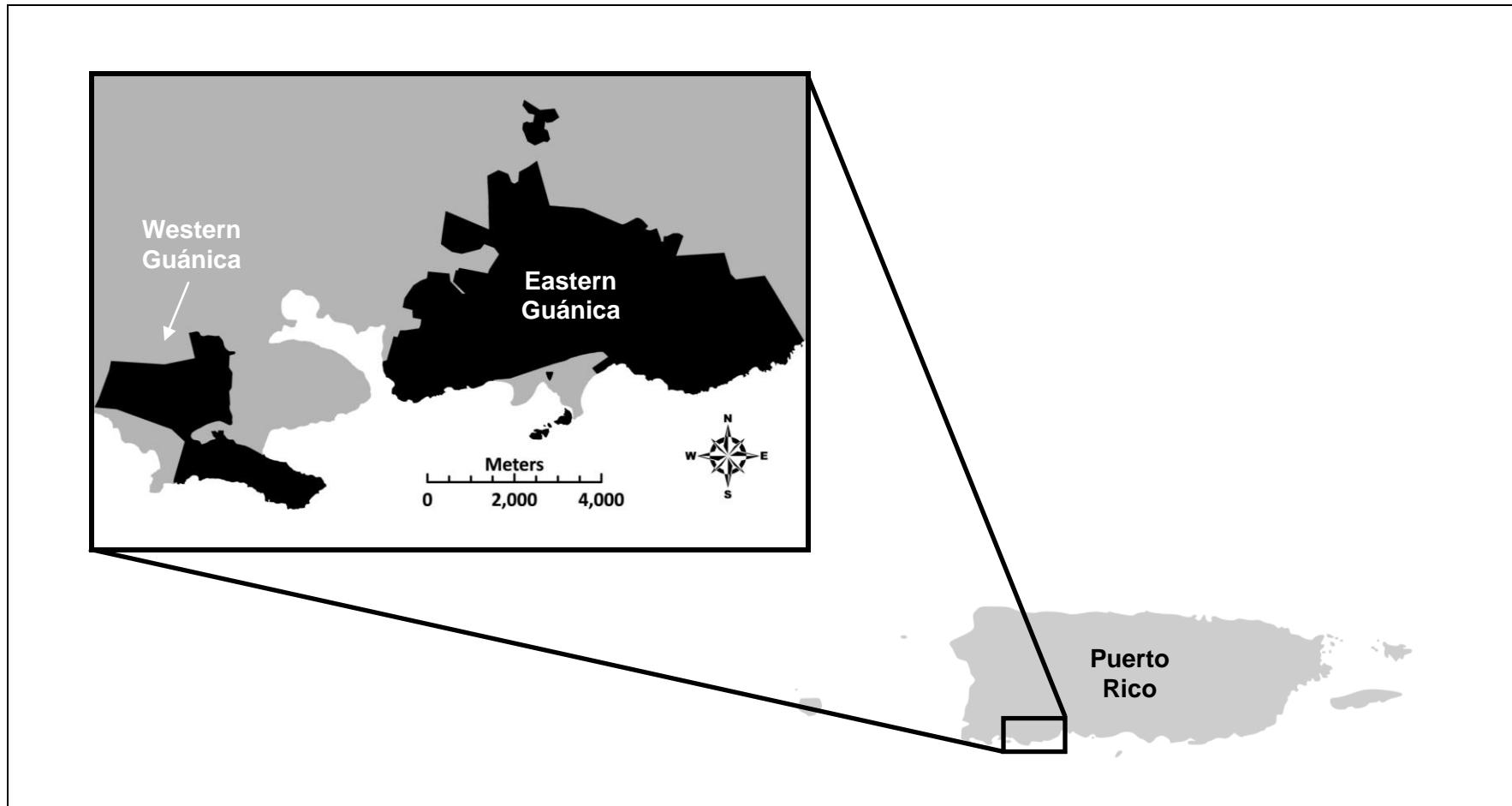
Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.2179	0.1408	0.0522	0.5846
p (mix1, t1)	0.8956	0.0430	0.7770	0.9548
p (mix1, t2)	0.7101	0.0840	0.5241	0.8449
p (mix1, t3)	0.8616	0.0534	0.7212	0.9375
p (mix1, t4)	0.8742	0.0498	0.7411	0.9440
p (t1)	0.0560	0.0583	0.0068	0.3403
p (t2)	0.0167	0.0182	0.0019	0.1305
p (t3)	0.0413	0.0437	0.0049	0.2728
p (t4)	0.0458	0.0483	0.0055	0.2948
c (mix1, t2)	0.7101	0.0840	0.5241	0.8449
c (mix1, t3)	0.8616	0.0534	0.7212	0.9375
c (mix1, t4)	0.8742	0.0498	0.7411	0.9440
c (t2)	0.0167	0.0182	0.0019	0.1305
c (t3)	0.0413	0.0437	0.0049	0.2728
c (t4)	0.0458	0.0483	0.0055	0.2948
N hat (East)	63.6956	42.6954	30.5194	243.2489
N hat (West)	77.8555	53.6419	35.1588	300.0046

**Table 2.24** Closed capture models for Pearly-eyed Thrasher point count data from the eastern unit of Guánica in 2009-10 ranked by their respective AIC<sub>c</sub> values.

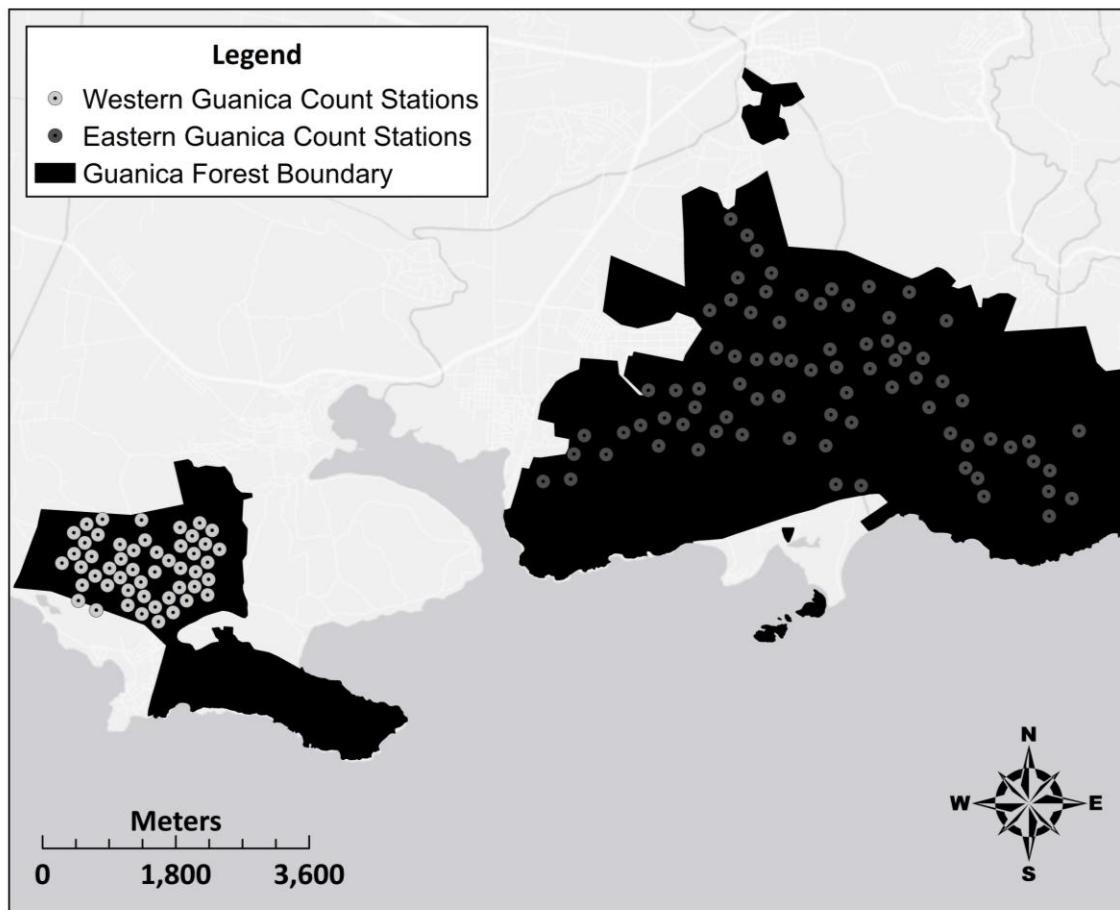
Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>c</sub> Weight	Model Likelihood	Parameters	Deviance
{gMh+SEMIDE+STRATUM1+STRATUM2}	394.7990	0.0000	0.6548	1.0000	8	378.3475
{gMh+SEMIDE}	400.0782	5.2792	0.0468	0.0714	6	387.8165
{gMh}	400.1292	5.3302	0.0456	0.0696	5	389.9429
{gMh+STRATUM1}	400.5962	5.7972	0.0361	0.0551	6	388.3345
{gMh+STRATUM2}	400.6772	5.8782	0.0347	0.0529	6	388.4155
{gMh+SEMIDE+HMAX}	400.9214	6.1224	0.0307	0.0468	7	386.5714
{gMh+CC}	401.1901	6.3911	0.0268	0.0409	6	388.9284
{gMh+aspect}	401.2328	6.4338	0.0262	0.0401	6	388.9712
{gMh+HMAX}	402.0979	7.2989	0.0170	0.0260	6	389.8362
{gMh+ELEV}	402.1153	7.3163	0.0169	0.0258	6	389.8536
{gMh+UC}	402.1507	7.3517	0.0166	0.0253	6	389.8890
{Mhb}	403.1091	8.3101	0.0103	0.0157	4	394.9853
{gMth}	403.4364	8.6374	0.0087	0.0133	11	380.6009
{gMh+STRATUM3}	403.9155	9.1165	0.0069	0.0105	6	391.6538
{Mh}	404.1407	9.3417	0.0061	0.0094	3	398.0667
{Mth}	404.2226	9.4236	0.0059	0.0090	6	391.9609
{gMh+SEMIEV}	404.9360	10.1370	0.0041	0.0063	6	392.6743
{gMh+SEMIDE+CC}	405.1972	10.3982	0.0036	0.0055	7	390.8472
{gMh+SLP}	406.9205	12.1215	0.0015	0.0023	6	394.6588
{gMh+DFD}	408.1484	13.3494	0.0008	0.0013	6	395.8867
{Mb}	437.2651	42.4661	0.0000	0.0000	2	433.2281
{Mtb}	439.1666	44.3676	0.0000	0.0000	4	431.0428
{gMb}	440.4931	45.6941	0.0000	0.0000	4	432.3693
{Mo}	440.9600	46.1610	0.0000	0.0000	1	438.9477
{gMo}	440.9600	46.1610	0.0000	0.0000	1	438.9477
{Mt}	442.0482	47.2492	0.0000	0.0000	4	433.9244
{gMt}	447.1391	52.3401	0.0000	0.0000	8	430.6876

**Table 2.25** Estimates of model parameters for the top-ranked model for Pearly-eyed Thrasher point count data from the eastern unit of Guánica in 2009-10.

Parameter	Estimate	SE	Lower CI	Upper CI
pi	0.9456	0.0293	0.8504	0.9815
p (2009, mix1)	0.3013	0.0660	0.1892	0.4434
p (2009, mix1)	0.3013	0.0660	0.1892	0.4434
p (2009, mix1)	0.3013	0.0660	0.1892	0.4434
p (2009, mix1)	0.3013	0.0660	0.1892	0.4434
p (2009)	0.9940	0.0063	0.9551	0.9992
p (2009)	0.9940	0.0063	0.9551	0.9992
p (2009)	0.9940	0.0063	0.9551	0.9992
p (2009)	0.9940	0.0063	0.9551	0.9992
p (2009)	0.9940	0.0063	0.9551	0.9992
p (2010, mix2)	0.0277	0.0192	0.0070	0.1035
p (2010, mix2)	0.0277	0.0192	0.0070	0.1035
p (2010, mix2)	0.0277	0.0192	0.0070	0.1035
p (2010, mix2)	0.0277	0.0192	0.0070	0.1035
p (2010)	0.9052	0.0412	0.7885	0.9607
p (2010)	0.9052	0.0412	0.7885	0.9607
p (2010)	0.9052	0.0412	0.7885	0.9607
c (2009, mix1)	0.3013	0.0660	0.1892	0.4434
c (2009, mix1)	0.3013	0.0660	0.1892	0.4434
c (2009, mix1)	0.3013	0.0660	0.1892	0.4434
c (2009)	0.9940	0.0063	0.9551	0.9992
c (2009)	0.9940	0.0063	0.9551	0.9992
c (2009)	0.9940	0.0063	0.9551	0.9992
c (2010, mix2)	0.0277	0.0192	0.0070	0.1035
c (2010, mix2)	0.0277	0.0192	0.0070	0.1035
c (2010, mix2)	0.0277	0.0192	0.0070	0.1035
c (2010)	0.9052	0.0412	0.7885	0.9607
c (2010)	0.9052	0.0412	0.7885	0.9607
c (2010)	0.9052	0.0412	0.7885	0.9607
N hat (2009)	142.8639	60.5308	77.4355	344.4718
N hat (2010)	358.2391	260.5984	116.2326	1330.2130



**Figure 2.1** Map showing the location and relative size of the eastern and western tracts of Guánica State Forest, the two parts of the reserve in which this study was conducted.



**Figure 2.2** Map showing the locations of 50 point count stations in the western tract and 79 point count stations in the eastern tract of Guánica State Forest.