SURVIVAL RATES OF A NEOTROPICAL PARROT: IMPLICATIONS FOR LATITUDINAL COMPARISONS OF AVIAN DEMOGRAPHY

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Abstract. Latitudinal variation in avian demography played an important early role in the development of life history theory, especially in the idea of a cost of reproduction. Recent attempts to determine the survivorship of tropical birds with mark–recapture statistics have proved controversial. Here, we use a small neotropical bird, the Green-rumped Parrotlet (*Forpus passerinus*), as a model system for investigating sources of heterogeneity that might bias interspecific comparisons. Mark–resighting data were collected on 1334 adult parrotlets over a decade. We expected adult survival to be low because this parrot lays a large clutch (mean = 7 eggs), is a cavity nester, and breeds in a highly seasonal environment. A two-age-class term in local survival was nonsignificant, indicating that an age or transience effect was unimportant. Local survival of males did not vary annually, but 19.3% of the yearly variation in female survival was explained by rates of nest loss during stages when females were incubating or brooding young. The overall local survival rate of parrotlets (ϕ = 0.565) was identical to temperate hole-nesting species of the same body size but was lower than that of tropical birds that lay smaller clutches. However, we also detected considerable heterogeneity in parrotlet survival. Females and males that were sighted but did not breed comprised a mean 23.5% and 52.9% of our population, respectively. Using multistate models, we found that breeders had significantly higher probabilities of local survival (ϕ = 0.678 vs. 0.486), of retaining their status as breeders (ψ = 0.719 vs. 0.279), and of detection (p = 0.997 vs. 0.375) than did nonbreeders. Overall, males and females had comparable local survival rates (breeders ϕ = 0.698 vs. 0.658, nonbreeders ϕ = 0.536 vs. 0.436). Our estimates of local survival could be affected by breeding dispersal, but site fidelity of parrotlets was strong: 95% of adults moved <500 m in consecutive years. A literature review for tropical birds showed that mark–resighting studies usually report return rates based on resightings of breeding or territorial adults, whereas mist net studies rely on recaptures and pool birds of different age and social status in their calculations of local survival. Future studies should attempt to compare subsets of avian populations that are similar in demography. Because rates of site fidelity and social system may differ among species, these factors must also be considered in interspecific comparisons of avian life histories.

Key words: avian demography; Forpus passerinus; Green-rumped Parrotlet; mark–recapture; multistate models; nonbreeder; site fidelity; social systems; survival; tropical vs. temperate.

INTRODUCTION

A central issue in evolutionary ecology is understanding why species differ in their life history traits. One basic concept of life history theory is the cost of reproduction, which is expressed as a trade-off between fecundity and survival (Stearns 1992). This idea was developed, in part, by consideration of demographic differences between birds breeding in tropical and

northern temperate areas. Early workers noted that the clutch size of tropical birds was smaller than that of their temperate counterparts, and that survival rates were apparently high (reviewed by Murray 1985, Skutch 1985, Martin 1996). These life history differences were thought to be adaptations to tropical environments typically characterized by a less seasonal climate, a more stable food supply, a longer breeding season, and higher nest predation rates. The small clutch size of tropical birds has been well established for several regions (Skutch 1985, Yom-Tov 1987, Brosset 1990), but systematically higher survival rates are presently disputed (Karr et al. 1990, Johnston et al. 1997). Murray (1985) argued that adult survivorship should be high in tropical birds precisely because fe-

cundity rates are low. Nevertheless, empirical estimates of survival are required because clutch size could covary with other life history traits, including age of first breeding, number of breeding attempts, or juvenile survival.

Interspecific comparisons of survival are often compromised by biases inherent to the techniques used to estimate survival. For example, age ratios assume that population size is stable (Ricklefs 1997), maximum longevity is sensitive to sample size and outliers (Krementz et al. 1989), and life tables assume that survival or reporting rates do not vary among years (Anderson et al. 1985, Francis 1995). Stochastic recovery models (Brownie et al. 1985) generally have limited utility for land birds because few bands (<1%) are recovered from nonhunted species (Oatley and Underhill 1993, Francis 1995). Mark–recapture data provide a useful alternative and have been used in two general approaches. "Mark–resighting studies" capture and individually mark breeding or displaying birds, and then use intensive resighting observations to monitor populations of one or only a few species. "Mist net studies" use grids of mist nets to capture and mark birds, and then use recaptures to systematically resample multiple species at the same time and location.

One commonly used index of survival is the "return rate" or the proportion of marked birds resighted in the following year. Return rates for northern temperate birds are variable and range from 0.40 to 0.70 (reviewed by Greenberg 1980, Sæther 1989, Martin and Li 1992, Johnston et al. 1997). Despite considerable overlap, tropical birds tend to have higher return rates than temperate birds, ranging from 0.55 to 0.90 (Snow and Lill 1974, Willis 1974, Greenberg and Gradwohl 1986). Nevertheless, return rates are a problematic index of survival because they fail to control for the probability of detection (Lebreton et al. 1992, Martin et al. 1995). The Cormack-Jolly-Seber (CJS) model is an improvement because it permits calculation of local survival rates (ϕ) that are corrected for recapture or resighting rates (p; Lebreton et al. 1992). The CJS model, denoted ϕ_t, p_t, has time dependence in both probabilities and has been widely applied to tropical and temperate birds in both mark–resighting (McDonald 1993, Ralph and Fancy 1995) and systematic mist net studies (Karr et al. 1990, Faaborg and Arendt 1995).

Karr et al. (1990) used the CJS model to derive estimates of survivorship for forest birds at sites in the eastern United States and Panama. They found little difference in median local survival (0.57 vs. 0.55), which led them to challenge the conventional view that survivorship is high among tropical birds. Similar methodology yielded median local survival estimates of 0.68 and 0.65 for avian communities in Puerto Rico (Faaborg and Arendt 1995) and Trinidad (Johnston et al. 1997), respectively. Unfortunately, the CJS model may underestimate survival because it fails to account

for birds that are captured once and never seen again (Johnston et al. 1997, Brawn et al. 1999). This effect can be controlled by the use of age-structured or transient models (denoted ϕ_{2ac*t}, p_t, and τ_t, ϕ_t, p_t; Pradel et al. 1997). A significant age effect in a sample of birds banded as adults can indicate an effect of relative age, transience, or heterogeneity of capture (Johnston et al. 1997, Prévot-Julliard et al. 1998). The CJS model may also yield biased estimates because it ignores other potential sources of variation such as the survival differences between breeders and nonbreeders. Multistate models can control for this heterogeneity by including breeding status as a dynamic state variable (Nichols et al. 1994, Cam et al. 1998).

In this paper, we examine the local survival and resighting rates of a tropical parrot using mark–resighting data based on an intensive population study conducted over a decade. We recognize that single-population studies are unlikely to resolve the debate about survivorship differences between tropical and temperate birds. Indeed, the advantage of systematic mist net studies is that their standardized methodology facilitates interspecific comparisons. However, mist net studies are often characterized by small samples (median < 10 birds/yr), low recapture rates (median p < 0.3), and failure to control for breeding status, movement rates, and other sources of heterogeneity (e.g., Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997). Intensive mark–resighting studies can be subject to the same problems, but may permit closer examination of these potential sources of bias.

The life history characteristics of our study species, the Green-rumped Parrotlet (*Forpus passerinus*), make it particularly relevant to the debate about survivorship differences between tropical and temperate birds. Parrotlets are unusual, compared with most tropical species, because they lay large clutches (mean = 7 eggs), are nonexcavating cavity nesters, and live in a highly seasonal environment where they are exposed to a large array of predators that threaten nests and adults (Beissinger and Waltman 1991, Waltman and Beissinger 1992, Beissinger and Gibbs 1993). Life history theory predicts that survival should be low under all three conditions (Martin and Li 1992, Stearns 1992, Martin 1996). Thus, parrotlets could be an exception that proves the rule, if estimates of their survivorship are comparable to those of temperate zone species, but are low within the range of survival expected for tropical birds.

Our objectives were to determine the local survival rates of adult parrotlets and to examine whether local survival was affected by transience, breeding status, or emigration. These sources of heterogeneity affect many small land birds. We use the Green-rumped Parrotlet as a model system for understanding how such sources of bias could affect interspecific comparisons of avian survivorship.
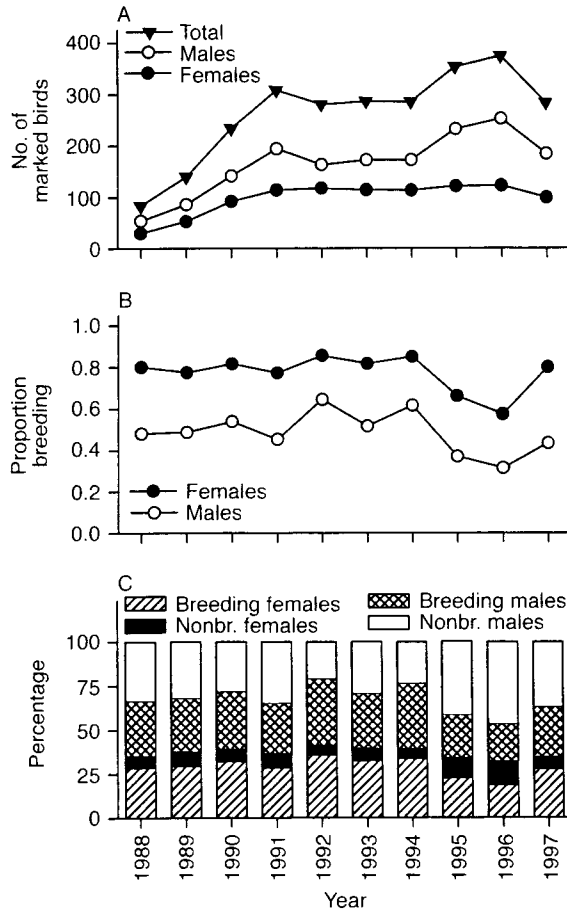
FIG. 1. (A) Number of adult Green-rumped Parrotlets marked or resighted in the study area in Venezuela each year. (B) proportion of the marked adults known to have bred, and (C) relative percentages of breeders and nonbreeders of either sex. The number of birds sighted is not corrected for the probability of resighting.

METHODS

Study site and species

The study was conducted at Hato Masaguaral, a cattle ranch 45 km south of Calabozo, in Guárico, Venezuela (8°34' N, 67°35' W). The habitat of the 4-km²; study area included flat, brushy savannah (or llanos) and unimproved pasture. Troth (1979) provides further descriptions of the study area. Rainfall is highly seasonal, with a dry season (January–March), two transitional months (December, April), and a wet season (May–November). Fieldwork was conducted from late May to mid-December during 1988 to 1997.

The Green-rumped Parrotlet is a small (25–34 g) parrot that lives in savannah, pasture, and forest edge habitats throughout northeastern South America (Forshaw 1973). This species feeds primarily on fruits and the seeds of herbaceous plants (Waltman and Beissinger 1992). It is monomorphic in body size, but is readily sexed by plumage differences: males have blue wing

bars and green foreheads, whereas females have green wings and yellow foreheads. Parrotlets breed during the rainy season at our field site; most used artificial nest boxes made of polyvinyl chloride tubing that were attached to fence posts (Beissinger and Bucher 1992). Forty nest boxes were installed in 1988. The number of boxes in the study area was increased to 100 in 1989 and to 106 in 1994, where it has remained constant. Parrotlets nesting in nest boxes have fecundity and rates of nest success comparable to those of parrotlets nesting in natural cavities (Beissinger and Bucher 1992, Stoleson and Beissinger 1997a, b; S. R. Beissinger, unpublished data).

Green-rumped Parrotlets are socially monogamous, and no more than two birds participate in a nesting attempt. Pairs defend nest sites but are otherwise nonterritorial. Eggs are laid from early June through late October, and mean clutch size is seven eggs (range = 4–11 eggs). Clutch hatching is highly asynchronous (Stoleson and Beissinger 1997a). Females incubate alone, beginning with the first-laid egg, and males feed females during incubation and brooding (Beissinger and Waltman 1991, Waltman and Beissinger 1992, Grenier and Beissinger 1999). Once all of the eggs have hatched, both parents provision the brood and roost outside of the nest box at night (Curlee and Beissinger 1995). Pairs raise up to two broods per year (Waltman and Beissinger 1992). Both sexes breed as yearlings, but delayed age of first breeding is common, especially for males (S. R. Beissinger, unpublished data). Nonbreeding birds are regularly observed, and they sometimes harass breeding pairs. Nest sites and mating opportunities appear to be limited, because nonbreeding parrotlets investigate unattended nests and sometimes destroy eggs or commit infanticide (Beissinger et al. 1998). During the dry season, parrotlets roost together in large groups and forage in flocks (Waltman and Beissinger 1992).

Study methods

We tried to mark all nesting and prospecting birds. In total, 1334 adult parrotlets were captured in the first nine years of the study. Because no parrotlet has been detected breeding during its natal year, adults were assumed to have survived at least one dry season. Parrotlets were captured in mist nets at roosting sites and in the vicinity of nest boxes, or were trapped in the nest box while feeding young. In 1988, a few adults (24 of 84, 28.6%) were individually marked with two plastic color rings, but no numbered metal bands. Some plastic band loss occurred, and we treated birds with partial plastic bands as being of unknown identity when recaptured. From 1989 onward, adults were marked with either two colored aluminum bands or one aluminum and one plastic band. Thus, with the exception of a few birds marked in 1988, all birds received a numbered, permanent band. Philopatric young were rebanded with colored aluminum bands if recaptured as

TABLE 1. Numbers of adult Green-rumped Parrotlets captured for the first time (F) or resighted from a previous year (R), and annual conditions at Hato Masaguaral, Venezuela.

Year	No. adult females		No. adult males		Rainfall (mm)		Nest occupancy (% of boxes used)	No. attempts per box[†]	Percentage of nests lost[‡]
	F	R	F	R	Dry season	Wet season			
1988	30		54		6	1424	72.5	1.20 ± 0.13	8.0 (50)
1989	40	12	60	24	3	986	49.1	0.71 ± 0.08	5.9 (102)
1990	47	41	96	45	27	1511	70.8	1.22 ± 0.09	4.3 (139)
1991	62	49	118	75	93	1372	79.3	1.31 ± 0.08	7.3 (151)
1992	59	56	73	89	222	1754	86.8	1.37 ± 0.07	9.2 (163)
1993	49	63	96	75	143	1597	73.6	1.10 ± 0.08	20.0 (130)
1994	52	60	84	86	11	1346	79.3	1.42 ± 0.09	10.2 (157)
1995	79	40	138	92	146	1275	69.8	1.04 ± 0.08	21.1 (128)
1996	67	54	130	121	21	1540	61.3	0.98 ± 0.09	20.4 (108)
1997		47		95	13	1268	65.1	1.00 ± 0.08	5.4 (112)

Notes: Birds newly banded in 1997 were not used in the survival analyses. Rainfall was pooled for January–April (dry) and May–December (wet).

† Number of nesting attempts per nest box (mean ± 1 SE).

‡ Percentage of nests lost indicates the percentage of clutches that were destroyed by predators during early stages of the nesting cycle (i.e., the start of laying to the end of brooding), when females are regularly in the nest box. Sample size (number of nests) is given in parentheses.

adults. This was treated as the first handling event, so that mark–recapture histories were based solely on adults. Parrotlets were resighted near nest boxes, at communal roosts, and in feeding flocks. Band combinations and sometimes band numbers were read with binoculars (10×) and spotting scopes (40–60×) at distances of 10–75 m. Field effort consisted of daily surveys over a 7-mo period, and was similar in all years. Starting in 1995, however, we made a more concerted effort to resight and identify nonbreeding birds in the study population.

Nest boxes were checked daily during the breeding season, and parrotlet clutches were found early in laying (with 1–2 eggs). We were confident in assigning individuals to breeder or nonbreeder status because the nest boxes were monitored intensively. A parrotlet was considered to be a breeder if it was associated with at least one nesting attempt during the study year, regardless of the fate of the nest. Few nesting attempts were made in natural nest cavities (Beissinger and Bucher 1992, Stoleson and Beissinger 1997b), and it is unlikely that breeders were overlooked. Nonbreeders were also identified by their behavior, as they were often observed in small groups and in male–male pairs (Beissinger et al. 1998). Occasionally, a pair that was apparently mated was observed defending a nest box but did not produce a clutch. Nonbreeders included yearlings and older birds that failed to nest (S. R. Beissinger, *unpublished data*). Parrotlet nests were considered depredated if all eggs or nestlings disappeared before any young had fledged.

Local survival rates are influenced by site fidelity. To evaluate the relative importance of permanent emigration, we measured the distances that adult parrotlets moved between years. We mapped the study area using a compass, range finder, and measuring tape; the map

was then analyzed in a digitized format. If a bird was sighted multiple times in a year, we used the first location where a bird was encountered in a given year. Dispersal of adults was estimated as the distance moved between sighting or breeding locations in consecutive years.

Broods of parrotlets were manipulated as part of several experiments during the 10 years of our study. Offspring number and hatching synchrony were manipulated in a subset of nests during 1989–1996. We ignored these treatments in our survival analyses because rigorous analyses have shown that these prior manipulations had no effect on the local survival of either nestling or adult parrotlets (Stoleson and Beissinger 1997a).

Survival analyses

Return rates have often been used as an index of survival in land birds (Martin and Li 1992, Johnston et al. 1997), but are the product of the probabilities of true survival, local site fidelity, temporary emigration, and detection. We analyzed mark–resighting data to decompose return rates into local survival (ϕ) and resighting rates (p), following the approach outlined by Lebreton et al. (1992). Local survival is an improvement over return rates, but the effects of mortality and permanent emigration are confounded because local survival is the product of true survival and local site fidelity. We used estimates of breeding dispersal distance to separate the effects of these two probabilities. Resighting rates are usually considered to be an index of detectability, but may also be biologically relevant because they are the product of temporary emigration and detection.

Local survival and resighting rates were estimated in two steps. Program RELEASE (version 2.6; Burn-

ham et al. 1987) was first used to calculate goodness-of-fit to a time-dependent model (ϕ_t, p_t). This procedure tests for overdispersion (i.e., a lack of independence) in the data structure. The component statistics of Test 3 (3.SR, 3.Sm) and Test 2 (2.Ct, 2.Cm) were used to detect heterogeneity among individuals in local survival and resighting rates, respectively. (For further details regarding these tests, see Burnham et al. 1987, Lebreton et al. 1992.) We only included transitions with sufficient data in the overall χ^2 test for goodness-of-fit, and we examined the individual contingency tables of each transition for evidence of systematic bias.

Program SURGE (version 5; Pradel et al. 1998) was then used to model local survival and resighting rates. Adult parrotlets were coded as either not sighted (0) or present (1) in the capture histories, and birds known to be dead ($n = 27$) were treated as not released on the last handling occasion. SURGE used a maximum likelihood approach to fit hierarchical models to mark-recapture histories. Fit of a given model was described by the deviance (DEV) and number of parameters (np) of the model. The most parsimonious model was the one with the lowest value for Akaike's Information Criterion (AIC = DEV + 2 × np; Burnham and Anderson 1992). Likelihood ratio tests were used to contrast nested models; the difference in deviances between two nested models was compared to a χ^2 distribution in which the difference in number of parameters was used as the degrees of freedom. If a likelihood ratio test was nonsignificant, the reduced model was accepted and tested against models with fewer parameters. Factors tested in the models included year of study (t), sex (sex), and age class (2ac). We started with saturated models that included all of these terms, and modeled resighting rate first so that we had the best fit for p before we started modeling local survival. User-defined models and external constraints were used to supplement the default model choices of SURGE.

To investigate the effect of social system on the demography of adult parrotlets, we recoded the adult capture histories to include breeding status as a state variable. In this analysis, birds were coded as not sighted (0), present as a nonbreeder (N), or present as a breeder (B). Dead birds were treated as not released. We used program MSSURVIV (version 1; Brownie et al. 1993) to analyze the capture histories, following Nichols et al. (1994), Spendelow et al. (1995), and Cam et al. (1998). Local survival is the product of survival rate (S) and the transitional probability of breeding (ψ; notation after Nichols et al. 1994). The multistate models of MSSURVIV allow calculation of estimates of S and ψ that are specific to breeders and nonbreeders. Survival rate (S) is an improvement over local survival because it controls for heterogeneity due to breeding status, but the consequences of mortality and permanent emigration are still confounded. Here, ψ for breeders and nonbreeders is the transition probability of remaining or becoming a breeder in a subsequent year,

respectively. We started with models that assumed that S and ψ at time $i + 1$ were dependent on breeding status at time i, but not at time $i - 1$ (i.e., models with Markovian transitions; Brownie et al. 1993). We did not model external covariates or additive constraints in this set of analyses because it was not possible to implement such models with this version of MSSURVIV.

Data handling and statistical analyses

All additional statistical analyses were performed using procedures from SAS (SAS Institute 1990). In our analyses of dispersal distance vs. breeding status, we found that adult parrotlets were often observed in more than one year. To avoid pseudoreplication, we selected one dispersal distance record at random for each bird; our conclusions were unchanged if we used the entire data set. Years were pooled, as we did not have adequate data to examine annual variation in dispersal. Dispersal distances of adults were tested for assumptions of normality and found to be significantly nonnormal (Shapiro-Wilks test, $P < 0.001$). Box-Cox transformations indicated that the log transformation was most appropriate for our data, and all dispersal distances were adjusted (ln [$x + 0.5$]) before analysis with standard parametric statistics (Proc GLM).

The resighting rate of breeders was close to unity (see *Results*), and we used logistic regression (Proc LOGISTIC) to analyze local survival rates in relation to aspects of reproductive performance. The number of eggs laid per year had a bimodal distribution ranging from 1 to 30 eggs. Birds laying ≥12 eggs had laid either one exceptionally large clutch or two smaller clutches. Although egg production is a female reproductive trait, we reasoned that egg number could affect male survival because males feed their mates during laying, and clutch size is related to provisioning rates (Waltman and Beissinger 1992). Annual nesting success was categorized for parents as: (1) fledged no young from any nesting attempts, or (2) fledged at least one nestling from one nesting attempt. For the subset of nests that fledged at least one chick, we examined the effect of number of young fledged on local survival. The distribution of number of young fledged was positively skewed, with a median of six young, and ranged from one to 16 young per season. All means are presented ± 1 SE. All tests were two-tailed and were considered significant at $P < 0.05$.

RESULTS

Population size, annual conditions, and causes of mortality

The number of marked parrotlets sighted per year increased during the first four years of the study (1988–1991) as we began marking the population (Fig. 1A). After 1990, the number of marked females sighted remained relatively constant at 100–120 birds/yr. Simi-

TABLE 2. General models for estimating local survival (ϕ) and resighting rates (p) of adult Green-rumped Parrotlets in Venezuela (females, $n = 485$; males, $n = 849$).

Model	DEV	np	AIC	Comparison between models
Modeling resighting rates (p)				
1) $\phi_{2ac*t*sex}, p_{2ac*t*sex}$	3868.0	64	3996.0	
2) $\phi_{2ac*t*sex}, p_{2ac+t*sex}$	3884.1	52	3988.1	Age $\times$ year interaction effect on p within each sex, model 2 vs. model 1: $\chi^2_{12} = 16.1$, $P = 0.187$
3) $\phi_{2ac*t*sex}, p_{t*sex}$	3886.0	50	3986.0	Age effect on p, model 3 vs. model 2: $\chi^2_2 = 1.9$, $P = 0.387$
4) $\phi_{2ac*t*sex}, p_{t+sex}$	3893.3	43	3979.3	Year $\times$ sex interaction effect on p, model 4 vs. model 3: $\chi^2_7 = 7.3$, $P = 0.398$
5) $\phi_{2ac*t*sex}, p_t$	3904.2	42	3988.2	Sex effect on p, model 5 vs. model 4: $\chi^2_1 = 10.9$, $P < 0.001$
6) $\phi_{2ac*t*sex}, p_{sex}$	3919.2	36	3991.2	Year effect on p, model 6 vs. model 4: $\chi^2_7 = 25.9$, $P < 0.001$
Modeling local survival (ϕ)				
7) $\phi_{2ac+t*sex}, p_{t+sex}$	3901.9	30	3961.9	Age $\times$ year interaction effect on ϕ within each sex, model 7 vs. model 4: $\chi^2_{13} = 8.7$, $P = 0.795$
8) ϕ_{t*sex}, p_{t+sex}†	3904.6	27	3958.6	Age effect on ϕ, model 8 vs. model 7: $\chi^2_3 = 2.7$, $P = 0.440$
9) ϕ_{t+sex}, p_{t+sex}	3924.3	20	3964.3	Year $\times$ sex interaction effect on ϕ, model 9 vs. model 8: $\chi^2_7 = 19.7$, $P = 0.006$
10) $\phi^f_c, \phi^m_c, p_{t+sex}$	3911.3	20	3951.3	Year effect on male ϕ, model 10 vs. model 8: $\chi^2_7 = 6.7$, $P = 0.462$
11) $\phi^f_{dry\ season}, \phi^m_c, p_{t+sex}$	3937.6	13	3963.6	Residual year effect on female ϕ, model 11 vs. model 10: $\chi^2_7 = 26.3$, $P < 0.001$. Dry-season rainfall as a constraint on female ϕ, model 11 vs. model 14: $\chi^2_1 = 0.7$, $P = 0.403$
12) $\phi^f_{wet\ season}, \phi^m_c, p_{t+sex}$	3938.3	13	3964.3	Residual year effect on female ϕ, model 12 vs. model 10: $\chi^2_7 = 27.0$, $P < 0.001$. Wet season rainfall as a constraint on female ϕ, model 12 vs. model 14: $\chi^2_1 < 0.01$, $P > 0.99$
13) $\phi^f_{predation}, \phi^m_c, p_{t+sex}$	3933.1	13	**3959.1**	Residual year effect on female ϕ, model 13 vs. model 10: $\chi^2_7 = 21.8$, $P = 0.003$. Annual nest predation as a constraint on female ϕ, model 13 vs. model 14: $\chi^2_1 = 5.2$, $P = 0.023$
14) $\phi^f_c, \phi^m_c, p_{t+sex}$	3938.3	12	3962.3	
Additional models				
15) ϕ_{t*sex}, p_{t*sex}	3897.3	24	3965.3	
16) ϕ_{sex}, p_{sex}	3971.7	4	3979.9	

Notes: The fit of each model is described by the deviance (DEV) and the number of parameters (np); a low value for Akaike's Information Criterion (AIC = Dev + 2 $\times$ np) indicates a good model fit. Model 13 (bold type) was the model that best fit the data. Likelihood ratio tests are used to compare nested models ($\chi^2 = \Delta$ DEV, df = Δ np). Model subscripts include: 2ac, two age classes; c, constant; t, time dependent; and sex, sex dependent. The season and predation subscripts indicate models that constrain time-dependent variation to be a function of those annual covariates (see data in Table 1). In models 10–14, superscript f indicates females, and superscript m indicates males.

† This model is equivalent to $\phi^f_t, \phi^m_t, p_{t+sex}$.

larly, 160–190 marked males/yr were observed in 1991–1994, although >200 individuals/yr were recorded in the last three years. Females were much more likely than males to be breeders (Fig. 1B), and the proportion of each sex breeding was relatively constant (0.77 ± 0.03 in females and 0.49 ± 0.03 in males), especially in the first seven years of our study. Changes in breeding frequencies in the last three years were presumably a result of our increased effort to identify nonbreeders in 1995–1997, and an increase in the number of marked birds. The composition of the parrotlet population was relatively constant during the 10 years of our study, and overall, males outnumbered females 1.7 : 1.0 (Fig. 1C).

Annual conditions varied over the 10-yr study period. Total annual precipitation ranged from ~1000 to 2000 mm, and varied greatly during the dry and wet seasons (Table 1). The proportion of nest boxes that received parrotlet eggs varied among years ($G_9 = 51.5$, $P < 0.001$), but occupancy rate did not change during the study period (Mantel-Haenszel test, $\chi^2_1 = 0.03$, $P = 0.873$). Similarly, the number of attempts per box
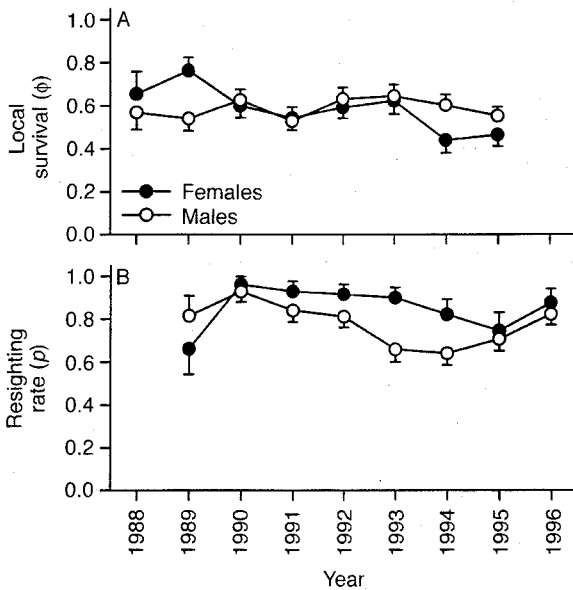
FIG. 2. (A) Estimates of local survival (ϕ) and (B) resighting rates (p) of Green-rumped Parrotlets banded as adults (females, n = 485; males, n = 849). Point estimates were calculated from model 15 (ϕ_{t*sex}, p_{t*sex}; see Table 2), and were inestimable for 1996–1997 because of time dependence in both rates. Model 15 illustrates the unconstrained variation in ϕ and p. Estimates are shown as mean ± 1 SE.

differed among years ($F_{9,990}$ = 6.6, P < 0.001), but showed no long-term trends ($F_{1,998}$ = 0.06, P = 0.812). Female parrotlets are most vulnerable to predators during the first two-thirds of the nesting cycle, when they spend most of their time in the nest box (Beissinger

and Waltman 1991, Curlee and Beissinger 1995). Rates of early nest loss to predators (Table 1) differed among years (G_9 = 48.8, P < 0.001), and were significantly higher during the later years of the study (Mantel-Haenszel test, χ_1^2 = 12.4, P < 0.001).

Cause of death was known for 27 marked parrotlets. Eight adult parrotlets were found dead in nest boxes with no signs of external injury. These birds may have died of starvation, disease, or other causes. Adult parrotlets were killed in nest boxes by snakes (n = 4; *Boa constrictor*, *Epicrastes cenchra*, and *Spilotes pullatus*), and small mammals (n = 6; mouse opossum *Marmosa robinsoni*, black rat *Rattus rattus*). One marked adult was killed by an Aplomado Falcon (*Falco femoralis*), and we witnessed successful attacks on unmarked parrotlets by falcons (Waltman and Beissinger 1992) and Roadside Hawks (*Buteo magnirostris*). A further eight losses were accidental deaths caused by handling.

General models of local survival and resighting rates for adult parrotlets

During the 10 years of the study, 1334 adult Green-rumped Parrotlets were color-banded and released (Table 1). A few birds were long-lived, with minimum life-spans of ≥7–8 yr (n = 2 females and 4 males) or 9–10 yr (n = 2 males). Overall, the resighting data of adults did not fit a Cormack-Jolly-Seber model (sum of Tests 2 and 3 of RELEASE; χ_{29}^2 = 52.8, P < 0.01). The model was not rejected for females (χ_8^2 = 2.2, P = 0.740), but we had sufficient data to calculate only one test (3.SR). The tests were nonsignificant in males (sum of 3.SR, 3.Sm and 2.Cm: χ_{18}^2 = 19.6, P = 0.355), except for one component of Test 2 (2.Ct, χ_3^2 = 30.9,

TABLE 3. Multistate models for estimating probability of survival (S), transitional probability of breeding (ψ), and resighting rates (p) of adult female Green-rumped Parrotlets (n = 485).

Model	DEV	np	AIC	Comparison between models
Modeling resighting rates (p)				
1) $S_{status*t}$, $\psi_{status*t}$, $p_{status*t}$	195.4	52	299.4	
2) $S_{status*t}$, $\psi_{status*t}$, p_{status}	208.8	38	**284.8**	Year effect on p, model 2 vs. model 1: χ_{14}^2 = 13.3, P = 0.503
3) $S_{status*t}$, $\psi_{status*t}$, $p_{constant}$	255.5	37	329.5	Breeding status effect on p, model 3 vs. model 2: χ_1^2 = 46.7, P < 0.001
Modeling transitional probability of breeding (ψ)				
4) $S_{status*t}$, ψ_{status}, p_{status}	240.8	22	284.8	Year effect on ψ, model 4 vs. model 2: χ_{16}^2 = 32.0, P = 0.010
5) $S_{status*t}$, ψ_t, p_{status}	281.9	29	339.9	Breeding status effect on ψ, model 5 vs. model 2: χ_9^2 = 73.2, P < 0.001
Modeling probability of survival (S)				
6) S_{status}, $\psi_{status*t}$, p_{status}	241.2	22	285.2	Year effect on S, model 6 vs. model 2: χ_{16}^2 = 32.4, P < 0.001
7) S_t, $\psi_{status*t}$, p_{status}	238.1	29	296.1	Breeding status effect on S, model 7 vs. model 2: χ_9^2 = 29.4, P < 0.001
Additional model				
8) S_{status}, ψ_{status}, p_{status}	282.3	6	294.3	

Notes: Model 2 (AIC entry in bold type) was the model that best fit the data. Model subscripts include: status, breeding status (breeding vs. nonbreeding); t, time dependent. See Table 2 *Notes* for further explanation of headings.
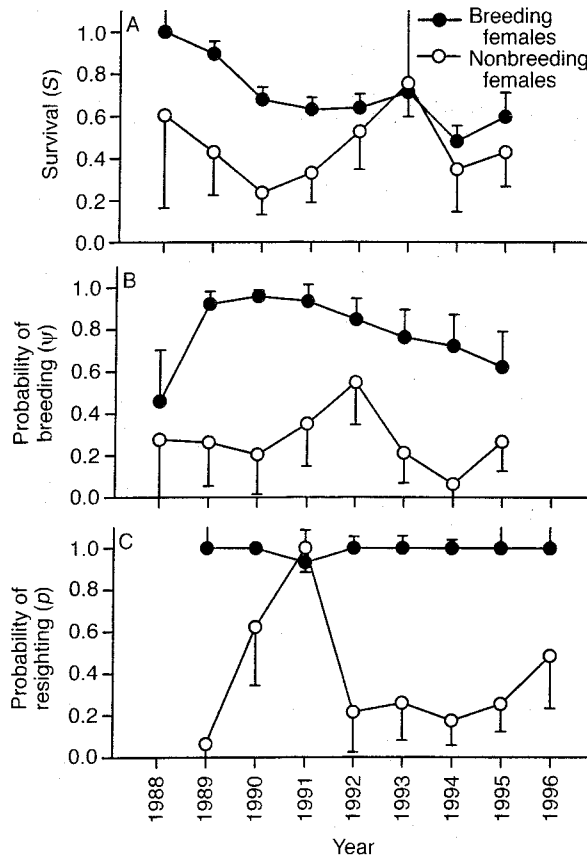
FIG. 3. (A) Estimates of the probability of survival (S), (B) transitional probability of breeding (ψ), and (C) resighting rates (p) of adult females that are breeders or nonbreeders $(n = 485)$. Point estimates were calculated from model 1 $(S_{status*t}, \psi_{status*t}, p_{status*t}$; Table 3), and were inestimable for 1996–1997. Estimates are shown as mean ± 1 SE.

$P < 0.001$). In this special case, the goodness-of-fit test indicated that the resighting data were consistent with a model with age dependence in resighting rate $(\phi_{t*sex}, p_{2ac*t*sex})$. Thus, we started the survival analyses with a model that included age dependence in both local survival and resighting rates (Table 2). We explored models with greater age structure (3–4 age classes) in local survival and resighting rate, but they were nonsignificant and collapsed to this initial model.

The model that best fit the resighting rate was one in which the annual variation was constrained to be a constant difference between the sexes (model 4; Table

2). Resighting rates varied among years, and females were detected more readily than males (Fig. 2). The local survival of adults was not affected by age dependence, but year and sex interacted significantly (model 9 vs. 8). Females initially had higher and then lower local survival than males in the early and late years of the study, respectively (Fig. 2). The local survival of adult males was nearly constant (model 10 vs. 8; Fig. 2), so we did not model environmental covariates for this sex. Annual variation in rainfall during the dry and wet seasons accounted for <3% of the variation in female survivorship. The best fit model was one in which the local survival of females was constrained to be a function of early nest loss to predation (Table 2; model 13 vs. 14). However, nest loss explained a relatively small percentage of the total variation in female survival (partial χ^2/total $\chi^2 = 5.2/27.0 = 19.3\%$), and local survival contained significant residual annual variation that was not explained by the covariates that we tested (models 11, 12, and 13 vs. 10). Overall, females had local survival rates comparable to those of males (0.547 ± 0.018 vs. 0.582 ± 0.014, from model 16), but resighting rates were higher among females (0.862 ± 0.023 vs. 0.745 ± 0.021).

The effect of breeding status on local survival and resighting rates

We modeled the effect of breeding status separately for male and female parrotlets because we found significant differences between the sexes in their local survival and resighting rates. In females, goodness-of-fit tests showed that all models tested were an adequate fit to the capture histories with breeding status ($P > 0.650$, all tests). Female resighting rates did not vary yearly (model 2 vs. 1, Table 3), but there was significant annual variation in the transitional probability of breeding and in survival rates (models 4 vs. 2, 6 vs. 2; Fig. 3). Breeding status had a significant effect on all three probabilities in females (models 3 vs. 2, 5 vs. 2, 7 vs. 2; Table 3). Breeders had higher survival, breeding, and resighting rates than nonbreeders (Fig. 3, Table 4). Data requirements of multistate models increase quickly with the number of levels in the state variables. Point estimates and their confidence limits were variable in early years of the study and for nonbreeders (Fig. 3), presumably because fewer females were marked in early years (Fig. 1A, Table 1) and because most bred (Fig. 1B). Nonetheless, there appeared to be long-term de-

TABLE 4. Estimates of the survival rate (S), transitional probability of breeding (ψ), and resighting rate (p) of adult Green-rumped Parrotlets.

	Females		Males	
Rate	Breeders	Nonbreeders	Breeders	Nonbreeders
Probability of survival (S)	0.658 ± 0.030	0.436 ± 0.042	0.698 ± 0.024	0.536 ± 0.021
Probability of breeding (ψ)	0.781 ± 0.044	0.266 ± 0.049	0.657 ± 0.038	0.291 ± 0.025
Probability of resighting (p)	1.000 ± 0.023	0.306 ± 0.062	0.994 ± 0.038	0.444 ± 0.039

Note: Estimates (±1 SE) were calculated from model 8 $(S_{status}, \psi_{status}, p_{status}$; see Tables 3 and 5).

TABLE 5. Multistate models for estimating probability of survival (S), transitional probability of breeding (ψ), and resighting rates (p) of adult male Green-rumped Parrotlets ($n = 849$).

Model	DEV	np	AIC	Comparison between models
Modeling resighting rates (p)				
1) $S_{status*t}$, $\psi_{status*t}$, $p_{status*t}$	303.6	52	**407.6**	
2) $S_{status*t}$, $\psi_{status*t}$, p_{status}	334.0	38	410.0	Year effect on p, model 2 vs. model 1: χ^2_{14} = 30.4, $P = 0.007$
3) $S_{status*t}$, $\psi_{status*t}$, p_t	349.1	44	437.1	Breeding status effect on p, model 3 vs. model 1: $\chi^2_8 = 45.5$, $P < 0.001$
Modeling transitional probability of breeding (ψ)				
4) $S_{status*t}$, ψ_{status}, $p_{status*t}$	344.0	36	416.0	Year effect on ψ, model 4 vs. model 1: χ^2_{16} = 40.4, $P < 0.001$
5) $S_{status*t}$, ψ_t, $p_{status*t}$	426.8	43	512.8	Breeding status effect on ψ, model 5 vs. model 1: $\chi^2_9 = 123.2$, $P < 0.001$
Modeling probability of survival (S)				
6) S_{status}, $\psi_{status*t}$, $p_{status*t}$	372.2	36	444.2	Year effect on S, model 6 vs. model 1: χ^2_{16} = 68.6, $P < 0.001$
7) S_t, $\psi_{status*t}$, $p_{status*t}$	379.7	43	465.7	Breeding status effect on S, model 7 vs. model 1: $\chi^2_9 = 76.0$, $P < 0.001$
Additional model				
8) S_{status}, ψ_{status}, p_{status}	416.4	6	428.4	

Note: Model 1 (AIC entry in bold type) was the model that best fit the data. See Table 2 *Notes* for further explanation of headings.
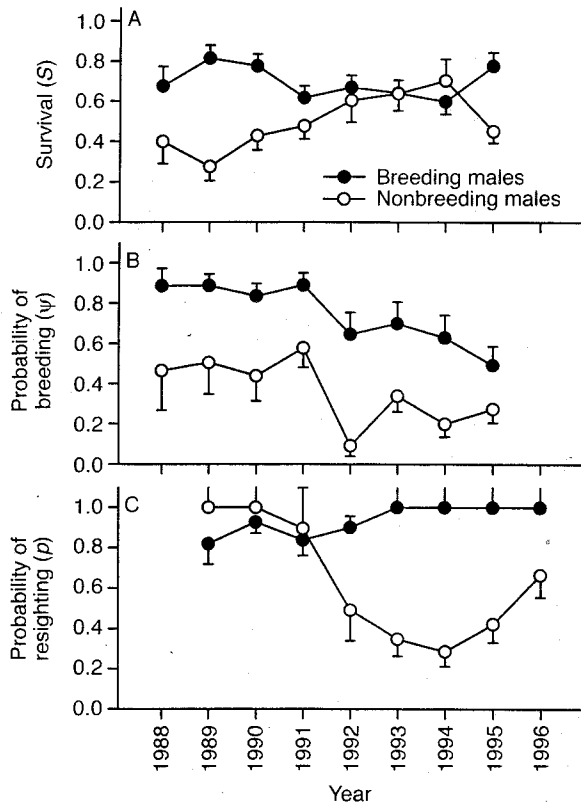

FIG. 4. (A) Estimates of the probability of survival (S), (B) transitional probability of breeding (ψ), and (C) resighting rates (p) of adult males that are breeders or nonbreeders ($n = 849$). Point estimates were calculated from model 1 ($S_{status*t}$, $\psi_{status*t}$, $p_{status*t}$; Table 5), and were inestimable for 1996–1997. Estimates are shown as mean ± 1 SE.

clines in both survival and the transitional probability of breeding in breeding females (Fig. 3).

We had better information for males because we marked more individuals (Fig. 1, Table 1) and because a greater proportion were nonbreeders (Fig. 1B). Seven of the eight models tested met the assumption of internal homogeneity (goodness-of-fit tests, $P > 0.30$), and only model 5 ($S_{status*t}$, ψ_t, $p_{status*t}$, Table 5) was rejected ($P < 0.001$). The probability of resighting (model 2 vs. 1; Table 5), transitional breeding (model 4 vs. 1), and survival (model 6 vs. 1) varied across years in males. Breeding status had a significant effect on all three probabilities as well (models 3 vs. 1, 5 vs. 1, and 7 vs. 1), and the saturated starting model (model 1) could not be further reduced. As in females, male breeders had higher survival rates, were more likely to remain breeders, and had resighting rates near unity (Fig. 4, Table 4). The transitional breeding rate appeared to decline in this study for males of either breeding status (Fig. 4B). Resighting rates of male and female nonbreeders increased after 1995, when we increased our effort to read bands on this group of birds.

The effect of reproductive performance on local survival

The estimated resighting rate of breeding females and males (Figs. 3C and 4C) was essentially 1.0 (Table 4). We made the assumption that this was the case, and used uncorrected return rates as an index of local survival (ϕ') for breeders. Logistic regression analysis showed that local survival rates increased with the number of eggs laid (regression coefficient $B = 0.079$; Table 6), after controlling for the effects of year and

TABLE 6. Logistic regression models testing the effects of fecundity (total number of eggs laid, annual nesting success, and number of young fledged), year, and sex on the local survival rates (ϕ') of breeding parrotlets. B is the regression coefficient (± 1 SE). Higher-order interactions were nonsignificant.

Source of variation	B	χ^2	df	P
No. eggs laid	0.079 ± 0.013	39.4	1	0.001
Year	-0.112 ± 0.025	19.6	1	0.001
Sex	0.040 ± 0.112	0.1	1	0.721
Residual	223.1 ± 50.6	19.4	1	0.001
Annual nesting success	1.022 ± 0.202	25.6	1	0.001
Year	-0.130 ± 0.028	22.3	1	0.001
Sex	0.078 ± 0.114	0.5	1	0.491
Residual	257.7 ± 54.8	22.1	1	0.001
No. young fledged	0.081 ± 0.021	14.2	1	0.001
Year	-0.120 ± 0.029	16.6	1	0.001
Sex	0.207 ± 0.128	2.6	1	0.107
Residual	237.8 ± 58.4	16.6	1	0.001

Notes: Females produced 1–30 eggs per year. Annual nesting success was classed as "no" (parents bred but did not successfully fledge young from any nesting attempt), or "yes" (parents fledged at least one nestling from at least one nesting attempt). This test did not include 1988, as data were sparse. Parrotlets fledged 1–16 young per year.

sex. Females that produced ≥12 eggs had higher local survival in nine of nine years, and this was also the case in six of nine years for males. Overall, the local survival rates of birds laying ≥12 eggs (females: ϕ' = 0.622, n = 288; males: ϕ' = 0.536, n = 252) were 13–20 percentage points higher than those of birds laying 1–11 eggs (females, ϕ' = 0.415, n = 371; males, ϕ' = 0.404, n = 431). Local survival rates increased as a function of annual nesting success (B = 1.022; Table 6). Parrotlets that successfully fledged young had higher overall rates of local survival (females, ϕ' = 0.577, n = 489; males, ϕ' = 0.488, n = 492) than did birds with nests that failed (females, ϕ' = 0.274, n = 146; males, ϕ' = 0.343, n = 166). Local survival rates also increased with the number of young fledged (B = 0.081; Table 6). Females and males that fledged ≥6 young had higher rates of local survival in six of nine

years and in seven of nine years, respectively. Overall, the local survival rates of birds fledging ≥6 young (females, ϕ' = 0.622, n = 254; males, ϕ' = 0.550, n = 240) were 7–9 percentage points higher than those of birds fledging 1–5 young (females, ϕ' = 0.523, n = 258; males, ϕ' = 0.433, n = 275).

Was variation in local survival due to mortality or to emigration?

To investigate whether the variation in local survival was due to permanent emigration, we examined the movements of adults in consecutive years. The dispersal of adults was influenced by breeding status and sex, but the interaction was nonsignificant (two-way ANOVA, $F_{3, 590}$ = 0.4, P = 0.787). Males moved farther than females in search of breeding opportunities, regardless of their breeding status (Fig. 5). The difference
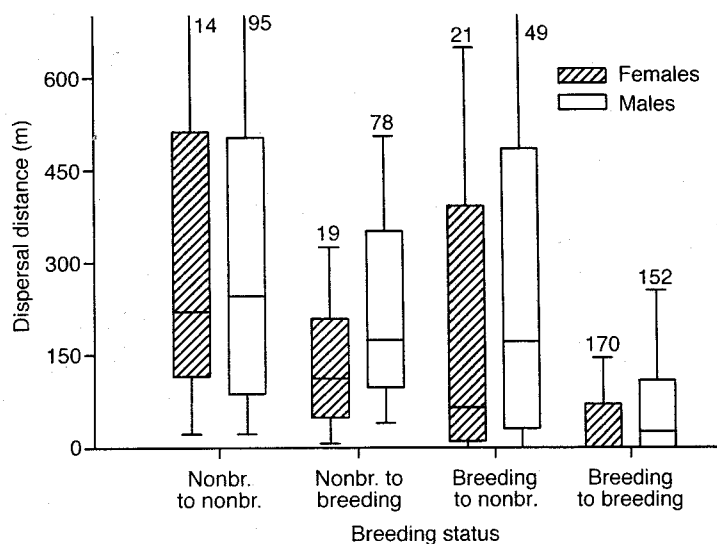
FIG. 5. Site fidelity of adult Green-rumped Parrotlets as a function of breeding status. We used the first location where a bird was sighted as a nonbreeder (nonbr.) or as a breeder in consecutive years. One dispersal distance record was selected at random for each adult. Box plots indicate median and interquartile range; error bars are the 10–90% quantiles. Sample size (no. birds) is indicated above each error bar.

was significant in a main-effects model without the interaction term ($F_{1,593} = 5.3$, $P = 0.021$). Breeding status also had a significant effect on dispersal distance ($F_{3,593} = 52.5$, $P < 0.001$), and nonbreeders moved farther in search of nest boxes and mates than did birds that were breeders (Fig. 5). Birds that changed breeding status moved intermediate distances. Adult parrotlets showed strong site fidelity, as the median dispersal distances of all groups were <250 m.

We obtained an index of detectable dispersal by calculating the distance between all possible pairs of nest boxes. The median of this distribution (970 m, range 7–2633 m) was about four times greater than the observed rates of adult dispersal. This suggests that once a parrotlet began to reside in the study area, emigration was unlikely to occur. Thus, permanent emigration does not appear to be a major source of bias in our estimates of local survival. Nevertheless, if the dispersal distances of adults were bimodally distributed, we might have missed birds that dispersed long distances (>2.5 km).

DISCUSSION

Green-rumped Parrotlets have life history traits that are atypical for most land birds breeding at equatorial latitudes: they lay a large clutch, nest in cavities, and inhabit a highly seasonal environment (Beissinger and Waltman 1991, Waltman and Beissinger 1992, Beissinger and Gibbs 1993). For these reasons, we predicted that their survival would be low for a tropical species. Nonetheless, the local survival rate of parrotlets ($\phi = 0.565$) from mark–resighting data was almost identical to the median rates reported for a mist net study of 11–25 species in Panama, and was only slightly lower than median rates reported for birds in Puerto Rico and Trinidad (Table 7). Furthermore, parrotlet survival was comparable to the local survival of several small cavity nesters that breed at northern temperate latitudes ($\phi = 0.57$ for Blue Tits, *Parus caeruleus*, Blondel et al. 1992; $\phi = 0.62$ for Black-capped Chickadee *P. atricapillus*, Loery et al. 1997).

At first glance, our study supports the finding of Karr et al. (1990) that survival rates of tropical and temperate birds are similar. This conclusion seems equivocal, however, if the substantial heterogeneity in local survival rates of adult Green-rumped Parrotlets is considered. Comparative studies usually control for correlated life-history traits (e.g., body size, clutch size) and phylogeny (Sæther 1989, Martin 1995, Johnston et al. 1997), but only rarely consider the potential sources of bias that could affect survival rates. Thus, we discuss how the sources of heterogeneity and bias that affected parrotlet survival could affect latitudinal and interspecific comparisons of avian survivorship.

Age, transience, and heterogeneity of capture

In a sample of adult birds of unknown age, a significant two-age-class term may indicate an effect of relative age, the presence of transients, or heterogeneity of capture (Johnston et al. 1997, Pradel et al. 1997, Prévot-Julliard et al. 1998). Many analyses of survivorship for birds fail to control for these three effects because they use the CJS model to derive estimates of survival (e.g., 12 of 15 studies; Table 7). Analyses based on two-age-class models have shown that individuals captured once and then never resighted can be an important source of bias in studies of tropical and temperate birds (Johnston et al. 1997). Similarly, controlling for transience led to a significant increase in estimates of survival for Panamanian birds, although the difference in overall means was relatively small (0.53 vs. 0.58; Brawn et al. 1999). The two age class term was not significant in our analyses of local survival for adult Green-rumped Parrotlets, but we have found strong age class effects in separate analyses of parrotlets banded as nestlings (B. K. Sandercock and S. R. Beissinger, *unpublished data*). Two age class models fit the mark–recapture data for 11 of 17 species studied by Johnston et al. (1997); these could have been age effects because they were able to identify juveniles in only one species.

Remsen and Parker (1983) speculated that age and transience effects may be more likely in tropical ecosystems because breeding seasons are longer and young are produced over more months of the year than in northern temperate areas. Similarly, Johnston et al. (1997) argued that inclusion of young and dispersing birds at tropical sites and exclusion at temperate sites could result in under- and overestimates of survival in the two regions, respectively. Nonetheless, it seems unlikely that the effects of age, transients, and heterogeneity of capture will completely explain latitudinal or regional differences in avian survivorship. Return rates are already high for many tropical birds (Table 8). In general, controlling for age, transients, heterogeneity of capture, emigration, and detection rates can only increase estimates of survival for resident adults of tropical or temperate species.

The importance of social system

Return rates of from mark–resighting studies of tropical land birds (Table 8) often appear to be higher than local survival rates derived from mist net studies (Table 7). This pattern is counterintuitive because return rates are not corrected for detection rates and should be lower. Although mark–resighting studies use both recapture and resighting data, mist net studies generally use only recaptures (Tables 7 and 8). Estimates of survival may be low in mist net studies if the capture histories of older birds are truncated because they learn to avoid nets or traps (Elder 1985; but see Nichols et al. 1984). More importantly, survival rates could be low because mist net studies capture a broader and more representative sample of avian populations. Most mark–resighting studies typically report return rates for portions of the population that are easily surveyed, such as breed-

TABLE 7. Estimates of annual local survival for birds breeding at latitudes between the tropics of Cancer (23°27′ N) and Capricorn (23°27′ S).

Species	Local survival (ϕ)	Detection rate (p)	No. birds	No. years	Model[†]	Type of data[‡]	Birds sampled[§]	Latitude (N)	Reference
A) Systematic mist net studies									
25 species	0.55 (0.33–0.73)	0.28 (0.10–0.49)	70 (20–618)	10	CJS or age	recapture	all	9°10′	Karr et al. (1990), Brawn et al. (1995)
11 species	0.59 (0.41–0.73)	. . .	. . .	21	transient	recapture	all	9°10′	Brawn et al. (1999)
17 species	0.65 (0.45–0.85)	0.20 (0.08–0.47)	51 (10–376)	10	age	recapture	all or adults	10°30′	Johnston et al. (1997)
9 species	0.68 (0.51–0.79)	0.20 (0.10–0.32)	72 (19–348)	18	CJS	recapture	all	18°00′	Faaborg and Arendt (1995)
B) Mark–resighting studies									
Iiwi (*Vestiaria coccinea*)	0.55	0.22	123	6	CJS	both	adults	19°30′	Ralph and Fancy (1995)
Green-rumped Parrotlet (*Forpus passerinus*)	0.56	0.81	1334	10	age	both	adults	8°34′	**This study**
Long-tailed Hermit (*Phaethornis superciliosus*)	0.57	. . .	. . .	5	CJS	both	males at leks	10°26′	Stiles (1992)
Palila (*Loxioides bailleui*)	0.63	0.16	. . .	6	CJS	both	adults	19°50′	Lindsey et al. (1995)
Omao (*Myadestes obscurus*)	0.66	0.62	153	6	CJS	both	adults	19°30′	Ralph and Fancy (1994a)
Akepa (*Loxops coccineus*)	0.70	0.60	61	6	CJS	both	adults	19°30′	Ralph and Fancy (1994b)
Akiapolaau (*Hemignathus munroi*)	0.71	0.80	20	5	CJS	both	adults	19°30′	Ralph and Fancy (1996)
Apapane (*Himatione sanguinea*)	0.72	0.07	201	6	CJS	both	adults	19°30′	Ralph and Fancy (1995)
Hawaii Creeper (*Oreomystis mana*)	0.73	0.73	49	6	CJS	both	adults	19°30′	Ralph and Fancy (1994b)
8 species	0.76 (0.67–0.86)	0.61 (0.38–0.92)	18.5 (12–25)	3	CJS	both	adults	4°05′	Jullien and Thiollay (1998)
Long-tailed Manakin (*Chiroxiphia linearis*)	0.77	0.83	186	10	CJS	both	adults at leks	10°18′	McDonald (1993)
Red-billed Leiothrix (*Leiothrix lutea*)	0.79	0.18	338	6	age	both	adults	19°31′	Ralph et al. (1998)
Akepa (*Luxops coccineus*)	0.79	0.81	158	7	age	both	adults	19°30′	Lepson and Freed (1995)

Notes: All estimates were calculated with mark–recapture statistics. Rates were pooled across sexes, years, and different sites. Median rates and sample sizes (range in parentheses) are given for studies that considered multiple species.

† Model used to derive survival estimates: age = a model with a two-age-class term in local survival (ϕ_{2ac*t}, p_t); CJS = Cormack-Jolly-Seber model, time dependence in local survival and recapture (or resighting) rates (ϕ_t, p_t); transient = a model that controls for transience and yields estimates of local survival for residents (τ_t, ϕ_t, p_t).

‡ "Both" indicates that both resighting and recapture data were used to construct the mark–recapture histories.

§ Subset of the population sampled: all = breeding adults, nonbreeding adults, and juveniles; adults = breeding and nonbreeding adults.

ing, territorial, or lek-holding individuals (Table 8). Nonbreeding birds that are young or senescent are often excluded.

Nonbreeders were common in our population of Green-rumped Parrotlets, comprising, on average, ~23.5% of the females and 52.9% of the males sighted each year (Fig. 1). If we corrected these estimates for the lower probability of resighting nonbreeders (Table 4), the estimated percentages of nonbreeding females and males in our population rose to 50.1% and 71.6%, respectively. Breeding parrotlets had survival rates that were ~20 percentage points higher than nonbreeders (Table 4). Moreover, local survival was highest among parrotlets that laid more eggs and fledged more young. These results are contrary to the patterns predicted by a cost of reproduction, but could be due to phenotypic correlations among life history traits.

Nonbreeders have been reported to have lower survival than breeders in a variety of birds (e.g., Willis 1974, Smith and Arcese 1989, Orell et al. 1994, Cam et al. 1998). In some of these species, breeders presumably had higher survival because they held general-purpose territories that were used for feeding and attracting a mate. This is an unlikely explanation for Green-rumped Parrotlets because pairs defend a nesting cavity and not a territory (Beissinger et al. 1998). Nonbreeding parrotlets may have had lower survival for three reasons. First, nonbreeders could have ranged farther than breeders in search of reproductive opportunities. We would not have detected nonbreeders that moved >2.5 km, and some of the difference in local survival could have been due to emigration. However, it seems unlikely that emigration can completely account for the differential survival between breeders and nonbreeders, because adult parrotlets generally showed strong site tenacity (Fig. 5). Second, the difference in survival between breeders and nonbreeders may have been partly an age effect in males. Yearling males are likely to be nonbreeders and also have low survival (S. R. Beissinger, *unpublished data*). Third, the transitional probability of breeding was low for nonbreeders, and this segment of the population could have included low-quality birds that were unable to obtain or retain a mate. Nonbreeders are observed in the older age classes of both sexes.

We would have greatly overestimated the overall survival rates of the Green-rumped Parrotlet if we had considered only breeding birds. Worse, we would have used as little as 36% of the parrotlet population to calculate survivorship. How representative are parrotlets likely to be among tropical land birds? Nonbreeders might be common in the Green-rumped Parrotlet because nest sites are usually limited for cavity nesters (Brawn and Balda 1988, Newton 1994), and because snags are less common in equatorial than in temperate forests (Gibbs et al. 1993). It is also possible that provision of nest boxes has increased the size of the nonbreeding population. This notion has some support be-

cause the transitional probability of breeding declined among breeders during the study (Figs. 3 and 4), possibly as a density-dependent response.

Interspecific comparisons are difficult because nonbreeders are rarely surveyed in population studies (Beissinger 1996). Nonbreeders were relatively easy to detect in Green-rumped Parrotlets because they actively search for mates and available nest sites (Beissinger et al. 1998). Direct observation is usually difficult because nonbreeders are secretive (Smith 1978, Arcese 1987), have larger home ranges than breeders (Zack and Stutchbury 1992, Nur and Geupel 1993, Rohner 1997), and range from nonterritorial floaters to mated pairs that do not produce young (Dowsett-Lemaire 1985, Robinson et al. 1990, Westcott and Smith 1994). Nonetheless, nonbreeders have been reported in both temperate (Thompson and Nolan 1973, Smith and Arcese 1989, Nur and Geupel 1993, Orell et al. 1994) and tropical land birds (Smith 1978, Dowsett-Lemaire 1983*a, b,* 1985, Dowsett and Dowsett-Lemaire 1986, Freed 1987, Jullien and Thiollay 1998), including other parrots (Beissinger and Bucher 1992).

At present, it is unclear whether the frequency of nonbreeders varies with latitude. A conventional view of tropical birds is that population numbers are close to carrying capacity and habitats are saturated (Martin 1996). This is supported in cases where territory boundaries show long-term stability despite turnover (Greenberg and Gradwohl 1997). If so, limited breeding opportunities might be a common feature of tropical social systems. On the other hand, nest predation rates can be high among tropical birds (Skutch 1985; but see Martin 1996), and low productivity may reduce the size of nonbreeding populations (Stiles 1992). In future research, the demographic importance of nonbreeders should be given greater attention.

The effect of breeding-site fidelity on local survival

Mist net studies have been criticized for their failure to account for the effect of spacing systems in estimating the abundance of tropical birds (Remsen and Good 1996). Movements also affect the estimation of local survival rates because it is not possible to distinguish permanent emigration from mortality. It is somewhat surprising that past mist net studies have not presented information on movement rates (Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997). Rates of permanent emigration could be a systematic source of bias that affects interspecific comparisons of survivorship.

Permanent emigration appeared to be relatively unimportant among adult Green-rumped Parrotlets. Adult site fidelity was quite strong, as 95% of all parrotlets moved <500 m in consecutive years. Dispersal distance is likely to be underestimated if birds move off of a study area of limited size (Moore and Dolbeer 1989, Baker et al. 1995, Koenig et al. 1996). The size of our study area (4 km²) is typical of many intensive

TABLE 8. Annual return rates of birds breeding at latitudes between the tropics of Cancer (23°27' N) and Capricorn (23°27' S).

Species	Annual return rate	No. birds	No. years	Type of data†	Birds sampled‡	Latitude	Reference
A) Systematic mist net studies							
Black-billed Seedcracker (*Pyrenestes ostrinus*)	0.21	608	4	recapture	adults	3°46' N	Smith (1990)
14 species	0.45§ (0.11– 0.87)	34.5 (4– 266)	11	both	territorial	10°30' S	Dowsett (1985)
34 species	0.91 (0.50– 1.00)	5 (2–20)	2	both	all	1°12' N	Fogden (1972)
B) Mark–resighting studies							
Common Fiscal Shrike (*Lanius collaris*)	0.39	18	2	resighting	territorial	0°40' S	Zack and Ligon (1985)
Slaty Antshrike (*Thamnophilus punctatus*)	0.54	85	8	resighting	territorial	9°10' N	Greenberg and Gradwohl (1986)
Galapagos Mockingbird (*Nesomimus parvulus*)	0.61	377	11	resighting	territorial	0°20' N	Curry and Grant (1989)
Checker-throated Antwren (*Myrmotherula fulviventris*)	0.62	82	8	resighting	territorial	9°9' N	Greenberg and Gradwohl (1986)
White-flanked Antwren (*Myrmotherula axillaris*)	0.64	51	8	resighting	territorial	9°9' N	Greenberg and Gradwohl (1986)
Gray-backed Fiscal Shrike (*Lanius excubitorius*)	0.66	53	3	resighting	territorial	0°40' S	Zack and Ligon (1985)
Green Woodhoopoe (*Phoeniculus purpureus*)	0.66	130	7	resighting	territorial	0°40' S	Ligon and Ligon (1989)
Stripe-backed Wren (*Campylorhynchus nuchalis*)	0.69	365	6	resighting	territorial	8°34' N	Rabenold (1985)
Medium Ground Finch (*Geospiza fortis*)	0.69	...	8	both	adults	0°	Gibbs and Grant (1987)
Ocellated Antbird (*Phaenostictus mcleannani*)	0.70	160‖	10	resighting	territorial	9°9' N	Willis (1974)
Bicoloured Antbird (*Gymnopithys bicolor*)	0.71	280‖	10	resighting	territorial	9°9' N	Willis (1974)
White-browed Sparrow Weavers (*Plocepasser mahali*)	0.71	112	3	resighting	adults	11°22' S	Lewis (1982)
Purple-crowned Fairy-wren (*Malurus coronatus*)	0.72	206	4–6	resighting	breeders	15°40' S 19°01' S	Rowley and Russell (1993)
White-fronted Bee-eater (*Merops bullockoides*)	0.74	163	5	resighting	breeders	0°22' S	Emlen and Wrege (1991)
Groove-billed Ani (*Crotophaga sulcirostris*)	0.75	330‖	5	resighting	breeders	10°30' N	Vehrencamp et al. (1988)
Spotted Antbird (*Hylophylax naevioides*)	0.81	1032‖	10	resighting	territorial	9°9' N	Willis (1974)
Dusky Antbird (*Cercomacra tyrannina*)	0.82	65	8	both	territorial	9°5' N	Morton and Stutchbury (2000)
Cactus Ground Finch (*Geospiza scandens*)	0.82	...	8	both	adults	0°	Gibbs and Grant (1987)
Silvereye (*Zosterops lateralis*)	0.83	1657‖	8	resighting	adults	23°27' S	Catterall et al. (1989)

Table 8. Continued.

Species	Annual return rate	No. birds	No. years	Type of data†	Birds sampled‡	Latitude	Reference
Tooth-billed Bowerbird (*Scenopoeetes dentirostris*)	0.88	24	16	resighting	males at courts	19°00′ S	Frith and Frith (1995)
White-bearded Manakin (*Manacus manacus*)	0.89	38	4.5	both	males at leks	10°30′ N	Snow (1962)
Puerto Rican Parrot (*Amazona vittata*)	0.91	46‖	7	resighting	breeders	18°27′ N	Snyder et al. (1987)

Notes: Return rates were pooled across sexes, years, and sites. Median rates and sample sizes (range in parentheses) are given for studies that considered multiple species.

† "Both" indicates that both resighting and recapture data were used to calculate return rates.

‡ Subset of the population sampled: all = breeding adults, nonbreeding adults, and juveniles; adults = breeding and nonbreeding adults; territorial = adults (and helpers) holding a breeding territory; breeders = breeding adults.

§ Return rates based on all subsequent years, and not just the following year.

‖ The study did not give the number of individual birds banded; the number of bird-years is shown instead.

population studies, but our estimates of dispersal should be reasonably accurate because adult parrotlets moved short distances relative to the potential movements that we could have detected (Fig. 5). Comparable data for other tropical birds are limited, but median distances of breeding dispersal were < 250 m for 16 of 18 land birds in Malawi (Dowsett 1985), < 300 m for 10 of 12 species in Trinidad (Snow and Lill 1974), and < 400 m for Puerto Rican Vireos (*Vireo latimeri*; Woodworth et al. 1998).

Return rates and local survival rates could be higher among tropical than northern temperate birds, not because absolute survival rates are higher, but because adults disperse over shorter distances. Tropical species that are nectivorous or frugivorous are known to show low site fidelity because their food resources are spatially and temporally dispersed (Martin and Karr 1986, Stiles 1988, Franklin et al. 1989, Kinnaird et al. 1996). Low site fidelity may also be a feature of tropical birds that make long-distance seasonal movements (Stiles 1988, Robinson et al. 1990, Loiselle and Blake 1992, Powell and Bjork 1995). However, there are relatively few estimates of adult survival for such species. Tropical studies are often based on small, usually insectivorous species that hold territories or leks for the duration of their life-span (Tables 7 and 8). Switches among sites are typically rare and often only to adjacent areas (Snow and Lill 1974, Willis 1974, McDonald 1993, Greenberg and Gradwohl 1997, Jullien and Thiollay 1998). Adult dispersal may be uncommon in other tropical species (Tables 7 and 8) because cooperative breeders and cavity nesters rarely move once they obtain a breeding territory or nesting site, and because insular species are less likely to show long-distance dispersal. Site fidelity is generally thought to be high in northern temperate land birds (Greenwood and Harvey 1982), and adult dispersal distances are often < 500 m (Harvey et al. 1979, Shields 1984, Drilling and Thompson 1988, Holmes and Sherry 1992,

Montalvo and Potti 1992, Murphy 1996, Morton 1997). However, other temperate species readily switch territories both within and between years, often in response to nesting failure (Darley et al. 1971, Thompson and Nolan 1973, Weatherhead and Boak 1986, Bensch and Hasselquist 1991, Haas 1998). It remains to be seen whether site fidelity differs between tropical and temperate birds.

The effect of sex on local survival

The potential effects of social system and rates of site fidelity are likely to differ between the sexes. Male Green-rumped Parrotlets had similar or higher survival rates than did females, and the difference in probabilities was 4–10 percentage points, depending on the subset of the population. Adult males moved farther than females in consecutive years, so the difference in local survival was not due to female-biased emigration. We obtained better model fit when we used early nest loss as a constraint on female survival (Table 2), presumably because females are vulnerable while they incubate and brood the young alone. The small differences in adult mortality are unlikely to explain the male-biased sex ratio in adult parrotlets, whereas differential mortality and differential emigration between female and male fledglings appear to be important (S. R. Beissinger, *unpublished data*).

Although female and male parrotlets showed little difference in survival or site fidelity, this pattern is unlikely to hold for all tropical birds. For example, local survival and recapture rates might differ between the sexes in lekking species because males are sedentary at display sites whereas females are mobile (Graves et al. 1983, Stiles 1992, McDonald 1993). This presents a problem for mist net studies that pool the sexes, which was done for lek-mating manakins and other species by Karr et al. (1990) and Johnston et al. (1997). Variation in local survival rates among mist net

studies could have been partly due to sex differences in the composition of their samples.

Statistical considerations

Our intensive mark–resighting effort has yielded accurate estimates of survival for Green-rumped Parrotlets, but this is only one of many tropical bird species. Mist net studies consider multiple species (Karr et al. 1990, Faaborg and Arendt 1995, Johnston et al. 1997), but band fewer birds (median $n < 75$ birds) and have lower recapture rates ($p < 0.30$; Table 7). Demographic studies of tropical birds are difficult because most species occur at low densities (Karr 1990). Nevertheless, small sample sizes and low recapture rates reduce the power to detect differences among survival models (Lebreton et al. 1992).

One index of power in mark–resighting and mist net studies could be their ability to detect time dependence in ϕ. Annual variation in local-survival is a common feature of many long-term studies of northern temperate land birds (e.g., Peach et al. 1995, Chase et al. 1997, Loery et al. 1997). Tropical land birds might be expected to show little annual variation in survival if they experience constant climatic conditions. However, seasonal variation in precipitation is fairly common at tropical latitudes (Fogden 1972, Karr et al. 1990), and rainfall can affect the annual survivorship of tropical birds (Gibbs and Grant 1987, Stiles 1992). Johnston et al. (1997) did not consider time dependence in survival for any of their 17 study species. A time-dependent model was retained for only 12% and 22% of the species in Karr et al. (1990) and Faaborg and Arendt (1995), respectively. Lack of time dependence in local survival was also observed in some mark–resighting studies of tropical birds (McDonald 1993, Lepson and Freed 1995, Jullien and Thiollay 1998). Moreover, time-dependent models of local survival tended to be retained in species with larger sample sizes and collapsed to the most simple model in most others. A lack of annual variation in survival may indicate that some mist net and mark–resighting studies are constrained by low statistical power.

CONCLUSIONS

Our present understanding of the comparative demography of birds has been hampered by inappropriate comparisons that do not account for methodological or sampling differences among studies. Mark–recapture statistics yield more accurate estimates of survival but have not yet been widely applied to tropical birds (Tables 7 and 8). Few studies have calculated local survival rates where age/transience effects or breeding status have been controlled (Table 7). Movement rates have rarely been considered, so that permanent emigration and mortality are often confounded. Moreover, survival estimates are often based on different subsets of avian populations. Most mark–resighting studies of tropical species have examined only breeding birds (Table 8), whereas mist net studies have pooled all individuals without regard to age, breeding status, or sex (Table 7). Similar problems exist in estimates of survivorship for land birds of northern temperate regions. Many broad-scale analyses do not describe the methods used to calculate survival (Sæther 1988, Martin 1995), or treat all estimates as equally robust (Sæther 1989, Martin and Li 1992, Johnston et al. 1997). Local survival rates are available for some northern temperate birds (see references in Martin and Li 1992, Chase et al. 1997, Johnston et al. 1997), but more are needed before valid broad-scale comparisons can be made.

Finally, we believe that most comparative analyses of life history traits should be reassessed because they are usually based on mean survival rates. Given that so much heterogeneity can occur in survival rates, it is unclear whether analyses of mean rates are meaningful. Different species could have the same mean survival rate, but have markedly different survivorship curves due to age-specific variation in survival. A more profitable approach may be to estimate age- or sex-specific rates of survival for birds of different social status (e.g., McDonald 1993). If this is not possible, future analyses should at least compare similar subsets of populations, such as the individuals that are territorial breeders. Resolution of the tropical vs. temperate debate awaits better estimates of survivorship and a more comprehensive understanding of avian life histories.

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