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DEMOGRAPHY OF ZENAIDA DOVES IN PUERTO RICO[1]

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Abstract. We conducted a capture-recapture study of Zenaida Doves (*Zenaida aurita*) in three neighboring dairy farms in eastcentral Puerto Rico during 1984–1997. During 46 sampling periods, mean survival rate per sampling period was 0.77 (range = 0.1–1.0), mean recruitment was 911 individuals (range = 182–5,124), and mean population size was 1,569 individuals (range = 233–7,354). Survival increased during 1984–1991 and decreased during 1992–1997. Recruitment did not show a trend, but population size increased during 1984–1997. Rate of increase was a curvilinear decreasing function of population size. A demographic model with a fixed mortality rate stabilized at 1,350 individuals. When mortality rate was defined as a normal random variable, mean population size was 1,421 individuals, and there was a 0.95 probability of observing population sizes from 467 to 2,375 individuals. The size of the Zenaida Dove population varied widely over time, but periods of high recruitment rapidly offset periods of low survival in the dairy farms.

Key words: capture-recapture data, demographic model, demography, population dynamics, Puerto Rico, Zenaida aurita, *Zenaida Dove.*

Resumen. Efectuamos un estudio de captura-recaptura de la tórtola cardosantera (*Zenaida aurita*) en tres vaquerías colindantes en el estecentral de Puerto Rico durante 1984–1997. Durante 46 períodos de muestreo, el promedio de la tasa de sobrevivencia por período de muestreo fue 0,77 (rango = 0,10–1,0), el reclutamiento promedio fue 911 individuos (rango = 182–5.124), y el tamaño poblacional promedio fue 1.569 individuos (rango = 233–7.354). La sobrevivencia aumentó durante 1984–1991 y disminuyó durante 1992–1997. El reclutamiento no mostró una tendencia, pero el tamaño poblacional aumentó durante 1984–1997. La tasa de crecimiento fue una función curvilinear decreciente del tamaño poblacional. Un modelo demográfico con una tasa de mortandad fija se estabilizó en 1.350 individuos. Cuando la tasa de mortandad fue definida como una variable normal aleatoria, la media del tamaño poblacional fue 1.421 individuos, y hubo una probabilidad de 0,95 de observar tamaños poblacionales entre 467 y 2.375 individuos. El tamaño de la población de tórtolas cardosanteras varió ampliamente a través del tiempo, pero los períodos de alto reclutamiento rápidamente compensaron a los períodos de baja sobrevivencia en las vaquerías.

INTRODUCTION

A major portion of ecology is concerned with understanding how wildlife populations change over time and which factors determine the magnitude of their numerical change (Krebs 1994). Recruitment (births + immigrants), survival (1 − deaths − emigrants), and population size are fundamental demographic parameters of wildlife populations (Lebreton and Clobert 1991). Capture-recapture methods can be used to estimate demographic parameters and monitor temporal changes in population abundance (Pollock et al. 1990, Lebreton et al. 1992, Loery et al. 1997).

Zenaida Doves (*Zenaida aurita*) are abundant and widely hunted in Puerto Rico (Rivera-Milán 1992, 1995). We conducted a capture-recapture study of Zenaida Doves in three dairy farms in eastcentral Puerto Rico during 1984–1997. Our objectives were to estimate temporal variation of demographic parameters (survival, recruitment, and population size) and build a demographic model to describe and predict annual changes in population size due to changes in survival and recruitment rates.

METHODS

STUDY AREA

Our study area comprised three neighboring dairy farms (approximately 729 ha) in the municipality of Cidra, Puerto Rico (18°10′N, 66°97′W). In the dairy farms, pastures were dominated by Guinea grass (*Panicum maxi-*

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mum), and second-growth forests were dominated by bamboo (*Bambusa vulgaris*), African tuliptree (*Spathodea campanulata*), matchwood (*Didymopanax morototoni*), trumpet tree (*Cecropia schreberiana*), and other trees typical of the subtropical moist zone (Birdsey and Weaver 1982).

Hunting was not allowed in Cidra (U.S. Fish and Wildlife Service 1982), but illegal hunting occurred occasionally in agricultural areas near the dairy farms. During 1993–1995, a large portion of the pastures inside the dairy farms was developed by a housing project, but surrounding second-growth forest patches (approximately 163 ha) were left untouched.

CAPTURE-RECAPTURE DATA

We trapped Zenaida Doves with mist nets and funnel traps baited with cracked corn during 46 sampling periods: February–November 1984, 1991, and 1992, April–November 1996, and 1997. Intervals between sampling periods per year were about 30 days. We marked captured Zenaida Doves with U.S. Fish and Wildlife Service numbered aluminum bands and released them immediately after data collection.

DATA ANALYSIS

Because of limited sample sizes in 1984, 1996, and 1997, we did not stratify the capture-recapture data of Zenaida Doves by age. However, survival and capture rates of hatching-year and after-hatching-year Zenaida Doves did not differ significantly in 1991 and 1992 (Rivera-Milán 1999). Both age classes showed similar survival and recapture patterns during 20 of 46 sampling periods. Thus, we analyzed the capture-recapture data with age classes combined (Lebreton et al. 1992).

We used between-model tests for model selection and goodness-of-fit tests to evaluate the fit of models in program JOLLY to the capture-recapture data of Zenaida Doves (Pollock et al. 1990). We used Test 2 and Test 3 in program RELEASE to conduct a more detailed assessment of the goodness-of-fit of the standard Jolly-Seber model (Cooch et al. 1997), and the Brownie-Robson test statistic (Model 2 or marking-effect model in JOLLY) to examine whether newly marked and previously marked individuals had different survival and capture probabilities.

The bootstrap method (Efron and Tibshirani 1993, Simon 1997) was used to establish frequency distributions and 95% confidence intervals of estimates of survival rate ($\hat{\phi}_i$), recruitment ($\hat{B}_i$), and population size ($\hat{N}_i$). We randomly resampled the original datasets with replacement 1,000 times (bootstrap replications) and generated bootstrap datasets with the program RESAMPLING STATS (Simon 1997).

Simple linear regression was used to test for decreasing or increasing trends in transformed and non-transformed demographic parameter estimates ($\hat{\phi}_i$, $\hat{B}_i$, $\hat{N}_i$) versus time (i). Plots of residuals versus fitted values and residual statistics (e.g., Durbin-Watson d statistic and serial autocorrelation index) allowed us to examine whether the assumptions of regression were met (Ryan 1997).

DEMOGRAPHIC MODEL

A demographic model for Zenaida Doves was built and evaluated with STELLA II (Peterson and Richmond 1993, Hannon and Ruth 1997), Microsoft Excel 5, and StatView (SAS Institute, Inc. 1998). We wanted to build a basic demographic model, parameterized with capture-recapture data, to describe and predict annual changes in the size of the Zenaida Dove population in the dairy farms. The structure of the model is presented in a compartmentalized form. Population size (N) was the system state variable and it was estimated as the number of individuals per time step (DT = 1 year; time period: T = 25 years). Simple linear regression and nonlinear transformations (exponential, logarithmic, power, and growth models) were used to specify in mathematical terms the feedback between the size of the population and its rate of increase due to density dependence (Rodenhouse et al. 1997). Annual mortality rate was defined as fixed over time or as a normal random variable with mean μ and standard deviation σ. We conducted sensitivity analysis using a uniform random distribution covering the range of observed population sizes during 46 sampling periods. Means $\pm$ SD for population size were computed from 500 25-year model runs.

RESULTS

CAPTURE-RECAPTURE DATA

Goodness-of-fit and likelihood-ratio tests indicated that the standard Jolly-Seber model with time-specific survival and capture rates fit the

TABLE 1. Mean estimates of survival rate ($\bar{\hat{\phi}}_i$), recruitment ($\bar{\hat{B}}_i$), and population size ($\bar{\hat{N}}_i$) and bootstrapped 95% confidence intervals (1,000 bootstrap replicates), under the standard time-specific Jolly-Seber model (Model A in JOLLY), for the capture-recapture data of Zenaida Doves collected in Cidra, Puerto Rico, during 1984–1997.

Date	$\bar{\hat{\phi}}_i$[a]	95% CI	$\bar{\hat{B}}_i$	95% CI	$\bar{\hat{N}}_i$	95% CI
Feb–Nov 1984	0.55	0.27–0.81	772	188–1,757	991	489–1,659
Feb–Nov 1991	0.89	0.82–0.96	792	430–1,424	1,364	860–2,063
Feb–Nov 1992	0.73	0.50–0.93	928	512–1,477	1,582	1,037–2,207
Apr–Nov 1996	0.77	0.62–0.92	1,296	325–2,879	2,500	1,421–4,147
Apr–Nov 1997	0.69	0.44–0.86	889	260–1,888	1,560	883–2,167
1984–1997	0.77	0.69–0.85	911	561–1,344	1,569	1,224–2,094

[a] $\bar{\hat{\phi}}_i$ = estimated mean survival rate (1 − mortality rate − emigration rate) from period i to i + 1; $\bar{\hat{B}}_i$ = estimated mean number of recruited individuals (births + immigrants) from period i to i + 1; and $\bar{\hat{N}}_i$ = estimated mean population size in period i. Intervals between sampling periods (i) per year were about 30 days.

capture-recapture data of Zenaida Doves (Model A in JOLLY and Test 2 and Test 3 in RELEASE: P-values > 0.1). Survival and capture rates of newly captured and previously captured individuals did not differ significantly (Model 2 in JOLLY: P-values > 0.1). However, goodness-of-fit and likelihood-ratio tests indicated that survival and capture rates varied significantly over time (that is, Model B and Model D in JOLLY were rejected; P-values < 0.05).

We captured 2,490 Zenaida Doves and recaptured 480 of them at least once during 46 sampling periods between February–November 1984 and April–November 1997 (mean capture rate per sampling period = 0.05, bootstrapped 95% CI = 0.04–0.07). Mean survival rate per sampling period was 0.77 (range = 0.1–1.0), mean recruitment was 911 individuals (range = 182–5,124), and mean population size was 1,569 individuals (range = 233–7,354; Table 1, Fig. 1a–c).

Mean survival rate per sampling period ranged from 0.55 in 1984 to 0.89 in 1991 (Table 1). Only 3 of 380 Zenaida Doves captured in 1984 were recaptured during 1991–1997. The oldest Zenaida Dove recaptured was at least 8 years old. Mean recruitment ranged from 772 individuals in 1984 to 1,296 individuals in 1996, and mean population size from 991 individuals in 1984 to 2,500 individuals in 1996 (Table 1). Survival increased during 1984–1991 and decreased during 1992–1997 (quadratic regression: $F_{2,33}$ = 3.4, P < 0.05). Recruitment (births + immigrants) did not show a trend (linear regression: $F_{1,25}$ = 0.4, P > 0.5), but population size increased during 1984–1997 (linear regression: $\hat{b} \pm$ SE = 0.16 ± 0.07; $e^{\hat{b}}$ = 1.17 or 17% per year; $F_{1,37}$ = 5.7, P < 0.05). Residual plots and residual statistics indicated that the assumptions of regression were met (that is, ln[$\hat{N}_i$] vs. time [i]: d = 1.1, P > 0.1; first-degree serial autocorrelation = 0.2).

Mean rate of increase was 1.35 (bootstrapped 95% CI = 1.04–1.75), and the probability of it being equal or less than 1 was approximately 0.03. Rate of increase was a curvilinear decreasing function of population size (power regression: $68.653N^{-0.592}$, t_{35} = −3.9, P < 0.001), which stabilized at 1,350 individuals (Fig. 1c and Fig. 2a, b).

DEMOGRAPHIC MODEL

Model runs with a fixed mortality rate ($\bar{x}$ = 0.96) stabilized at 1,350 individuals after 6 years (Fig. 3 and 4a). When mortality rate was defined as a normal random variable (with mean ± SD = 0.96 ± 0.25), mean population size was 1,421 individuals (bootstrapped 95% CI = 1,318–1,664), and there was a 0.95 probability of observing population sizes from 467 to 2,375 individuals (Fig. 3 and 4b).

DISCUSSION

CAPTURE-RECAPTURE DATA

The standard time-specific Jolly-Seber model (Model A in JOLLY) fit the capture-recapture data of Zenaida Doves. Model 2 in JOLLY and Test 2 and Test 3 in RELEASE ("recapture" and "survival" tests, respectively; Burnham et al. 1987, Cooch et al. 1997) did not detect capture and survival rate differences among newly and previously captured individuals. However, Zenaida Doves had low capture probabilities and high turnover rates (that is, low survival and high recruitment), and under these circumstances goodness-of-fit tests have low power (Pollock

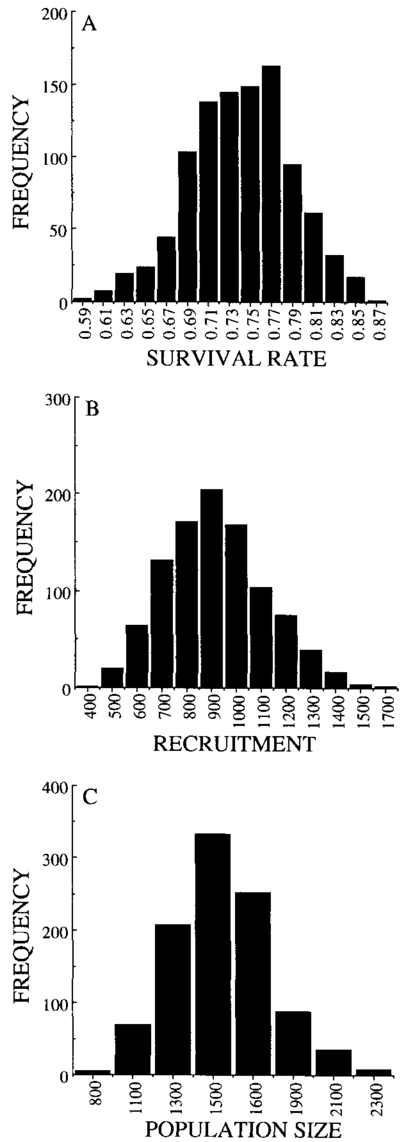


FIGURE 1. Frequency distributions of mean estimates of (A) survival rate per sampling period, (B) recruitment, and (C) population size based on the capture-recapture data of Zenaida Doves collected in three dairy farms in Cidra, Puerto Rico, during 46 sampling periods between February–November 1984 and April–November 1997. Bootstrap replications = 1,000.

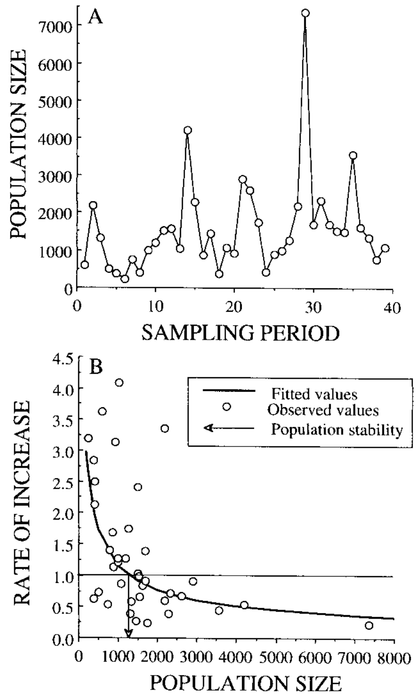
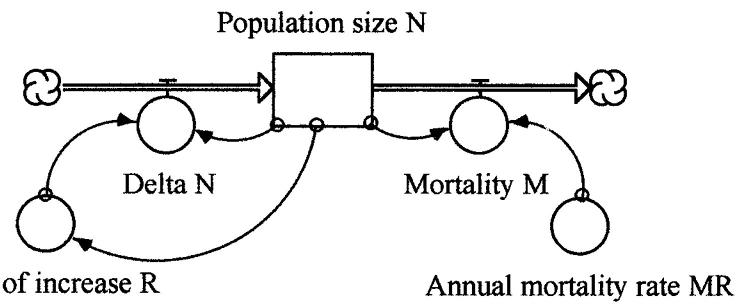


FIGURE 2. (A) Population size estimates of Zenaida Doves in three dairy farms in Cidra, Puerto Rico, during 46 sampling periods between February–November 1984 and April–November 1997. (B) Power regression model for the negative feedback between the size of the Zenaida Dove population ($\hat{N}_i$) and its rate of increase ($\hat{R} = \hat{N}_{i+1}/\hat{N}_i$), showing population stability ($\hat{R} = 0$) at 1,350 individuals.

et al. 1990, Lebreton et al. 1992). Moreover, these tests cannot detect a permanent trap response, such as avoidance of funnel traps and mist nets after initial capture, or a lowering of survival due to long-term trauma induced by trapping and handling.

Of 480 recaptures during 1984–1997, 86% were recaptured in one sampling period, 11% in two sampling periods, 2% in three sampling periods, 1% in four sampling periods, and none in five sampling periods or more. Recaptures were low even though 25% of captured individuals (bootstrapped 95% CI = 21–29%) remained marked in the population per sampling period ($\hat{\bar{M}}_i$ in Model A). Less than 1% of the individuals that were trapped died, and about the same percentage of those that were released had signs of trauma or injuries resulting from trapping or handling. Thus, we believe that the recapture pattern of Zenaida Doves mainly reflected a permanent trap response after initial capture and the effect of their daily movements across the boundaries of the dairy farms.

Permanent trap avoidance cannot bias the survival rate estimator, although its precision can be reduced. However, the population size estimator can be positively biased by permanent



Model runs = 500.
Time period (T) = 25 years and time step (DT) = 1 year.
System conditions: $N(t) = N(t - dt) + (DN - M) \cdot dt$.
Initial N = 233.
Sensitivity analysis: uniform distribution range = 233-7,354 (which are the lowest and highest values of N estimated during 46 sampling periods).
Inflow: Delta N (DN) = $R \cdot N$.
Outflow: $M = N \cdot MR$, where M = deaths + emigrants, and $MR = 1 - 0.77^{12} = 0.96$ fixed over time or as a normal random variable with mean ± SD = 0.96 ± 0.25 (monthly survival rate was 0.77 during 1984-1997; that is, annual survival rate was the product of 12 monthly survival rates = 0.04).
$R = 68.65285 \cdot N^{-0.59241}$ (which is the model of best fit for the feedback between the size of the population and its rate of increase).

FIGURE 3. Structure of the demographic model used to describe and predict the population dynamics of Zenaida Doves in three dairy farms in Cidra, Puerto Rico. The demographic model was based on bootstrap analyses of the capture-recapture data of Zenaida Doves collected in the dairy farms during 1984–1997. Mean survival rate ($\bar{\phi}_i$) per sampling period was changed to annual mortality rate ($1 - \bar{\phi}_i^{12}$) to simulate annual changes in abundance (500 25-year model runs).

trap avoidance (Nichols et al. 1984). Using line transect surveys, Rivera-Milán (1999) estimated a population size of 933 Zenaida Doves (bootstrapped 95% CI = 765–1,144) in the dairy farms in 1991. This independent estimate of population size was within the bootstrapped 95% confidence intervals of population size estimates from capture-recapture data in 1991 (Table 1). Thus, we believe that population size estimates from capture-recapture data were not severely biased by low recapture probabilities and high turnover rates.

Second-growth forests in the dairy farms provided suitable habitats for foraging, nesting, and roosting Zenaida Doves. On the 163 ha of second-growth forests, Rivera-Milán (1999) estimated 398 active nests (95% CI = 215–580), a nesting success of 0.62 (95% CI = 0.52–0.74), and 1.24 young fledged per nest (95% CI = 1.07–1.41) in 1991. Zenaida Doves had a diverse diet, including tree fruits, grass seeds, corn and other high protein grains given to cattle in the dairy farms. Thus, high recruitment rapidly offset low survival because habitat conditions and food sources in the dairy farms not only sustained a large and relatively successful nesting population, but also attracted Zenaida Doves from neighboring and distant areas (F. F. Rivera-Milán and M. Vázquez, unpubl. data).

DEMOGRAPHIC MODEL

Zenaida Doves are multibrooded habitat generalists capable of opportunistically changing their nesting and foraging preferences (Wiley 1991, Rivera-Milán 1996, 1997). They track environmental fluctuations closely and exploit foraging resources (tree fruits, grass seeds, and cultivated grains) such that their abundance can increase rapidly in response to fluctuations in foraging resources. Because of low survival and high recruitment rates, their populations can be highly variable and can reach or surpass ceiling levels

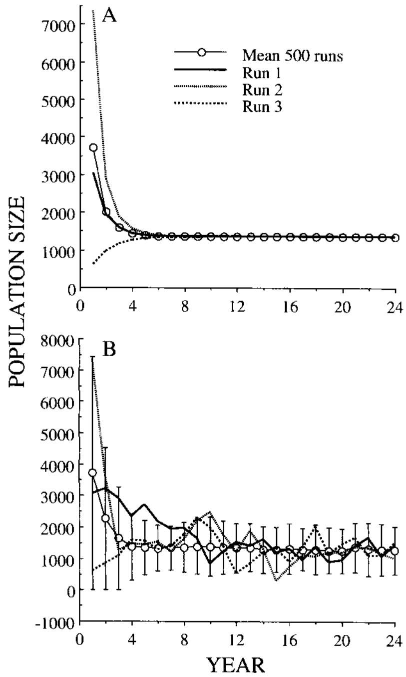


FIGURE 4. (A) Demographic model with a fixed annual mortality rate and a negative feedback between the size of the Zenaida Dove population and its rate of increase in three dairy farms in Cidra, Puerto Rico. (B) Demographic model with annual mortality rate defined as a normal random variable and a negative feedback between the size of the Zenaida Dove population and its rate of increase. Means and 95% confidence intervals (vertical lines marking lower and upper population size thresholds) were computed from 500 25-year model runs. The first three single-model runs are presented to depict the direction and magnitude of numerical changes over time.

causing short-term density dependence in demographic parameters (Rivera-Milán 1999).

We built a demographic model for Zenaida Doves based on bootstrap analyses of their capture-recapture data. To simulate density dependence, we incorporated a negative feedback between the size of the population and its rate of increase. We defined annual mortality rate as fixed over time to determine how fast and at what size the population would reach stability (births + immigrants = deaths + emigrants). Despite initial conditions (that is, a uniform distribution covering the range of capture-recapture population size estimates), the simulated system reached a stable equilibrium at 1,350 individuals after 6 years (Fig. 2b and 4a).

In addition, we defined annual mortality rate as a normal random variable to examine the magnitude of numerical changes in the population under increased stochasticity. Estimates of population size and bootstrapped 95% confidence intervals from capture-recapture data were within or overlapped with predicted lower and upper population thresholds of the demographic model (Table 1, Fig. 1c and 4b). Single model runs mimicked observed numerical changes during 46 sampling periods. Thus, we believe that the structure of the demographic model captured the essential features of the population dynamics of Zenaida Doves in the dairy farms. As expected, population size varied widely over time, but periods of high recruitment rapidly offset periods of low survival.

Overall, our capture-recapture data and demographic model provide a baseline for understanding the population dynamics of Zenaida Doves in the dairy farms. We believe that maintaining high recruitment via local reproduction and immigration is the key for keeping annual changes in abundance within predicted levels. However, modeling efforts can be improved by quantifying demographic parameters separately and introducing spatial dimensions explicitly, especially if we need to integrate basic principles of their population ecology operating at multiple scales (Nichols and Pollock 1990, Starfield and Bleloch 1991, Rodenhouse et al. 1997).

In an integrated project, we can combine the use of distance sampling and capture-recapture methods with telemetry and Geographic Information System technologies for population monitoring (Strong and Bancroft 1994, Rivera-Milán 1999). Then, the spatial dimensions of population processes can be simulated within a system dynamics framework incorporating data about habitat use and availability, demographic parameters, and the movements of Zenaida Doves in the study area and its surroundings.

The capture-recapture data and demographic model presented here support the view that Zenaida Doves can cope with increased stochasticities, and that they can be irruptive under favorable habitat and environmental conditions. In the context of conservation and management of Zenaida Doves, we believe that high recruitment rates will make them resilient to environmental disturbances and responsive to habitat manipulations aimed to maintain second-growth forests in the dairy farms and other agricultural areas in eastcentral Puerto Rico.

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