

JUVENILE AND ADULT SURVIVAL OF SWAINSON'S THRUSH (*CATHARUS USTULATUS*) IN COASTAL CALIFORNIA: ANNUAL ESTIMATES USING CAPTURE-RECAPTURE ANALYSES

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ABSTRACT.—We estimated annual rates of survival for juvenile and adult Swainson's Thrushes (*Catharus ustulatus*) using capture–recapture analyses from 22 years of mist-netting data in coastal California ($n = 2,651$ individual captures). Our apparent survival estimate was 56% for adults and 25% for juveniles. We are the first to estimate an annual juvenile survival rate for a Neotropical migrant using capture–recapture probability estimates. Like most estimates of annual survival, we could not distinguish between dispersal away from our study area (which is likely high for juveniles) and mortality. Hence, survival is underestimated. However, our juvenile survival estimate did not include the period from fledging to independence, a time when mortality can be high. Many researchers have assumed juvenile survival to be half that of adult survival in population models (e.g. source–sink). Our juvenile to adult survival ratio was 45% (95% CI = 27 to 65%). We caution researchers from simply assuming that juvenile survival approximates half of adult survival when modeling populations and suggest using a range of values. Using a range of values is prudent because of the potential for annual variation, site-specific variation, and especially because estimates are imprecise or completely lacking. Received 10 April 2003, accepted 6 June 2003.

RESUMEN.—Estimamos tasas anuales de sobrevivencia de juveniles y adultos de *Catharus ustulatus* utilizando análisis de captura-recaptura de 22 años de redeo en la costa de California ($n = 2651$ capturas individuales). Nuestra estimación aparente de sobrevivencia fue de 56% para adultos y 25% para juveniles. Este es el primer estudio que estima una tasa de sobrevivencia juvenil anual para una migratoria neártica-neotropical utilizando estimaciones de probabilidad de captura-recaptura. Al igual que la mayoría de las estimaciones de sobrevivencia anual, no pudimos distinguir entre dispersión fuera de nuestra área de estudio (probablemente alta en juveniles) y mortalidad. Por tanto, la sobrevivencia está subestimada. Sin embargo, nuestra estimación de sobrevivencia juvenil no incluyó el período desde que el pollo abandona el nido hasta el momento en que alcanza la independencia, un período en el que la mortalidad puede ser alta. En modelos poblacionales muchos investigadores han supuesto que la sobrevivencia juvenil es la mitad de la adulta (por ejemplo en modelos de fuente-resumidero). Nuestra proporción de sobrevivencia de adultos a juveniles fue de 45% (95% IC = 27% a 65%). Advertimos del riesgo de suponer que la tasa de sobrevivencia juvenil es la mitad de la adulta y sugerimos usar una serie de valores. Utilizar una serie de valores es prudente debido a factores potenciales como la variación anual, variación local y especialmente porque las estimaciones son imprecisas o inexistentes.

INVESTIGATIONS INTO THE viability or growth rate of animal populations often require estimates of adult survival and juvenile survival to breeding age. Estimates of adult survival currently exist for many migratory passerines (e.g. DeSante et al. 1998), yet estimates of juvenile survival remain elusive. Accurate estimation of the population growth rate, critical for assess-

ing metapopulation dynamics, is dependent upon an accurate estimate of juvenile survival. For passerines in general and migratory passerines in particular, that parameter is notoriously difficult to estimate, because natal site fidelity of migratory passerines is apparently extremely low and dispersal distances may be great. Hence, the convention in many population models (e.g. source–sink assessment) has been to divide adult mortality by the average number of offspring fledged (Ricklefs 1973) or,

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as has been more frequently done, assume juvenile survival to be half of adult survival (e.g. Temple and Cary 1988, Noon and Sauer 1992, Donovan et al. 1995). Researchers acknowledge the limitations of such an approach and are employing models to predict demographic parameters not measurable in the field (Powell et al. 1999, Perkins and Vickery 2001) as well as statistical methods that adjust potentially low estimates of juvenile survival (possible when data on natal dispersal distances are available; Baker et al. 1995).

Estimates of survival from fledging to independence have been reported for year-round residents and short-distance migrants (e.g. Dhondt 1979, Krementz et al. 1989, Sullivan 1989, Magrath 1991), and recently, radiotelemetry studies have contributed to our knowledge of that stage of the life cycle for migratory passerines (Anders et al. 1997, Powell et al. 2000, Yackel Adams et al. 2001). However, juvenile survival estimates from a passerine's hatching-year to the following spring (breeding age for most species) are scarce. The majority of studies where juvenile survival has been estimated, either by capture-recapture-type analyses or enumeration (i.e. return rates), are from year-round resident species, many of which are confined to geographically isolated areas (e.g. Great Tit [*Parus major*], Clobert et al. 1988; Florida Scrub-Jay [*Aphelocoma coerulescens*], Woolfenden and Fitzpatrick 1996; island populations of House Sparrow [*Passer domesticus*], Ringsby et al. 1999; Puerto Rican Vireo [*Vireo latimeri*], Woodworth et al. 1999).

Juvenile survival has been loosely defined in the literature depending on the questions under investigation. Here we define juvenile survival as the period from postfledging independence to the following spring (breeding age for most passerines). Ours is a long-term mist-netting study of Swainson's Thrushes (*Catharus ustulatus*) and the majority of birds captured in their hatching-year have already reached independence (Johnson and Geupel 1996). A more accurate estimate of juvenile survival, however, would include mortality during the postfledging period (from fledging to independence). In North America, the length of time from hatching to the following spring is variable by species but can be roughly estimated at 9 to 11 months.

Johnson and Geupel (1996) noted a high return rate (18%) for young Swainson's Thrushes

to our Palomarin study area prompting us to examine whether we could use capture-recapture survival estimators to calculate juvenile survival. Hence, we used data from 22 years (1979 to 2000) of standardized mist-netting at a site in coastal California to estimate adult and juvenile survival and recapture probabilities for Swainson's Thrush. We followed Cormack-Jolly-Seber methods to calculate annual survival rates; we could not distinguish mortality from permanent dispersal, which results in underestimates of survival (i.e. we are estimating apparent survival, not actual survival). To our knowledge, however, we are the first to report a survival probability from hatching-year to the following spring for a Neotropical migrant.

METHODS

From 1979 to 2000, mist-netting was conducted at the Palomarin Field Station of the Point Reyes Bird Observatory (PRBO), located in the Point Reyes National Seashore, Marin County, California (37°56'N, 122°45'W). From 1979 to 1988, nets were run three days per week from December to March, seven days per week from April to November; from 1989 to 2000, nets were run three days per week from December to April, and six days per week from May to November. Detailed descriptions of the site and netting protocol have been presented elsewhere (e.g. DeSante and Geupel 1987, Johnson and Geupel 1996, Gardali et al. 2000).

We studied a subspecies of Swainson's Thrush endemic to California, *C. u. oedicus*. This subspecies breeds primarily within riparian areas of coastal California and apparently differs in breeding season habitat preferences from all other subspecies (riparian vs. coniferous; Evans Mack and Yong 2000). Population numbers were stable in California from 1966 to 2000 (Sauer et al. 2001), as well as at the Palomarin Field Station in summer 1980–1994 (Johnson and Geupel 1996) and during fall migration 1979–1999 (Ballard et al. in press). The wintering range of *C. u. oedicus* is thought to be the Tres Marias Islands and mainland Nayarit (Mexico) south and east along Pacific coast to Nicaragua, north to central and eastern Guatemala, possibly northeastern Chiapas (Phillips 1991). Hatch-year birds were distinguished from adults by the degree of skull pneumatization as well as the presence or absence of buffy tipped greater coverts (Pyle 1997).

Apparent survival and recapture probabilities were estimated using program MARK 2.0 (White and Burnham 1999) to fit nested models. Program RELEASE (Burnham et al. 1987) available in MARK was used to perform a goodness-of-fit test on the global model. Effects of age (*a*; juvenile and adult),

group (g ; transient and site-attached for those originally banded as juvenile or adult), and time (t ; year) on survival and recapture probabilities were examined. Following Cooch and White (2002), the notation $\Phi a2-./.$ represents survival of two age classes with no time-dependence; however, some individual birds were banded as both juveniles and adults, so age only for birds originally banded as juveniles was also parameterized. Models were developed on the basis of *a priori* biological hypotheses involving the explanatory variables mentioned above. Bias-corrected Akaike's information criterion (AIC_c) as computed in MARK was used to guide model selection, applying the principle of parsimony where appropriate (Lebreton et al. 1992, Anderson and Burnham 1999, White and Burnham 1999; Table 1). The model with the lowest AIC_c was considered to be the most appropriate, and differences in AIC_c between that model and every other model (ΔAIC_c) were used to identify other likely models. Models with $\Delta AIC_c < 2$ can be said to exhibit strong support and those with $\Delta AIC_c = 2-4$ exhibit some support (Burnham and Anderson 1998).

Recapture probability of transients has been shown to be lower than recapture probability of site-attached individuals in other species (Peach et al. 1991, Chase et al. 1997, Pradel et al. 1997). Such heterogeneous recapture probabilities violate an assumption of capture-recapture methodology (the "iii assumption"; see Lebreton et al. [1992] for discussion).

Whether that was the case for Swainson's Thrushes was examined by comparing recapture and survival probabilities of both groups: presumed transients and site-attached individuals during the breeding season. The breeding season was defined as 15 May to 31 July following Johnson and Geupel (1996). A double-capture criterion was used to distinguish transients from site-attached individuals; individuals that were caught at least two times during any breeding season (at least seven days apart) were presumed site-attached, other individuals (captured during the breeding season) were presumed transients (following Chase et al. 1997, Gardali et al. 2000, Bayne and Hobson 2002).

RESULTS

A total of 2,651 Swainson's Thrushes were captured during the breeding season over the course of the study. Of those, 365 were site-attached adults, 924 were transient adults, 215 were site-attached juveniles, and 1,147 were transient juveniles.

We found no reason to reject the global model: $\Phi(g^*t)p(g^*t)$ (goodness-of-fit, $\chi^2 = 86.90$, $df = 120$, $P = 0.989$). Models selected as most appropriate to these data were (1) where apparent survival and recapture probabilities varied

TABLE 1. Ranking models of apparent survival (Φ) and recapture (p) probabilities as a function of age (a ; juvenile and adult; $a2-./.$ represents two age classes with no time-dependence), group (g ; transient and resident, originally banded as hatch-year or after hatch-year), time varying (t ; year), constant ("."; not time varying) for capture-recapture mist-netting data, 1979-2000. np = number of estimable parameters. See text for further discussion of model notation.

Model	np	AIC_c	ΔAIC_c	AIC_c weights	Deviance	Δ Deviance
$\Phi(a2-./ + g)p(a2-./ + g)$	8	1,987.523	0	0.48042	593.364	191.022
$\Phi(a2-./ + g)p(g)$	8	1,987.84	0.317	0.41	593.682	191.34
$\Phi(a2-./ *g)p(g)$	10	1,990.479	2.956	0.10958	592.291	189.949
$\Phi(g)p(g)$	8	2,009.791	22.268	0.00001	615.632	213.29
$\Phi(.)p(g)$	5	2,025.243	37.72	0	637.116	234.774
$\Phi(t)p(g)$	25	2,031.131	43.608	0	602.531	200.189
$\Phi(.)p(a2-./ + g)$	5	2,037.173	49.65	0	649.046	246.704
$\Phi(g)p(g^*t)$	88	2,057.338	69.815	0	497.12	94.778
$\Phi(g)p(.)$	5	2,069.233	81.71	0	681.106	278.764
$\Phi(g)p(t)$	25	2,070.672	83.149	0	642.072	239.73
$\Phi(.)p(g^*t)$	85	2,072.986	85.463	0	519.182	116.84
$\Phi(g^*t)p(g)$	88	2,083.461	95.938	0	523.243	120.901
$\Phi(t)p(g^*t)$	104	2,088.07	100.547	0	493.388	91.046
$\Phi(g^*t)p(g^*t)$	157	2,114.347	126.824	0	402.342	0
$\Phi(g^*t)p(.)$	85	2,143.328	155.805	0	589.524	187.182
$\Phi(g^*t)p(t)$	104	2,153.499	165.976	0	558.817	156.475
$\Phi(.)p(.)$	2	2,397.297	409.774	0	1,015.188	612.846
$\Phi(.)p(t)$	22	2,401.26	413.737	0	978.771	576.429
$\Phi(t)p(.)$	22	2,415.034	427.511	0	992.544	590.202
$\Phi(t)p(t)$	41	2,418.608	431.085	0	957.184	554.842

by age (to two years) and group (transient vs. site attached for birds originally banded as juveniles and adults), and (2) where apparent survival varied by age and group and recapture probability varied only by group (Table 1). Both models assumed that after reaching maturity, birds originally banded as juveniles had similar survival rates or recapture probabilities to birds originally banded as adults (i.e. they were estimated as the same parameter by MARK). The former had a slightly lower AIC_c value and both models had the same number of parameters (Table 1). Estimates of apparent survival from both models were nearly identical, but here estimates from the model where both apparent survival and recapture probability varied with age and group are presented (Table 2). Recapture probability was found to be over 3× greater for site-attached adults than for transient adults and nearly 4× greater for site-attached juveniles than for transient juveniles (Table 2). Apparent annual survival probability of site-attached adults (56%) was considerably higher than for transients (36%; Table 2). The same was true for our apparent juvenile survival estimates as the estimate for site-attached individuals was 25% and only 9% for transients (Table 2). Ratio of juvenile to adult survival for site-attached individuals was 0.446 (95% CI = 0.27–0.65).

DISCUSSION

Recapture and survival probabilities of transients were far lower than those of site-attached individuals as has been shown in several studies (e.g. Peach et al. 1991, Chase et al. 1997). To pool both groups in capture–recapture analyses would violate the assumption of homogeneity of recapture probabilities between groups (Lebreton et al. 1992). Although grouping individuals on the basis of transient or resident status using our criteria may exclude birds that are actually residents, it is very unlikely that

it includes birds that are transients. Thus, it is a conservative method. Additionally, breeding season mortality has been found to be low (Powell et al. 2000, Sillett and Holmes 2002), and thus limiting our survival estimation to birds known to have survived through part or all of one breeding season is unlikely to bias our survival estimates high. Lacking real data on transient or resident status of individuals captured, this appears to be a viable option for estimating survival (Bayne and Hobson 2002). Survival estimates of transient individuals are likely so low as to not be very useful. We consider the models of site-attached individuals to provide our best estimates and those will be used in the following discussion.

Most studies of annual survival suffer from the inability to distinguish between permanent dispersal and true mortality. As a result, survival estimates are likely low and should be viewed as conservative. Our estimate of adult survival, 56%, is nearly identical to a 57% estimate reported from 11 years of capture–recapture–resighting data for Swainson's Thrushes from a single site in New Hampshire (Nichols et al. 1981). Adult Swainson's Thrush survival estimates from the Monitoring Avian Productivity and Survivorship (MAPS) program were 62% from the Northwest Region (63 sites combined), 47% from the Southwest Region (1 site), and 44% from the Alaska and Boreal Canada Regions (8 sites combined; DeSante et al. 1998).

Interpretation of our juvenile survival estimate, 25%, is difficult. On one hand, it can be viewed as an underestimate because we could not distinguish dispersal from mortality. Juvenile dispersal away from the natal areas for migrants appears to be the norm and it is likely that Swainson's Thrushes dispersed beyond the range of our sampling effort. On the other hand, our juvenile survival estimate does not account for the mortality that occurs between fledging and independence. Indeed, mortality during

TABLE 2. Apparent survival and recapture estimates for adult and juvenile residents and adult and juvenile transients. The final survival (Φ) and recapture (p) models contained eight parameters: age (juvenile and adult) and group (transient and resident); Φ (age + group) p (age + group).

	Survival probability (SE, 95% CI)	Recapture probability (SE, 95% CI)
Juvenile residents	0.247 (0.043, 0.173–0.340)	0.741 (0.103, 0.499–0.891)
Adult residents	0.564 (0.025, 0.515–0.612)	0.598 (0.040, 0.518–0.674)
Juvenile transients	0.087 (0.029, 0.045–0.162)	0.225 (0.083, 0.103–0.424)
Adult transients	0.364 (0.041, 0.288–0.448)	0.161 (0.031, 0.109–0.231)

that stage can be great for other songbirds (e.g. Magrath 1991, Anders et al. 1997, Yackel Adams et al. 2001) as well as for Swainson's Thrush in coastal California (J. D. White unpubl. data). For example, postfledging mortality of Wood Thrush (*Hylocichla mustelina*) ranges from 25 to 58% (14 and 8 weeks postfledging, respectively; Anders et al. 1997, Powell et al. 2000). To what extent those discrepancies offset each other is unknown. However, it is unlikely that they are equal, further complicating the interpretation of our juvenile survival estimate.

Why does this Swainson's Thrush population exhibit high natal site-fidelity? Johnson and Geupel (1996) suggested that because this subspecies breeds "almost exclusively" in coastal riparian woodlands the options for dispersal are few (relative to habitat generalists) potentially causing young to return closer to their natal grounds. However, this subspecies of Swainson's Thrush does breed in nonriparian habitats in coastal California where vegetative structure is suitable (Shuford 1993, J. D. White pers. obs.). Natal philopatry for other populations of Swainson's Thrush has not been examined. Hence, although dispersal possibilities may be limited for this population, other factors that have the potential to explain such high natal site-fidelity should be explored for this thrush (e.g. behavior and social structure).

To our knowledge, we are the first to calculate an annual juvenile survival estimate for a Neotropical migrant using capture-recapture methodology. Our data on survival of adult and juvenile Swainson's Thrushes supports the commonly used assumption that juvenile survival is about half of adult survival. That assumption appears to have originally progressed from Ricklefs (1973) suggestion that juvenile survival from fledging to breeding age can be estimated by dividing the adult mortality rate by the number of fledglings per adult (assuming a stable population). For year-round resident passerines, Ricklefs (1973) concluded that the juvenile to adult survival ratio was ~25%. Greenberg (1980), however, hypothesized that for migrants, the ratio was more likely closer to 50%. Using Ricklefs (1973) approach, other researchers have found that juvenile survival for migrants is ~50% of adult survival (Temple and Cary 1988, Noon and Sauer 1992, Donovan et al. 1995), and that ratio is still currently used in source-sink models (e.g. Budnik et al. 2000,

Simons et al. 2000). Nolan (1978) used return rates to estimate survival from postfledgling independence to the first breeding season (39%) and annually as adults (65%) for the migratory Prairie Warbler (*Dendroica discolor*). That yields a juvenile to adult survival ratio of 60%. However, when incorporating Nolan's (1978) estimate of survival from fledging to independence (82%) into the equation, the ratio drops to 49%.

Because estimates of juvenile survival for other Neotropical migrants are currently very difficult to measure, and even the estimate reported here suffers from the inability to account for permanent dispersal and mortality during the postfledging period, we strongly recommend that researchers use a range of values when modeling population dynamics.

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