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CORRECTING BIASED ESTIMATES OF DISPERSAL AND SURVIVAL DUE TO LIMITED STUDY AREA: THEORY AND AN APPLICATION USING WRENTITS[1]

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Abstract. Accurate estimates of dispersal distributions and survival to breeding are essential for estimating gene flow and population demographics, and for testing the predictions of mechanistic models. We derive a method that corrects for the underestimate of dispersal and survival inherent in studies conducted within a finite area. Each dispersal event is weighted by the inverse of the probability of observing that event, calculated by dividing the observable dispersal events of a given distance by all possible dispersal events of that distance. The method takes into account the shape of the study area and suitability of habitat. The method is applied to a twelve-year field study of natal dispersal in Wrentits (*Chamaea fasciata*) resulting in an increase in the estimate of mean and median dispersal from observed values of 267 and 248 m to corrected values of 375 and 387 m. The correction method also estimates the number of second year birds recruiting to potential breeding territories on and off the study area. Seventy-five of the 799 locally born fledglings recruited onto the study plot (9.3%). We estimate that an additional 101 birds recruited off the study plot, increasing the estimate of yearling survival to recruitment from 9.3% to 21.9% of young fledged. We used a simulation approach to generate testable predictions that validate the assumptions and results of the method. The method is easy to apply, and is easily extended to incorporate greater realism and detail.

Key words: Dispersal; survival; recruitment; Wrentits; Chamaea fasciata.

INTRODUCTION

Natal dispersal is usually defined as that movement from an animal's fledging site to its first breeding location (Greenwood and Harvey 1982). How far to disperse may be one of the most important decisions individuals make, involving such factors as competition and cooperation with parents and relatives (Woolfenden and Fitzpatrick 1984), inbreeding avoidance (Koenig and Pitelka 1979), and predictability of habitat type. Distributions of natal dispersal distances in birds and mammals have been used to make several types of inferences, including the survival costs of dispersal (Miller and Carroll 1989), the search patterns and degree of knowledge of dispersers (Waser 1985), possible competition among siblings (Tonkyn and Plissner 1991), the heritability of dispersive tendency (Greenwood et al. 1979), and the avoidance of inbreeding (Packer 1979). A left skewed distribution, or one with a preponderance of short distance dispersal events, has been taken as evidence of low competition, philopatry, or optimal search strategies of the surrounding area. A more uniform distribution has been taken to imply competition, a straight line dispersal search pattern, or an innate dispersive tendency above and beyond foraging a suitable breeding site. Accordingly, accurate estimates of dispersal would greatly improve our understanding of population genetics and habitat choice for a given species. Unfortunately, much of the theory surrounding natal dispersal has been developed to explain a pattern that may be an artifact of artificially truncated dispersal distributions recorded on limited study areas (Porter and Dooley 1993; Koenig and Hooge, unpubl. manuscript).

In most population studies, recruitment and dispersal distance are measured within a limited study area (Weise and Meyer 1979, Drilling and Thompson 1988, Morton 1992). Young are banded in the nest, and if they remain on the study site or return to it to breed, they are counted as local recruits. A mean or median distance

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is calculated from these observed dispersal events and an estimate of survival to first breeding is drawn from the number of observed recruitment events. Because some birds will disperse beyond the study site, it is understood that these estimates of dispersal and survival calculated within the study site are lower than the actual values. The longer the dispersal distance of an individual, the less likely its breeding site will fall within the study area. Despite these shortcomings, such values are often used to make comparisons which may not be justified. For example, Perrins (1965) used recaptures of Great Tits (*Parus major*) three months after fledging to conclude that earlier fledging young survive better than those fledging later in the season. These conclusions were disputed by Dhondt (1979), who conducted a study of dispersal involving large scale trapping of Great Tits during the postfledging period. Dhondt netted beyond the boundaries of his nest sites, and did not find later fledging young to incur higher mortality than earlier fledging young. Dhondt analyzed the recovery data from within the original study area, and concluded that inferences based on local recaptures or recruitment alone would have been misleading. Dhondt (1979) also pointed out that Kluyver's (1971) conclusion that survival of fledglings was density dependent based upon the result that artificial reduction of first broods led to higher recaptures of young from second broods was unwarranted, because an equally valid explanation was that dispersal, rather than survival had shown density dependence.

If survival to breeding is measured by the proportion of fledged young observed breeding the following year, then an observed difference in survival between early and late broods, or between sexes, or between heavier and lighter young, may be an artifact of differences in dispersal. While noted in passing, this limitation is often ignored in practice and differences in return rate often are interpreted as differences in survival. For example, Smith (1993), Reed and Oring (1993), and Campbell and Slade (1993) all used recapture rates to estimate survival in Marsh Tits (*Parus palustris*), Spotted Sandpipers (*Actitis macularia*), and Northern Cotton Rats (*Sigmodon hispidus*), respectively, though all mention that return rate is not necessarily a measure of survival and that differences in dispersal between different classes of individuals could affect survival estimates. In fact, Reed and Oring (1993) analyzed return rates on the natal site as compared to the entire study site censused in order to examine biases due to study area size and recorded higher return rates and a change in sex bias in return rate on the enlarged study area.

Different approaches have been used previously to deal with the constraints of a limited study site. Some assume a certain distribution, for example the normal distribution, and fit the missing data to that form (Wetzler and Risch 1984). A study by van Noordwijk (1984) compared observed dispersal events to all possible dispersal events within the study plot to measure the effect of position within a site on apparent dispersal patterns. Barrowclough (1978) proposed a method for using the observed distribution of dispersal events to estimate those events lost due to a limited study area. Porter and Dooley (1993) used Monte Carlo methods weighting observed recruitment events by observation sites to test a null model of uniformly distributed dispersal against the observed geometric distribution. Sandell et al. (1990) and Bowen et al. (1989) used methods similar to those derived here to generate a corrected number of territories moved by field voles (*Microtus agrestis*) and Groove-billed Anis (*Crotophaga sulcirostris*), respectively.

Methods that weight observed natal dispersal events by the probability of their observation can also be used to correct estimates of survival to recruitment into the breeding population. This approach has not been applied to survival estimates in birds. In this paper we present a method that corrects for dispersal events outside the study area, and then extend the method to estimate survival to recruitment of yearlings. The correction techniques are easy to program (True Basic® code is available from the authors), take into consideration both the shape of the study area and the distribution of preferred habitat around the study area, and are amenable to the addition of greater complexity and realism. Here, we use the method to analyze twelve years of dispersal data for Wrentits at the Palomarin Field Station of the Point Reyes Bird Observatory, and we attempt to validate the results and test the assumptions upon which it is based.

METHODS

DERIVATION

For dispersal distances short enough to be observed within a study site, the distribution of observed dispersal distances is a function of the actual dispersal of the birds born in a study site and the probability of observing recruitment events of the different distances. The following method uses the observed distribution of dispersal distances and the probability of observing those distances to generate a corrected distribution of dispersal distances and successful establishment of a potential breeding territory, which will be called "recruitment" from now on.

The method used here is derived from an application of probability theory using Bayes Theorem (Fleiss 1981). Let A_r be a recruitment event at a distance r from the natal nest, and B the observation of any recruitment event. Then $P(A_r)$ is the probability of recruiting a certain distance r, while P(B) is the probability of the recruitment being observed, irrespective of distance. In that case, by Bayes Theorem:

$$P(B \mid A_r) = \frac{P(A_r \mid B)P(B)}{P(A_r)}. \qquad (1)$$

Where $P(B \mid A_r)$ is the conditional probability that a dispersal event is observed given that it takes place at a certain distance, and $P(A_r \mid B)$ is the conditional probability that recruitment takes place at a certain distance r, given that it is observed. What we wish to derive is $P(A_r)$, the probability of recruiting at a certain distance from the fledging site whether or not it was observed. Rearranging the equation above,

$$P(A_r) = \frac{P(A_r \mid B)P(B)}{P(B \mid A_r)}. \qquad (2)$$

$P(A_r \mid B)$ is estimated using the observed frequency distribution of dispersal distances. $P(B \mid A_r)$ is calculated by a process to be described later. P(B), the probability of observing any recruitment event, requires knowledge of the total number of recruitment events on and off the study area. This is one of the figures that we are trying to estimate, but the term cancels and is not needed to perform the correction. To see how this formula relates to collected data, it is now expressed numerically.

$$N_{A_r}/N_{\text{recruits}} = (N_{A_rB}/N_B)(N_B/N_{\text{recruits}})/P(B \mid A_r)$$

where N_{A_r} is the number dispersing a distance r, N_{recruits} is the total number of recruits, N_{A_rB} is the number of individuals dispersing distance r that were observed (the uncorrected data), and N_B is the total number of observed recruits. Thus

$$N_{A_r} = (N_{A_rB})/P(B \mid A_r). \qquad (3)$$

The total number dispersing a distance r, N_{A_r}, equals the number observed to disperse a distance r, divided by the probability that a dispersal event of distance r is observed. The method calculates a weighting factor based on $P(B \mid A_r)$ for each observed dispersal event. If we consider a single observed event,

$$N_{A_rB} = 1$$

Then

$$N_{A_r} = 1/P(B \mid A_r). \qquad (4)$$

Differentiating the various available weighting correction techniques are the methods for calculating $P(B \mid A_r)$. In our method, the shape of the study site is first defined graphically and approximated as a grid, the resolution determined by the simplest approximation that describes the shape accurately. In addition to the shape of the study site, the areas which are suitable and the areas which are unsuitable or marginal for breeding are defined (Fig. 1). The probability of observing a dispersal event from each point on the study site is calculated by drawing a circle with a radius r, the distance of the observed dispersal event originating from that point. Let x be the number of potential endpoints that fall in suitable habitat within the study area and y be the number of potential endpoints falling on any suitable habitat inside and outside the study area. Then x/y equals the probability of observing a recruitment event of distance r from that point on the study area (Fig. 2). $P(B \mid A_r)$ is calculated by averaging the probability of observing a dispersal event of the given distance over every point of origin in the study plot. This is done by drawing a circle of radius r from each point on the study site and dividing x by y for each point on the site and taking the mean (in this case the sum of all x divided by the sum of all y). The weight for a single dispersal event is then $1/P(B \mid A_r)$. The sum of the weights for all observed dispersal events also estimates the number of successful recruits including those which are observed and those which were not observed because of dispersal off the study plot, and serves as a corrected estimate of survival to recruitment.

ASSUMPTIONS

Certain assumptions must be made to apply this technique, and when possible, the assumptions were tested or validated. The model assumes no heterogeneity in productivity on the study site.

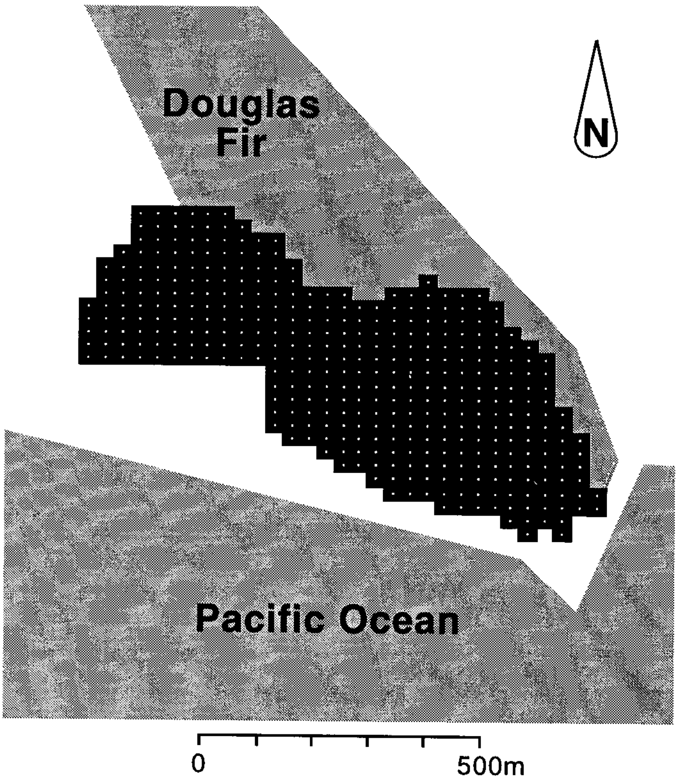

FIGURE 1. A schematic drawing of the study plot, shown in black. White dots represent the 30 m markers used to locate nests and the discrete points used to calculate the probability of observing individual dispersal events. Unsuitable habitat is shown by the shaded regions.

This allows use of an average value of productivity to represent all sites, and allows one to calculate a correction weighting function for a specific site that does not have to be recalculated with each addition of new data. A simulation approach for assessing the effect of deviation from this assumption is discussed later.

One assumption for which deviations are difficult to measure directly is that there is no significant dispersal longer than the longest dimension of the study area. Significant long distance dispersal will cause the correction weightings to underestimate the true survival to recruitment of juveniles. Long distance dispersal will also not be represented in the corrected dispersal distance distribution. Since these recruitment events are unobservable an indirect approach was taken to estimate the missing recruitment. We compared the recruitment of juveniles using the weighting correction to that which is required to replace the mortality in breeding adults to estimate the proportion of individuals dispersing longer distances than the longest observable distance on the study site.

Wrentits are assumed to disperse with equal probability in any direction, and this was tested with a Rayleigh test (Batshelet 1981). Another assumption is that aside from preventing birds from recruiting, habitat has no effect on recruitment patterns. Birds can recruit beyond obstacles of poor habitat, and are not more or less likely to be found on the borders of poor habitat. Furthermore, birds are assumed to attempt to recruit only on suitable habitat. Thus, in the present example, the Pacific Ocean on one side of the study site does not lower recruitment directly, but it forces all the recruitment onto suitable habitat. While this assumption is likely met in cases of grossly unsuitable habitat, the presence of population sinks, areas where recruitment occurs but productivity is very low, cannot be ruled out, and were not treated in this study. The mod-

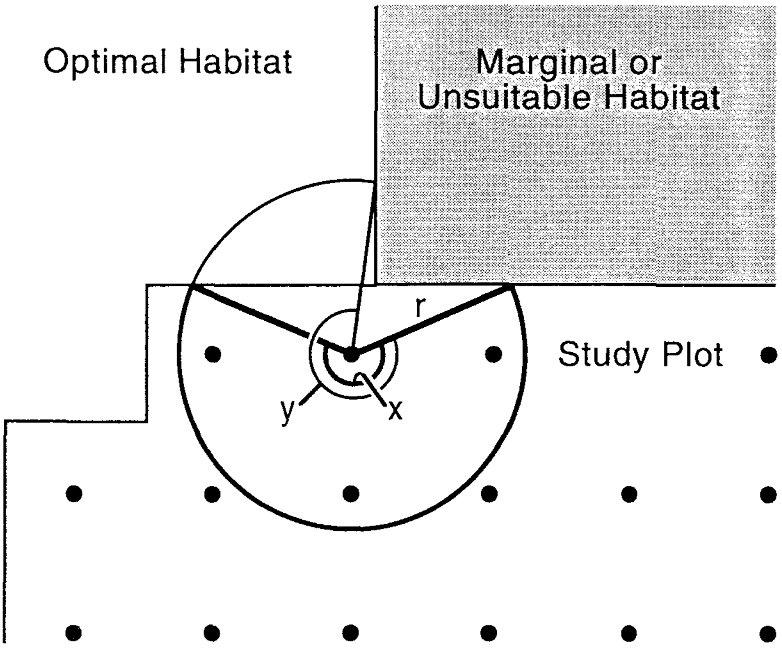

FIGURE 2. The method for estimating the probability of observing a single dispersal event of distance r from a single point on the study site. The ratio of x/y is the proportion of possible endpoints falling on suitable habitat within the study plot to the number of endpoints on all suitable habitat. This estimation is carried out for every point on the study site grid.

el assumes no rebound or aversion effect at the boundaries of unsuitable Wrentit habitat.

The longest observed dispersal events have a large impact on the estimate of juveniles that recruit off the study site, and by extension the overall estimate of survival to recruitment. To estimate confidence limits around the corrected survival estimate, and to examine the effects of sampling from the observed recruitment events, a bootstrapping (Efron and Gong 1983) program was written that sampled randomly from the observed recruitment events 75 times with replacement, and calculated the corrected estimate of survival from that "bootstrap sample." The program repeated this procedure 1,000 times, and the 2.5th and 97.5th percentiles of the histogram of 1,000 bootstrap replications provided 95% confidence intervals around the estimate of survival.

The effects of violations of these assumptions will vary with each study and study area. A directional bias will have a greater effect on dispersal and recruitment estimates as study area shape diverges more from a circle or square. This is because the detectability of dispersal events in different directions will vary within an irregularly shaped study area more than in a regular one. For example, if the study area is a long, narrow rectangle that extends from east to west, very few north-south dispersal events will be observable. A similar relationship exists for nonrandom productivity. The observable dispersal events from different parts of a study area are not the same (van Noordwijk 1984). If nests are concentrated in the center of the study, higher return rates will likely be recorded than if the nests were distributed along the periphery, however, the dispersal distribution will be skewed to shorter distance events, because the longest observable dispersal events can only originate from nests at the periphery of the study site. Since statistically significant biases in productivity or directionality of dispersal may be difficult to demonstrate with small sample sizes, it may be preferable to use a simulation approach to observe the potential effects of these biases on the corrected estimates, rather than correcting the data for these biases as well.

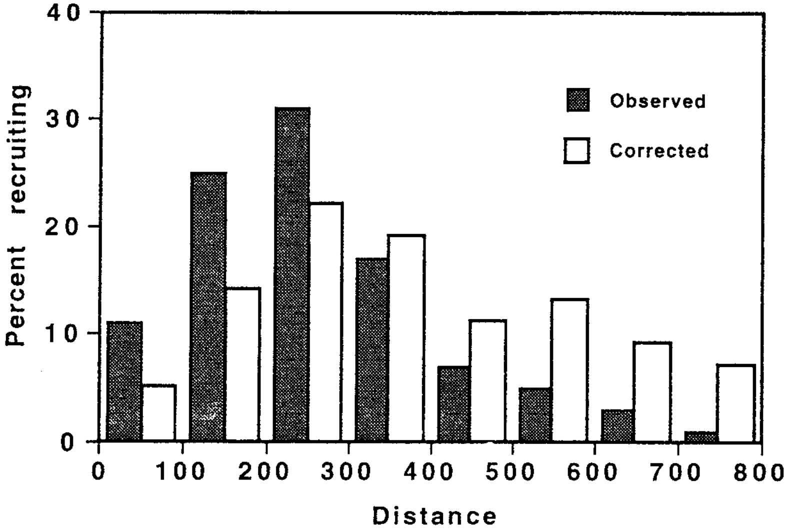

FIGURE 3. Histograms of the observed (shaded) and corrected (white) dispersal data. Bars show proportion of successful second year recruits dispersing a given distance.

THE WRENTIT STUDY

The data used in this analysis were gathered in a study of Wrentits at the Point Reyes Bird Observatory from 1980 to 1992. For further description of the study site see DeSante (1981), DeSante and Geupel (1987), and Geupel and DeSante (1990). The study plot consists of two types of "Northern Coastal Scrub" (Shuford and Timosi 1990), 18 ha of mature/undisturbed habitat—composed of dense, homogeneous shrubs, primarily California sage (*Artemesia californica*), coyote bush (*Baccharus piluaris*), bush monkey flower (*Mimulus aurantiacus*), poison oak (*Toxicodendron diversiloba*), and coffee berry (*Rhamnus californica*), and 14 ha of successional/disturbed habitat, composed of less dense coyote bush interspersed with coastal prairie grassland, thistles (*Cirsium*) and small (<9 m) Douglas fir (*Pseudotsuga menziesii*).

All Wrentits captured in the course of a standardized netting program (DeSante and Geupel 1987) or located in their nests received a color band combination for individual recognition. Age was determined by the degree of skull pneumatization or maroon color in the outer iris (Pyle et al. 1987). Juveniles refer to birds either banded as nestlings or banded with the above characteristics during their hatching year. Unknown age refers to individuals banded in late fall (after 31 October with complete skull pneumatization) through July of their first breeding season or individuals that never received bands. Individuals are considered recruits if they are observed to successfully establish a territory or join a territorial male (successfully fledging young is not a requirement). Effort was constant throughout the study site. A concentrated effort was made to locate all nests for all pairs for every year except 1986. Therefore the following breeding season, 1987, was not included in analysis of natal dispersal distance and local recruitment.

The study plot is marked by 387 stakes placed in a grid at 30 m intervals. The area surrounding the study site consists of disturbed successional coastal scrub, grazed coastal grassland, Douglas fir forest, and the Pacific Ocean. Though Wrentits have been observed in Douglas Fir forest (unpubl. data), its use by breeding Wrentits is sufficiently rare to allow it to be treated as unsuitable habitat for this correction. The grazed land and ocean were also treated as unsuitable or marginal Wrentit habitat for breeders (Fig. 1). For the analysis, the study site was approximated by a grid of points 30 m apart, in the same positions as the marker stakes.

RESULTS

There were 75 observed natal dispersal events for the years covered by the study (Fig. 3). There was no significant trend in the direction of natal

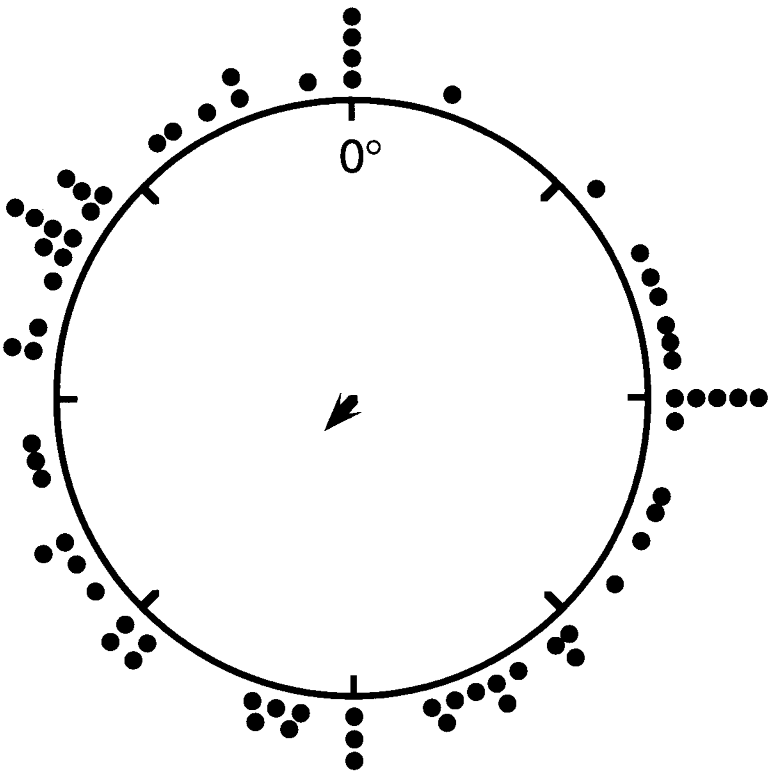

FIGURE 4. The compass directions of the observed dispersal events. The length of the directional arrow (relative to the radius of the compass circle) is equal to 1 minus the P value for the orientation of the points (Rayleigh z = 0.58, $P > 0.9$).

dispersal from the fledge site (Fig. 4). The weighting method as outlined above was applied to the observed dispersal distances, and the corrected number of birds surviving to recruit was calculated, as well as the corrected dispersal distribution. The longer dispersal distances were weighted more heavily, as the probability of observing a recruitment event ranges from 1 when the distance is 0 meters to 0 when the dispersal distance is longer than the largest dimension of the study plot, approximately 1 km in our case. The longest observed dispersal event in the Wrentit study, 720 meters, was weighted 12.6 times, while the shortest dispersal distance of 33 meters was weighted 1.05 times. This had the effect of shifting the distribution from what was originally right skewed and leptokurtic (skewness = 0.86, $g_2 = 0.22$, where $g_2 = 0$ for a normal distribution) to a more uniform, more platykurtic distribution (skewness = 0.22, $g_2 = -0.98$, Fig. 3). The uncorrected mean dispersal distance was 267 ± 153 meters, and the median distance was 248. The corrected mean dispersal distance was 379 ± 184 meters, an increase of 42%, and the corrected median distance was 372, an increase of 50%. The corrected estimate of recruits was 176, 2.33 times the original estimate. This increase in recruitment does not take into account dispersal longer than the longest observable distance. There were 799 birds that fledged on the study site over the years of the study, and so the correction increased the estimate of recruitment from 9.3% to 21.9% of fledged birds, with a bootstrap confidence interval of 0.18–0.26.

To determine whether there were any apparent or real differences between sexes in survival that were confounded by dispersal effects, we compared corrected and uncorrected dispersal and recruitment by sex. Thirty-seven known males and 35 known females were recovered on the study plot, and the correction method estimates that 78 males and 86 females successfully re-

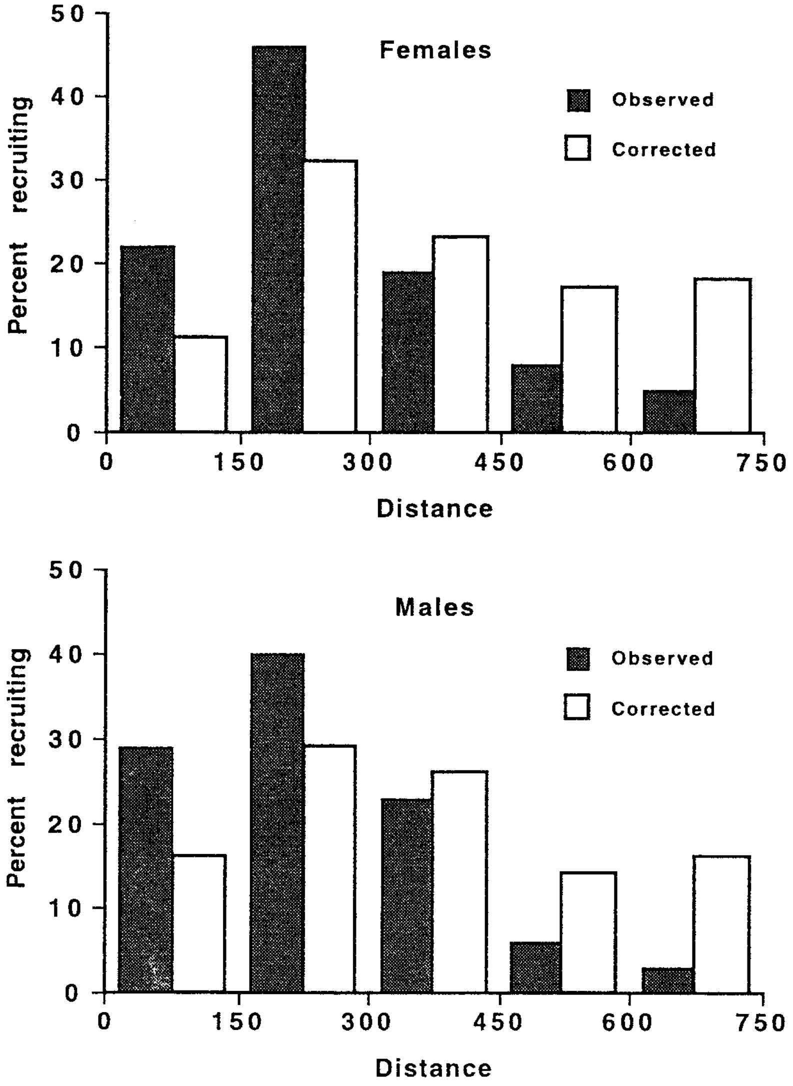

FIGURE 5. Observed (shaded) and corrected (white) dispersal distributions for males (top) and females (bottom).

cruited. Both the corrected and uncorrected average dispersal distance did not vary between males and females (Fig. 5). The corrected mean dispersal distance for males was 373 ± 201 m and for females was 368 ± 171 m. Juvenile Wrentits do not appear to vary in either their dispersal patterns or survival by sex, so there were no observed differences in the survival estimate after correction for dispersal bias. Whereas the observed number of male recruits was slightly lower than females, after correcting for recruitment beyond the study grid recruitment of females was estimated to be slightly higher than in males.

The corrected dispersal and recruitment were used to simulate the observed local recruitment, in order to test whether nonuniform productivity on the study site led to bias in the corrected dispersal and survival estimates. The average productivity was calculated by taking the corrected recruitment, in this case 176, and dividing it by the "area" of the study plot, in this case the 387 grid points. This yielded an average productivity of 0.45 recruits per study grid point.

From each point in the plot, circles were drawn that were weighted with the corrected dispersal distribution. In this case, the dispersal distribution was approximated by concentric bands of 100 m width. The sum of predicted local recruits was 76.5, which is close to the observed number of 75 recruits. In contrast, using the *uncorrected* dispersal distance distribution and productivity to predict local recruitment in this way gives a prediction of 23 local recruits.

Survival to recruitment was estimated from adult survival and fecundity, and the demographic estimate of survival was used to estimate the number of individuals surviving to recruitment. A breeding Wrentit pair produces 2.54 fledglings per year, on average and experiences 0.36 mortality (n = 10 years, Nur and Geupel, unpubl.). Using 64% adult survival, recruitment probability must be 0.28 to balance adult mortality. This figure is an overestimate to some degree, because there is recruitment of older floaters in addition to second year birds (O. Williams, G. Geupel, and N. Nur, unpubl. manuscript). This type of extrapolation rests upon the assumptions of no net immigration and population stability, consistent with the observation of no significant trend in breeding population size in this population (Geupel and Nur, unpubl.). This indirect measure of offspring survival indicates that long distance dispersal (dispersal over 700 m) accounts for 22% of juvenile survival to recruitment, calculated as the fraction of the demographic recruitment estimate not accounted for by the corrected survival, (0.28–0.219)/0.28. In contrast, use of the observed recruitment as an estimate of survival leaves 66% of the demographic estimate of survival to recruitment unaccounted for. A conclusion of significant long distance dispersal is consistent with the corrected dispersal distribution, which does not end in a narrow tail, but in a wide band, implying dispersal beyond the longest distance observed. This conclusion is also consistent with mist netting data (Nur and Geupel 1993) which show a plateau in probability of net capture of juveniles with increasing distance from the fledging site from 400 to beyond 700 meters.

DISCUSSION

Our method avoids some assumptions of some earlier methods. In particular, the method takes the shape of the study site into account. Study sites are often extremely nonregular (noncircular), as they are often constrained by physical boundaries, e.g., a Douglas fir forest and the Pacific Ocean at the Palomarin site. The method can also factor in quality of habitat in or around a study site. When analyzing the Wrentit data, all of the habitat within the study site was counted as suitable. Some of the habitat outside the study site was treated as unsuitable (the Pacific Ocean and a stand of Douglas Fir trees) and the rest was treated as suitable. While some marginal habitat was simplified and treated as unsuitable in this case, the method can be made more sensitive. The programs can be modified to weight habitat quality, although the weighting criteria will vary with different species and different objectives. We use productivity as a measure of habitat quality, which is a function of the number of breeding individuals and their nesting success. In different combinations of habitat quality and numbers of breeding age individuals, productivity can depend on the density of individuals, the density of nest sites, or the density of resources (Brown 1969), and on the quality of nest sites (susceptibility to predators or weather) as well. Weighting the likelihood of recruitment in or outside of the study site by habitat quality requires extra information, but is especially important in systems with very different productivity inside and outside of the research site.

While the methods presented here are more flexible and give more realistic results than a previous method developed by Barrowclough (1978), they work on a similar principle. Barrowclough's method assumes a circular study area. The ratio of all circles with a radius of the given dispersal distance with the center within the circular study area are integrated in order to determine the percentage falling inside the approximating circle. This method is not easily applicable to a noncircular study site and does not take habitat suitability into consideration. The differences in correction weightings can be significant. The Barrowclough correction cannot be used with the Wrentit data because a circle with an area equal to the study plot has a diameter smaller than one of the observed dispersal events. The probability of observing that dispersal event is zero, meaning that the observed event is given infinite weight. Use of an approximating circle does not just lower precision, but also changes estimates of survival and the shape of the dispersal distribution in ways that are not always predictable. If there are long observed dispersal events relative to the dimensions of the study site, their weights are overestimated by a circular approximation due to the reduction of possible long distance recruitment events in a circle, and short dispersal events are underweighted due to the smaller amount of edge. More importantly, discrete methods such as the one developed here and earlier (Sandell et al. 1990, Porter and Dooley 1993, Bowen et al. 1989) are more easily extended in a realistic way to test predictions. For example, in addition to simulating the local recruitment of birds hatched within the study site, recruitment of immigrants from off the study site can be simulated in the same manner to estimate the effects of long distance dispersal, if productivity beyond the study area is known and immigrants are easily recognized.

The methods developed here are similar to those used by Sandell et al. (1990) and Porter and Dooley (1993). Those studies implicitly take study area shape into account by weighting for trapping or observation locations. Because of the constant effort over the entire Palomarin study area, there was no need to weight by trapping location, and study area shape was implicitly built into the correction. Though Sandell et al. do not take habitat quality into consideration, Porter and Dooley do consider habitat quality to the extent that they eliminated the Pacific ocean (as we did) as a dispersal sink in one of the studies they reanalyzed. Porter and Dooley use the coefficient of variation of correction weights to measure the degree of truncation due to limited study area. In the five studies analyzed, the CV of the correction weightings ranged from 82–127%, compared to the CV of our correction weightings, which was 81%, low on their scale. The importance of correcting for bias due to limited study area can be seen in the comparison of radiotracking data to observed dispersal. In a study on acorn woodpeckers (Koenig and Hooge, unpubl. manuscript), the average distance moved by radiotracked dispersers was an order of magnitude higher than the observed dispersal of individuals remaining on the study site. While the largest dimension of the study area precluded dispersal observations greater than 1 km, the distribution within that range was correctable.

Our method allows one to construct a more accurate distribution of dispersal distances, to more accurately estimate survival to recruitment, and to quantify the effects that limited study plots have on observed dispersal distributions and survival estimates. While it is possible to take into consideration directional biases in dispersal and more levels of variation in site quality, the method as used here gave reasonable results with only very simple descriptions of study site shape and surrounding habitat quality. This is important if the method is to be applied to a wide range of completed or continuing studies where additional data may not be available.

Though other methods for correcting dispersal distributions have been developed, they have thus far been used mostly to construct null models of uniform dispersal distance to compare with the predictions of models using a geometric probability of stopping, or models of philopatry. The potential for these weighting methods to correct natal recruitment estimates has not been fully appreciated, and as is seen here, the effect of limited study area on survival estimates is at least as dramatic as the effect on dispersal distributions. Though area bias correction of survival estimates has not been previously exploited in the study of natal dispersal, a conceptually similar method for using corrected estimates of undetectable dispersers to correct survival estimates of kangaroo rats, Dipodomys merriami, was proposed by Zeng and Brown (1987). A potential benefit of simultaneous correction of dispersal and survival bias is the ability to decouple differential survival from differential dispersal. For example, Arcese (1989) points out that the simulation models of natal dispersal mentioned earlier (Waser 1985, see also Tonkyn and Plissner 1991) suggest that sex-biased dispersal arises from differential mortality rates of males and females. Since the more dispersive sex will always appear to have higher mortality, this hypothesis will always receive support from biased data sets. Correction for limited area effects allows survival to be compared between groups with different dispersal rates, and will provide a true test of Arcese's hypothesis. The ease of implementing the method proposed here, its ability to take habitat quality and study plot shape into consideration, and the ability to extend the method to measure the effects of violating certain assumptions, make it useful for better estimating dispersal distributions and survival to recruitment.

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