

Validating the use of constant effort mist-netting to monitor avian populations

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Summary: Validating the Use of Mist-nets in Monitoring Avian Populations

Constant-effort mist-netting has been proposed as a means of obtaining information on demographic processes of avian populations. To determine whether data gathered from a standardized regime of mist-netting yields valid results regarding adult survival, to determine the probability of capture and recapture of individuals, and to determine whether these probabilities might be biased by one or more factors, the Point Reyes Bird Observatory analyzed data on Wrentits (*Chamaea fasciata*) gathered over eleven years. On the study site, at Palomarin Field station, Point Reyes National Seashore, Wrentits were mist-netted, nests of all breeding birds were located and their young banded, and the adults were individually color-banded and their territories determined.

Capture probability was strongly related to distance from the nest to the nearest mist-net, for both juveniles and adults. Breeding Wrentits were seldom caught more than 200 m from their nest, but juveniles were regularly caught to 700 m and beyond. The catchment area for juveniles likely extends to several kilometers. The probability a juvenile was caught declined with fledging date. Juveniles were almost always first caught 20 to 60 days after fledging. Most adults caught were non-breeders. Non-breeders were very transient; consequently recapture probability in the following year was very low (estimated to be 4%, using the statistical program SURGE). In contrast, recapture probability was high for breeders (71%). There was no evidence for net-avoidance. Most breeders were caught three times or more during the same season, most non-breeders were never recaptured. Age, reproductive success and sex did not influence capture probability of breeders; the earliest breeding Wrentits were least likely to be caught.

Analyzing capture/recapture data from mist-nets with SURGE and differentiating breeders and non-breeders, yielded a survival estimate of 57.4% for breeders, a value close to those obtained from re-sightings of color-banded birds in a subsequent year (59% to 64%). However, pooling data from breeders and non-breeders, yielded a survival estimate of 31% and recapture probability of 38%. The aberrant value for survival is due to non-breeders (with very low recapture probability) being lumped with breeders (whose recapture probability was high). We present recommendations for further work and to guide monitoring programs. In particular, we stress the importance of attempting to distinguish breeders from non-breeders if one wishes to infer survival from capture/recapture data. We suggest that restricting the analysis to individuals caught more than once in the same season may be helpful in this regard.

INTRODUCTION

Populations of many North American landbird species appear to be declining at an alarming rate (reviewed in Hagan & Johnston 1992; Finch, Stangel & Martin in press). Migrant species, especially those wintering in the Neotropics, seem particularly threatened, though it is hard to determine how widespread problems are, in the face of sparse data for many species and for many regions of the continent. Government agencies and Non Governmental Organizations are faced with the challenge of identifying the factors precipitating this decline, as a first step in formulating effective management responses. To understand the causes of population decline requires detailed demographic information, information that established national monitoring programs, specifically the Breeding Bird Survey (which uses point counts to derive an index of breeding abundance) cannot provide.

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 and only these components (provided that immigration balances emigration). The need for researchers, managers and agencies to assess such primary demographic parameters has been stressed by many in recent time (Temple & Wiens 1989, DeSante in press, Martin & Nur in press, Ralph et al. in press).

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), and more recently, the Monitoring Avian Productivity and Survivorship (MAPS) program, of the Institute of Bird Populations (DeSante in press). However, the accuracy and validity of mist-netting have yet to be established, nor we do know the limitations or qualifications of data derived from

constant effort mist-netting. Finally, in the absence of knowledge of the population from which mist-netted birds originate, it is impossible to develop methods of data collection and data analysis that best measure their intended targets.

In 1992 the Point Reyes Bird Observatory (PRBO) commenced a project, funded by Grant Agreement No. 14-48-00009-92-1278 between U.S. Department of Interior Fish and Wildlife Service and PRBO, to investigate the accuracy and validity of mist-net data for collecting certain demographic parameters that are of critical importance for interpreting the significance of population trends detected by other national monitoring programs, such as the Breeding Bird Survey.

The original proposal for the project (submitted to U.S. Fish & Wildlife Service in fall 1991) was to investigate several demographic parameters, but the scope of the project was subsequently reduced (to coincide with the reduced budget of the project). The objectives of the current project were four-fold.

Our first objective was to examine mist-net based measures of adult survival that rely on state-of-the-art statistical analysis of capture-recapture data, and in particular to compare results from constant-effort mist-netting with PRBO's detailed observations on individually colorbanded birds that breed at PRBO's coastal scrub study site, Palomarin Field Research Station. Our goal was to determine whether mist-net data can indeed provide valid estimates of adult survival and/or reliable indices of trends in adult survival.

The second objective was to examine an important assumption of demographic inferences based on constant-effort mist-netting data: that birds caught are a random sample of those alive (or breeding). More generally, the second objective was to investigate what factors influenced the probability a bird was caught in a standardized mist-netting regime. Such factors, if they exist, can lead to bias and imprecision in estimating survival and productivity of avian species on the basis of mist-net data. This component of the project was carried out on both juveniles (Hatching Year birds) and adults. We compared the known population of birds breeding or fledging at Palomarin with the sample obtained from mist-netting.

Likewise the third objective was to examine recapture probability to determine whether recapture probability of birds in subsequent years is high and, if not, to examine factors that might influence recapture. In this part of the analysis we focused on adults.

The fourth objective was to make recommendations for the conduct of constant-effort mist-netting, as part of a population monitoring program, and for the analysis of such mist-net data.

The statistical analyses have been conducted on the Wrentit (*Chamaea fasciata*), a species for which we have very good data from 12 years of intensive study on a 36 ha study plot, coupled with 16 years of standardized mist-netting conducted in or near the study plot.

It is our strong desire to investigate the validity of using mist-net data to infer demographic parameters besides survival, such as production of young and survival and recruitment of young into the breeding population, and we have made a proposal to the U.S. Fish & Wildlife Service to do just that in 1993. The proposed work would be on several species in addition to Wrentits. In addition, though not part of the funded project, we have analyzed the accuracy and validity of mist-net data for measuring avian productivity in the Wrentit and refer to some of these results in this report (Nur & Geupel in press, included as an Appendix to this report).

STUDY SPECIES AND STUDY SITE

The study species is the Wrentit a species restricted to California, Oregon and Baja California, which has been the subject of little prior study (Erickson 1938, Geupel & DeSante 1990). Wrentits are monogamous, resident year-round and both parents share parental-care roles (e.g. both nest-build and incubate). The Wrentit is considered to be quite sedentary (Erickson 1938, Johnson 1972), which we have confirmed: less than 1% of breeders move their territories between years on our study site (Geupel & DeSante 1990). The lack of dispersal tendency makes them well suited for estimating survivorship on the basis of capture/recapture data. Wrentits maintain year-round territories and that, together with their sedentary nature, makes them good candidates for a validation study, i.e. birds observed on the study grid are likely to be the same ones caught in the nets.

The field work has been 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 study site, 36 ha in size, we have carried out, simultaneously, constant effort mist-netting, nest searches, intensive spot-mapping, and behavioral observations of color-banded individuals.

Constant effort mist-netting was conducted using twenty 12-m mist nets composed of

14 netting sites (Figure 1). Eight sites (14 nets) were located on the edge of mixed, evergreen forest habitat comprised primarily of coast live oak (*Quercus agrifolia*), California bay (*Umbellularia californica*), Douglas fir (*Pseudotsuga menziesii*), and California buckeye (*Aesculus californicus*). The other six single nets were located in disturbed coastal scrub comprised 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). Coastal scrub habitat is the preferred habitat of Wrentits (Erickson 1938, AOU Checklist 1983).

The net locations are adjacent to and extend across approximately 25% of the 36 ha study plot (Figure 1). Net locations were selected so as to maximize the number of birds caught (L. R. Mewaldt personal communication). The standardized operation of mist-nets is described by DeSante and Geupel (1987) and has continued without change. In summary, nets were run daily for 6 hours, beginning 15 minutes after local sunrise (weather permitting) from 1 May (1 April prior to 1989) to approximately 25 November, and 3 days per week (Wednesday, Saturday and Sunday) from December through end of March (or April, since 1989).

The detailed monitoring of individuals was conducted on the 36 ha study plot and has been described elsewhere (Geupel and DeSante 1990). In summary, identities and territory boundaries of color-marked individuals were determined from detailed spot-mapping censuses conducted a minimum of 3 days per 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 1987 through 1991. No attempt was made to locate nests in 1986 and effort was reduced in 1980, hence we have generally excluded these years from the analyses of fledged young. The method of locating and monitoring of Wrentit nests are described in Geupel and DeSante (1990). Nearly all successful nests (those fledging one or more young) are found before fledging and their young individually color-banded. Additional individuals are color-banded when first caught in mist-nets as hatching year (HY) or as after-hatching year (AHY) birds.

Locals are defined as juveniles banded as nestlings and fledged from nests on the study plot. Nonlocals are juveniles first captured and banded in the standard operation of mist nets and are assumed to have dispersed onto the study area.

RESULTS

Who is caught in mist-nets?

In the analysis we consider first who is caught in mist-nets, in particular, What factors, if any, influence the probability a Wrentit is caught? We consider first juvenile Wrentits and then adults.

Juveniles

Among juveniles there were two classes of individuals: those fledged on the study grid ("locals") and those fledged elsewhere ("non-locals"). It is possible that some individuals fledged on the grid were not identified, but these individuals undoubtedly make up a small percentage of all juveniles. Table 1 shows the number of locals and non-locals caught over a 10 year period. In every year non-locals caught in the nets outnumber locals, but the ratio varies among years ($P < 0.0001$, G test). If immigrant juveniles outnumber locally-born young in other species as well, this implies that year-to-year variation in the total number of Hatching Year birds caught (or ratio of HY to AHY birds) will mainly reflect conditions elsewhere rather than in the immediate neighborhood of the mist-nets.

Figure 2 shows the distribution of Hatching Year birds with respect to first capture date. Two distinct distributions are present, with the second, larger peak (that of non-locals) lagging the first peak by about two weeks. We feel that this pattern is likely very prevalent among landbird species, i.e., that a wave of locally-born young are caught first and then those born elsewhere.

Capture Probability among Locally born Young: We analyzed data obtained on locally born young to determine what factors influenced the probability a juvenile was caught (there being relatively little known about the immigrant young). The data come from 790 fledged young, from 10 breeding seasons (1981-1991, with the exception of 1986, when no attempt was made to locate nests). The most important factor influencing capture probability was distance from the nest to the mist-nets (here measured as distance to the nearest net) (Figure 3). Young fledged within 100 m of a mist-net had a 40% chance of being caught; beyond that distance the probability of capture declined ($P < 0.0001$, a significant decline in capture probability

with increasing distance; analyzed with logistic regression). However beyond about 300 m the capture probability reached an asymptote, of about 14%. This asymptotic level was maintained until beyond 600 m, at which point our data become scant. However, it is reasonable to suppose that capture probability stayed at about 14% until at least 900 m (the maximum distance between a juvenile's nest and the net it was caught in). Given that the preponderance of juveniles caught were non-locals (and most of these would have fledged 900 m or more away from the mist-nets), the capture range for juvenile Wrentits at Palomarin is likely to be measured in kilometers (for contrast with adults, see below).

The other two significant factors to influence capture probability were age of the juvenile and date of fledging. Figure 4 shows that Wrentits were almost always first caught between 20 and 60 days after fledging, with most caught between 30 and 50 days. The onset of capture of juveniles at 20 days post-fledging, closely coincides with the minimum period of post-fledging parental care in this population (18 days; Geupel & DeSante 1990). Furthermore, if a Wrentit had not been caught within 70 days of fledging, it was almost never caught subsequently (see Figure 4). Thus there was a finite window of opportunity to catch Hatching Year birds. Terminating a mist-netting program too early in the season would lead to a biased measure of productivity (e.g. second-brood young might be missed).

Young fledging later in the season were less likely to be caught in mist-nets than those reared earlier in the season ($P = 0.006$, logistic regression; Figure 5). Because netting effort remained constant during the entire summer and fall (through late November) this result was not an artifact of a seasonal change in netting effort. This result might reflect differences in post-fledging survival (late-fledging young might be less likely to live 20 or more days post-fledging) or it may reflect differences in dispersal tendencies. If netting had terminated in middle to late August (as is the usual practice in constant effort mist-netting programs, such as MAPS), this bias against late-fledged young would have been very much more severe.

The probability a fledged Wrentit was caught in a mist-net during the breeding season did not vary among years, with one exception (Table 2). In 1983, which was a year with very exceptional rainfall, only 2% of fledged young were caught. Perhaps excessive rainfall led to diminished post-fledging survival that year. For most years, and in every year since 1983, about 22% of fledglings are caught. There was significant variation in capture probability between years, but only if 1983 is included in the analysis ($P < 0.0001$ with 1983; $P > 0.2$, without 1983; logistic regression).

Capture of Adults

Breeding Status: The two most important factors influencing capture probability were distance to the nets and breeding status. Surprisingly, most adult Wrentits caught were not territory-holders and thus, we infer, non-breeders (Table 3). The ratio of breeders to non-breeders among those caught did not vary significantly between years ($P = 0.076$, G test), though in 1984, the proportion of breeders was unusually high (53%). In general there were about three times as many non-breeders as breeders ($X = 26.4$ and $X = 8.4$, respectively; Table 3). Here we present results regarding all captures during the year, but the results were quite similar when only breeding season captures were considered. The number of non-breeders caught in a year varied markedly between years (Table 3), between 9 and 47, but the number of breeders did not vary so much, between 5 and 12. The difference in year-to-year variability in number of breeders as opposed to number of non-breeders caught reflects 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 (see below). Annual fluctuations in the number of non-breeders has been discussed elsewhere (Geupel et al. 1992) and is influenced by demographic processes such as last year's production of fledglings and breeding population size.

Breeders and non-breeders were caught throughout the season (first capture dates during the breeding season shown in Figure 6). The two groups did not differ in mean first capture date, $\bar{X} = 24$ May (SD = 35.3 days) and $\bar{X} = 29$ May (SD = 29.6 days), ($P > 0.15$, ANOVA). In general, in July and August fewer adults (whether breeders or non-breeders) were caught.

Breeding status, in turn, influenced the number of times an individual was recaptured in the same season (Table 4). Non-breeders were usually caught but once during a given year (78%), whereas breeders were usually caught multiply (71% were caught more than once, and 53% were caught three times or more in the same year). The fact that breeders were caught so often in the same year, and usually in the breeding season, implies little net-avoidance among breeding Wrentits, even though these birds had ample opportunity to learn where nets were placed. The implications of this result are discussed below.

That a greater number of non-breeders were caught in the nets than breeders does not imply that non-breeders outnumbered breeders in the population. The non-breeders were, for the most part, just "passing through" the study site, whereas

breeders stayed put. The transience of these non-breeders is indicated, first of all, by the fact that few were ever seen again, in nets (see above) or on the study grid (Geupel et al. 1992). Secondly, most (74%) of these non-breeders were first caught in the winter or spring of their after-hatching year (i.e., they were neither locally born nor caught in the nets in their first year of life). In contrast, 52% of breeders caught in nets had been locally born or were caught in nets in their first year of life. Thus, most non-breeders caught during the breeding season had never been seen before nor were they ever seen again. Over the course of a breeding season, many non-breeders, or floaters, passed through the study area and were caught, though at any one time the number of non-breeders may have been fairly small.

Capture probability among breeders: In this section we analyze capture probability among known breeders. Over an 11 year period (1981-1991), a total of 523 breeders were identified on the study grid (the same individual is counted multiply if it bred in more than one year); of these, 93 (17.8% of all breeders) were caught sometime during the year (in almost all cases during the breeding season). By far, the most important influence on capture probability was distance to the mist-nets (distance measured from the nest to the nearest net). Individuals breeding within 50 m of a net were caught with 100% probability ($n = 40$), those breeding more than 200 m from the nearest net were rarely caught (0.8%, $n = 389$; Figure 7). In between 50 and 200 m, the proportion of breeders caught in the nets declined in a smooth fashion (Figure 7), ranging from 82% caught among those breeding 50 to 75 m from a net, to 17% caught among those breeding 175 to 200 m from the nearest net. The statistical significance of distance to the net in predicting capture of a breeder was very high ($P < 0.0001$, logistic regression).

To examine whether territorial boundaries influenced capture probability we compared proportion captured with respect to number of territories a Wrentit had to traverse in order to reach the nearest net (Table 5). This analysis was restricted to birds breeding within 200 m of a net, since 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 5). A multiple logistic regression analysis demonstrated that distance to nearest net and number of intervening territories to nearest net both had statistically significant and independent effects on capture probability ($P = 0.001$ and $P = 0.011$, respectively).

Using logistic regression analysis we examined whether age, date of breeding or

reproductive success/effort influenced capture probability. Of these factors, only date of breeding, specifically date first clutch was completed, had an unambiguously significant effect. Earlier breeding birds were less likely to be caught than those breeding in the middle or later in the breeding season (Table 6). However, for all breeders whose first clutch was completed from about 21 April on, capture probability was similar, about 26% (note that minimum, median and maximum first clutch completion dates were 23 March, 26 April and 30 June, respectively). We used multiple logistic regression analysis to confirm that there was an effect of breeding date on capture probability independent of the effect of distance-to-the-nearest-net on capture probability ($P = 0.044$ for the effect of clutch completion date, while controlling for distance to nearest net; date was transformed as the square of days elapsed since 21 March).

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 for distance to nearest net in a multiple logistic regression analysis ($P > 0.1$). Capture probability showed no significant association with the number of young hatched or fledged or the number of clutches or broods or the sex of the breeder ($P > 0.4$, in each analysis, logistic regression). There was a tendency for individuals who failed to rear any young to hatching to be more likely caught than others (29.8% vs. 19.1%, respectively; $P > 0.3$, logistic regression).

Analysis of survival and recapture probability

To analyze survival 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). All analyses have been conducted on the mist-net capture data (data from 333 different individuals caught over the 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 have analyzed, first, all captures, stratifying on breeding status, and then carried out analyses on capture data that pooled all adults.

Stratifying the analysis according to breeding status, i.e., allowing survival and recapture to differ for the two groups, resulted in an estimated survival probability of 57% for breeders and 38% for non-breeders (Table 7). Recapture probability was estimated to be 71% for breeders and 4% for non-breeders. The difference in recapture probability between the two groups is significant ($P = 0.0001$), but the difference in survival probability is not ($P > 0.3$), due to the large confidence interval

surrounding the estimate of non-breeder survival. Thus, a breeder caught in one year is **likely** to be recaptured the following year, if it is alive, whereas a non-breeder is very **unlikely** to be recaptured the following year.

On the basis of observation of color-banded birds, we estimated survival to be 58.6% (S.E. = 3.9%) for females and 64.2% (S.E. = 3.8%) for males, for the study population during the same period (1981-1991). These represent minimal estimates of survival: they are the proportion of breeders re-sighted in the following breeding season. We suspect that dispersal off the study grid is infrequent (Geupel & DeSante 1990) and that, once identified, few birds are missed in the following year, but nevertheless there are likely to be some birds of each category. If so, the true survival rate would be slightly higher. The value obtained by SURGE for breeders (57.4%) using mist-net data is a little lower than that derived from direct observations, but the confidence interval (47 - 67%) obtained includes the latter estimates. Conversely the confidence interval around the estimates of female and male survival includes the SURGE survival estimate. Thus, SURGE estimates for breeders are consistent with those derived from direct observation.

The above-stated SURGE estimates were obtained assuming survival to be constant among years and constant with age (where age, in SURGE, is defined with reference to years since first capture). Survival of breeders did not vary significantly with age (Likelihood Ratio Statistic [LRS] = 7.96, $P > 0.5$) or year (LRS = 8.26, $P > 0.5$), according to SURGE analyses. Survival tended to increase with age, consistent with our observations on the color-banded population (Nur & Geupel, unpublished). Annual survival of breeders, as estimated by SURGE, varied from 17% to 82%, with most years, seven out of ten, between 41 and 78%.

Most investigators running a constant-effort mist-netting program will not be able to distinguish breeders from non-breeders, and therefore, we performed analysis with SURGE on all adults, pooling data from breeders (59 different individuals) and non-breeders (274 different individuals). The results of the pooled analysis were a very discrepant survival estimate of 30.6% (95% Confidence Interval is 22 - 41%) and a recapture probability estimate of 38.2% (95% C.I. is 23 - 56%). These estimates were obtained assuming year-constant and age-constant survival and recapture probabilities. There was no evidence that survival or recapture probability varied with year ($P > 0.5$, for either parameter). The previous, stratified analysis makes clear why the results from the pooled analysis were so aberrant: (1) non-breeders, which are very transient and thus unlikely to be recaptured, have been included with

breeders, which are site-faithful and likely to be recaptured, and (2) the analysis did not differentiate between breeders and non-breeders.

Even if analysis of capture/recapture data, pooled with respect to breeding status, gives skewed estimates of survival, it may still provide a reasonable index of annual survival. Hence we considered whether such an annual index (derived from mist-net capture data) could reliably predict annual survival as determined by observations on color-banded birds. There was a trend for the two survival estimates to vary in the same direction (Figure 8), but the correlation was not significant ($P = 0.18$, linear regression). 1986 was an outlier, yielding the highest resighting survival estimate of the 10 years, but a relatively low estimate of survival, according to capture/recapture data (fourth lowest). That year was aberrant in other respects (DeSante and Geupel 1987), and if 1986 is excluded, there is a marginally significant correlation between the two survival indices ($P = 0.0529$, linear regression). Interestingly, female survival (as determined by resighting) correlated better with the mist-net survival estimates than did males (for females the linear regression was significant, $P = 0.016$, excluding 1986), even though mist-nets were catching male and female breeders equally.

Recapture Probability

We do not treat recapture probability in the same detail as capture probability because the main results have already been outlined above, with the SURGE analysis.

The overwhelming determinant of recapture probability was breeding status (see above). Among non-breeders SURGE estimated 4% of those alive were recaptured in a subsequent year. Among breeders the same parameter was estimated to be 71%. Only four breeders (out of 59) had any breaks in their capture-recapture records (i.e., a non-capture interrupting a string of captures). Because of the small sample size, we have not attempted to analyze individual life histories further with respect to factors favoring recapture or failure to recatch individuals. Results from SURGE indicated that recapture probability among breeders did not vary between years or with age.

The pattern of recapture for breeders and non-breeders observed within a season was magnified when one considered the pattern of recapture during the entire study (1981-1991). Breeders were recaptured up to 43 times during the study period; 56% were recaptured twice or more and 31% were recaptured six times or more (Table 8). Non-breeders were rarely recaptured at all; only 5% were recaptured more than once (Table 8). The differences in number of captures for the two groups is highly significant ($P < 0.0001$, Poisson regression).

CONCLUSIONS AND IMPLICATIONS FOR AVIAN MONITORING PROGRAMS

The most important result of the study, we feel, is that survival estimates, based on capture/recapture data obtained from mist-nets, can only provide valid results if breeders and non-breeders can be differentiated. In this study, the two classes could be differentiated, because we were able to establish the identity of territory holders within range of the mist-nets. Consequently, mist-net derived estimates of survival we obtained appear to be accurate. In the absence of distinguishing these two groups, capture/recapture analysis provided extremely skewed and inaccurate estimates of survival. The reason for the difficulty with the pooled, undifferentiated analysis was also apparent: the recapture probabilities of these two groups are very different. There is almost an eighteen-fold difference between the two groups in this parameter.

Unfortunately, Wrentit breeders and non-breeders cannot be distinguished in the hand. Both groups of individuals commonly display partial brood patches (Williams, Geupel & Nur, MS). The same problem, of being unable to distinguish breeders and non-breeders in the hand, is likely to apply to other species as well. For example in many species, males do not develop brood patches and breeding condition (as indicated by cloacal protuberance) is not an indicator of local breeding. For females, even if the 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 exist at other times during the breeding season (nets usually being run in constant-effort mist-netting programs for a period of three months or more). In addition, in the Palomarin Wrentit population, date of capture does not allow one to distinguish breeders from non-breeders. We expect that this pattern will hold for other species as well, especially more transient, migrant populations.

One solution to the problem of differentiating breeders and 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). 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 400 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 concern.

A second, more expedient solution relies on our observation that non-breeders were

rarely recaptured (within the same or different season), whereas breeders were usually recaptured (Table 4). Survival could, we suggest, be estimated from only those individuals that had been recaptured in the same season. This does not eliminate the problem of non-breeders, but it would reduce the magnitude. Some breeders would be discarded, but not many; all but 29% of Wrentit breeders were recaptured 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**, not just caught. Running nets often (as many days per 10-day period as is feasible) would further that goal.

Even though survival estimates are severely skewed when breeders and non-breeders cannot be distinguished, there still would be value, we suggest, to a survival index based on the year-by-year estimates for the pooled data. We could not show a significant correlation between the mist-net index and estimates based on individually-marked birds, which means only that survival **in any one year** could not be accurately predicted by the mist-net index. However, there was reasonable correspondence between the two survival measures, suggesting that a trend in survival over time, might be detected by the pooled mist-net survival index. Peach et al. (1990) found a strong correlation between rainfall in west Africa and annual survival as estimated from constant-effort mist-netting data, indicating the value of such an approach.

Another important result of this study is the apparent absence of net-avoidance, with respect to initial capture or recapture. On the contrary, recapture probability of breeders, as estimated by SURGE, was high (71%). There is no evidence that Wrentits learned to avoid nets. Breeders were repeatedly caught within a season and between seasons. Wrentits breeding within 50 m of a net were always caught at least once during a breeding season. These are results obtained from a scheme of permanently-established mist-nets, nets that are run 52 weeks of the year, and that for more than 6 months of the year are run daily. Where mist-nets are run less often (once or twice per 10 days) and for fewer months per year, net-avoidance is even less likely to be a problem.

The most important determinant of capture probability, for both juveniles and adults, was distance from the net. This result was not unexpected. What is very valuable, and what was never been calculated before in any species (to our knowledge), is the quantitative relationship between distance and capture probability. For adults, few were captured who were more than 200 m from the nearest net. Juveniles, however,

were caught with a near-constant probability of c. 14% probability beyond 300 m, up to a least 700 m. The catchment area for juveniles is likely more than a kilometer, maybe several. Thus, the populations being sampled by nets are very different for the two age classes. This calls into question the standard practice of estimating productivity by dividing the number of HY birds caught by the number of AHY birds caught (as is done by the Constant Effort Sites Scheme and MAPS program). The problem is exacerbated because the numbers of HY birds relatively close to the nets (the area which samples adults) will not always fluctuate in parallel with numbers of HY birds further from the nets (but close enough to be caught by the nets). This problem is evident in Wrentits: there was no correlation between the number of HY birds fledged on the study grid and caught in the nets, and the number of HY birds caught in the nets who fledged elsewhere (off the grid) (Nur & Geupel in press; see Appendix).

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. However, for juveniles, two important factors influencing capture probability were date of fledging and age of the individual. If these results apply to other species, they imply constant-effort mist-netting programs can be biased in measuring production of late-fledging young in two respects: these birds would be less likely to be caught, if netting effort remained constant throughout the summer and early fall (as we have found), and the bias would be even more severe if netting terminated before these young were of catchable age. The window of opportunity for catching juveniles undoubtedly varies with species; in the Wrentit, and probably most species, the window of opportunity seems to be related to the cessation of parental care.

Our validation study is limited in two respects. First, we have only considered temporal variation in survival and not spatial variation. Mist-nets may or may not be able to accurately assess differences in survival between sites. Secondly, we have only considered a single species. We think it would be extremely valuable to consider additional species, and for that reason have proposed a comparable study on the Song Sparrow in 1993.

RECOMMENDATIONS

- 1) We recommend that calculations of adult survivorship from mist-net capture/recapture data be restricted to data sets where breeders and non-breeders

can be distinguished. If non-breeders cannot be distinguished by any other means, we recommend restricting survivorship analysis to adults caught twice or more in the same breeding season. However, in many cases, it may not be necessary to obtain an accurate estimate of survival from capture-recapture data (i.e., it can be obtained from other data), and an annual index indicating trends in survival may still be very valuable. We recommend deriving such an index based on capture-recapture data from all adults, even where breeding status is unknown.

- 2) **We recommend running mist-nets as often as is feasible.** This will increase the number of adults which are recaptured, thus facilitating the differentiation of breeders and non-breeders. It will also increase the sample size of juveniles that are caught, improving our ability to infer trends in productivity and juvenile survival/recruitment.
- 3) **We recommend adjusting mist-net monitoring periods to suit local breeding seasons.** If the breeding season starts in April, nets should be run at that time, in order to increase the number of times breeders are caught (assuming multiple capture is to be used as a way to select breeders, i.e., non-transient individuals). The spring is a time that migrants may be passing through, and it would be desirable to exclude these individuals from calculations of survival. We recommend running nets in May (and April if the breeding season has started then) and using the multiple-capture criterion to exclude migrants, rather than not running nets in April and/or May as has been recommended by the MAPS program. Netting should continue as late in the breeding season as is necessary to catch late-fledged young; this might mean netting one month or more after the last young fledged. Again, migrants or long-distance dispersing individuals might prove a problem late in the season in some species, but data can be truncated on a species by species basis.
- 4) **We recommend multi-level, integrated monitoring, especially if species of special concern have been identified.** We discuss this in detail in Nur & Geupel in press (see Appendix). By multi-level, we mean using several techniques at once, i.e., using point counts and mist-netting in conjunction with territory-mapping of individually-banded birds and nest-monitoring. The use of several techniques in concert, rather than being redundant, provides one with information that could not otherwise be attained.

An example of the power of a multi-level, integrated approach is our ability to track abundance of non-breeder Wrentits (floaters). Through spot-mapping or point counts

we can potentially track the number of breeders, but floaters are an important component of landbird demography, yet are hard to observe in the field due to their secretive nature. Mist-netting allowed us to track the total number of adults (whether breeding or not), but by itself could not tell us which were breeders. Putting both together (total adult abundance and breeder abundance) allows inference as to non-breeder abundance. The abundance of non-breeders was related, in turn, to several demographic parameters (Geupel et al. 1992). The ability of a population to respond to perturbation might well be related to the existence and abundance of non-breeders (as exemplified by the Northern Spotted Owl *Strix occidentalis caurina*, Verner 1992).

5) More work is needed in evaluating, validating and optimizing monitoring methods relying on constant-effort mist-netting. Mist-netting has been a method for trapping birds for several decades, but it has only recently been adopted and promoted as a means for monitoring bird populations. Even in England, where the British Trust for Ornithology has been conducting the Constant Effort Sites Scheme for about a decade, there has been little work on validation. This omission applies, for example, to the report by Baillie et al. (1986), which evaluates the Constant Effort Sites Scheme, but does not attempt to validate results. Work is needed with regard to: monitoring of spatial variation and not just temporal variation, a consideration of additional species, evaluating the ability to infer juvenile survival and recruitment from mist-net data, and an in-depth consideration of the ability of mist-nets to monitor avian productivity. We believe that mist-nets have the potential to provide a good tool for monitoring trends in avian productivity, but the best method to measure productivity remains to be established.

ACKNOWLEDGEMENTS:

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Table 1. Capture of locally-born young and non-locally born fledglings, 1981 - 1991, breeding season only. (No local fledglings banded in 1986.)

Year	Number Locals Caught	Number Non-locals Caught	Per cent of HY birds that were local
1980	15	59	20.3
1981	13	66	16.5
1982	33	88	27.3
1983	1	63	1.6
1984	19	63	23.2
1985	21	61	25.6
1987	11	50	18.0
1988	27	57	32.1
1989	20	35	36.4
1990	13	27	32.5
1991	22	43	33.8

¹ - Proportion of juveniles among all HY birds varies between years (Likelihood ratio statistic = 44.21, $P < 0.0001$)

Table 2. Probability of capture of locally-born fledglings, 1981 - 1991, during the breeding season.

Year	Number Fledged	Per cent Caught
1981	66	18.2
1982	95	33.7
1983	57	1.8
1984	91	17.6
1985	83	25.3
1987	38	26.3
1988	99	23.2
1989	94	21.3
1990	73	17.8
1991	94	23.4

Table 3. Capture of AHY Wrentits over 10 yrs in relation to Breeding Status.

Year	Number Breeder's	Number Non-breeder's	Per cent Breeder's ¹
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

¹ - Proportion of breeders, among all AHY birds, did not vary significantly between years (Likelihood ratio statistic = 26.94, df = 10, P = 0.076)

Table 4. Frequency of capture and recapture within a year, in relation to breeding status. (Includes only individuals caught at least once during the breeding season.)

Number of Captures	Breeder		Number of Captures	Non-breeder	
	Frequency ¹	Percent		Frequency ¹	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

¹ - The same individual is included more than once if it was caught in different years.

Table 5. Capture probability in relation to territory location. Only Wrentits breeding within 200 m of the nearest mist-net are included in the analysis.

Number ¹ Territories	Per cent	Sample size
0	96.4	56
0.5	62.5	24
1	6.7	15
1.5	14.3	7
2	25.0	12
2.5-3	0.0	4

¹ - coding: 0, net is within Wrentit's territory; 0.5, net is in territorial no-man's land, i.e., outside territorial boundary but not within neighbor's territory; 1, 2, 3, net one, two or three territories away; 1.5, 2.5, as with 0.5 but an additional territory or two away.

Table 6. Effect of breeding date (date first clutch completed) on capture probability. Date categorized into 10-day intervals.

Date first clutch completed	Per cent Caught	Sample size
before 11 Apr	7.7	65
11 - 20 Apr	14.3	63
21 - 30 Apr	26.9	67
1 - 10 May	26.5	49
11 - 21 May	21.2	33
after 22 May	27.7	36

Table 7. Results of SURGE Analysis on mist-net capture data, by breeding status.

	Survival Probability		Recapture Probability	
	Estimate	95% C.I.	Estimate	95% C.I.
Breeders	0.574	0.47 - 0.67	70.8	0.53 - 0.84
Non-breeders	0.376	0.13 - 0.72	4.8	0.01 - 0.18

Test for differences in parameter estimates, between breeders and non-breeders:

Likelihood ratio		
statistic = deviance	1.06, $P > 0.3$	14.69, $P = 0.0001$

Table 8. Frequency of recapture, cumulative for the period 1981-1991, in relation to breeding status.

Number of Recaptures	Breeder		Number of Captures	Non-breeder	
	Frequency	Percent		Frequency	Percent
0	20	33.9	0	218	79.6
1	6	10.2	1	41	15.0
2	4	6.8	2	7	2.6
3	7	11.9	3	3	1.1
4	2	3.4	4	2	0.7
5	2	3.4	5	0	0.0
6	5	8.5	6	2	0.7
7	3	5.1	7	1	0.4
8	3	5.1	-	-	-
9	2	3.4	-	-	-
10-19	4	6.8	-	-	-
44	1	1.7	-	-	-
Total	59	100.0	Total	274	100.0

Figure Captions:

Figure 1. Map of the study area, 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, totalling 36 ha in area. Constant effort mist-netting was conducted at nets marked with asterisks. Dotted lines enclose Wrentit territorial boundaries for a typical year, 1985.

Figure 2. Frequency distribution of first capture dates for local and nonlocal juveniles, data from 1980-1990, grouped into ten day periods.

Figure 3. Capture probability of juveniles (locally born young only) in relation to distance from the nest to the nearest mist-net, data from 1981-1991. Filled triangles show proportion of fledged young caught, grouped in 100 m intervals: 0 - 100 m, 100 - 200 m, etc. Total sample size is 790 fledglings. Solid line gives the best fit to the data using logistic regression. The relationship is highly significant ($P < 0.0001$, logistic regression).

Figure 4. Frequency distribution of capture in relation to age (days since fledging), data from 1981-1991. The smooth line depicts a normal distribution with the same mean and variance as the observed data.

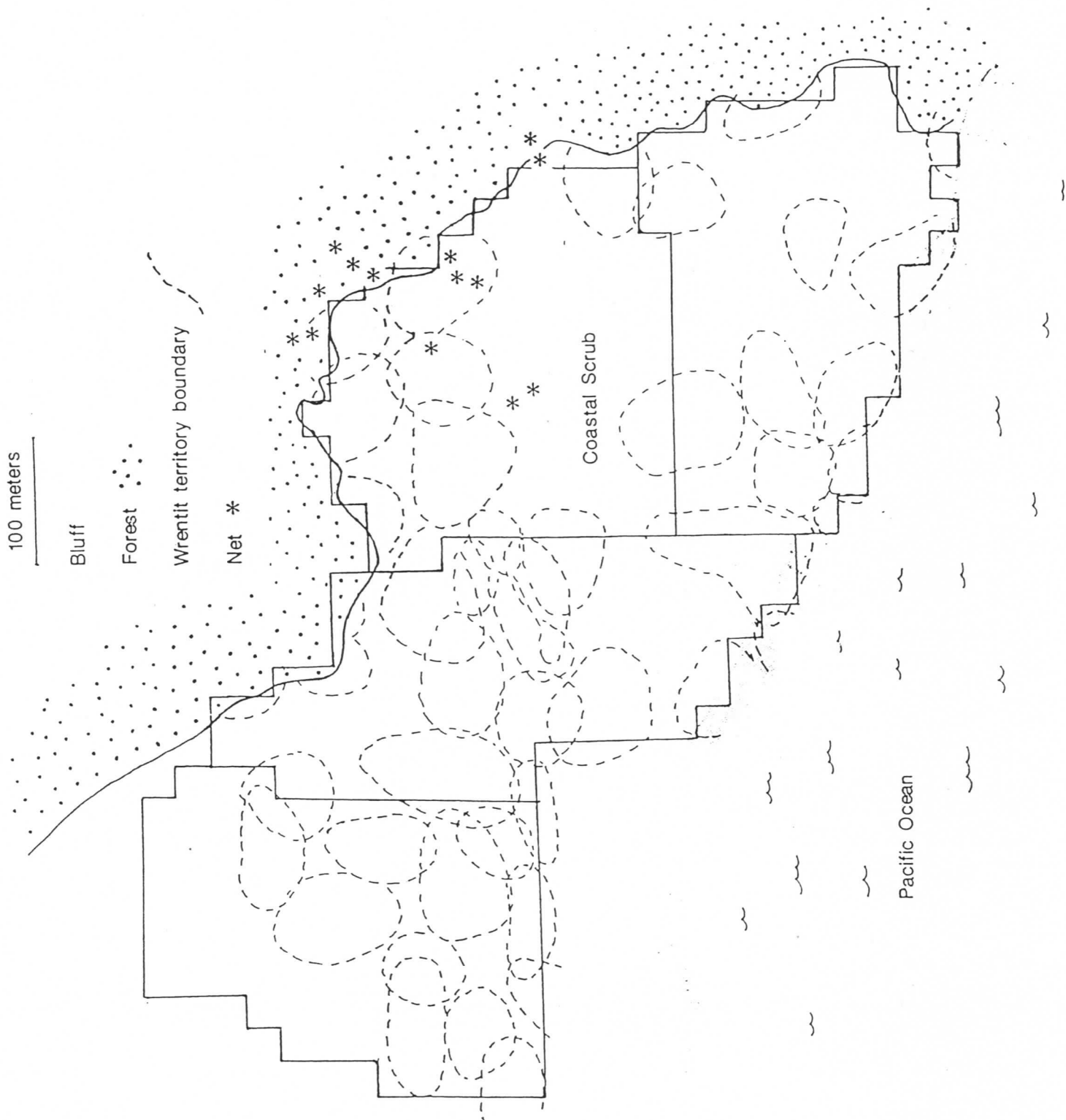
Figure 5. Capture probability of juveniles (locally born young only) in relation to fledging date, data from 1981-1991. Filled triangles show proportion of fledged young caught, grouped in semi-monthly intervals: end of April, early May, late May, etc. Total sample size is 790 fledglings. Solid line gives the best fit to the data using logistic regression.

Figure 6. Frequency distribution of first capture dates for breeders and non breeders, data from 1981-1991. 91=1 April, 121=1 May, 152=1 June, 182=1 July, and 213=1 August. A) Breeders. B) Non-breeders. Data have been grouped into three-day intervals.

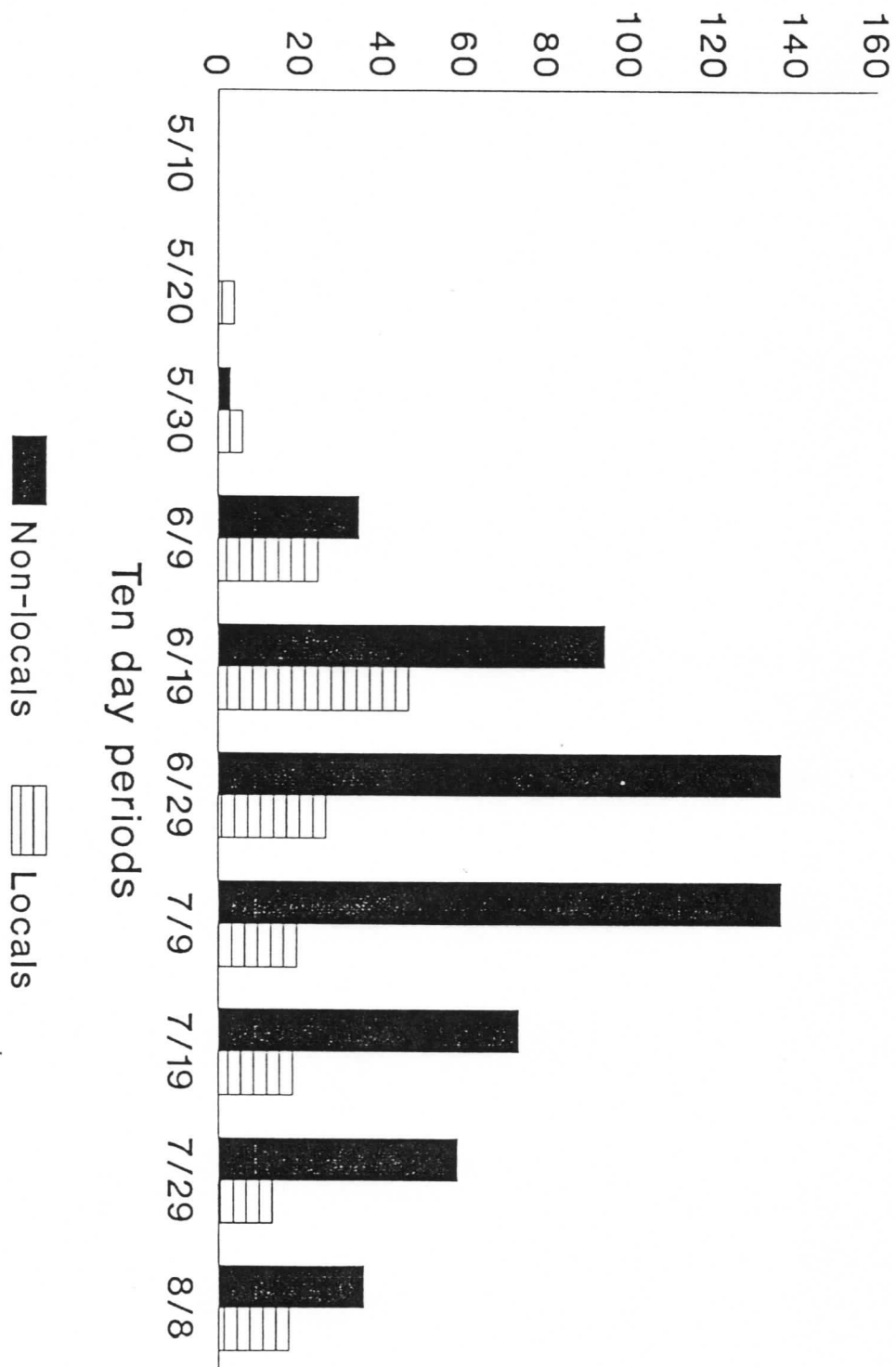
Figure 7. Capture probability of breeders in relation to distance from the nest to the nearest mist-net, data from 1981-1991. Distance measured in meters. Filled circles show proportion of breeders caught for breeders grouped in 50 m intervals: 0 - 50 m, 50 - 100 m, etc. Beyond 500 m, data are show in 100 m intervals. Solid line gives the best fit to the data using logistic regression.

Figure 8. Comparison of Survival Indices. Values for each year are shown by two digit codes. 1983 and 1987 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 is shown excluding 1986.

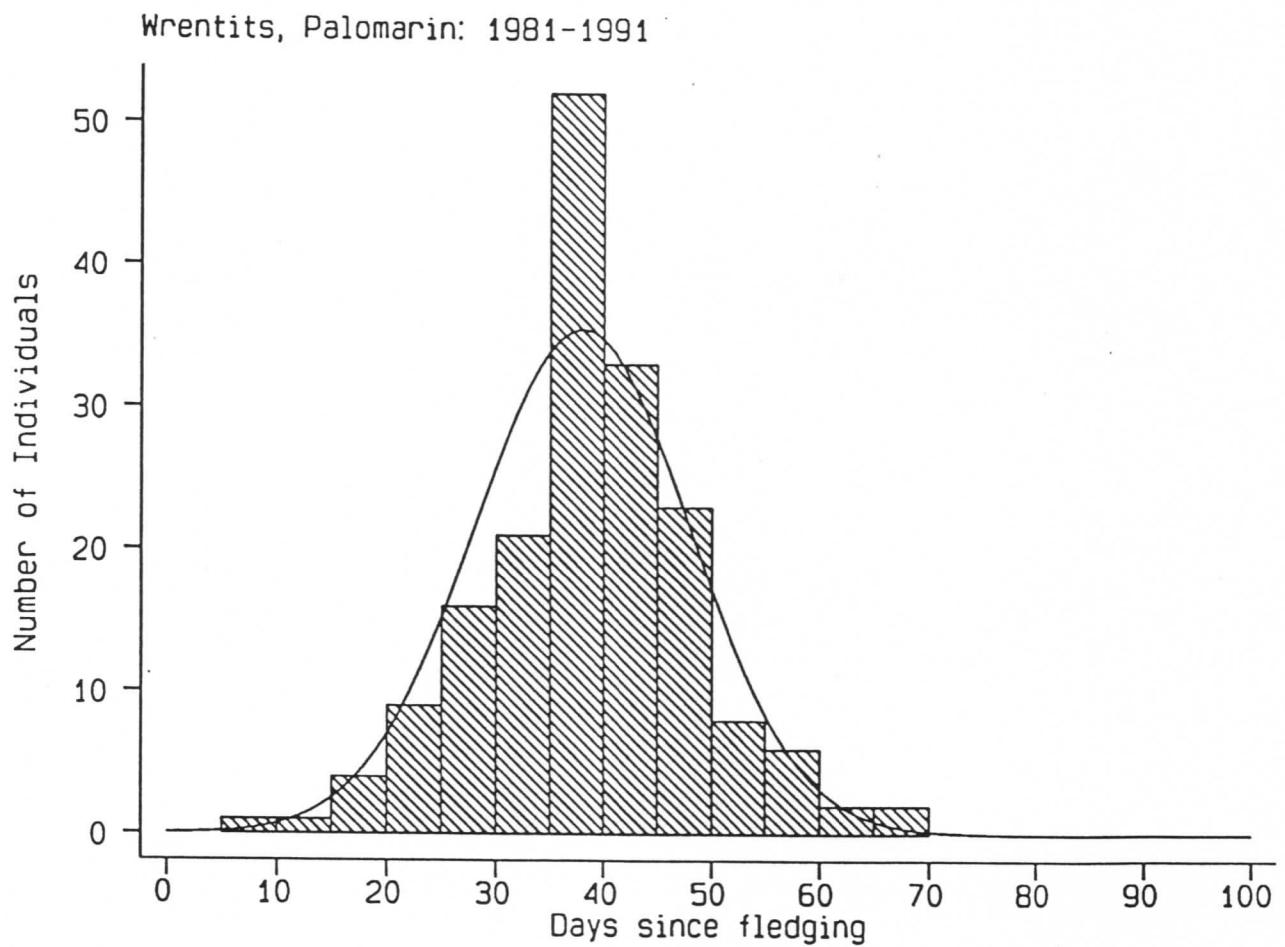
PRBO Report Fig 1



The number of juveniles captured over ten 10 day periods from 1980 to 1990.

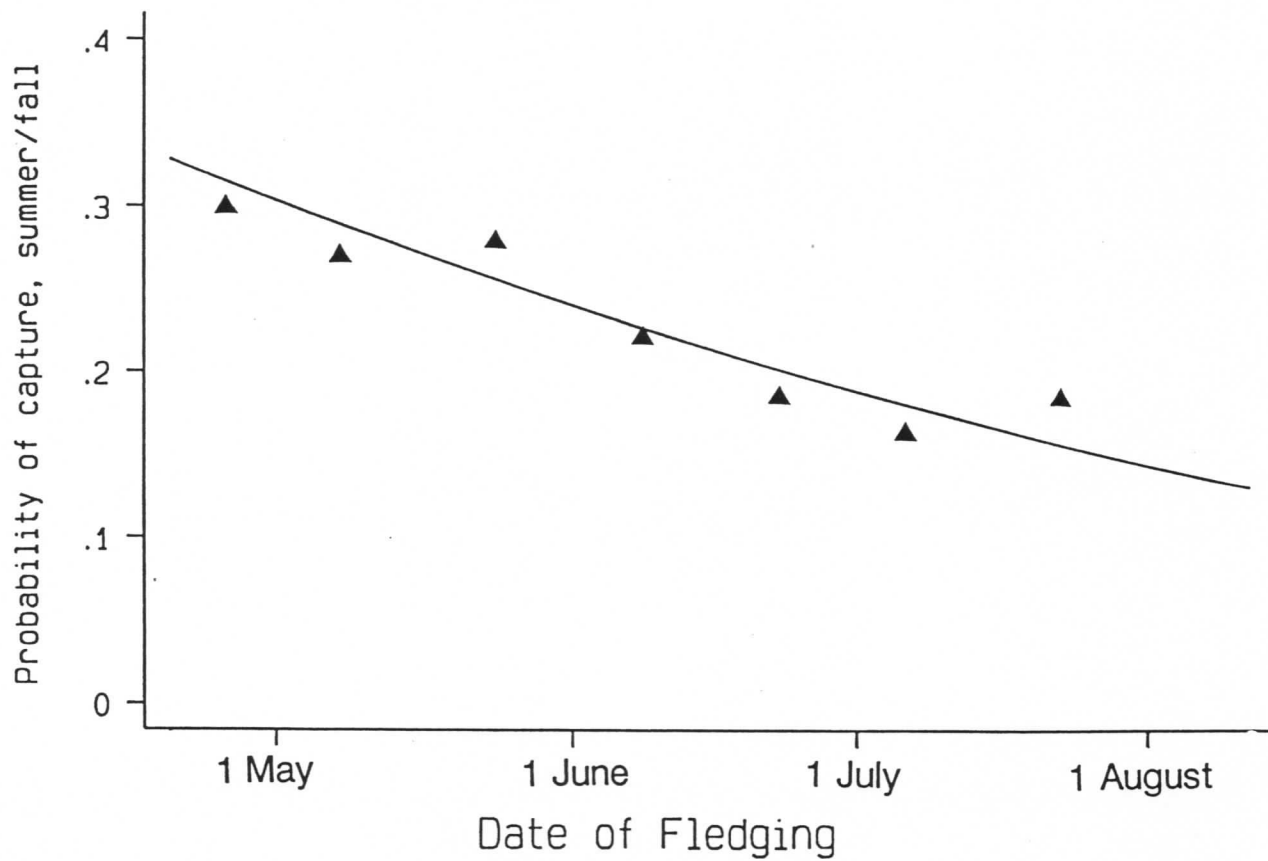


PRBO Report Fig 4



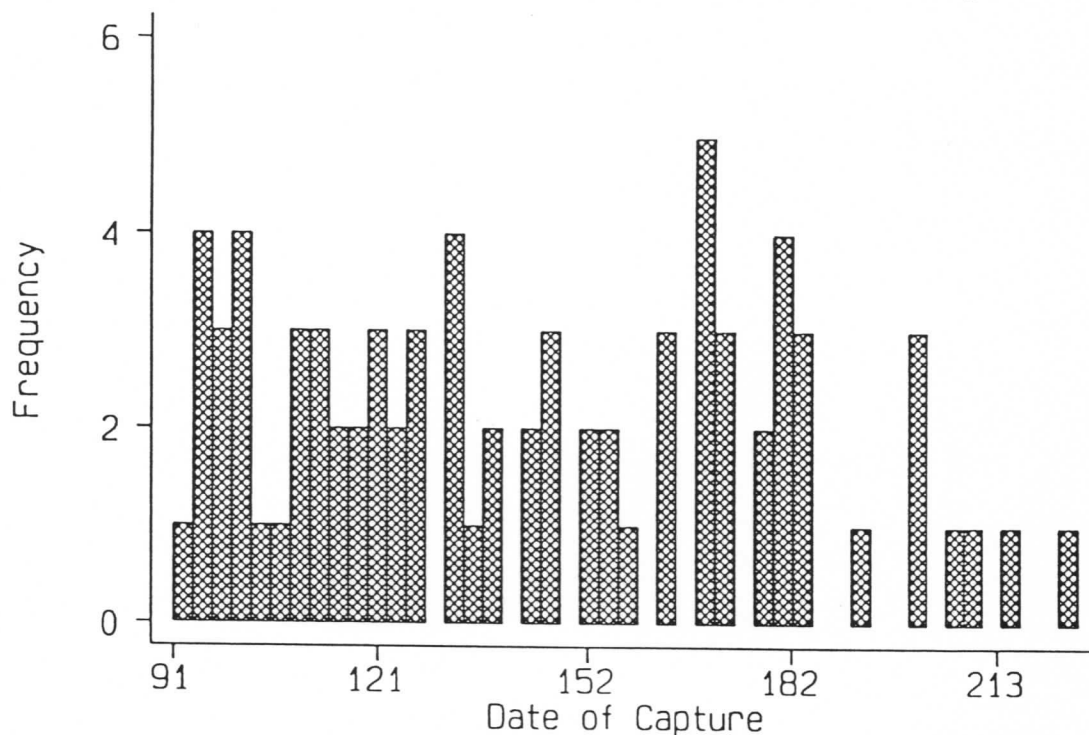
PRBO Report Fig 5

Wrentits, Palomarin: 1981-1991
Logistic regression, $P=0.006$



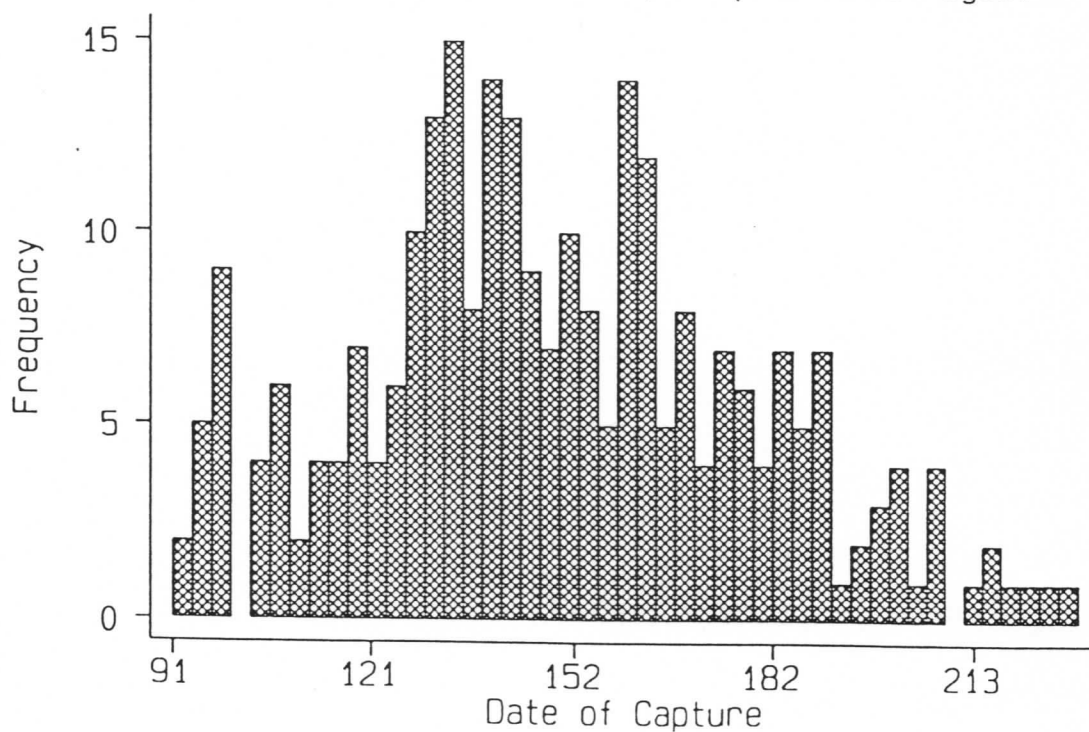
a)

Distribution of capture dates: Breeders
First capture in the season, 1 April - 18 August



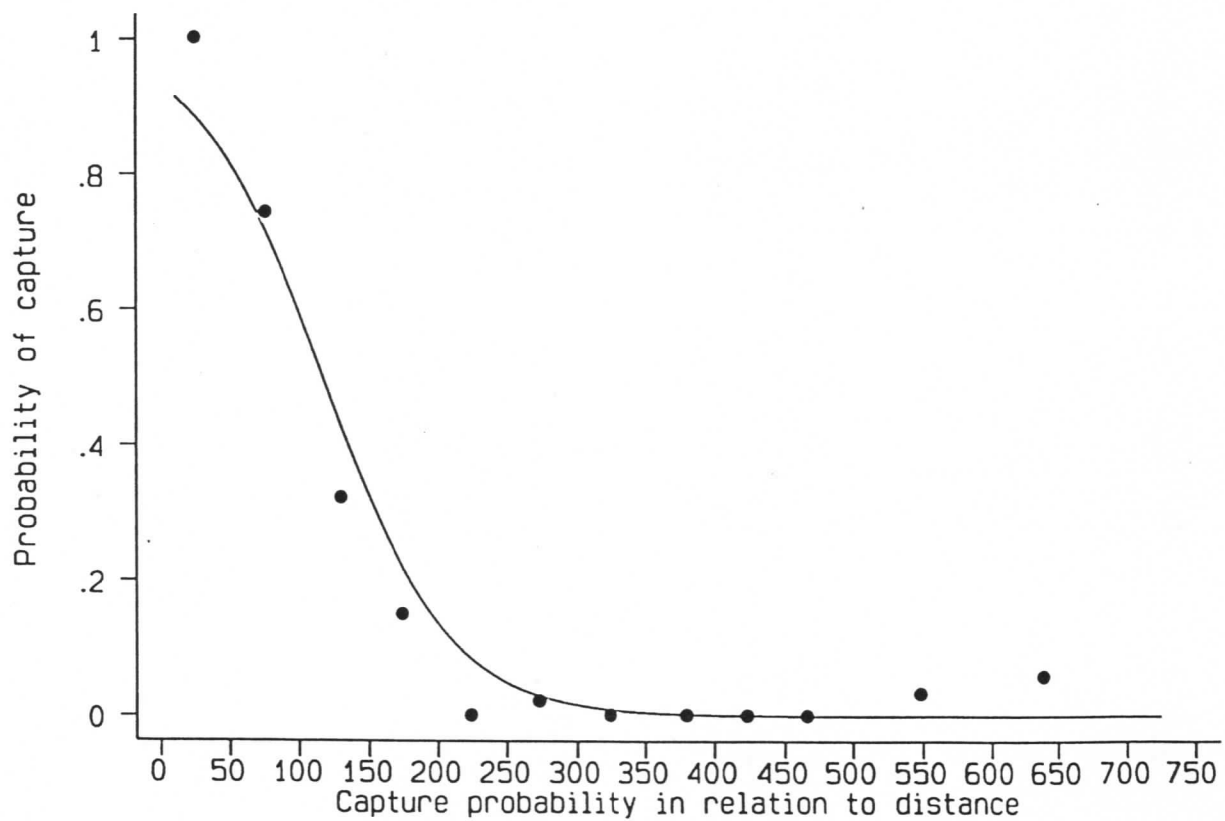
b)

Distribution of capture dates: Non-breeders
First capture in the season, 1 April - 18 August

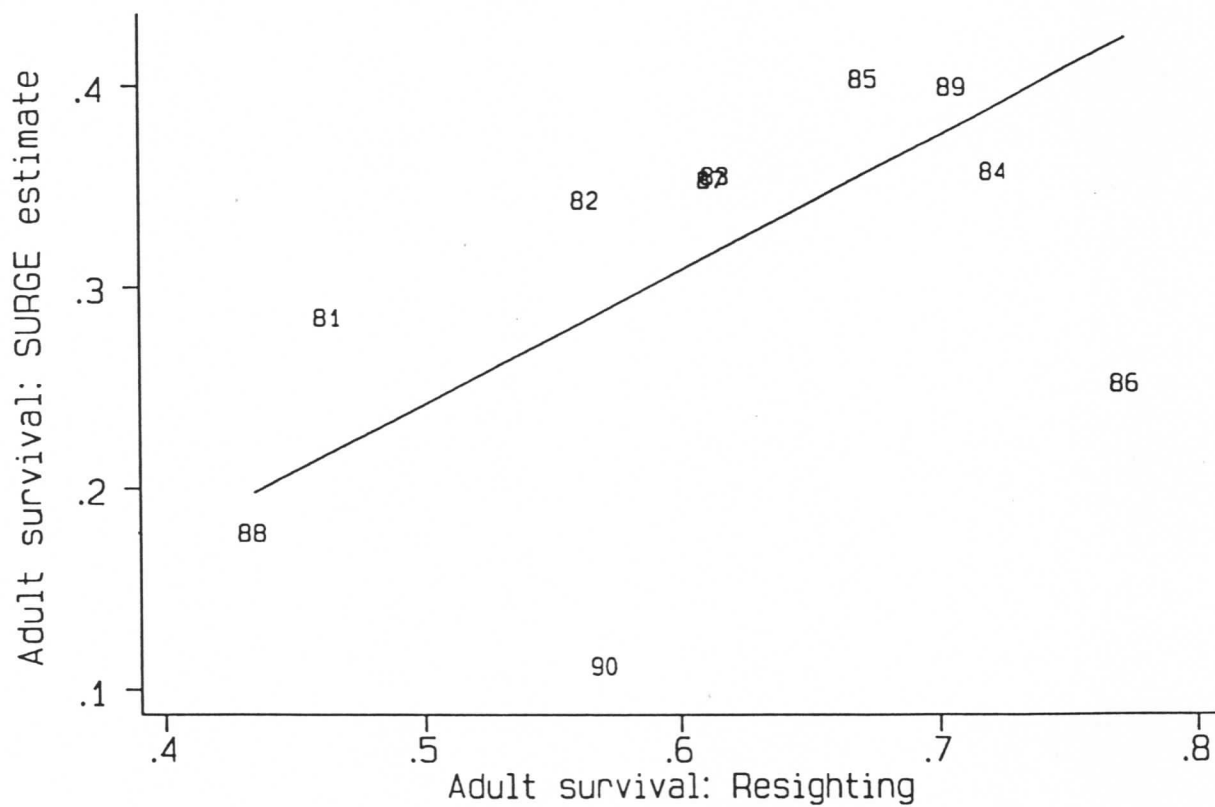


PRBO Report Fig 7

Effect of distance to net on capture of breeders
Logistic regression, $P < 0.0001$



Comparison of SURGE estimates and direct observations
Palomarin: 1981-1990



APPENDIX:

Draft of Paper to be published in Proceedings of National Conference on Status and Management of Neotropical Migrant Birds--Partners in Flight. Edited by D. Finch, P. Stangel, and T. Martin.

Evaluation of mistnetting, nest-searching and other methods for monitoring demographic processes in landbird populations

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INTRODUCTION

The starting point for this paper is the question, What does a manager need to know to manage a species or a set of species? In our opinion, **A manager needs to identify problems (or potential problems), to identify possible solutions, and then needs to monitor these species to determine success of the management action.** To accomplish these objectives requires detailed information on demographic processes (Temple & Wiens 1989). Four critical components of demography are:

- 1) Adult survivorship
- 2) Reproductive success (i.e., production of young or productivity),
- 3) Recruitment of young into the breeding population, and
- 4) Population size or density (especially breeding population size).

There is widespread consensus that monitoring population density of neotropical migrant birds is critical, but the same consensus has not been reached with regard to the first three demographic components. We focus on these three components 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 the first three components and only these components (provided that immigration balances emigration). Our goal in this paper is not so much to persuade managers that measuring productivity and survivorship is critical for species of concern (see, for example, Martin & Nur [this volume] and DeSante [this volume]), but to consider **how** to carry out a program of monitoring demographic processes.

The Point Reyes Bird Observatory has been involved in research and monitoring of migrant and resident landbird populations for over two decades (Geupel & Nur, this volume). Building on the work of L. Richard Mewaldt, C. J. Ralph, David DeSante, and others at the Observatory, PRBO has developed an integrated, four-level approach to the study of avian population processes. The levels, in order of increasing precision and/or scale of resolution, are:

- 1) Point counts, to assay breeding population density over a large area,
- 2) Constant-effort mistnetting (CEM) to provide indices of productivity (specifically, production of independent young) over a moderately large area, and, potentially, to provide information on survivorship,
- 3) Nest-searching and -monitoring to provide site-specific and habitat-specific information regarding success at producing young, and
- (4) Spot-mapping of color-banded individuals, to determine breeding status, absolute breeding density and survival of adults.

We recognize that not all managers will be able to implement all the enumerated

levels of monitoring, but we wish to encourage the adoption of as many as feasible. One of the goals of this paper is to provide a persuasive argument that implementing all four levels will provide superior information about the population dynamics of a species of concern and mechanisms underlying observed dynamics.

The accuracy, validity and/or utility of these different monitoring methods, however, remains to be established. Constant-effort mistnetting is a relatively new monitoring technique that forms the basis of a North American monitoring program (DeSante this volume) and that has attracted a lot of interest because it can provide information on demographic processes, yet is not as labor-intensive as other methods, e.g., nest-searching (Martin & Geupel in press). Nevertheless, there has been little work to date to validate CEM as a monitoring technique nor to examine underlying assumptions of its use - and those are our two overall objectives in this paper. Some more specific questions that we wish to address are:

(1) Does the variation in number of Hatching Year birds caught during Constant Effort Mistnetting accurately reflect production of young and other demographic variables? Is there variation among species?

(2) Which individuals (among adults) are likely to be caught in nets? How likely are they to be recaptured? Are there biases in capture and recapture of individuals?

The work we report here is work-in-progress; the results are still preliminary, but the great interest in this subject, in North America and elsewhere, would seem to justify an early report.

We wish to emphasize that in this paper we are evaluating methods to measure year-to-year variation in demography, that is **temporal variation**. Managers will often be interested in variation between patches - even between habitats - that is, **spatial variation**. No one, to our knowledge, has attempted to validate constant-effort mistnetting with respect to spatial variation, though we are currently collecting data that will address this point (Nur & Geupel, unpublished).

STUDY SPECIES AND STUDY SITE

We have concentrated our efforts to date on evaluation of methods on two species, the Song Sparrow (*Melospiza melodia*), a widespread and well-studied species (Nice 1937), and the Wrentit (*Chamaea fasciata*), a much more localized species, restricted to California, Oregon and Baja California, which has been the subject of little study to date (Erickson 1938, Geupel & DeSante 1990).

The field work has been 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 our main study site, 36 ha in size, we carry out all four levels of monitoring: point counts, constant effort mistnetting, nest searches and intensive

spotmapping (and behavioral observations) of color-banded individuals. In this paper we discuss data from the last three mentioned levels. Fourteen permanent mistnet locations have been established in one portion of the 36 ha study grid (Fig. 1), and netting is conducted throughout the year, in a standardized fashion, for three to seven days per week (depending on season). The study site is described in DeSante and Geupel (1987) and Geupel and DeSante (1990); methods are detailed in the same publications. Suffice it to say that we attempt to locate all nests of the study species and follow the fate of those nests. Nearly all successful nests (those fledging one or more young) are found before fledging and their young individually color-banded. Additional individuals are color-banded when first caught in mistnets as hatching year (HY) or as after-hatching year (AHY) birds.

Both species are year-round residents at Palomarin. The Wrentit is particularly sedentary (Erickson 1938, Johnson 1972) and thus would be well suited for estimating survivorship on the basis of capture/recapture data (adults are unlikely to disperse between years). Song Sparrow shows intraspecific variability in dispersal and migratory tendencies, though our population at Palomarin appears fairly sedentary. It is precisely in sedentary populations such as these that we would expect constant-effort mistnetting to be most successful at accurately tracking the local production of young.

RESULTS

Monitoring Productivity

The more Wrentit fledglings were produced on the plot, the more of these locally-born young were caught as part of our Constant Effort Mistnetting program, conducted during the breeding season (Fig. 2). Almost fifty per-cent of the year-to-year variation in number of locally born young caught in nets can be accounted for by the variation in number of fledglings produced. This finding provides some confirmation that mist nets are indeed measuring local production of young. Another way to view this result is to consider the proportion of fledged young which were caught in the nets. Over a ten-year period, 24.2% of Wrentit fledglings were caught in nets during the summer months ($n = 714$). In most years, a fairly consistent percentage of Wrentit fledglings were caught, usually between 19% and 28%, but there were exceptions, especially 1983, during which only one out of 57 fledged young was caught (1.8%). That year was one of unusually heavy rainfall (a record-breaking El Nino event), which may have depressed post-fledging survival of Wrentits.

Of wider interest, though, is the question, Did the total number of HY Wrentits caught in the nets--no matter what their origin--provide a good measure of Wrentit fledgling production? This answer is disappointing. There was not a good relationship (and certainly no significant relationship) between production of fledglings on the 36 ha

study grid and the total number of HY birds caught in the nets. The relationship is marginally improved by considering the ratio of HY birds to AHY birds caught in the nets as the dependent variable rather than simply the total number of HY birds and considering the fledgling production per pair as the independent variable, but we are still left with a result that falls short of statistical significance (Fig. 3).

This result seems to present a paradox. To resolve the paradox, we note first that the total number of HY birds is the sum of locally born young and those which are non-local (born outside the study grid). Above, we showed that the number of locally born young caught in the nets correlated with fledgling production, but it turns out that the number of non-local young caught in the nets had nearly nothing to do with local fledgling production ($r = +0.065$, $P > 0.8$). One explanation for this last-mentioned result is that the production of local young is not correlated with the production of non-local young, in other words, reproductive success for Wrentits is very patchy. An alternative explanation is that the number of non-local young caught in the nets reflects dispersal tendencies of those young more than it reflects reproductive success.

Whereas HY captures did not predict local productivity well, it did predict a different demographic parameter, the proportion of Wrentits breeding in the next year that were one year of age. This parameter is an index of the success of a cohort in recruiting in the following year. The greater the ratio of HY to AHY birds caught during the breeding season, the greater the proportion of one-year old birds breeding in the next year ($R^2 = 0.444$, $P = 0.035$). In fact, the mistnet-based measure of productivity did a slightly better job at predicting next year's age structure than did productivity as measured by nest-searches (number of fledglings reared per pair), $r = +0.666$ vs. $r = +0.608$, respectively. Why might that be? Our answer is that mistnets performed well in predicting recruitment because they are sampling juveniles at a later stage in life--a few weeks post-fledging, rather than at the time of fledging, as is the case for nest-searches.

Turning to Song Sparrows we see a different picture: there is a very good relationship between fledgling production on the grid (total number of Song Sparrows fledged) and number of HY birds caught in the nets (Fig. 4A). In fact, 67% of the between year variation in HY captures can be accounted for differences in local fledgling production and vice versa. We stress that the very same comparison for Wrentits is unambiguously not significant ($P > 0.4$) and the corresponding R^2 is only 6% (Fig. 4B). In other words, there is marked variation between species in the ability of mistnets to track year to year changes in the local production of young.

Captures of adults: breeders vs. floaters

Considering the capture and recapture of adults, we found that most Wrentits caught in

mistnets were apparently non-breeders, that is, floaters (O. Williams, G. Geupel & N. Nur, unpublished; Geupel et al. 1992). On average about two floaters were caught in our nets each season for every breeder caught ($X = 18.9$ non-breeders per year vs. $X = 9.1$ breeders caught per year, $n = 10$ years). This difference arose not because floaters outnumbered breeders, but rather because breeders stayed put; only breeders with territories near to mist nets--one or at most two territories away--were caught. Breeders further away were not caught. In contrast the non-breeders were very transient. Over the course of the breeding season a high number "passed through" our study site. The degree of transience is indicated, first of all, by the fact that of 188 non-breeders captured over a 10-year period, only 18 (9.6%) had been previously banded in their first summer or fall of life. Four individuals were locally-born (one of more than 700 banded fledglings) and the other 14 had been first caught as independent juveniles in their first fall. Moreover, once caught, most of these nonbreeders were never seen again. Only 52 out of 189 individuals (28%) were seen again in the same season, either caught in mistnets or observed and identified by means of their color-bands. In contrast, most breeders were caught repeatedly during the breeding season. Sixty-two percent of breeders were recaptured in the same breeding season ($n = 91$), some repeatedly (Table 1). This result implies little net-avoidance among breeding Wrentits, even though these birds had ample opportunity to learn where nets were placed.

In short, within a season, breeders were much more likely to be recaptured than non-breeders. The same pattern held between seasons. Many breeders (more than 40%) were recaptured in a subsequent season, whereas few non-breeders were (less than 8%). In other words, breeders were more than five times as likely to be recaptured in a subsequent season as were non-breeders (G test, $P < 0.001$). We don't think this necessarily indicates any difference in survival between these two groups, just a difference in recapture probability. We are just now analyzing our data to calculate survival probabilities for Wrentits (breeding and otherwise) using SURGE (Lebreton et al. 1992), but in the meantime it appears that capture-recapture data collected with constant effort mistnetting can provide a good index of survival--among breeders. The difficulty is to distinguish breeders from non-breeders, which cannot be determined in Wrentits by the presence or absence of brood patch or cloacal protruberance (unpublished data). One suggestion would be to calculate survival rates using only adults that had been caught twice or more in the same breeding season, since most breeders (62%) were caught more than once, whereas most non-breeders (72%) were not.

CONCLUSIONS AND RECOMMENDATIONS

To summarize, among Wrentits the number of locally-born young caught in nets

mirrored the total local production of fledglings, but the overall number of HY birds caught did not track local production of young. In contrast, the number of HY Song Sparrows caught as part of a constant-effort mistnetting regime did mirror local production of Song Sparrow young. Thus, there is variation between species in the ability of CEM to track changes in local productivity. Our results are similar to that of Feu and McMeeking (1991) who found that in Blackbirds *Turdus merula*, the number of juveniles caught with CEM (part of the Constant Effort Sites Scheme of the British Trust for Ornithology) was correlated with local productivity, but that in the Song Thrush *Turdus philomelos* there was no such relationship. With regard to Wren tit adults, we found that mistnets tended to catch non-breeders (floaters) rather than breeders, and that recapture probability (within season and between seasons) was strongly related to breeding status. In particular, breeders were likely to be recaptured, thus providing no evidence of net-avoidance. Our results suggest that a low probability of recapturing adults in subsequent breeding seasons (obtained in some CEM studies) reflects inclusion of transient non-breeders with more philopatric breeders, rather than being due to avoidance of mistnets.

Our recommendations are:

1) Before implementing a monitoring program, determine what are the objectives. For example, some monitoring programs might be geared toward studying temporal variation whereas others might focus on spatial variation in demographic parameters. Our own attempt to validate mistnetting and that of Feu & McMeeking (1991) have investigated temporal variation. The limited data gathered to date suggests that mistnets might provide a valid index of productivity, albeit with species-to-species variation in their efficacy. It remains to be seen, though, whether mistnets provide a good index of spatial variation. The answer would depend on degree of patchiness, extent of spatial coverage by mistnets, differences in catchability as a function of habitat, etc. With nest-searching, spatial variation presents a different sort of problem: the connection between nesting success and the patch sampled is clear, but the problem may be that nesting success in an investigated patch may not easily extrapolate to other patches, whether nearby or far away. Other objectives to be considered are the identity of the demographic parameters (all? just productivity? just survivorship?) and the spatial scale (tens of acres or thousands of acres?)

2) More work is needed in developing and validating different monitoring methods. This holds for all monitoring methods but we feel it is particularly true for mistnetting. Mistnetting has been a method for trapping birds for several decades, but it has only recently been adopted and promoted as a means for monitoring bird populations. Even in England, where the British Trust for Ornithology has been conducting the Constant Effort Sites Scheme for about a decade, there has been little work on validation. This

omission applies, for example, to the report by Baillie et al. (1986), which evaluates the Constant Effort Sites Scheme, but does not attempt to validate results. Other points requiring some "fine-tuning" are, Which months to run nets in? Where best to place nets? How many days to run nets per standard, ten-day period? What is the effect of habitat on efficacy and validity of mistnetting data? What is the "catchment" area for juvenile and adult birds (O'Connor 1992)?

3) We recommend that calculations of adult survivorship from mistnet capture-recapture data be restricted to (presumed) breeders. If non-breeders cannot be distinguished on the basis of brood patch, we recommend restricting survivorship analysis to adults caught twice or more in the same breeding season. One implication of our work is that those who wish to infer survivorship from capture-recapture data should run the same set of nets relatively often (thereby increasing the sample of birds caught twice in the same season).

4) We recommend multi-level, integrated monitoring, especially if species of special concern have been identified. Our study at Palomarin has indicated ways in which a multi-level approach to monitoring is the most powerful. Our point is that using several techniques in concert, rather than being redundant, provides one with information that could not otherwise be attained. In other words, the whole is greater than the sum of the individual parts. Consider these two examples from our field study. First, fledgling production of wrentits in 1983 was fairly high but only one independent locally-born fledgling was caught in the nets. With only nest-monitoring to go on, we would have thought productivity was reasonably good that year. With only mistnetting to go on, we would have identified poor productivity of the 1983 cohort but we would have had little idea as to cause. From mistnetting data alone we could not separate poor nesting success (e.g. high nest-predation) from poor post-fledging survival.

The second example of the power of a multi-level, integrated approach is our ability to track abundance of non-breeders (floaters). Through spot-mapping or point counts we can potentially track the number of breeders, but floaters are an important component of Neotropical migrant demography, yet are hard to observe in the field due to their secretive nature. Mistnetting allowed us to track the total number of adults (whether breeding or not), but by itself could not tell us which were breeders (as mentioned above, in wrentits, neither brood patch nor cloacal protruberance are indicators of breeding status). Putting both together (total adult abundance and breeder abundance) allows inference as to non-breeder abundance. The ability of a population to respond to disturbance might well be related to the existence and abundance of non-breeders (as exemplified by the Northern Spotted Owl *Strix occidentalis caurina*, Verner 1992).

A multi-level monitoring program might be more labor-intensive (and thus

expensive) than a single-level approach (e.g., point counts), but if such a program can alert us to problems and help us identify solutions **before** a species is certifiably endangered, the effort will represent an economical investment.

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Table 1. Same-season Recaptures of Wrentit Breeders at Palomarin (1982-1990)

Capture Status ¹	Frequency	Percent
Caught but not recaptured	26	38%
Caught once, recaptured once	23	33%
Caught once, recaptured twice	13	19%
Caught once, recaptured three or more times	7	10%

Average number of recaptures¹ = 1.22

¹Breeding individuals caught April - July, inclusive, and recaptured in same time period. Thus, an individual caught in March and again in June of the same year is listed as caught once, but not recaptured.

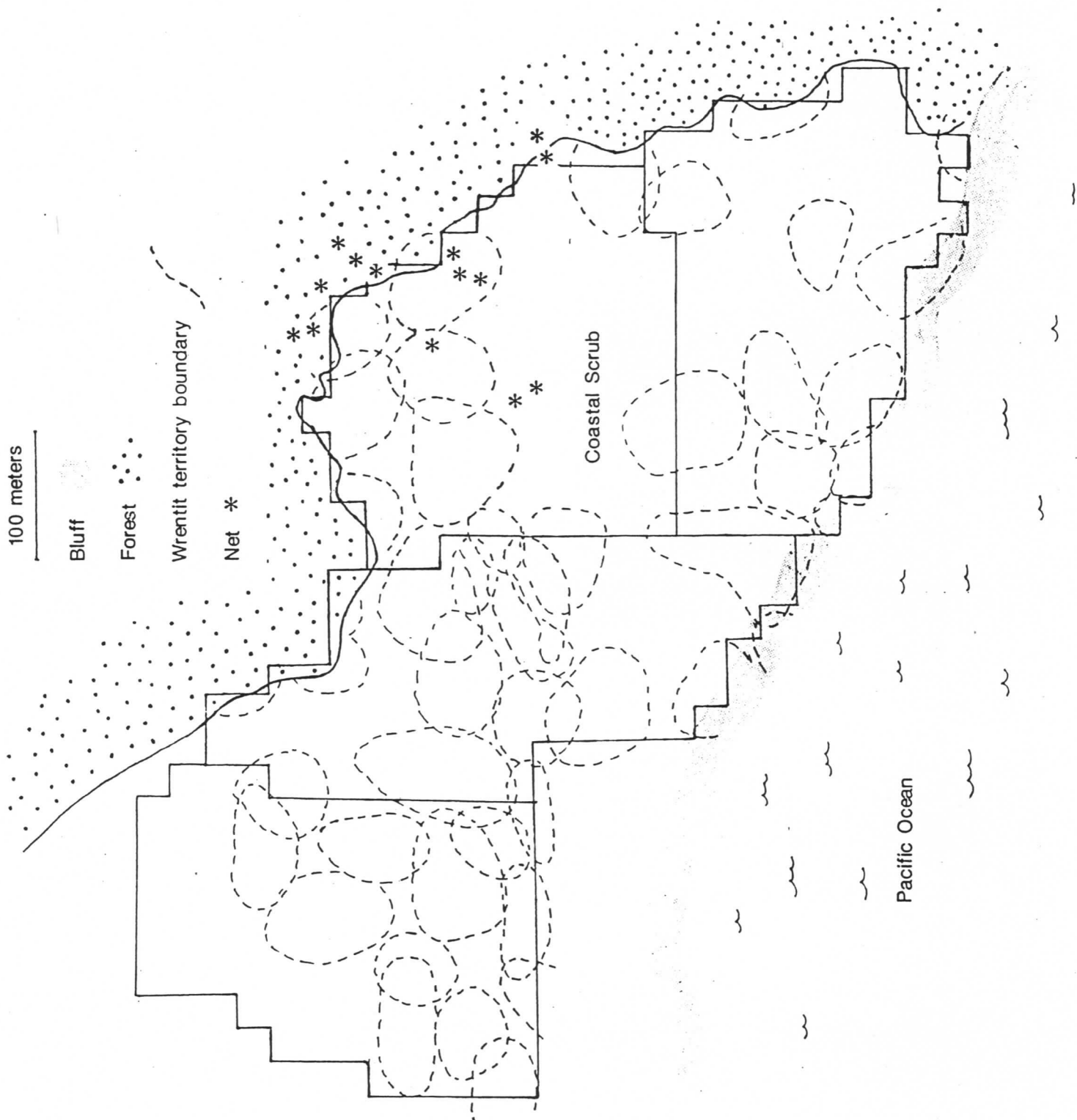
Figure Captions:

Figure 1. Map of the study area, Palomarin Field Station, Point Reyes National Seashore. Nest-searches and spot-mapping of color-banded birds took place in the four contiguous area marked by solid, rectilinear lines, totalling 36 ha in area. Constant effort mistnetting was conducted at nets marked with asterisks. Dotted lines enclose Wrentit territorial boundaries (1985 shown).

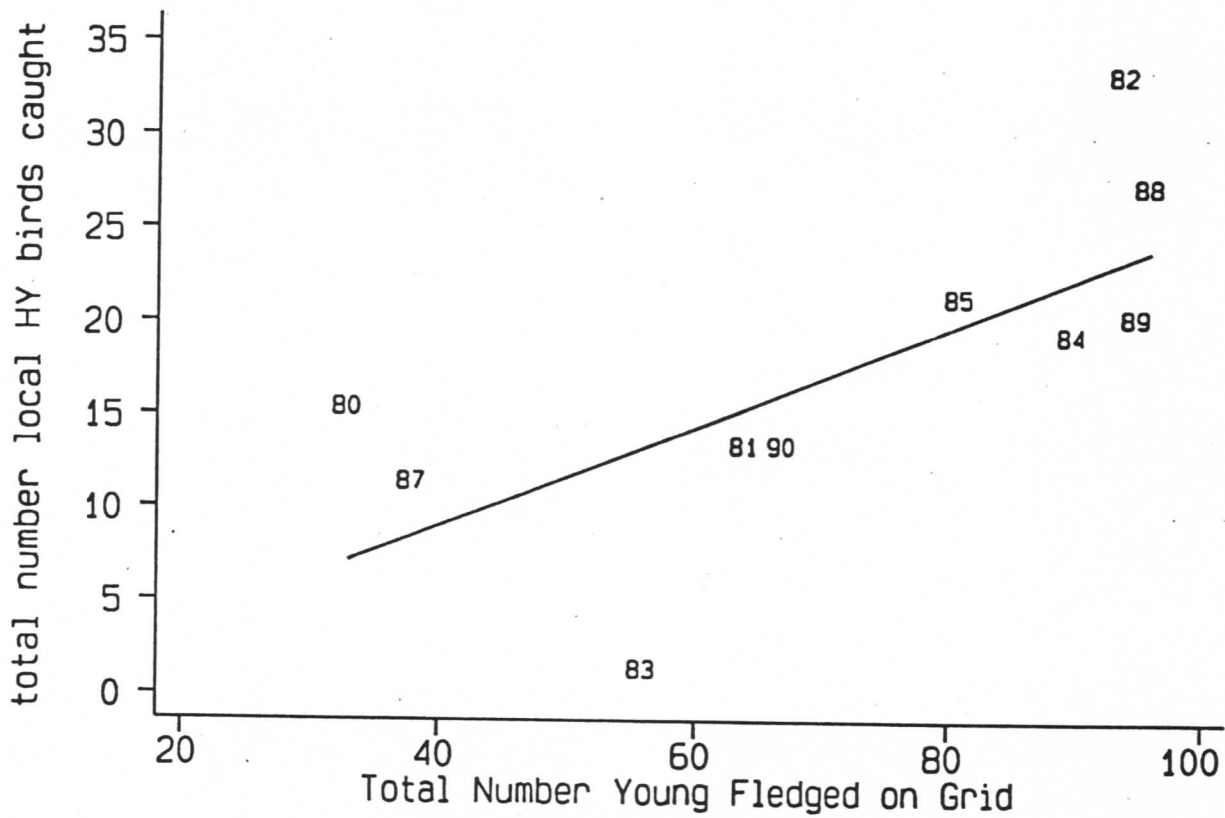
Figure 2. Number of locally-born Hatching Year (HY) Wrentits caught in each breeding season in relation to total number of Wrentit young fledged on the study grid (see text). '80' refers to 1980 breeding season, etc. The solid line is the best least squares fit to the data; regression statistics are provided in the figure.

Figure 3. Ratio of Hatching Year (HY) Wrentits to After Hatching Year Wrentits caught in each breeding season in relation to fledging productivity on the study grid (i.e. Number of fledglings produced per pair per breeding season). Substituting total HY birds caught for the ratio HY/AHY or total number of fledged young for fledged young per pair did not improve the statistical relationship between nest-based and net-based measures of Wrentit productivity. '80' refers to 1980 breeding season, etc. The solid line is the best least squares fit to the data; regression statistics are provided in the figure.

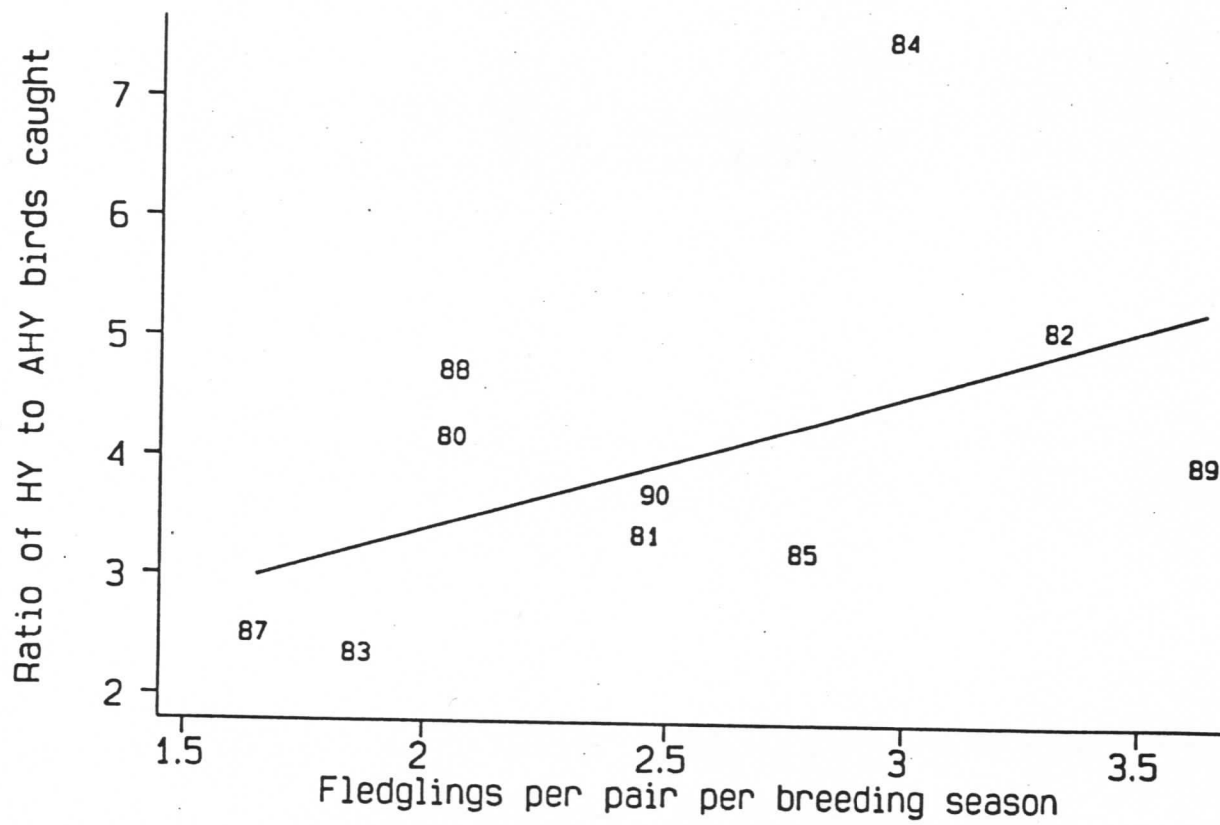
Figure 4. A) Number of Hatching Year (HY) Song Sparrows caught in each breeding season (regardless of origin) per 100 net-hours in relation to total number of Song Sparrow young fledged on the study grid (see text). '80' refers to 1980 breeding season, etc. The solid line is the best least squares fit to the data; regression statistics are provided in the figure. B) Same variables and same years of data as in part A), but for Wrentits. The solid line is the best least squares fit to the data; regression statistics are provided in the figure.



Wrentits, Palomarin: 1980-1990
 $R^2=0.492$, $P=0.024$

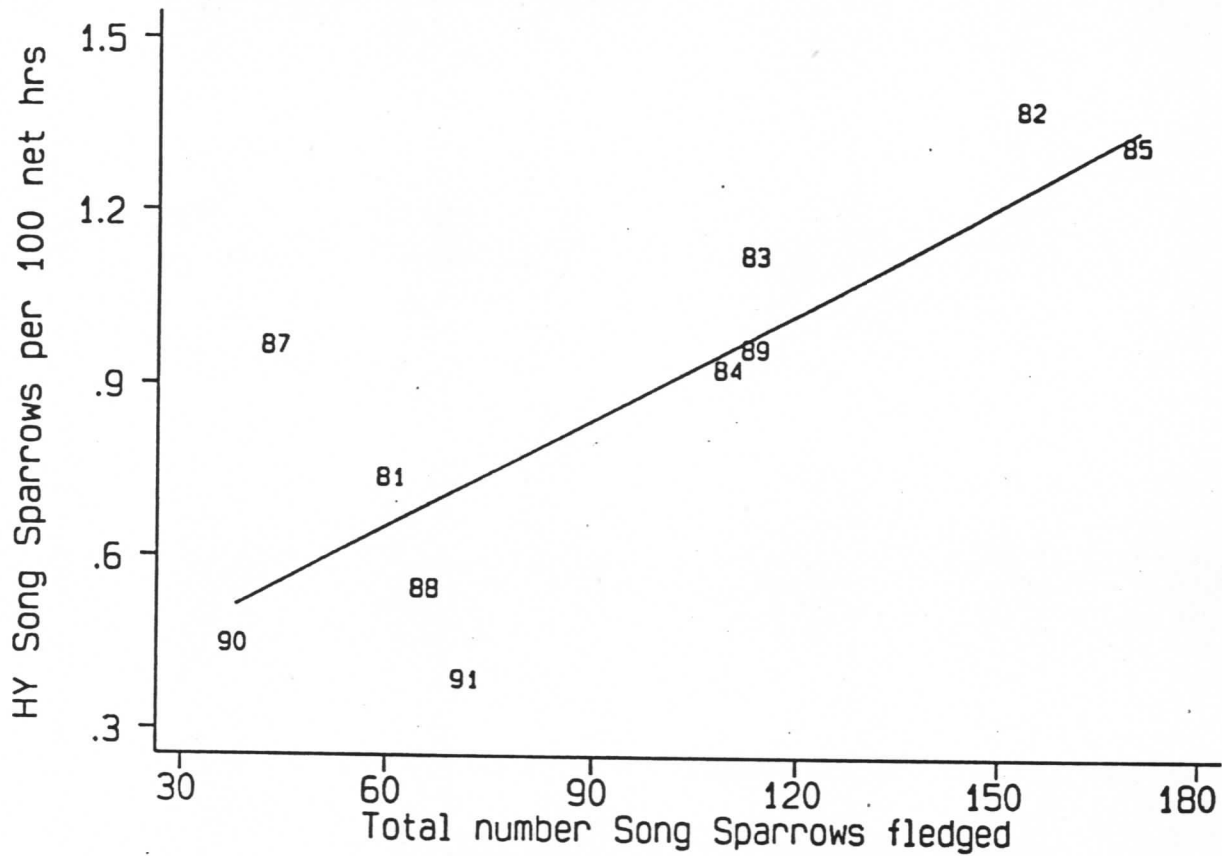


Wrentits, Palomarin: 1980-1990
 $R^2=0.248$, $P=0.143$



R square = 0.67, P = 0.004

A)



R square = 0.06, P = 0.49

B)

