The Auk 119(1):149–165, 2002

ANNUAL SURVIVAL RATES OF WINTERING SPARROWS: ASSESSING DEMOGRAPHIC CONSEQUENCES OF MIGRATION

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ABSTRACT.—The demographic consequences of migration have important implications for both evolutionary ecology and conservation biology. We investigated local survival rates for six populations of sparrows at a wintering site. Recent developments in mark–recapture statistics were applied to a 13 year dataset with large numbers of marked individuals ($n = 1{,}632$ to 4,394). The study taxa were closely related, and included one resident species (Song Sparrow [*Melospiza melodia gouldii*]), one short-distance migrant (''Puget Sound'' White-crowned Sparrow [*Zonotrichia leucophrys pugetensis*]), two moderate-distance migrants (Lincoln's [*Melospiza lincolnii*] and Fox [*Passerella iliaca*] sparrow), and two long-distance migrants (''Gambel's'' White-crowned [*Zonotrichia leucophrys gambelii*] and Golden-crowned [*Zonotrichia atricapilla*] sparrow). A literature review demonstrated a cline in fecundity among these sparrows: resident and short-distance migrants laid multiple clutches of few eggs, whereas long-distance migrants tended to produce one large clutch. Annual rates of local survival were low in the interval after first capture (<0.35), possibly because of variation in true survival, site-fidelity, presence of transients and heterogeneity of capture. Estimates of local survival among birds that returned at least once were more robust and were comparable among Song (0.558 ± 0.054 SE), Puget Sound White-crowned (0.461 ± 0.026), Lincoln's (0.456 ± 0.066), Fox (0.352 ± 0.0), Golden-crowned (0.422 ± 0.023) and Gambel's White-crowned (0.432 ± 0.0) sparrows. Estimates of survivorship for Lincoln's and Fox sparrows are among the first values available for those species. Local survival was not higher among resident than migratory taxa, nor did it covary with migration distance among migratory species. These results did not support the time-allocation hypothesis of Greenberg (1980), but are consistent with aspects of bet-hedging theory. While these analyses have potential implications for conservation of migratory birds, further work is required to establish whether these patterns are applicable to Neotropical migrants. *Received 27 September 2000, accepted 1 September 2001.*

RESUMEN.—Las consecuencias demográficas de la migración tienen importantes implicaciones tanto en ecología evolutiva como en biología de la conservación. En un sitio de invernada investigamos las tasas de supervivencia en seis poblaciones de gorriones. Se aplicaron estadísticos recientemente desarrollados para el análisis de datos de marca y recaptura a una base de datos de 13 años en la que se marcó gran número de individuos ($n = 1{,}632$ a 4,394). Los taxa estudiados se encontraban altamente emparentados e incluyeron una especie residente (*Melospiza melodia*), una especie migratoria de corta distancia (*Zonotrichia leucophrys* de Puget Sound), dos especies migratorias de distancia moderada (*Melospiza lincolnii* y *Passerella iliaca*) y dos especies migratorias de larga distancia (*Zonotrichia atricapilla* y *Zonotrichia leucophrys* de Gambel). Los resultados de una revisión bibliográfica demostraron un gradiente en la fecundidad de estos gorriones: las especies residentes y migratorias de corta distancia presentaron nidadas múltiples de pocos huevos, mientras que las especies migratorias de larga distancia presentaron una tendencia a producir una sola nidada grande. Las tasas anuales de supervivencia local fueron bajas durante el intervalo posterior a la primera captura (<0.35), posiblemente debido a variación en la supervivencia verdadera, fidelidad de sitio, presencia de individuos transeúntes y a la heterogeneidad de las capturas. Las estimaciones de supervivencia local entre las aves que retornaron por lo menos una vez fueron

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más robustas y fueron comparables entre *M. melodia* (0.558 ± 0.054 ES), *Z. leucophrys* de Puget Sound (0.461 ± 0.026), *M. lincolnii* (0.456 ± 0.066), *P. iliaca* (0.352 ± 0.0), *Z. atricapilla* (0.422 ± 0.023) y *Z. leucophrys* de Gambel (0.432 ± 0.0). Las estimaciones de la supervivencia de individuos de *M. lincolnii* y *P. iliaca* representan uno de los primeros valores disponibles para estas especies. La supervivencia local no fue mayor en los taxa residentes que en los migratorios, ni covarió con la distancia de migración entre las especies migratorias. Estos resultados no apoyaron la hipótesis de Greenberg (1980) sobre la asignación de tiempo, pero fueron consistentes con aspectos de la teoría de ''bet-hedging''. Aunque estos análisis tienen potenciales implicaciones para la conservación de aves migratorias, se requieren estudios adicionales para establecer si estos patrones son aplicables a las aves migratorias neotropicales.

ONE THEORETICAL APPROACH to the study of evolution of avian migration has been to compare demographic differences between resident and migratory populations of the same or different species. In early work, migratory birds were regarded as ''*r*-selected'' strategists with high population-growth potential and good dispersal ability to occupy ephemeral or marginal environments in breeding and wintering areas (von Haartman 1968, O'Connor 1985). More recently, migrant birds have been recognized to be an integrated part of avian communities at wintering sites (Sherry and Holmes 1995). Fecundity, which is a function of number of broods and number of offspring produced per brood, tends to be lower in migrants than species that are resident at northern temperate latitudes. Moreover, migrants tend to have higher annual survival than residents (reviewed by Sherry and Holmes 1995, Nichols 1996). The high survival rates of some migratory land birds (e.g. >0.7; Murphy 1996) raises the possibility that certain species might be ''*K*-selected'' strategists that make large investments in few offspring to maximize fitness in stable environments, or ''bet-hedgers'' that reduce reproductive effort per breeding episode to cope with unpredictable conditions (Boyce 1988, Sæther et al. 1996). Understanding demographic consequences of migration is of interest from both theoretical and applied viewpoints. Identification of demographic patterns associated with different migratory options would help to explain the origin and diversity of avian life histories (Martin 1995) and could also aid conservation efforts for migratory land birds with declining population numbers (Peterjohn et al. 1995).

Greenberg (1980) proposed the time-allocation hypothesis to explain demographic differences between resident and migratory species. This hypothesis states that reproductive output should increase as a function of time spent at breeding sites and that survival will increase with time spent at nonbreeding areas of presumably milder climate. Mortality associated with migration is viewed as a migratory cost that increases with distance travelled, but one that is independent of time spent at breeding and nonbreeding sites. Several studies have tested predictions of the time-allocation hypothesis by comparing vital rates of resident and migrant species or by relating vital rates to migration distance. Some reviews have reported that residents produce more eggs or fledglings than migrants (Greenberg 1980, Mönkkönen 1992), whereas others have found opposite results (O'Connor 1985) or no difference (O'Connor 1981). Such inconsistencies may be partly due to covariation between migration tendencies and habitat use, and to the effect nest-site location has on components of fecundity (Martin 1995). Differences in annual survival have also been reported: von Haartman (1968), Greenberg (1980), Morse (1989) and Mönkkönen (1992) concluded that migrant lineages had higher adult survivorship than resident taxa, at least for some regions of Europe and North America. In contrast, O'Connor (1981) and Dobson (1990) found that resident species of British birds tended to higher survivorship than migrants, but that differences were not significant. Finally, intraspecific analyses have found that survivorship is correlated positively with migration distance in different populations of Mallards (*Anas platyrhynchos*; Hestbeck et al. 1992), but not Red Knots (*Calidris canutus*; Harrington et al. 1988).

Many of the comparisons above are problematic for one or more of several reasons. First, most studies have contrasted vital rates of birds from unrelated lineages. Life-history traits can be influenced by historical events, and interspecific comparisons are more robust if phylogenetic relationships are taken into account (Martin 1995). Second, previous reviews have relied on empirical studies that have applied different capture techniques at a range of temporal and spatial scales. In particular, indices of both recruitment and survivorship can be sensitive to the size of study plots because of difficulties in distinguishing mortality from emigration (Lambrechts et al. 1999). Finally, past studies have used estimates of annual survival that have been calculated with statistics that have proven to be unreliable (e.g. age-ratios, longevity, life-table analyses, return rates, references in Sandercock et al. 2000). Mark–recapture statistics can be a useful alternative (Burnham and Anderson 1998, White and Burnham1999), particularly when applied to systematic mist-net sampling. One potential concern for studies using mark–recapture methods is that estimates of survivorship may be biased low if the sample contains a large number of individuals that have been captured on one occasion but are never resighted again (DeSante et al. 1995, Johnston et al. 1997). This phenomenon may be due to one or more of several different processes including age-specific variation in true survival or site fidelity, presence of transient individuals, or to heterogeneity of capture (Pradel et al. 1997, Prévot-Julliard et al. 1998). However, such effects can be controlled by use of age-structured models that separate local survival in the interval after first capture from subsequent transitions.

In this paper, we examine annual survivorship of sparrows at a wintering site in northern California. The six taxa of sparrows examined in this study range from sedentary, resident species to long-distance migrants that travel to northern regions to breed (Table 1). This study improves on past work by restricting the set of study taxa to closely related species or subspecies, by standardizing the mist-net sampling effort for all study species over a 13 year period, and by using mark–recapture statistics to calculate estimates of local survival corrected for probability of resighting and for potential bias in rates introduced by birds captured on only one occasion. Our objectives were to determine local survival rates for immature and adult sparrows, to relate interspecific variation in local survival rates to tendency to migrate and migration distance, and to evaluate potential

TABLE 1. Aspects of migration and fecundity for selected sparrows that winter at Coyote Creek Field Station, California.

Species or subspecies	Life-history	Migration distance	Breeding range	Modal clutch size	Re-nesting	Broods per year	Sources[a]
Song Sparrow *Melospiza melodia gouldii*	Resident	None	Upland areas around San Francisco Bay	3–4	Y	2–3	1–4
Puget Sound White-crowned Sparrow *Zonotrichia leucophrys pugetensis*	Migrant	Short	Coastal areas of southwest British Columbia to northern Oregon	4	Y	2–3	5–9
Lincoln's Sparrow *Melospiza lincolnii*	Migrant	Moderate	Boreal forests of Alaska and northern Canada, southern Rocky Mountains	4	Y	1	10
Fox Sparrow *Passerella iliaca, unalaschcensis* lineage	Migrant	Moderate	Coastal areas of southwest Alaska to northern British Columbia	4	Y	1–2	11–14
Golden-crowned Sparrow *Zonotrichia atricapilla*	Migrant	Long	Alaska, Yukon, and northern British Columbia	4	Y	1	15–16
Gambel's White-crowned Sparrow *Zonotrichia leucophrys gambelii*	Migrant	Long	Alaska and northern Canada	5	N / Y	1	6–8, 17–18

[a] 1. Marshall 1948, 2. Johnston 1954, 3. Johnston 1956, 4. Halliburton and Mewaldt 1976, 5. Lewis 1975, 6. Morton 1976, 7. Cortopassi and Mewaldt 1965, 8. Chilton et al. 1995, 9. DeWolfe and Baptista 1995, 10. Ammon 1995, 11. Gabrielson and Lincoln 1959, 12. Rogers 1994, 13. Zink 1994, 14. Bell 1997, 15. Kessel 1989, 16. Norment et al. 1998, 17. Wingfield and Farner 1979, 18. Norment 1992.

for estimating demographic rates from populations of wintering birds.

METHODS

Study area.—Wintering sparrows were studied at the Coyote Creek Field Station of the San Francisco Bay Bird Observatory (hereafter, ''Coyote Creek'') at the southern end of San Francisco Bay, California (37°28′N, 122°03′W) over a 13 year period from September 1985 to December 1997. Habitats at the study site include riparian forest vegetation and open fields. Riparian forests were established in early 1980s as part of a restoration scheme, and are now dominated by Freemont cottonwood (*Populus fremonti*), willows (*Salix* spp.), boxelder (*Acer negundo*), and coyote brush (*Baccharis pilularis*). Open field habitats are located within and adjacent to an overflow channel. The channel floods during years of heavy winter rains, but is otherwise dry. Woody vegetation is not permitted to grow in the channel to ensure a maximal carrying capacity during flood conditions, and channel vegetation is composed of an assortment of short ($<$1 m) herbaceous plants. Qualitative observations suggest that plant communities and vegetative structure have varied over the years in both habitats.

Study species.—Six taxa of sparrows, including five species and two subspecies were examined in this study (Table 1). Phylogenetic analyses based on morphological or genetic characters are concordant, and indicate that sparrows in the genera *Melospiza*, *Passerella*, and *Zonotrichia* are closely related and form a single clade within Emberizid sparrows (Zink and Blackwell 1996, Patten and Fugate 1998). The breeding ecology of these sparrows is also similar, all are male-territorial and socially monogamous, with uniparental incubation by females and biparental care of young. The species vary in their tendency to migrate but all are common as wintering birds at Coyote Creek and elsewhere in the San Francisco Bay area.

Sparrows could be readily identified to species, and sometimes subspecies, by features of plumage, bill color, and wing length (Pyle 1997). Song Sparrows (*Melospiza melodia gouldii*, here treated as synonymous with *M. m. santaecrucis*) are nonmigratory residents of upland areas around San Francisco Bay (Table 1). Large body size, white bellies and dark plumage distinguish *M. m. gouldii* from *M. m. pusillula*, an endemic subspecies confined to nearby saltmarshes (Marshall and Dedrick 1994). Song Sparrows with rufous plumage (possibly *M. m. oriantha*, a migratory subspecies) are captured at Coyote Creek only rarely ($<$1–3 individuals per year; A. Jaramillo pers. obs.). Three subspecies of Lincoln's Sparrows (*M. lincolnii*) are thought to winter in San Francisco Bay (C. Cicero pers. comm.), but plumage differences among those forms are subtle (Ammon 1995). No attempt was made to separate subspecies among Lincoln's Sparrows, and the breeding grounds of our wintering population remain speculative. Fox Sparrows (*Passerella iliaca*) wintering at Coyote Creek were pale-plumaged members of the ''sooty group'' (i.e. the *unalaschcensis* lineage), a collection of subspecies known to breed in coastal areas of western Alaska (Zink 1994, Bell 1997).

Our sample included three taxa of crowned sparrows. Golden-crowned Sparrows (*Zonotrichia atricapilla*) are a monotypic species that breeds in northern areas of Alaska and Canada (Norment et al. 1998). In contrast, White-crowned Sparrows (*Zonotrichia leucophrys*) exhibit considerable geographical variation in morphology. Two of five subspecies were examined in this study, the ''Puget Sound'' White-crowned Sparrows (*Z. l. pugetensis*) and ''Gambel's'' White-crowned Sparrows (*Z. l. gambelii*). These two forms are readily identifiable in the hand, both as immature birds and as adults, and can be distinguished by differences in bill color, wing length, and plumage coloration (Pyle 1997). *Zonotrichia l. pugetensis* is a short-distance migrant that travels to coastal areas of Washington and southern British Columbia to breed, whereas *Z. l. gambelii* is a long-distance migrant that breeds in northern Alaska and Canada (Cortopassi and Mewaldt 1965, DeWolfe and Baptista 1995, Norment et al. 1998). Two other subspecies breed in California but do not occur at Coyote Creek. ''Nuttall's'' White-crowned Sparrows (*Z. l. nuttalli*) are resident breeders at nearby coastal sites and areas north of San Francisco Bay (Baker et al. 1981, Petrinovich and Patterson 1982). ''Mountain'' White-crowned Sparrows (*Z. l. oriantha*) are a migratory race that breeds at higher elevations at sites farther inland (Morton et al. 1972, Morton et al. 1991). Finally, the nominate subspecies (*Z. l. leucophrys*) is also migratory but is an eastern form that breeds mainly in Ontario and Quebec (Cortopassi and Mewaldt 1965).

Published information was used to categorize the six taxa as resident or migratory, and their relative migration distance as short, moderate, or long (Table 1). We also reviewed papers that reported clutch size and nesting rates for our six study taxa. Resident Song Sparrows in the local area lay relatively small clutches of three to four eggs, whereas the migratory species lay modal clutches of four or five eggs. Latitudinal variation in clutch size has been reported in several of these species as well (Johnson 1954, Morton 1976, Norment et al. 1998). Resident Song and Puget Sound White-crowned sparrows that migrate short distances frequently renest and are also multibrooded. Lincoln's, Fox, and Golden-crowned sparrows are similar in their reproductive output. Gambel's White-crowned Sparrows migrate one of the longest distances, and are unusual because females produce one relatively large clutch, and in some populations, do not renest following nest failure. Despite a smaller clutch size, Song and Puget Sound White-crowned sparrows seem to have the highest fecundity because they produce more clutches per year than sparrows migrating longer distances. Although it would be preferable to use the average number of fledglings produced per female as an index of fecundity, the data from available population studies were not adequate for such calculations.

Capture, banding, and aging of sparrows.—Sparrows were captured with two methods at the Coyote Creek Field Station: Potter ground traps baited with seeds (1985–1993) and mist nets set in a $\sim$13.5 ha grid (1985–1997). Traps and nets were set in the same locations each year and were operated for an average of 22 days ($\sim$1,320 net-hours) per month during the eight month winter period from September 1 to April 30. Upon capture, each sparrow was marked with one uniquely numbered leg band. Colored leg bands were not used and no effort was made to resight banded birds. Sparrows were classed as ''immature'' (i.e. banding codes: L = local hatchling, HY = hatch year, and SY = second year; Gustafson et al. 1997) or ''adult'' (i.e. AHY = after hatch year and older) at first capture. ''Immature'' indicates birds captured before their first breeding season; reproductive condition was unknown. Immature sparrows captured in fall or early winter were identified by extent of skull pneumatization, juvenal plumage (Song Sparrows only) and crown coloration (White-crowned Sparrows only; Pyle 1997). White-crowned Sparrows could be aged for a longer period because the Puget Sound and Gambel's subspecies retain age differences in crown coloration into late winter. Immature birds of migratory species had completed one southward migration from their natal area before capture at wintering sites.

No attempt was made to sex birds because all taxa of sparrows were monomorphic during winter. Latitudinal clines in sex ratios of wintering birds have been reported for White-crowned Sparrows (King et al. 1965, Morton 1984) and other sparrows (Ketterson and Nolan 1976), and would be a concern if survival rates differed between sexes. Although return rates sometimes differ between sexes in sparrows (Nice 1937, Petrinovich and Patterson 1982), most studies report small or no sexual differences in survival (Morton et al. 1972, Halliburton and Mewaldt 1976, Baker et al. 1981, Sullivan 1989, Smith et al. 1996, Wheelright and Mauck 1998). For the purposes of this study, heterogeneity due to intersexual variation in survival and site-fidelity is assumed to be small relative to interspecific differences.

Repeated captures demonstrated that a few individuals were long-lived. Longevity was calculated as maximum recorded lifespan plus estimated duration of the bird's natal period. Following conventions of the U.S. Bird Banding Laboratory (Gustafsen et al. 1997), the natal year was set as the previous or penultimate summer for birds first captured as juveniles or adults, respectively, and sparrows were assumed to have hatched in June of their natal year.

Construction of capture histories.—Migratory species of sparrows were generally present from late August to early May, whereas resident Song Sparrows were captured year-round. To facilitate comparisons among the six taxa of sparrows, we restricted our sample of handling records to the period that both migrants and residents were present—September 1 to April 30. Thus, each sampling period in the sparrow capture histories was composed of an eight month winter period that spanned two calendar years. Sparrows were considered present if captured at least once during a winter period, and multiple captures were not considered further. Records of migratory birds from outside the winter period, and early hatching juvenile Song Sparrows captured in April were discarded. The sampling periods were longer than the intervals between periods. Although this study design can be a problem if mortality losses occur within a winter period, simulation modeling has shown that estimates of local survival are unbiased if capture effort is standardized among years (Smith and Anderson 1987), as was the case in this study.

Survival analyses and model selection.—Return rates, or proportion of individuals that are recaptured in a subsequent year, are often used as an index of survival in migratory birds. Annual return rates to a wintering or breeding site are the product of four independent probabilities: (*i*) true survival, (*ii*) site-fidelity (i.e. $1-$probability of permanent emigration), (*iii*) annual variation in local site use or breeding propensity (i.e. $1-$probability of temporary emigration), and (*iv*) detection rates. Mark–recapture statistics were used to distinguish among those probabilities and to calculate local survival ($\phi = i \times ii$) and recapture rates ($p = iii \times iv$). Local survival improves on return rates because it is corrected for probability of recapture. However, mortality and dispersal events are still confounded and both processes must be considered when comparing estimates.

Mark–recapture analyses were conducted in three steps with program MARK (version 1; White and Burnham 1999), following procedures discussed by Burnham and Anderson (1998). Each taxa of sparrow was modeled separately. First, we selected a global model. Age and annual conditions were included because these factors affect local survival and recapture rates of many land birds. Age at first capture was treated as a group effect (grp = immature or adult) and all probabilities were modeled with time-dependence (t = time or winter period). Local survival was modeled with a modified ''age'' model that separated the interval after first capture (ϕ^1) from all subsequent transitions (ϕ^2). Two age-class models are functionally equivalent to the transient models of Pradel et al. (1997). In our global model ($\phi^1_{grp\times t}$, ϕ^2_t,

$p_{grp\times t}$), the local survival of immature and adult sparrows was treated separately in the transition after first capture ($\phi^1_{grp\times t}$) but was pooled in subsequent years (ϕ^2_t).

Second, we tested for two possible violations of the assumptions of mark–recapture methods: unequal catchability (e.g. heterogeneity or overdispersion) and nonindependence of individuals (e.g. pseudoreplication). A simulation approach was used to calculate the goodness-of-fit between our data and the global model. A distribution of expected deviances for the global model was generated from 1,000 random simulations of the capture histories of each taxon, under the assumption of equal catchability. Observed deviance was then compared to the distribution of simulated values to determine whether the global model was an adequate fit to the data. A variance inflation factor ($\hat{c}$) was calculated by dividing the observed deviance by the mean expected value. If $\hat{c}$ was <1, it was set to one (Burnham and Anderson 1998).

Third, we proceeded to improve model fit by fitting nested models with reduced numbers of parameters. Factorial models that included interactions among the factors (e.g. $grp \times t$) and main effects models (e.g. ''additive'' model: $grp + t$) were constructed by using dummy variables in design matrices (White and Burnham 1999). All models were constructed using the logit-link function, and model fit was assessed with quasi-Akaike's Information Criterion (AIC) values that included correction terms for $\hat{c}$ and small sample size (QAIC$_c$; Burnham and Anderson 1998):

$$\mathrm{QAIC_c} = -[\mathrm{Dev}/\hat{c}] + 2K + 2K(K+1)/(n-K-1),$$

where Dev is the model deviance or $-2\ln[L(\hat{\theta})]$, $\hat{c}$ is the variance inflation factor, K is the number of parameters, and n is sample size. Model selection was based on the difference in QAIC$_c$ values between models (ΔQAIC$_c$). By definition, the best fit model had a ΔQAIC$_c$ of zero but other models were considered equally parsimonious if $\Delta\mathrm{QAIC_c} \leq 2$. Akaike weights ($w_i$) were used to determine the relative likelihood of a model within the set of candidate models (Burnham and Anderson 1998):

$$w_i = \exp(-0.5\Delta_i) \bigg/ \sum_{r=1}^{R} \exp(-0.5\Delta_r)$$

where Δ_i is the difference in QAIC$_c$ between model i and the best-fit model. The ratio of Akaike weights between two candidate models (w_i/w_j) was used to quantify relative degree that a particular model was better supported by the data than another model.

All possible combinations of our global model ($\phi^1_{grp\times t}$, ϕ^2_t, $p_{grp\times t}$) yielded a candidate set of 50 models for each sparrow. To reduce total number of models to be tested, we used a hierarchical procedure to guide model construction. Probabilities were modeled in the following order: recapture rates (p), local survival of adults (ϕ^2), and local survival of immature birds (ϕ^1). Each probability was modeled in the following order: the factorial model ($grp \times t$), a main effects model without an interaction term ($grp + t$), single factor models (c) (grp or t), and then constant models (c). Liberal criteria for retention of factors were used at first ($\Delta\mathrm{QAIC_c} \leq 4$) to obtain a coarse model fit. The three probabilities were then modeled in the same sequence but using more rigorous criteria (minimum ΔQAIC$_c$). In a final step, factors were replaced in model with the lowest QAIC$_c$ value to determine whether closely related models with better fit had been overlooked.

Estimation of local survival and probability of capture.—Parameter estimates were calculated with two methods. First, annual $\hat{\phi}$ values were calculated using the model averaging procedure of program MARK. In this method, parameter estimates for each transition were obtained from all models in the set of candidate models, and a weighted average was calculated using the Akaike weights specific to each model (Burnham and Anderson 1998). Estimates of variance for each weighted average were unconditional and included the conditional sampling variance and the variation associated with model uncertainty.

Overall $\hat{\phi}$ and $\hat{p}$ values were calculated by applying the variance components procedure of program MARK to the unconstrained global model. The total variance of overall means includes process variation due to temporal causes and undesired sampling variation due to measurement error. The variance-components procedure was used to estimate the process variance (δ) of the overall mean ($\hat{\beta}$); the SE was calculated as $\delta\sqrt{n}$, where n is the number of annual estimates included in the overall estimate. Program CONTRAST (Sauer and Williams 1989) was then used to make *post hoc* comparisons of the overall mean rates of local survival among sparrows. To retain an α level of 0.05 in multiple pairwise comparisons of means, the sequential Bonferroni method was used to adjust the significance level for the number of tests (i.e. $0.05/15 = 0.003$; Rice 1989). Tests were two-tailed and considered significant at $\alpha < 0.05$; all means are presented ±1 SE.

RESULTS

In the first 12 years of the study, a total of 1,632 to 4,394 individuals were banded in each of the six taxa of sparrows. At first capture, most sparrows were aged as immature birds, and this age-class constituted 54 to 80% of the samples (Table 2). Estimates of longevity ranged between 6 to 9 years for the six taxa (Song Sparrow: 8 years 3 months, Puget Sound

TABLE 2. Numbers of sparrows banded and goodness-of-fit testing to global model $\phi^1_{grp\times t}$, ϕ^2_t, $p_{grp\times t}$.

Species	Age at banding	No. birds banded	Deviance[a] Observed	Deviance[a] Expected	$\hat{c}$[b]	$P\geq$[c]
Song Sparrow	Immature	1107	315.5	300.2	1.05	0.447
	Adult	825				
	Total	1932				
Puget Sound White-crowned Sparrow	Immature	3516	254.8	260.7	1.00	0.570
	Adult	878				
	Total	4394				
Lincoln's Sparrow	Immature	1347	141.1	119.5	1.18	0.161
	Adult	1130				
	Total	2477				
Fox Sparrow	Immature	1139	140.4	113.0	1.24	0.076
	Adult	493				
	Total	1632				
Golden-crowned Sparrow	Immature	2605	243.1	224.7	1.08	0.248
	Adult	1494				
	Total	4099				
Gambel's White-crowned Sparrow	Immature	3109	235.2	213.7	1.10	0.207
	Adult	1091				
	Total	4200				

[a] Observed deviance refers to the deviance of the global model. A distribution of expected deviances was generated from 1000 random simulations of the mark–recapture histories of each species under the assumptions of equal catchability.

[b] The overdispersion correction factor or $\hat{c}$ equals observed deviance divided by mean expected deviance, and was set to 1 if <1.

[c] P-values were obtained by examining rank of observed deviance within distribution of simulated values.

White-crowned Sparrow: 7 years 9 months, Lincoln's Sparrow: 7 years 4 months, Fox Sparrow: 6 years 7 months, Golden-crowned Sparrow: 8 years 7 months, Gambel's White-crowned Sparrow: 6 years 9 months). Longevity was not correlated with our best estimate of annual survival (i.e. ϕ^2, see below), and should probably be avoided ($r_s = 0.43$, $P = 0.40$, $n = 6$; see also Krementz et al. 1989).

Goodness-of-fit tests based on simulations indicated that the global model ($\phi^1_{grp\times t}$, ϕ^2_t, $P_{grp\times t}$) was a satisfactory starting point for all six taxa of sparrows (P-values > 0.05, Table 2). In all cases, low values of the variance inflation factor ($\hat{c} < 1.25$) indicated that the mark–recapture data were not overdispersed and that assumptions of equal catchability and independence of individuals were met.

Model selection.—Mark–recapture modeling revealed that several alternative models were usually a good fit to the data for each sparrow taxa (Table 3). In Lincoln's and Fox sparrows, five models had good support (i.e. $w_i > 0.10$) and the top three to four models were considered equally parsimonious (i.e. $\Delta\text{QAIC}_c < 2$). Nonetheless, in both species the best-fit model had better support than the other candidate models ($w_i/w_j > 1.8$). In Song, Puget Sound White-crowned, and Gambel's White-crowned sparrows, a smaller number of models were a good fit to the data. In these taxa, support for the best-fit model was only marginally better than that of the second best model ($w_i/w_j = 1.1$ to 1.5). In Golden-crowned Sparrows, only one model received strong support and was $>7.9\times$ better than any other candidate model for this species.

Four of six sparrows had best-fit models that included annual variation in the probability of capture during the study period, and all taxa had at least one parsimonious model that indicated capture rates differed between birds marked as immature and adults. Overall probabilities of capture ranged from 0.44 to 0.80 (Table 4), and sparrows first captured as immature birds were usually more likely to be recaptured than adults (4 of 6 taxa, Table 4). Annual $\hat{p}$ are not presented because p was a nuisance parameter without biological relevance.

Age-structured models that separated the interval after first capture from subsequent transitions were the best fit for local survival in all six taxa of sparrows (Table 3). Models with greater age structure were not supported, nor were models that pooled local survival in the first and subsequent transitions (i.e. Akaike weights $w_i < 0.01$). Thus, local survival was modeled separately within each of the two age

TABLE 3. Mark–recapture modeling for six taxa of sparrows wintering at Coyote Creek Field Station, California.

	Model structure[a]			Model statistics[b]			
Species	ϕ^1	ϕ^2	p	Dev.	K	$\Delta QAIC_c$	w_i
Song Sparrow	t	c	$t + grp$	352.7	28	0.00	0.457
	$t + grp$	c	$t + grp$	351.4	29	0.87	0.296
	c	c	$t + grp$	381.5	16	3.05	0.100
Puget Sound White-crowned Sparrow	$t \times grp$	t	t	277.7	50	0.00	0.364
	$t \times grp$	t	$t + grp$	275.8	51	0.20	0.329
	$t \times grp$	t	$t \times grp$	254.8	62	1.62	0.162
Lincoln's Sparrow	$t + grp$	c	c	207.3	16	0.00	0.356
	t	t	grp	182.2	27	1.21	0.197
	$t + grp$	c	grp	206.7	17	1.56	0.165
	t	c	c	211.7	15	1.70	0.153
	$t + grp$	t	grp	181.2	28	2.37	0.110
Fox Sparrow	$t + grp$	c	c	215.3	16	0.00	0.380
	t	c	c	219.3	15	1.22	0.207
	t	t	grp	189.6	27	1.94	0.144
	$t + grp$	c	grp	215.2	17	2.01	0.139
	$t + grp$	t	grp	187.4	28	2.18	0.128
Golden-crowned Sparrow	$t + grp$	t	$t + grp$	283.7	39	0.00	0.888
Gambel's White-crowned Sparrow	t	c	$t \times grp$	277.2	40	0.00	0.554
	$t + grp$	c	$t \times grp$	275.7	41	0.66	0.399

[a] Models were structured to separate local survival immediately after banding (ϕ^1), local survival in later transition (ϕ^2), and recapture rates (p). Model notation includes: c = constant, grp = group effect of age at banding (immature or adult), t = time or annual variation, $t + grp$ = main effects or ''additive'' model (t and grp only), $t \times grp$ = factorial model (t, grp, and interaction).

[b] Model fit is described by the deviance (Dev), number of parameters (K) and quasi-Akaike's Information Criterion corrected for small sizes ($QAIC_c$). Models are presented in order of fit relative to the best-fit model (i.e. $\Delta QAIC_c = 0$). Only models with good support (Akaike weight $w_i \geq 0.1$) are included in the table.

classes. In the interval immediately after first capture (ϕ^1), local survival usually differed between immature birds and adults. Interaction between age at banding and year was significant in Puget Sound White-crowned Sparrows (Table 3), and local survival after first capture was greater in immature birds than adults in 6 of 12 years (Fig. 1). In Lincoln's, Fox, and Golden-crowned sparrows, main-effects models including age at banding, year, and no interaction term were the best fit (Table 3). Difference between immature birds and adults in local survival after first capture was slight in Lincoln's and Fox sparrows and larger in Golden-crowned Sparrows (Fig. 1). The local survival of immature birds and adults did not differ in either Song or Gambel's White-crowned sparrows (Table 3, Fig. 1). Overall, probability of local survival after first capture was lower among immature birds than adults in five of six taxa (Table 4).

Local survival in subsequent intervals (ϕ^2) exhibited annual variation in Puget Sound White-crowned and Golden-crowned sparrows, but collapsed to a constant in the best-fit models for the remaining four taxa (Table 3). At least one model with annual variation in ϕ^2 was equally parsimonious in Lincoln's and Fox sparrows. Thus, model averaging yielded traces that exhibited annual variation in local survival for those four taxa and a constant probability in Song and Gambel's White-crowned sparrows (Fig. 1). In all six taxa, local survival among returning adults (ϕ^2) was greater than the rates for adults in the interval after first capture (ϕ^1, Table 4).

Local survival and migratory behavior.—Local survival was greater in resident than migratory species but was not related to distance travelled among the five migratory species. Resident Song Sparrows had local survival rates after first capture that were 6 to 11% higher than migratory taxa of sparrows; the difference was significant among immature birds but not adults (Table 4). Within the sample of migratory taxa, estimates of local survival after first capture were generally low. Local survival after first capture was negligible (<0.15) in Lincoln's and immature Fox and Gambel's White-crowned sparrows, and only moderate (0.15 to 0.29) in Puget Sound White-crowned and adult Fox and Golden-crowned sparrows. Local sur-

TABLE 4. Overall annual probabilities of local survival after first capture and in later years ($\hat{\phi} \pm 1$ SE) and recapture ($\hat{p}$) for six taxa of sparrows wintering at Coyote Creek Field Station, California during 1985 to 1997.

Species	Local survival (ϕ)[a]			Recapture (p)[a]	
	Immatures after first capture	Adults after first capture	Adults in later years	Immatures	Adults
Song Sparrow	0.310 ± 0.023^{1}	0.340 ± 0.000^{1}	0.558 ± 0.054^{1}	0.543 ± 0.036^{1}	0.437 ± 0.035^{1}
Puget Sound White-crowned Sparrow	0.197 ± 0.001^{2}	0.165 ± 0.031^{2}	0.461 ± 0.026^{1}	0.636 ± 0.025^{1}	0.591 ± 0.068^{1,2}
Lincoln's Sparrow	0.059 ± 0.009^{3}	0.085 ± 0.010^{2}	0.456 ± 0.066^{1,2}	0.502 ± 0.058^{1}	0.605 ± 0.061^{2}
Fox Sparrow	0.108 ± 0.012^{4}	0.274 ± 0.081^{1,2}	0.352 ± 0.000^{2}	0.603 ± 0.065^{1,2}	0.496 ± 0.086^{1,2}
Golden-crowned Sparrow	0.179 ± 0.015^{2}	0.280 ± 0.023^{1}	0.422 ± 0.023^{1}	0.801 ± 0.022^{2}	0.669 ± 0.057^{2}
Gambel's White-crowned Sparrow	0.110 ± 0.017^{3,4}	0.122 ± 0.023^{2}	0.432 ± 0.000^{1}	0.552 ± 0.039^{1}	0.618 ± 0.070^{2}

[a] Overall means were obtained by applying the variance components procedure of program MARK to the global model for each species. The SE of the overall mean (i.e. $\hat{\beta}$) contains process variance only, the sampling variance has been removed. Means with the same superscript are not significantly different.

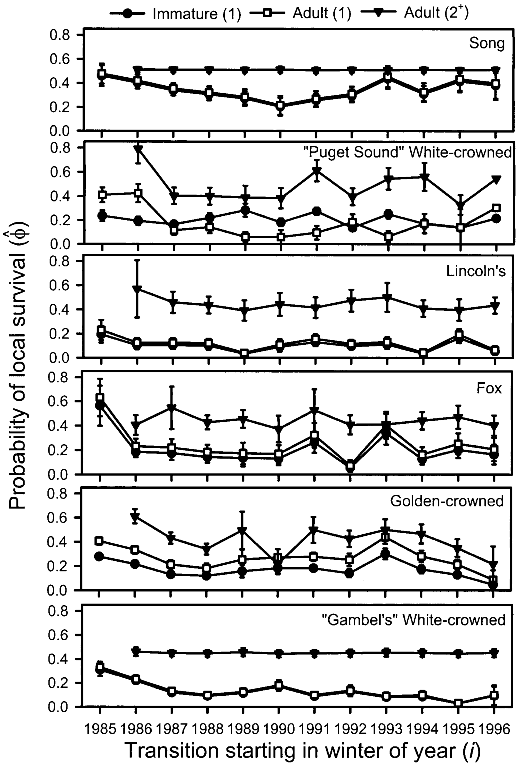

FIG. 1. Annual variation in probability of local survival for six species of wintering sparrows at Coyote Creek Field Station, California. Age-structured models were used to estimate local survival separately for immatures after first capture, adults after first capture and all birds during later intervals. Parameter estimates ($\bar{x} \pm 1$ SE) were calculated by taking a weighted average of estimates from all candidate models (Table 3), using Akaike weights (w_i) as a weighting criteria. The unconditional SE include sampling variance and the variance associated with model uncertainty.

vival after first capture did not covary with migration distance among the five migratory taxa but was higher among Puget Sound White-crowned than Gambel's White-crowned sparrows.

Among older adults that returned to Coyote Creek at least once, the highest probability of local survival was observed in Song Sparrows (0.56). The local survival of four of five migratory taxa were remarkably consistent (0.42 to 0.46), with only Fox Sparrows having somewhat lower rates (0.35). Confidence intervals were generally larger for $\hat{\phi}^2$ because samples of returning adults were smaller. Thus, local survival rates of Song and Fox sparrows were significantly different, but Song Sparrows did not otherwise differ from the other four taxa nor did local survival significantly differ among the five migratory taxa.

DISCUSSION

In this study, survival rates were estimated for six sparrow taxa that differed in migratory behavior and distance. Our analyses resulted in two major findings. First, local survival rates of sparrows were lowest after first capture and higher in subsequent transitions. Second, interspecific differences in local survival rates of birds that returned at least once were not related to migration tendency nor to migration distance. We evaluate the variation in local survival with regard to mortality and dispersal, and conclude by discussing the value of population studies of wintering birds.

PROCESSES AFFECTING LOCAL SURVIVAL IN THE YEAR AFTER FIRST CAPTURE

Local survival rates were ranked immature birds after first capture $<$ adults after first capture $<$ site-faithful adults in five of six taxa of sparrows (Table 4, Fig. 1). Local survival has also been reported to be lowest in the interval following first capture for other populations of wintering birds (Karr et al. 1990, Warnock et al. 1997, Reed et al. 1998). Moreover, newly marked individuals had lower return rates to wintering sites than site-faithful birds in Puget Sound White-crowned (33 vs. 61%; Mewaldt 1976), Gambel's White-crowned (26 vs. 49%; Linsdale 1949; 28 vs. 53%; Mewaldt 1976), and Golden-crowned (18 vs. 57%; Linsdale 1949) sparrows. At least four nonexclusive explanations could account for such results.

1. *Age-specific variation in true survival.*—Low local survival among immature sparrows may have been due to low rates of true survival. All sparrows were banded quickly and released soon after capture, but handling may have been more stressful for immature birds. Competition for territories is strong in resident populations of Song Sparrows (Arcese et al. 1992), leading to high disappearance rates among immature birds (Arcese 1989, Smith and Arcese 1989). Wintering populations of *Zonotrichia* sparrows are structured by dominance hierarchies, and social status is signalled by age-related changes in plumage (Fugle et al. 1984, Keys and Rothstein 1991). Immature sparrows of subdominant status may have higher mortality during winter or subsequent migration periods because they have less access to food resources, take greater risks during foraging, or have poorer physiological condition (Piper and Wiley 1990a, Slotow and Rothstein 1995, Slotow and Paxinos 1997, Leary et al. 1999).

2. *Age-specific variation in site-fidelity.*—Local survival after banding could have been low if immature or migratory sparrows permanently emigrated to new wintering areas. Immature birds had the highest local survival among resident Song Sparrows, and dispersal may be low in this species because territories are held year round (Halliburton and Mewaldt 1976, Smith et al. 1996). In contrast, migratory sparrows are known to change wintering areas after their first year (Ketterson and Nolan 1982, Barrentine and McClure 1993). Indeed, migratory species have greater dispersal rates than resident birds (Weatherhead and Forbes 1994, Paradis et al. 1998), possibly because they are able to sample more habitats during their annual movements. Induction of site fidelity in sparrows is a function of time spent at a breeding or wintering site (Ralph and Mewaldt 1976, Ketterson and Nolan 1990, Morton et al. 1991), and displacement experiments have shown that immature sparrows return to previous wintering sites at lower rates than adults (Sumner and Cobb 1928, Ralph and Mewaldt 1975, Barrentine 1990), particularly if moved in early winter (Ralph and Mewaldt 1976). Thus, site fidelity of migratory sparrows appears to be flexible among immature birds but becomes fixed with increasing age.

3. *Presence of transients.*—Newly banded sparrows may have had low local survival if a large proportion of the sample was either dispersing individuals or passage migrants that were moving to breeding or wintering sites elsewhere (Johnston et al. 1997). At a nearby site, DeSante et al. (1995) estimated that 58% of Song Sparrows and up to 79% of other landbird species were transient individuals. Migratory passerines sometimes show fidelity to stopover sites (Cantos and Tellería 1994, Merom et al. 2000), but that phenomenon is unlikely to bias our estimates of local survival. Stopover duration is short in White-crowned

Sparrows (median <5 days, *Z. l. leucophrys*; Cherry 1982) and other land birds (<2 to 4 days; Woodrey and Moore 1997, Yong et al. 1998), and recaptures of migrants should be rare. Cortopassi and Mewaldt (1965) marked >6,000 White-crowned Sparrows at stopover sites in areas where the species does not breed or winter, but did not recapture any bird in more than one year.

4. Heterogeneity of capture.—Heterogeneity of capture can explain low local survival after first banding if some individuals are less likely to be recaptured than others, effectively leading to permanent emigration (Pradel et al. 1995, Prévot-Julliard et al. 1998). Sparrows on the margins of our study site would have less opportunity to be caught if they had large home ranges that encompassed few of our traps or mist nets. That problem may have affected some study species because our study area was large (~13.5 ha) compared to the territory size of resident Song Sparrows (<1.5 ha; Johnston 1956, Halliburton and Mewaldt 1976), but was similar or smaller than estimates of home-range size reported for wintering *Zonotrichia* sparrows (0.5 to 20 ha; Price 1931, Piper and Wiley 1990b, Ralph and Mewaldt 1975).

In summary, local survival of newly captured birds is best viewed as the integrated product of variation in true survival, site-fidelity, presence of transients, and heterogeneity of capture. Distinguishing among these processes is rarely possible in small-scale studies of vertebrate population dynamics, and would require additional information on large-scale movements that is currently unavailable. Thus, interspecific comparisons of local survival after first capture are unlikely to be meaningful. Nonetheless, our work joins DeSante et al. (1995) and Johnston et al. (1997) in demonstrating that two age-class ($\phi_{2ac \times t}$, p_t) or transient models (τ_t, ϕ_t, p_t) should be considered when analyzing mark–recapture data from systematic mist net sampling.

SURVIVAL RATES OF SPARROWS VERSUS MIGRATORY BEHAVIOR

The most robust estimates of local survival were those of sparrows that returned to the study area at least once. Local survival rates of returning birds are not affected by inclusion of transients or heterogeneity of capture, but variation in true survival and site-fidelity are both potentially relevant. Survival rates of sparrows are apparently constant once a bird becomes an adult (Baker et al. 1981, Nol and Smith 1987). Site-fidelity is often strong once a wintering area is selected (Ralph and Mewaldt 1976). On the other hand, *Zonotrichia* sparrows are sometimes sensitive to local conditions, immigrating into vacant areas if congeners are removed (Mewaldt 1964), and dispersing if food resources are reduced (Piper 1990). In other migratory passerines, fidelity to wintering sites can be either strong (Holmes et al. 1989, Holmes and Sherry 1992) or weak (Ketterson and Nolan 1982, Terrill 1990). Thus, some sparrows may be flexible in their use of wintering habitats at Coyote Creek, but we had no *a priori* reason to expect interspecific differences in site-fidelity among returning adults.

Site-faithful individuals had similar rates of local survival in the six study taxa examined here, ranging from 0.35 in Fox Sparrows, 0.42 to 0.46 in Lincoln's, Puget Sound White-crowned, Golden-crowned, and Gambel's White-crowned sparrows, to a high of 0.56 in Song Sparrows (Table 4). Our estimates of local survival for site-faithful birds were greater than return rates of migrants to wintering and breeding sites (Table 5), presumably because return rates did not correct for birds captured only once or recapture rates <1. Our estimates were more comparable to return rates in resident populations, possibly because those studies also examined site-faithful birds. Only Nichols et al. (1981) and Karr et al. (1990) have used mark–recapture models to estimate survival rates for sparrows, and reported annual rates of local survival of 0.53 for Dark-eyed Juncos (*Junco hyemalis*), 0.55 for Seaside Sparrows (*Ammodramus maritimus*), and 0.61 for White-throated Sparrows (*Zonotrichia albicollis*). Survival rates calculated with a variety of analytical methods range from 0.46 to 0.68 for other species of sparrows (*n* = 10, Martin 1995). Thus, most species of sparrows appear to have moderate probabilities of annual survival regardless of their ecology.

The time-allocation hypothesis of Greenberg (1980) predicts high fecundity and low survivorship among species that are resident or relatively short distance migrants. The prediction of high fecundity would be supported if variation in clutch size, renesting rates, and broods

TABLE 5. Mean annual return rates previously reported for our study taxa. No published estimates are available for Lincoln's or Fox sparrows.

Life-history	Site	Species or subspecies	Return rate	Sex[a]	Age[b]	No. birds or bird yr	No. yr	Source[c]
Migrant	Wintering grounds	*Z.l. pugetensis*	0.18	MF	IA	115	2	1
			0.42	MF	IA	123	2	2
		Z. atricapilla	0.12	MF	IA	143–331	3	3
			0.18	MF	IA	52–375	11	4
			0.28	MF	IA	197	2	1
		Z.l. gambelii	0.17	MF	IA	282	5	5
			0.26	MF	IA	27–185	11	4
			0.31	MF	IA	380	2	2
Migrant	Breeding grounds	*M. melodia*	0.20	M	A	152	4	6
			0.54	MF	A	47–75	3	7
		Z.l. oriantha	0.32	MF	A	81–84	3	8
			0.36	MF	A	69	7	9
		Z. atricapilla	0.37	MF	A	19	2	10
Resident	—	*M. melodia*	0.47	MF	A	45–177	5	11
			0.55	MF	A	—	16	12
			0.65	M	A	31	5	13
		Z.l. nuttalli	0.43	MF	A	402	6	14
			0.54	MF	A	131–465	4	15

[a] M = males only, MF = both sexes.

[b] A = adults only, IA = immature and adults.

[c] 1. Price 1931, 2. Mewaldt 1976. 3. Sumner 1933, 4. Linsdale 1949, 5. Blanchard and Erickson 1949. 6. Weatherhead and Boak 1986, 7. Nice 1937, 8. Morton et al. 1972. 9. King and Mewaldt 1987, 10. Norment et al. 1998, 11. Halliburton and Mewaldt 1976, 12. Arcese et al. 1992, 13. Wilson et al. 2000, 14. Petrinovich and Patterson 1982, 15. Baker et al. 1981.

per year prove to be positively correlated with number of fledglings produced per female (Table 1). However, the second prediction was clearly rejected: survivorship was not related to migratory behavior nor to migration distance among the six taxa of sparrows considered here (Table 4). Long-distance migrants did not appear to be *r*-strategists with high fecundity and low survival (cf. von Haartman 1968, O'Connor 1985). Instead, variation in fecundity but not adult survival is consistent with aspects of bet-hedging theory (Boyce 1988, Sæther et al. 1996). Sparrows that are resident or travelling short-distances may be producing multiple clutches of fewer eggs as a response to variable environmental conditions. Southerly breeding sites may be unpredictable for several reasons: a longer breeding season with a less abundant food supply, greater densities of nest predators, or clines in the abundance of interspecific nest parasites. Similarities in adult survival also suggest a tradeoff between fecundity and survival of juveniles. Although mortality rates after independence can be high in resident passerines (Smith and Arcese 1989, Sullivan 1989, Magrath 1991), comparable estimates are not yet available for migratory species.

In the best test of the time-allocation hypothesis to date, Hestbeck et al. (1992) found that survival rates but not fecundity were positively correlated with migration distance in Mallards, a result opposite to this study. However, they found little support for the underlying assumptions of the hypothesis, which are based on putative tradeoffs among vital rates at different stages of the annual cycle. Data on seasonal variation in survival are available for a few land birds but northerly populations of wintering sparrows have low overwinter survival (Ketterson and Nolan 1982, Arcese et al. 1992), whereas overwinter survival of migratory passerines can be high at Neotropical sites (Holmes et al. 1989, Rappole et al. 1989, Conway et al. 1995). A critical test of the time-allocation hypothesis will require estimates of mortality during breeding, migration, and winter periods for multiple closely related species.

As one of the first attempts to use robust estimates of survivorship to address the time-allocation hypothesis, it is not yet clear whether our findings can be generalized to other migratory birds, especially Neotropical migrants. All six sparrow taxa migrate and winter within the northern temperate-zone. Although distances travelled by Gambel's White-crowned and Golden-crowned sparrows rival those of some Neotropical migrants, ecological conditions likely differ between northern temperate and tropical wintering sites. In the past, demography of Neotropical migrants has usually been compared to temperate-zone residents (Sherry and Holmes 1995, Nichols 1996). If Neotropical migrants are derived from tropical ancestors (Cox 1985, Levey and Stiles 1992), comparisons to tropical residents may be more relevant in the future (e.g. Yellow vs. ''Mangrove'' Warblers [*Dendroica petechia*]; Wiedenfeld 1992).

Study of wintering birds: An underused approach in population biology?—To date, the potential for estimating vital rates from wintering populations has been unappreciated, even though migratory land birds are often faithful to wintering areas (Mewaldt 1976, Holmes et al. 1989, Piper and Wiley 1990a, this study). Fidelity to breeding sites is affected by genetic considerations related to mate selection, and by ecological factors such as local knowledge of food and predator dispersion. In contrast, fidelity to wintering sites should be determined by ecological factors alone, unless pairing occurs at nonbreeding areas, as in waterfowl (Robertson and Cooke 1998). For at least some migratory land birds, site attachment is stronger at wintering sites than at breeding areas (Holmes and Sherry 1992). Thus, application of mark–recapture methods to wintering populations could yield more reliable estimates of local survival if disappearances reflect mortality and not permanent emigration.

Depending on the structure of an avian population, estimates of survivorship from wintering sites may also give a better indication of overall population trends. For example, Puget Sound White-crowned Sparrows have discrete breeding populations where local song dialects are distinct (Chilton et al. 1995). Study of singing behavior in overwintering birds has shown that individuals from different breeding populations are often found at the same wintering sites (DeWolfe and Baptista 1995). Estimates of survivorship from wintering populations of that subspecies reflect conditions throughout the breeding range, and could be preferable to estimates of survivorship derived from a limited set of breeding sites.

Study of wintering populations has at least two limitations for estimating vital rates necessary for demographic models of population viability. Fecundity can only be estimated with indirect methods such as age-ratios (Bart et al. 1999, Newton 1999), and studies of breeding birds cannot be circumvented. Moreover, migratory species have to complete at least one southward migration to reach a wintering site, and postfledging survival of juvenile birds cannot be determined. Although results of this study are encouraging, it should be noted that our samples contained a high proportion of individuals that were never recaptured, resulting in low local survival in the interval after first capture. Calculation of adult survival was only possible here because consistently high netting effort over a 13 year period allowed a large sample of sparrows to be marked. Although our study demonstrates that study of wintering birds holds great promise for estimating survival rates in vagile species, it also indicates that this approach will be less suitable for short-term projects of low intensity, particularly for relatively short-lived species.

ACKNOWLEDGMENTS

We dedicate this article to the founders who established the Coyote Creek Field Station (formerly Coyote Creek Riparian Station) in 1982, particularly the late Dr. Richard Mewaldt and Michael Rigney. This long-term study would not have been possible without the dedicated efforts of numerous volunteers and interns who participated in banding sessions and entered handling records into a computer database. We thank all for their commitment to wildlife conservation in the San Francisco Bay Area. Previous versions of the manuscript were greatly improved by the comments of P. Arcese, S. A. Gauthreaux, Jr., J. L. Grenier, K. Martin, F. R. Moore, T. S. Sillett, and N. T. Wheelright. B.K.S. was supported by a Killam Postdoctoral Fellowship and National Science Foundation grants to S. R. Beissinger (DEB-9503194, IBN-9407349) during preparation of this manuscript. Partial funding for this project was provided by the Santa Clara Valley Water District, through their Coyote Creek Flood Control Project Wildlife Monitoring Program. This article is contribution number 82 of the San Francisco Bay Bird Observatory.

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Associate Editor: F. Moore