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ESTIMATES OF ADULT SURVIVAL, CAPTURE PROBABILITY, AND RECAPTURE PROBABILITY: EVALUATING AND VALIDATING CONSTANT-EFFORT MIST NETTING

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Abstract. We evaluate the use of capture–recapture data gathered with constant-effort mist-netting to infer adult survival, comparing estimates obtained using the program SURGE with direct observations on color-banded individuals. In addition, we determined capture probability of breeding adults in relation to several factors, such as distance from nest to nearest net. Data were collected as part of a long-term, on-going study of species breeding at the Palomarin Field Station, Point Reyes National Seashore, concentrating on Wrentits (*Chamaea fasciata*). Capture probability of breeding Wrentit adults was strongly related to distance from nest to nearest net and, independently, to the number of intervening territories between nest and net. In addition, females (and their mates) laying early in the season were less likely to be caught than those laying later. Breeding adults whose nests were more than 200 m from the closest mist net were rarely caught. Most adults caught were transient individuals, not holding local breeding territories. Territory-holders were caught repeatedly; non-territory holders were not. Recapture probability of territory-holders in the following year (if alive) was estimated at 71%, but only at 5% for those not holding local territories. Survival of Wrentit breeding adults was estimated to be 57%, which was slightly below estimates based on re-sightings (59% to 64%). However, survival estimated on the basis of capture–recapture of all adults (ignoring territorial status) was only 38%. We suggest that, in the absence of information regarding territorial status, survival analyses be restricted to individuals caught at least twice in a season. This is an effective method for screening out transient individuals.

Key Words: capture–recapture, constant effort netting, productivity, survival, transients, validation, Wrentit.

Populations of certain North American landbird species appear to be declining strongly (reviewed in Hagan and Johnston 1992, Finch and Stangel 1993). For effective management responses to be formulated, underlying causal factors responsible for the declines must be identified. To understand the causes of population decline requires detailed demographic information. However, the primary, long-established North American monitoring programs, specifically the Breeding Bird Survey, do not provide this information.

The three most critical demographic processes underlying population growth and decline are (1) adult survivorship, (2) reproductive success (i.e., production of young, or "productivity"), and (3) recruitment of young into the breeding population. These three demographic components are the most critical because the change in breeding population size from one year to the next, representing decline or recovery of a species, can be directly attributed to a combination of these three components (provided that immigration balances emigration). The need for researchers, managers, and agencies to assess such primary demographic parameters has been repeatedly stressed by many authors (Temple and Wiens 1989, DeSante et al. 1993b, Nur and Geupel 1993b).

Mist-netting appears to be a potentially powerful and efficient means of collecting critical data on demographic parameters such as annual survival and reproductive success, and is the cornerstone of several monitoring programs, including the Constant Effort Sites (CES) Scheme of the British Trust for Ornithology (Baillie et al. 1986, Bibby et al. 1992, Peach 1993, Peach et al. *this volume*), and, more recently, the Monitoring Avian Productivity and Survivorship (MAPS) program of the Institute of Bird Populations (DeSante et al. 1993b, *this volume*). However, the accuracy and validity of inferences based on mist-netting data have only recently been studied (though see du Feu and McMeeking 1991), and we know little about the limitations of data derived from constant effort mist-netting (CEM). Finally, in the absence of information on the specific portion of the sampled population to which mist-netted birds belong, it is impossible to develop methods of data collection and data analysis that best measure demographic parameters of the target portions of the population (such as local breeders).

Both CEM and intensive observations of color-banded individuals have been underway at the Point Reyes Bird Observatory (PRBO) since 1980. Because the same population has been studied with different methodologies, we are able to evaluate demographic inferences made using the CEM methodology, by comparing results with inferences made using a second methodology. In addition, we are able to estimate capture probability, which is rarely known for natural populations, and evaluate whether captured individuals are a random sample of those present at the breeding site.

Here we report selected results of a project that we refer to as "The Mist-Net Validation Study," with regard to adult survival, capture probability, and recapture probability. We consider factors influencing capture and recapture probability, which could therefore bias demographic estimates. In this paper, we report results from a single site over the period 1981–1991. Additional aspects of the project have been reported in Silkey et al. (1999) and Nur et al. (2000).

METHODS

The study species is the Wrentit (*Chamaea fasciata)*, which has been the subject of relatively little prior study (Erickson 1938, Geupel and DeSante 1990, Geupel and Ballard 2002). Wrentits are monogamous, year-round, territorial residents, and both parents share in parental care such as nest-building and incubation. The Wrentit is considered to be quite sedentary (Erickson 1938, Johnson 1972), and we found that <1% of breeders move their territories between years on our study site (Geupel and DeSante 1990, Geupel and Ballard 2002). This make the species well suited for estimating survivorship on the basis of capture–recapture data. Wrentits maintain year-round territories and that, together with the sedentary nature of this species, makes them good candidates for a validation study, because birds observed on the study grid are likely to be the same ones caught in the nets.

The field work was conducted at PRBO's Palomarin Field Station, located just within the southern boundary of the Point Reyes National Seashore and adjacent to the Pacific Ocean. On the main 36 ha study site, we simultaneously carried out constant effort mist-netting, nest searches, intensive spot-mapping, and behavioral observations of color-banded individuals.

Constant effort mist-netting was conducted using 20, 12-m mist nets comprising 14 netting sites (Fig. 1). Eight sites (14 nets) were located on the edge of mixed, evergreen forest habitat comprised primarily of coast live oak (*Quercus agrifola*), California bay (*Umbellularia californica*), Douglas-fir (*Pseudotesuga menziesii*), and California buckeye (*Aesculus californicus*). The other six single nets were located in disturbed coastal scrub, which is the preferred habitat of Wrentits (Erickson 1938, AOU Check-list 1983). This was composed primarily of coyote bush (*Baccharis pilularis*), California sage *(Artemisa californica*), bush monkey flower (*Mimulus aurantiacus*), poison oak (*Rhus diversiloba*), California blackberry (*Rubus vitifolius*), and California coffeeberry (*Rhamnus californica*) interspersed with introduced grasses. For further description of the study area see DeSante and Geupel (1987) and Silkey et al. (1999).

Net locations were adjacent to, and extended across, approximately 25% of the 36 ha study plot (Fig. 1). Net locations were selected so as to maximize the number of birds caught (L. R. Mewaldt, pers. comm.). The standardized mist-netting procedure was described by DeSante and Geupel (1987) and continued with only minor change during the study period, 1981–1991. Briefly, nets were run 7 days/week for 6 h, beginning 15 min after local sunrise (weather permitting) from 1 May (from 1 April prior to 1989) to approximately 25 November, and 3 days/week (Wednesday, Saturday, and Sunday) from December through end of March (through end of April, since 1989).

Detailed monitoring of individuals was conducted on the 36-ha study plot and has been described elsewhere (Geupel and DeSante 1990). In brief, identities and territory boundaries of color-marked individuals were determined from detailed spot-mapping censuses conducted a minimum of 3 days/week during the breeding season (15 March–31 July) throughout the 11 years of the study. Each territorial individual was observed a minimum of once every two weeks, and normally at least once per week.

Concentrated efforts were made to locate and monitor all nest attempts of all territorial pairs on the study area from 1981 through 1985, and from 1987 through 1991. No attempt was made to locate nests in 1986 and effort was reduced in 1980, hence we excluded those years from analyses of fledged young. The method of locating and monitoring Wrentit nests was described in Geupel and DeSante (1990). Nearly all successful nests (those fledging one or more young) were found before fledging, and nestlings were individually color-banded. Additional individuals were color-banded when first caught in mist-nets as hatching year (HY) or as after-hatching year (AHY) birds.

Here we analyze survival and capture probability with respect to territorial status; all individuals were classified as "territory holders" or "non-territory holders" according to whether or not they were known to maintain breeding territories on or adjacent to the study grid. Whereas all territory holders were presumed breeders (which could be confirmed through nest-finding and monitoring), non-territory holders were mostly transient individuals. Non-territory holders may have been "floaters" (*sensu* Stutchbury and Zack 1992), but it is also possible that some individuals bred outside the study area. Note that some non-territory holders were floaters displaying local site fidelity (Nur et al. 2000).

We examined differences in capture rates (per season and over the observed lifetime of individuals) for adults, comparing territory holders and non-territory holders, using Poisson regression (StataCorp 1997). We used linear models to test for differences in capture dates between known territory holders and non-territory holders (Neter et al. 1990), after determining that assumptions of this method were met (Nur et al. 1999). We evaluated differences in capture probability of territorial (breeding) adults with respect to distance of the nest from nearest net, number of

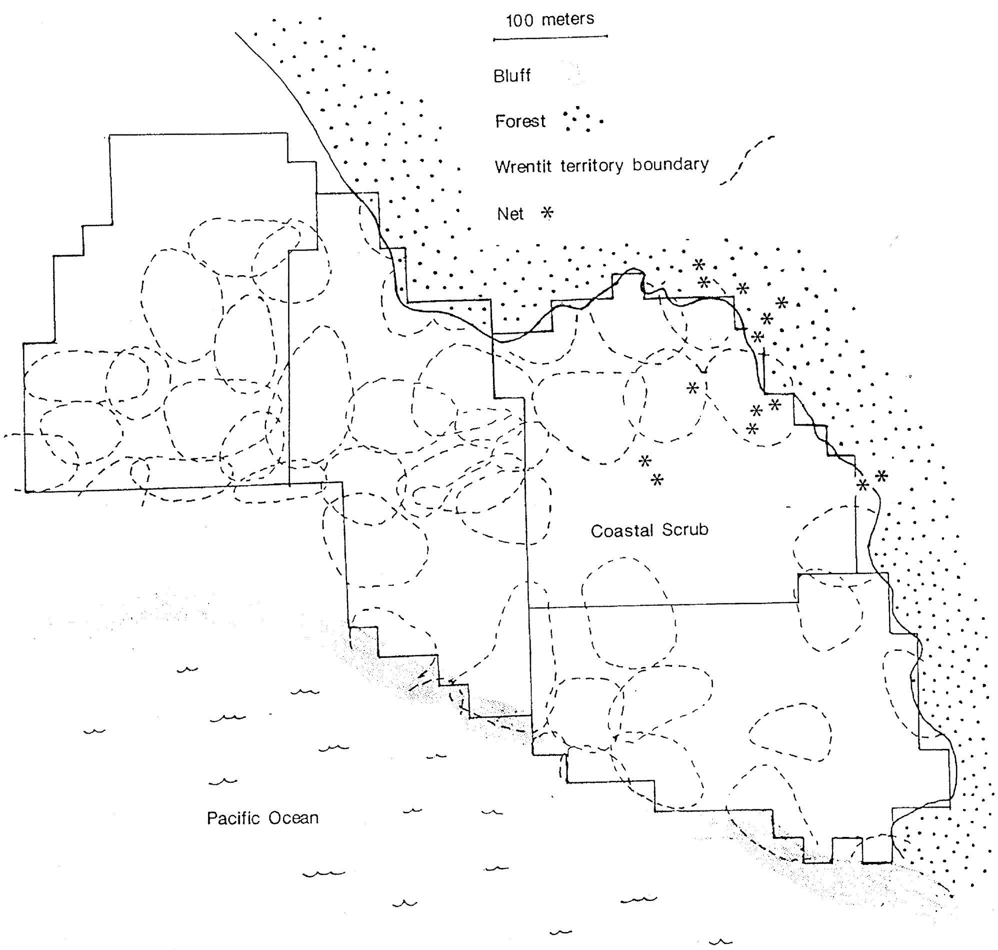

FIGURE 1. Palomarin Field Station, Point Reyes National Seashore. Nest-searches and territory-mapping of color-banded birds took place in the four contiguous area marked by solid, rectilinear lines, totaling 36 ha. Constant effort mist-netting was conducted at nets marked with asterisks. Dotted lines enclose Wrentit territorial boundaries for a typical year (1985).

territories between a bird's territory and the nearest net, sex, age, and various measures of reproductive success (date of completion of first clutch, number of young hatched or fledged, the number of clutches or broods), using multiple logistic regression (Hosmer and Lemeshow 2000). Date of clutch completion was transformed to the square of the number of days since 21 March (two days prior to the earliest first-egg date in the sample).

To analyze survival probability and recapture probability (i.e., the probability a bird that has survived to year x is caught in year x), we used the statistical program SURGE (Lebreton et al. 1992, Cooch et al. 1996). All analyses were conducted on the mist-net capture–recapture data from 333 different individuals caught over 11 years, and the results compared with detailed observations on individually color-banded Wrentits (244 different individuals for a total of 523 breeder-years). We first analyzed all captures, stratifying on territorial status, and then carried out analyses on capture data that pooled all adults.

Statistical analyses were carried out using STATA 5.0 (StataCorp 1997). Results give estimates ± SE, unless otherwise stated, and were considered significant if $P < 0.05$.

RESULTS

Influences on Capture Probability of Adults

Territorial status

Most of the adult Wrentits caught in the study did not hold territories within the study area (Table 1). In general, there were about three times as many non-territory holders as territory holders (means = 26.4 and 8.4, respectively; Table 1), although the

TABLE 1. CAPTURE OF AHY WRENTITS OVER 10 YEARS IN RELATION TO TERRITORIAL STATUS

Year	Number of local breeders	Number of non-territory holders	Percent local breeders
1981	8	35	19
1982	8	33	20
1983	12	30	29
1984	10	9	53
1985	9	28	24
1986	7	47	13
1987	8	32	20
1988	10	35	22
1989	5	14	26
1990	6	12	33
1991	10	16	39

Notes: Local breeders were birds known to hold territories in the study area. Non-territory holders were birds that either did not breed, or bred off the study area.

proportion of territory holders was unusually high in 1984 (53%). The number of non-territory holders varied more markedly among years than did the number of territory holders (Table 1), but the ratio of territory holders to non-territory holders did not vary significantly between years (Likelihood Ratio Statistic [LRS] = 26.94, df = 10, P = 0.076). Results were quite similar when only breeding season captures were considered.

Territory holders and non-territory holders were caught throughout the netting season. The two groups did not differ in mean first capture date (24 May ± 35.3 days [SD] for territory holders vs. 29 May ± 29.6 days [SD] for non-territory holders; ANOVA, P > 0.15). In general, fewer adults were captured in July and August (whether territory holders or non-territory holders).

Territorial status influenced the number of times an individual was recaught in the same season (Table 2). Non-territory holders were usually caught only once during a given year (78%), whereas local breeders were usually caught multiple times (71% more than once; 53% three or more times in the same year).

Over the entire study period, 66% of territory holders were recaptured at least once, whereas 56% were recaught more than once and 31% were recaught six times or more. Only four territory holders (out of 59) had any breaks in their capture–recapture records (i.e., a year in which they were not caught, flanked by one or more years in which they were caught). By contrast, only 20% of non-territory holders were recaptured at least once, and only 5% more than once. The difference in number of total captures for the two groups was highly significant (P < 0.001, Poisson regression).

Most (74%) non-territory holder birds were first caught in the winter or spring as after-hatching year individuals (i.e., they were neither locally fledged young nor caught in the nets in their first calendar year of life). In contrast, 52% of territory holders caught in nets were locally fledged young or were caught in nets in their first calendar year of life.

Capture probability of territory holders in relation to distance from nets

Over the 11-year study period, 523 breeders were identified on the study grid through intensive observations of color-banded individuals (the same individual was counted multiply if it bred in more than one year). Of these, 93 (17.8%) were captured in mist nets some time during the year, nearly all during the breeding season. By far the most important influence on capture probability was distance between the nest and the nearest mist net. All individuals breeding within 50 m of a net were caught (N = 40), while those breeding more than 200 m from the nearest net were rarely caught (0.8%, N = 389; Fig. 2). In between 50 and 200 m, the proportion of breeders caught in nets declined in a smooth fashion (Fig. 2), ranging from 82% caught among those breeding 50–75 m from a net, to 17% caught among those breeding 175–200 m from a net. The statistical significance of distance to the net in predicting capture of a known local breeder was very high (P < 0.001, logistic regression).

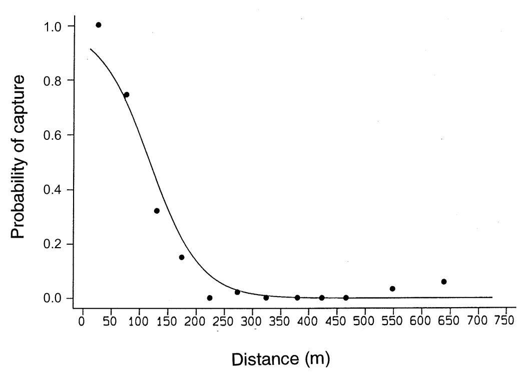

FIGURE 2. Capture probability of Wrentit breeders in relation to distance (m) from the nest to the nearest mist net, 1981–1991. Filled circles show proportion of breeders caught for breeders grouped in 50 m intervals: 0–50 m, 50–100 m, etc. Beyond 500 m, data are shown in 100 m intervals. Solid line gives the best fit to the data using logistic regression.

TABLE 2. FREQUENCY OF CAPTURE AND RECAPTURE OF WRENTITS WITHIN A YEAR, IN RELATION TO TERRITORIAL STATUS. (INCLUDES ONLY INDIVIDUALS CAUGHT AT LEAST ONCE DURING THE BREEDING SEASON)

Local breeders			Non-territory holders		
N times captured	Frequency[a]	Percent	N times captured	Frequency[a]	Percent
1	22	29	1	196	78
2	14	18	2	37	15
3	10	13	3	9	4
4	12	16	4	3	1.2
5	5	7	5	3	1.2
6	3	4	6	1	0.4
7	6	8	7	2	0.8
8–14	4	5	–	–	–
Total	78	100	Total	251	100

[a] Individuals were included more than once if caught in multiple years.

To examine whether territorial boundaries influenced capture probability, we compared proportion captured with respect to the number of territories a Wrentit had to traverse to reach the nearest net (Table 3). This analysis was restricted to birds breeding within 200 m of a net, because we showed above that Wrentits breeding at a greater distance from any net were rarely caught. Where a net was included within a Wrentit's territory, the Wrentit was almost always caught; conversely, Wrentits breeding more than two territories away were never caught (Table 3). Distance to nearest net and number of intervening territories to nearest net had independent and statistically significant effects on capture probability ($P = 0.001$ and $P = 0.011$, respectively).

Other factors influencing capture probability of breeders

Date of first clutch completion varied widely in the sample of breeders (minimum, median, and maximum first clutch completion dates were 23 March, 26 April, and 30 June, respectively). Earlier-breeding birds were less likely to be caught than those breeding in the middle or later in the breeding season (Table 4). However, for all breeders whose first clutch was completed from about 21 April on, capture probability was similar, at about 26%. First clutch completion date had a significant effect on capture probability when distance to nearest net was statistically controlled ($P = 0.044$).

Among breeders, there was a correlation between age and capture probability (one-year old individuals were more likely to be caught than older birds), but this relationship was not significant after controlling

TABLE 3. CAPTURE PROBABILITY IN RELATION TO TERRITORY LOCATION INCLUDING ONLY WRENTITS BREEDING WITHIN 200 M OF THE NEAREST MIST NET

Territory location[a]	Number of birds	Percent caught
0	56	96.4
0.5	24	62.5
1	15	6.7
1.5	7	14.3
2	12	25.0
2.5–3	4	0.0

[a] Coding for N territories: 0 = net was within Wrentit's territory; 0.5 = net was in territorial no-man's land (outside territorial boundary but not within neighbor's territory); 1, 2, 3 = net was one, two or three territories away; 1.5, 2.5 = as with 0.5, but an additional territory or two away.

for distance to nearest net ($P > 0.1$). Capture probability showed no significant association with the number of young hatched or fledged, the number of clutches or broods, or the sex of the breeder ($P > 0.4$ in each analysis).

SURVIVAL AND RECAPTURE PROBABILITY

Analyses stratified according to territorial status (territory holder vs. non-territory holder) resulted in estimated survival probabilities of 57% and 38%, respectively (Table 5). Recapture probability was estimated to be 71% for territory holders and 5% for those who were not. The difference in recapture probability between the two groups was significant ($LRS = 14.69$, $P = 0.001$), but the difference in survival probability was not ($P > 0.3$), due to lack of precision regarding the estimate of non-territory holder survival. Low precision was related to the fact that this category of individual was very unlikely to be recaptured the next year.

Annual survival of territory-holding birds caught in mist nets varied from 17–82%, and usually (7 out of 10 years) in a narrower range of 41–78%. Survival of territory holders did not vary significantly with age ($LRS = 7.96$, $P > 0.5$) or year ($LRS = 8.26$, $P > 0.5$). However, survival estimates showed a tendency

TABLE 4. EFFECT OF BREEDING DATE (DATE FIRST CLUTCH COMPLETED) ON CAPTURE PROBABILITY OF WRENTITS

Date 1st clutch completed	Number of breeders	% caught
Before 11 Apr	65	7.7
11–20 Apr	63	14.3
21–30 Apr	67	26.9
1–10 May	49	26.5
11–21 May	33	21.2
after 22 May	36	27.7

Note: Date categorized into 10-day intervals.

TABLE 5. RESULTS OF SURGE ANALYSIS ON MIST-NET CAPTURES OF WRENTITS, BY TERRITORIAL STATUS

	Survival probability	95% CI	Recapture probability	95% CI
Local breeders	0.574	0.47 – 0.67	70.8	0.53 – 0.84
Non-territory holders	0.376	0.13 – 0.72	4.8	0.01 – 0.18

to increase with age, consistent with our observations on the color-banded population (Geupel and Ballard 2002).

Analysis of resightings of color-banded birds gave an estimated survival probability of 58.3 ± 2.9% and resighting probability of 91.5 ± 3.1% for females. For males, the estimates were 69.1 ± 2.4%) and 93.4 ± 1.9%. Survival based on resightings differed for the two sexes (likelihood ratio test, P = 0.004), but resighting probability did not. Mean adult survival (averaging values for males and females) based on resighting data was 63.7%, which was somewhat greater than the adult survival estimate obtained from capture data for territory-holding individuals (57.4%), but the confidence intervals of the two estimates overlapped. Thus, survival estimates based on capture–recapture analyses of territory holders caught in mist nets were consistent with those derived from sighting–resighting analyses of color-banded territory holders.

Most investigators running a constant-effort mist-netting program can not distinguish local breeders from non-territory holders. We therefore analyzed data for all mist-net-caught adults, pooling data from territory holders (59 different individuals) and non-territory holders (274 different individuals). The pooled analysis showed no significant variation with year or age, and gave a survival estimate of 30.6% (95% Confidence Interval of 22–41%), vs. 57% for local breeders alone. Recapture probability was estimated at 38.2% (95% CI of 23–56%), as opposed to 71% for known local breeders.

Even though analysis of capture–recapture data gives skewed estimates of survival when non-territory holders are included, it may still provide a reasonable index of annual survival. We investigated whether such an annual index could reliably predict annual survival, by comparing it with survival analyses based on resightings of color-banded birds. There was a trend for the two survival estimates to vary in the same direction (Fig. 3), but the correspondence between the two indices was not significant (R^2 = 0.252, P = 0.14, linear regression). The year 1986 was an outlier, yielding the highest survival estimate of the ten years according to resighting,

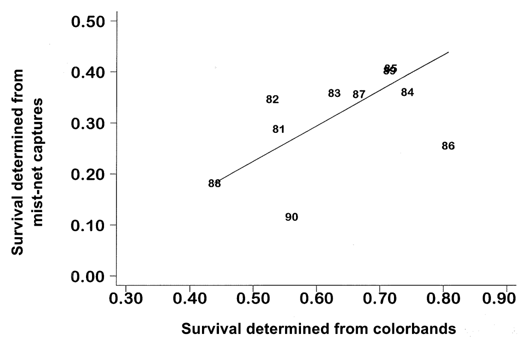

FIGURE 3. Comparison of Wrentit survival indices. Values for each year are shown by two digit codes. 1985 and 1989 are superimposed. On the *x*-axis is survival as estimated by resighting of color-banded individuals. On the *y*-axis is the SURGE estimate of survival using the pooled data (not differentiated by breeding status). Because 1986 was an aberrant year (see text), the best least-squares fit to the data excludes 1986.

but a relatively low estimate of survival according to capture–recapture data (third lowest). That year was aberrant in other respects (DeSante and Geupel 1987), and if 1986 was excluded, there was a significant correlation between the two survival indices (R^2 = 0.518, P = 0.029, linear regression).

DISCUSSION

The most important determinant of capture probability for adults in our study was distance from the net. A similar result was obtained for juveniles (see Nur et al. 1995), but the quantitative relationship between distance and capture probability differed for the two classes. For adults, few were captured that bred more than 200 m from the nearest net. Juveniles, however, were caught with a near-constant probability of ~14% beyond 300 m, up to a least 700 m. The catchment area for juveniles was likely more than a kilometer, maybe several. Thus, the populations being sampled by nets were very different for the two age classes. This has implications for the use of estimates of productivity derived by dividing the number of HY birds caught by the sum of AHY + HY captures (as is the practice of the Constant Effort Sites Scheme and MAPS program). This will not pose a serious problem if the numbers of HY birds within 200 m of nets (the area which samples adults) always fluctuate in parallel with numbers of HY birds further from the nets, but this may not be the case, and the subject deserves greater study.

Other than distance from the net, there appeared to be no important factors influencing capture probability of breeders, except that the earliest breeding birds were less likely to be caught. We have no explanation for this result. We speculate that seasonal differences in vegetation (and thus conspicuousness of the nets) may be responsible, but this needs to be examined directly.

The difference in year-to-year variability in number of breeders as opposed to number of transients caught reflected the greater constancy of capture among breeders, presumably because all those breeding close to the nets were caught in every year, whereas all those breeding some distance away were almost never caught. Annual fluctuations in the number of transients is discussed elsewhere (Nur et al. 2000), and is influenced by demographic processes such as last year's production of fledglings and breeding population size.

The most important result of the study was that survival derived from mist net capture–recapture data was underestimated unless local breeders and non-territory holders could be differentiated, due to an almost 18-fold difference between the two groups in recapture probability. If true non-breeders could be distinguished from those transient birds that bred off the study area, then at least non-breeding transients could be excluded from survival analyses. Unfortunately, Wrentit breeders and non-breeders cannot be distinguished in the hand, because both groups commonly display partial brood patches (PRBO, unpubl. data). The same problem is likely to apply to other species as well, such as those in which males do not develop brood patches. Even when the female brood patch is more highly developed among breeders than non-breeders in part of the breeding cycle (e.g., during incubation and the brooding phase), such differences are unlikely to persist throughout the three months or more that constant effort mist netting is conducted. Date of capture might provide some clues as to breeding status, but at least in the Palomarin Wrentit population, breeders and non-breeders cannot be distinguished by this means, and we expect this would also hold true for many other species.

One solution to the problem of differentiating local breeders and transients (whether the latter are breeders or non-breeders) would be to establish the identity of territory-holders within range of mist-nets through the use of unique color-bands or other markings, as in this study. For Wrentits, this identification need be done only within 200 m of the nets, but for other species a greater range would be prudent (perhaps 500 m or more, depending, in part, on territory size). Such an effort would be more time-consuming than the standard mist-netting protocol, but might be justified for a species of high concern.

A second, more expedient solution relies on our observation that non-territory holders were rarely recaptured within the same season, whereas territory holders were usually recaptured (Table 2). Survival could be estimated from only those individuals that had been recaptured in the same season. This would not eliminate the problem of transients, but should definitely reduce its magnitude. Data from some true breeders would be discarded, but at least in Wrentits, only 29% of breeders were not recaught at least once in the same year. An implication of this approach is that, in establishing a constant-effort mist-netting program, one goal would be to maximize the number of adults recaptured, as opposed to number of first captures. Running nets as many days per 10-day period as is feasible would further that goal, but would only be helpful if there was no net-avoidance. The fact that breeding Wrentits were caught so often in the same year, and usually in the breeding season, implies little net-avoidance in this species, even though these birds had ample opportunity to learn where nets were placed. Nets were in permanent locations, and operated at least 3 times/week (daily for more than 6 months of the year).

We applied the within-season recapture criterion to survival analyses of Wilson's Warbler (*Wilsonia pusilla*) capture–recapture data from the Palomarin Field Station (Chase et al. 1997). Individuals were classified as non-transient or transient on the basis of whether they were or were not caught two or more times in the breeding season, at least 7 days apart. Recapture probability for putative transients was only one-fifth that of non-transients (likelihood ratio test, $P < 0.001$). The survival estimate for all individuals pooled was 31%, whereas the estimate exclusive of putative transients was about 46%. True survival in this population was unknown, but is likely to be about 50%.

We have also analyzed data for the Song Sparrow (Nur et al. 2000), with similar results. Territory-holders and non-territory holders had very different recapture probabilities and pooling the two classes of adults resulted in low (biased) survival estimates, whereas distinguishing the two classes of individuals improved survival estimates. One difference between Palomarin Song Sparrows and Wrentits was that for the former, survival estimates for mist-net-caught, known territory holders were still substantially lower than survival as determined from analysis of resightings of color-banded breeders (47% vs. 60%, respectively; Nur et al. 2000). However, for the Song

Sparrow, the double-capture criterion (by which individuals caught twice in the same breeding season are considered non-transients) was very effective in yielding a survival estimate which matched the estimate obtained from capture–recapture analyses of color-banded individuals (both methods yielded estimates of 60% survival for males and females pooled). Thus, the use of the double-capture criterion was substantiated for the Song Sparrow, and that finding supports its use in analyses of Wilson's Warbler survival (Chase et al. 1997). Similar results were obtained by Peach (1993) for several European passerine species.

Even though Wrentit survival estimates were severely skewed when breeders and transients were not distinguished, there may still be value in a survival index based on year-by-year estimates for pooled data. We could not show a significant correlation between the mist-net survival indices and estimates based on individually marked birds, but there was reasonable correspondence between the two survival measures in most years. Any marked temporal trend in survival would probably be detected by the pooled mist-net survival index. We wish to point out, however, that mist-net studies may or may not be able to accurately assess differences in survival between sites. To our knowledge, no validation studies have been carried out to date on this topic.

Since this study, mark–recapture models have been developed to deal specifically with the effect of transients (Pradel et al. 1997). It would be valuable to analyze this data set (where territorial status of individuals is known, not inferred) using Pradel's model, to compare results with those based on color-band resighting data, and to analyze capture–recapture data for known local breeders only.

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