

ANNUAL SURVIVAL AND RECRUITMENT IN A RUBY-THROATED HUMMINGBIRD POPULATION, EXCLUDING THE EFFECT OF TRANSIENT INDIVIDUALS

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Abstract. We estimated annual apparent survival, recruitment, and rate of population growth of breeding Ruby-throated Hummingbirds (*Archilochus colubris*), while controlling for transients, by using 18 years of capture-mark-recapture data collected during 1984–2001 at Hilton Pond Center for Piedmont Natural History near York, South Carolina. Resident males had lower apparent survival (0.30 ± 0.05 SE) than females (0.43 ± 0.04). Estimates of apparent survival did not differ by age. Point estimates suggested that newly banded males were less likely than females to be residents, but standard errors of these estimates overlapped (males: 0.60 ± 0.14 SE; females: 0.67 ± 0.09). Estimated female recruitment was 0.60 ± 0.06 SE, meaning that 60% of adult females present in any given year had entered the population during the previous year. Our estimate for rate of change indicated the population of female hummingbirds was stable during the study period (1.04 ± 0.04 SE). We suggest an annual goal of ≥ 64 adult females and ≥ 64 immature females released per banding area to enable rigorous future tests for effects of covariates on population dynamics. Development of a broader cooperating network of hummingbird banders in eastern North America could allow tests for regional or meta-population dynamics in this species.

Key words: *Archilochus colubris*, mark-recapture, population growth, recruitment, Ruby-throated Hummingbird, survival, transients.

Sobrevivencia Anual y Reclutamiento en una Población del Picaflor *Archilochus colubris* Excluyendo el Efecto de Individuos Ocasionales

Resumen. Estimamos la sobrevivencia anual aparente, reclutamiento y tasa de crecimiento en una población reproductiva del picaflor *Archilochus colubris*, controlando por la presencia de individuos ocasionales. Utilizamos datos de 18 años de captura-marcaje-recaptura colectados entre 1984 y 2001 en Hilton Pond Center for Piedmont Natural History en cercanías de York, Carolina del Sur. Los machos residentes presentaron una sobrevivencia aparente menor (0.30 ± 0.05 EE) que las hembras (0.43 ± 0.04). Las estimaciones de la sobrevivencia aparente no difirieron entre edades. Estimaciones puntuales sugirieron que los machos marcados por primera vez tuvieron una menor probabilidad de ser residentes que las hembras, pero los errores estándar de estas estimaciones se sobrepusieron (machos: 0.60 ± 0.14 EE; hembras: 0.67 ± 0.09 EE). Para las hembras el reclutamiento estimado fue 0.60 ± 0.06 EE, lo que significa que el 60% de las hembras adultas presentes en un año determinado entraron a la población durante el año anterior. Nuestra estimación de la tasa de cambio indicó que la población de picafloros hembra fue estable durante el período de estudio (1.04 ± 0.02 EE). Para permitir futuras pruebas rigurosas sobre las covariables asociadas a las dinámicas poblacionales, sugerimos una meta anual de ≥ 64 hembras adultas y ≥ 64 hembras inmaduras liberadas por área de anillado. La creación de una amplia red cooperativa de anilladores de picafloros en el este de Norteamérica podría permitir estudiar y entender mejor las dinámicas regionales o metapoblacionales de esta especie.

INTRODUCTION

Understanding population dynamics of a species requires estimates of survival, reproduction, and dispersal. Capture-mark-recapture data have

been used in Jolly-Seber models (Jolly 1965, Seber 1965) to estimate annual apparent survival of many species (Seber 1982, Pollock et al. 1990). The term “annual apparent survival” is used because traditional Jolly-Seber models cannot distinguish between death and permanent emigration. Survival estimates from these models can be biased low if the banded sample includes animals from a resident population as

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well as transients. This bias can occur because transients typically disappear soon after being banded, and Jolly-Seber models assume these animals have died. Residents remain on the study area, albeit not necessarily year round, and have a recapture probability >0 . Recent advances in biometrics have enabled estimation of the proportion of the banded sample composed of transients (Loery et al. 1997, Pradel et al. 1997). Other recent advances in analysis of capture-mark-recapture data have enabled estimation of recruitment and rates of population change (Pradel 1996).

We combined these recently developed data-analytic techniques to estimate annual apparent survival, recruitment, and population growth of a population of Ruby-throated Hummingbirds (*Archilochus colubris*) breeding in north-central South Carolina. The population dynamics of hummingbirds as a group are poorly known. This likely is because hummingbirds, especially Ruby-throated Hummingbirds, are relatively solitary during most of the year, so that birds usually must be captured one individual at a time using labor-intensive methods. Our estimates of annual apparent survival are the first for Ruby-throated Hummingbirds using recently developed methods, and our estimates of recruitment are the first, to our knowledge, for any hummingbird species.

METHODS

STUDY AREA

As part of "Operation RubyThroat: The Hummingbird Project" (Hilton 2002), Ruby-throated Hummingbirds have been banded since 1984 at Hilton Pond Center for Piedmont Natural History near York, South Carolina (34°58'N, 81°13'W). The 5.5-ha study site, located in the heart of the Piedmont physiographic province, was in agricultural use (row crops and cattle grazing) for at least 65 years, and perhaps a century or more. Since 1982, natural vegetational succession has resulted in a mix of young pines and hardwoods. Small meadows are maintained by cutting and burning. A 0.5-ha pond is edged in hazel alders (*Alnus serrulata*), small hardwood trees, and herbaceous emergent plants. Stands of native trumpet creeper (*Campsis radicans*) and other native nectar-bearing plants are maintained to attract hummingbirds. Nature trails meander throughout the property and dou-

ble as lanes for mist nets. Between 30 June 1982 and 31 December 2001, 2483 Ruby-throated Hummingbirds were banded onsite.

CAPTURE-RECAPTURE TECHNIQUE

We banded hummingbirds from late March through mid-October, except in year one (1984), when banding began in late July. No attempt was made to standardize netting or trapping times or effort from year to year. Most hummingbirds (81%) were captured by placing a feeder containing sugar water (1:4 mix) inside a wire box trap with a manually activated trap door. The lead author watched the trap from a distance, and closed the trap door by pulling on an attached monofilament. Some hummingbirds (19%) were captured in mist nets (30-, 36-, or 38-mm mesh) deployed for general bird capture. Plumage and bill characteristics were used to determine the sex and age of each hummingbird (Baltosser 1987, Pyle 1997). Birds were aged as either hatch year or after hatch year. During each field season, every hummingbird was marked at initial capture with a "necklace" of nontoxic green dye on its upper breast or throat. This color mark, authorized by the federal bird banding laboratory (Laurel, Maryland), helped avoid re-trapping a banded hummingbird within a given year, thereby minimizing handling stress, as some birds entered the same trap dozens of times each day. Color-marked hummingbirds could be seen, but not identified individually, from a distance. Dye tended to wear off after 2 or 3 months, so birds with faded marks were recaptured and dye was reapplied. Since this color-marking scheme was unique to Hilton Pond, it also allowed for resightings of birds during migration away from the banding site.

STATISTICAL ANALYSES

Based on repeated captures of individual birds in the same or different years, we estimated that resident males were present on the study area in early April and resident females arrived in mid- to late April. Earliest date of capture for hatch-year birds was 9 June, indicating that breeding activity began by late April (Terres 1980). Some resident adult females were present throughout August. Some resident adult males remained on the study area at least until mid-August, and possibly throughout that month. Resident hatch-year birds of both sexes occasionally remained in the study area until mid-September, and pos-

sibly later. We restricted our analyses to 15 April–15 August 1984–2001.

Capture histories were formatted using SAS (SAS Institute 1997), and all banding analyses were performed using programs SURVIV (White 1983, 1992) and MARK (White and Burnham 1999, White 2002). All birds recaptured in a year other than the banding year were considered residents. All banded birds that were never recaptured after the banding year were considered potential transients (Pradel et al. 1997).

Program TMSURVIV can be used to estimate annual apparent survival (φ) controlling for transients (Pradel et al. 1996). However, that program does not allow estimation of annual survival for young birds (φ_Y) separately from adults (φ_A), primarily because transient probability for young birds ($1 - \psi_Y$) and φ_Y are confounded. Therefore, we used Brownie and Robson's (1983) Model 2 in MARK to estimate annual survival of adults the first year after banding (φ_{A1}) separately from other years (φ_{A2}), as well as to estimate annual survival of hatch-year birds (φ_Y). Note that the Brownie and Robson (1983) Model 2 and the transient model in TMSURVIV are really the same model, related in any given breeding season by the following equality (Pradel et al. 1997): $(1 - \psi) = [1 - (\varphi_{A1}/\varphi_{A2})]$, where $(1 - \psi) =$ transient probability in TMSURVIV. For example, if $\hat{\varphi}_{A1} = 0.25$ for adults banded in breeding season i and $\hat{\varphi}_{A2} = 0.40$ for recaptured adults in breeding season i , then estimated transient probability $(1 - \psi)$ for adults banded in breeding season i is $(1 - 0.62) = 0.38$. Note that ψ is resident probability, the probability that a newly banded adult is a resident.

We first constructed a most-general model in MARK that allowed survival to vary by sex (s) and year (t) for newly banded and previously banded adults (φ_{A1st} , φ_{A2st}), as well as for hatch-year birds (φ_{Yst}). Capture probability was also allowed to vary by sex and year (p_{st}). Fit of this model was evaluated with 500 bootstrap simulations in MARK and with χ^2 tests in a version of program RELEASE contained within MARK (Burnham et al. 1987, Anderson et al. 1994, Burnham and Anderson 1998, White 2002). A set of 22 competing models was constructed based on this most-general model to estimate φ_{A1st} , φ_{A2st} , φ_{Yst} , and p_{st} . In some models these parameters were constrained to be constant by

year, age, or sex, or by some combination thereof. Note that we did not test for true age effects (Nichols et al. 1997), but rather tested for differences in parameters between adults and immatures, and in some models allowed parameters to vary over time. In 10 models we constrained $\varphi_{A1st} = \varphi_{A2st}$, meaning all birds were considered residents ($\psi_{st} = 1$). In 12 models we allowed $\varphi_{A1st} \neq \varphi_{A2st}$, effectively allowing a transient term ($\psi_{st} \leq 1$). All young birds were considered residents in those models that estimated φ_Y separately from adult survival. When immature survival was constrained equal to adult survival, then one annual transient probability for all females and one for all males could be estimated using φ_{1st} and φ_{2st} . We estimated SE of ψ using the Delta Method (Seber 1982).

The best model of annual survival was identified using Akaike's Information Criterion adjusted for small sample size (AIC_c, Burnham and Anderson 1998) or for small sample size and overdispersion (QAIC_c, Anderson et al. 1994). The model with the lowest AIC_c or QAIC_c was considered best. The AIC_c is estimated using the number of identifiable parameters in a model, which we checked for accuracy, because program MARK occasionally miscounts these parameters. Akaike weights, w_i , were constructed to evaluate the strength of support for each model (Burnham and Anderson 1998, Anderson et al. 2001). In addition, Akaike weights were summed for several covariates to evaluate strength of support for variables that may not have been present in the lowest-AIC_c model (Burnham and Anderson 1998).

The earliest banding or recapture date for a Ruby-throated Hummingbird at Hilton Pond was 27 March, and the latest was 18 October. Thus, restricting our study period to 15 April–15 August required eliminating some potential residents. Birds color marked in late March or early April might have entered the pull-string trap in May, June, or July and been allowed to leave without being captured if their color mark was still visible: these birds would not have been identified individually and recorded as present during the breeding season. Conversely, these birds might have been identified individually and recorded if captured in a mist net at any time, or if recaptured in a pull-string trap after their dye had faded or disappeared. Nevertheless, 26 adult males and five adult females were banded before 15 April and not recorded later

that same year. None of these birds were recaptured in subsequent years. An additional four adult males were banded after 14 April, and recaptured before 15 April in a following year but not recorded later that breeding season. If these 35 birds were residents and were intentionally ignored upon entering the pull-string trap after 14 April, elimination of their pre-15 April capture records might have added heterogeneity to capture probabilities. We do not recommend increasing the annual sample period to capture such birds, at least not for studies of breeding population dynamics. Survival estimation is robust to heterogeneity in capture probabilities (Pollock et al. 1990). Furthermore, in the Discussion section of this paper we propose a possible solution to the dilemma of intentionally ignored residents that does not involve increasing the annual sample period.

After estimating annual survival, we estimated seniority probability (ζ) and rate of population change (λ). Seniority probability is the probability that a bird captured in year t was present in the study area in year $t - 1$. Note that $\zeta = (\varphi/\lambda)$, and $1 - \zeta$ is analogous to recruitment from immigration and *in situ* reproduction combined. Seniority probability and λ were estimated by analyzing reversed capture histories (Pradel 1996) of all birds banded as adult females during 15 April–31 August. Hatch-year birds cannot be included in recruitment estimation using live recapture data unless those data are collected following Pollock's Robust Design (Nichols et al. 2000). We deemed data for males banded as adults too sparse for recruitment estimation. Female survival and ζ were estimated simultaneously in MARK using a set of four competing models. The most-general model allowed ζ and p to vary over time. Fit of this model was evaluated with 375 bootstrap simulations in SURVIV. In other models, we constrained ζ , p , or both to be constant over time. As above, the best model was selected using AIC_c or QAIC_c. We then estimated ζ in the absence of possible transients by eliminating the first capture occasion of all adult females banded during 15 April–15 August before reversing their capture histories.

All hummingbirds in this study were captured in the same study area (Hilton Pond). To develop possible guidelines for future studies, we estimated the coefficient of variation (CV) of hypothetical survival rates, $CV = SE(\varphi)/\varphi$, and the

difference between those survival rates, $\hat{\theta}$, in one treatment and one control area over a 5-year period for a range of population sizes (N) and capture probabilities (Burnham et al. 1987, Pollock et al. 1990). Difference in survival, or effect size, was estimated as $\hat{\theta} = (\hat{\varphi}_{\text{control}}/\hat{\varphi}_{\text{treatment}})$. Variance of effect size was estimated as (Mood et al. 1974):

$$\widehat{\text{var}}(\hat{\theta}) = \hat{\theta}^2 \left[\frac{\widehat{\text{var}}(\hat{\varphi}_{\text{control}})}{(\hat{\varphi}_{\text{control}})^2} + \frac{\widehat{\text{var}}(\hat{\varphi}_{\text{treatment}})}{(\hat{\varphi}_{\text{treatment}})^2} + \frac{\widehat{\text{cov}}(\hat{\varphi}_{\text{control}}, \hat{\varphi}_{\text{treatment}})}{(\hat{\varphi}_{\text{control}} \cdot \hat{\varphi}_{\text{treatment}})} \right].$$

The 95% confidence interval on $\hat{\theta}$ was estimated as $\hat{\theta} \pm 1.96 \sqrt{\widehat{\text{var}}(\hat{\theta})}$. The CV of survival in the third year was obtained using program CAPQUOTA (Hines 1981, Pollock et al. 1990, Hines 1996). The CV of effect size was estimated using survival rates from the third year assuming N and p were equal in the treatment and control area. All results are reported as means \pm SE, except when stated otherwise.

RESULTS

We used a total of 1327 individually marked Ruby-throated Hummingbirds released during 15 April–15 August 1984–2000 at Hilton Pond Center for Piedmont Natural History. Of these, 17% were recaptured at least once during 1985–2001. Each year during 1984–2000, a mean of 73.6 ± 30.1 (SD) new hummingbirds was captured, and a mean of 91.4 ± 35.6 (SD) new or returning hummingbirds was released. At initial release, 32% of all hummingbirds were adult females, 20% were hatch-year females, 21% were adult males, and 27% were hatch-year males.

MODEL FIT

Evidence of overdispersion was detected with our most-general model of apparent survival with four age-sex classes and a transient term ($P = 0.11$; observed deviance = 165.85; \hat{c} = observed \hat{c} /mean simulated \hat{c} = 1.19, as deviance df = 0). Therefore QAIC_c was used for model selection. Output from program RELEASE indicated that tests 2, 3.SR, and 3.Sm were not significant for any age-sex class ($P \geq 0.18$), indicating little heterogeneity in survival and capture probabilities (Burnham et al. 1987). However, RELEASE also indicated insufficient data were available for 118 of 124 subtests within tests 3.SR and 3.Sm. All six subtests for which

TABLE 1. Set of competing models of annual apparent survival (φ), and capture probability (p) for all Ruby-throated Hummingbirds captured during 15 April–15 August 1984–2001 at Hilton Pond, South Carolina. In some models φ or p were allowed to vary by sex (s), age (A = after hatch-year, Y = hatch-year), or year (t). Some models included a transient effect by allowing survival the first year after banding (φ_1) to differ from survival in subsequent years (φ_2). Model selection was based on QAIC_c, which balances model fit against precision, adjusted for small sample size and overdispersion (Burnham and Anderson 1998). The model with the lowest QAIC_c is considered best. The difference between QAIC_c of the best model and a subsequent model (Δ QAIC_c) is used to calculate the degree of relative support for a given model, its QAIC_c weight. These weights sum to 1.0. The QDeviance is the difference between $-2\log(\text{likelihood})$ of a given model and $-2\log(\text{likelihood})$ of the saturated model (White 2002).

Model	QAIC _c	Δ QAIC _c	QAIC _c weights	No. of parameters	QDeviance
$\varphi_1 s \varphi_2 s p_t$	1468.98	0.00	0.53	21	289.52
$\varphi_s \varphi_2 s p_{st}$	1470.59	1.62	0.23	38	255.76
$\varphi_{A1} s \varphi_{A2} s \varphi_Y s p_t$	1471.88	2.90	0.12	23	288.30
$\varphi_{A1} s \varphi_{A2} s \varphi_Y s p_{st}$	1473.82	4.84	0.05	40	254.77
$\varphi_s p_t$	1474.45	5.48	0.03	19	299.11
$\varphi_A s \varphi_Y s p_t$	1475.98	7.01	0.02	21	296.53
$\varphi_A s \varphi_Y s p_{st}$	1476.83	7.85	0.01	38	262.00
$\varphi_s p_{st}$	1477.60	8.62	0.01	34	271.16
$\varphi_1 \varphi_2 p$	1482.11	13.14	0.00	3	339.26
$\varphi_1 \varphi_2 p_t$	1483.12	14.15	0.00	19	307.78
φp	1492.97	23.99	0.00	2	352.12
φp_t	1494.46	25.48	0.00	18	321.16
$\varphi_1 st \varphi_2 s p_{st}$	1495.60	26.62	0.00	70	211.93
$\varphi_{st} p_{st}$	1502.06	33.09	0.00	66	227.16
$\varphi_t p_t$	1503.96	34.98	0.00	33	299.62
$\varphi_{A1} st \varphi_{A2} s \varphi_Y s p_{st}$	1504.43	35.45	0.00	72	216.36
$\varphi_{1t} \varphi_{2t} p_t$	1509.38	40.40	0.00	49	271.22
$\varphi_{A st} \varphi_Y st p_t$	1517.03	48.05	0.00	84	202.28
$\varphi_1 st \varphi_2 st p_{st}$	1520.43	51.45	0.00	96	178.56
$\varphi_A st \varphi_Y st p_{st}$	1533.06	64.09	0.00	100	182.05
$\varphi_{A1} st \varphi_{A2} st \varphi_Y st p_t$	1542.66	73.69	0.00	116	154.56
$\varphi_{A1} st \varphi_{A2} st \varphi_Y st p_{st}$	1560.93	91.95	0.00	130	139.68

sufficient data were available pertained to test 3.SR for females. Test 3.SR is the most applicable one in RELEASE for detecting transients, and $P < 0.05$ for 2 of those 6 subtests. In addition, $P = 0.18$ for test 3.SR for adult females. As such, we felt it prudent to include a transient term in our most-general model.

SURVIVAL AND TRANSIENT MODEL

Our lowest QAIC_c model of apparent survival fit the data well ($P = 0.82$). Annual apparent survival differed by sex, but not by age or year (Table 1). Resident males had lower survival than females ($\hat{\varphi}_{A2\text{male}} = 0.30 \pm 0.05$; $\hat{\varphi}_{A2\text{female}} = 0.43 \pm 0.04$). First-year survival of newly banded hummingbirds differed from survival of marked, or resident, birds recaptured that same year ($\hat{\varphi}_{1\text{male}} = 0.18 \pm 0.02$; $\hat{\varphi}_{A1\text{female}} = 0.29 \pm 0.03$). Point estimates of ψ suggested females were more likely than males to be residents ($\psi_{\text{female}} = 0.67 \pm 0.09$; $\psi_{\text{male}} = 0.60 \pm 0.14$) al-

though standard errors of these estimates overlapped. Capture probability differed among years, but not by sex. Mean annual capture probability, estimated from annual point estimates and their standard errors (program CONTRAST, Sauer and Williams 1989), was $\hat{p} = 0.64 \pm 0.04$.

Akaike weights (Table 1) supported inclusion of a transient term in our best overall model, as did the sum of Akaike weights of all models including a transient term (0.93). Sum of Akaike weights provided strong support for a difference between male and female survival (1.00), but only weak support for a difference between adult and immature survival (0.20), and no support for temporal variation in survival (0.00).

SENIORITY AND λ MODEL

The most-general model of adult female survival and seniority, with $\psi = 1$, fit the data ($P = 0.24$), so we used AIC_c for recruitment model selection. In the lowest-AIC_c model seniority proba-

TABLE 2. Set of competing models of annual apparent survival (φ), capture probability (p), and seniority (ζ) for adult female Ruby-throated Hummingbirds captured during 15 April–15 August 1984–2001 at Hilton Pond, South Carolina. In some models φ , p , or ζ were allowed to vary among years (t). Model selection was based on AIC_c , which balances model fit against precision, adjusted for small sample size (Burnham and Anderson 1998). The model with the lowest AIC_c is considered best. The difference between AIC_c of the best model and a subsequent model, ΔAIC_c , is used to calculate the degree of relative support for a given model, its AIC_c weight. These weights sum to 1.0.

Model	AIC_c	ΔAIC_c	AIC_c weight	No. of parameters
$\varphi p_t \zeta$	3018.10	0.00	1.00	20
$\varphi p_t \zeta_t$	3034.20	16.10	0.00	35
$\varphi_t p_t \zeta$	3043.26	25.16	0.00	34
$\varphi_t p_t \zeta_t$	3054.24	36.14	0.00	50

bility was constant over time ($\hat{\zeta}_{female} = 0.36 \pm 0.03$, Table 2). Estimated rate of population change was $\hat{\lambda}_{female} = 1.02 \pm 0.02$. The 95% confidence interval (0.98 to 1.06) on this estimate overlapped 1.0, indicating a stable population of female Ruby-throated Hummingbirds in the study area.

After deleting the first capture record of each adult female to eliminate possible transients, seniority probability increased slightly ($\hat{\zeta}_{female} = 0.40 \pm 0.06$). Our point estimate of rate of population change also increased slightly, $\hat{\lambda}_{female} = 1.04 \pm 0.04$, but with a 95% confidence interval ranging from 0.95 to 1.13, indicating a stable female population.

EFFECT SIZE

Based on our parameter estimates above we used $\varphi_{control} = 0.40$ and $\varphi_{treatment} = 0.30$ when estimating CV of survival rates and effect size, $\hat{\theta}$. Results suggested a $CV \leq 0.20$ for $\varphi_{control}$ could be obtained when $p \geq 0.43$ if the control population, N , was 500 birds; when $p \geq 0.60$ if $N = 200$; and when $p \geq 0.74$ if $N = 100$ (Pollock et al. 1990). Similarly, a $CV \leq 0.20$ for $\varphi_{treatment}$ could be obtained when $p \geq 0.53$ if $N = 500$; when $p \geq 0.72$ if $N = 200$; and when $p \geq 0.86$ if $N = 100$.

A $CV \leq 0.20$ for $\hat{\theta}$ occurred when $p \geq 0.62$ in both areas if $N = 500$ in both areas; when $p \geq 0.82$ if $N = 200$; and when $p \geq 0.98$ if $N = 100$ (Fig. 1). A $CV = 0.20$ for $\hat{\theta}$ would be pos-

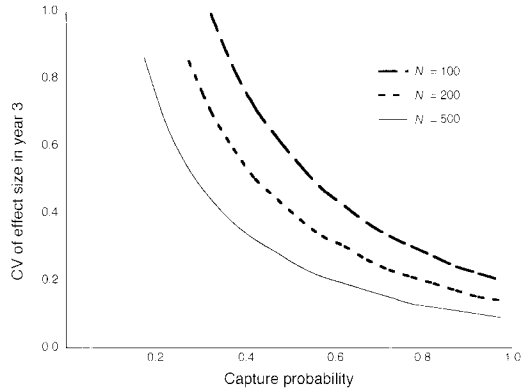


FIGURE 1. If annual apparent survival in a control area is 0.40 and annual apparent survival in a treatment area is 0.30, the difference in survival between those areas (the effect size) $\hat{\theta} = \hat{\varphi}_{control}/\hat{\varphi}_{treatment}$ is 1.33. Given equal population size, N , and equal capture probability in both areas, the coefficient of variation of effect size in the third year of a hypothetical 5-year study decreases as population size or capture probability increase. This figure may be helpful in designing future studies of Ruby-throated Hummingbirds. Similar figures using other estimates of annual survival can be created for any species using techniques described in Pollock et al. (1990).

sible given $p = 0.62$ in both areas if 310 females were captured annually ($N = 500$) from both populations. These sample sizes might be impossible for any one bander to reach. A $CV = 0.30$ for $\hat{\theta}$ would be possible given $p = 0.64$ in both areas if $N = 200$, corresponding to an annual release of 128 females in each area.

DISCUSSION

Our analysis suggests that the study population of breeding Ruby-throated Hummingbirds at Hilton Pond in north-central South Carolina is stable. Results from the Breeding Bird Survey also indicated a stable population in Ruby-throated Hummingbirds during 1980–2000 in South Carolina (trend = 1.1, $P = 0.66$; Sauer et al. 1997).

Mulvihill et al. (1992) reported 0.29 and 0.45 apparent annual survival for male and female Ruby-throated Hummingbirds respectively, although that difference between sexes was not statistically significant. Our point estimates of apparent annual survival were similar to those of Mulvihill et al. (1992). Although Mulvihill et al. (1992) did not have access to transient models, they restricted their analysis to humming-

birds captured in at least two different years, birds we define as known residents.

Female Ruby-throated Hummingbirds are larger than males. Mulvihill et al. (1992) suggested that reverse sexual dimorphism and relatively low male survival may be related in this species, noting that male Ruby-throated Hummingbirds attempt to mate with several females each breeding season and do not provide parental care (Trivers 1972, Payne 1984). Our results provide stronger evidence of sex-related differences in annual survival of this species.

The difference in annual apparent survival we detected may actually reflect a greater probability of permanent emigration by resident males, rather than lower annual male survival. Resident females may be more philopatric to breeding areas. We know of no studies of philopatry in Ruby-throated Hummingbirds. However, males defend territories (Mulvihill et al. 1992). If resident males that lose territorial disputes permanently vacate the study area, then male survival estimates could be biased low.

Our use of a 4-month annual sample period could introduce heterogeneity in annual survival. Such heterogeneity could arise because a bird captured 15 August would only have to survive eight months to enter the following sample period, while a bird captured 15 April would have to survive a minimum of 12 months, and up to 16 months to be captured in the following sample period. Heterogeneity violates assumptions of capture-recapture models and can bias parameter estimates (Nichols et al. 1982, Seber 1982). Furthermore, given the low estimated annual survival, particularly for males, a substantial proportion of birds banded early in a given year might have died before that sample period ended, unless most mortality occurs away from the breeding grounds. We know of no studies of seasonal hummingbird survival. Smith and Anderson (1987) studied bias in survival rates from band-recovery models resulting from long sample periods and low annual survival. They found that little bias occurred unless annual survival was low, which it was in our study, and the temporal distribution of captures within the sample period was extremely variable among years, which generally was not the case in this study. Nevertheless, potential bias in parameter estimates from capture-recapture studies resulting from long sample periods, combined with low annual survival, needs further study. Until then

we suggest that future studies of hummingbird population dynamics consider concentrating capture effort within a three-month period or less, perhaps 1 May–1 August in our study area.

The ability of capture-recapture techniques to detect temporal variation in parameters and effects of covariates on parameters increases as either sample size or capture probability increases. Our annual sample size of released birds was relatively small. However, our survival estimates had relatively small standard errors because of the long-term nature of the data set, and the relatively high probability of capture in any given year. Nevertheless, a larger banded sample might have enabled us to detect temporal variation in survival or recruitment. A large annual release of females in each of several areas might allow for tests for spatial and temporal effects of environmental factors on population parameters in the future. Our calculations suggest that a possible goal is to release ≥ 128 females annually in each study area.

Capturing ≥ 128 females each year at a specific study site would be very labor intensive, and may not always be possible. The CV of survival and effect size decreases as the length of a study increases, so a smaller annual sample size would be needed with a study longer than five years (Hines 1981). Another possible way to achieve high annual sample size would be to develop a spatial network of hummingbird banding sites, each operated independently. Banding sites could be characterized by habitat type and other environmental factors. Data from all sites could then be analyzed simultaneously to test for effects of environmental covariates on population dynamics. Sites with similar factors of interest would be considered replicates. Indeed, the Monitoring Avian Productivity and Survivorship (MAPS) Program attempts to do that with many landbird species (DeSante 1992, DeSante et al. 1995). Even with multiple sites large annual sample sizes at each site are still desirable.

Ideally, hummingbird banding efforts would be conducted so as to minimize possibility of catching migrants, as is done in the MAPS program (DeSante 1992). Trapping of migrants is valuable for studies of migration behavior, but not necessarily for studies of breeding population dynamics.

Our analysis excluded a small number of marked, but unrecorded, potential residents. We

doubt these few birds, which were never recaptured, substantially biased our survival estimates for resident birds, particularly for females. Ideally, however, all hummingbirds that enter a trap should be recaptured, identified individually, and recorded. This would enable later parsing of the data into any desired annual banding interval and would help eliminate transients and minimize heterogeneity in capture and survival probabilities resulting from excessively long banding periods (Smith and Anderson 1987, Lebreton et al. 1992). On the other hand, repeatedly capturing the same individual might expose a bird to high levels of handling stress. One possible solution would be to mark birds one way when mostly migrants are thought to be present and a second way, perhaps with a different color, when mostly breeders are thought to be present. In that manner, perhaps only breeders that arrive early or remain late in the breeding season would be subjected to several captures in the same year. Such a solution may not be easy to implement, however, as hummingbirds can be difficult to capture, band, and color mark because of their small size. Nevertheless, if a collaborating network of Ruby-throated Hummingbird banders were developed, perhaps drawing upon some of the techniques described here, it might eventually allow for fascinating tests of regional population dynamics in this species (Pulliam 1988, Gilpin and Hanski 1991), particularly using multistate models to address questions of dispersal, survival, and recruitment (Hestbeck et al. 1991, Nichols and Kendall 1995).

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