

NATAL DISPERSAL IN THE COOPERATIVELY BREEDING ACORN WOODPECKER¹

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Abstract. Dispersal data are inevitably biased toward short-distance events, often highly so. We illustrate this problem using our long-term study of Acorn Woodpeckers (*Melanerpes formicivorus*) in central coastal California. Estimating the proportion of birds disappearing from the study area and correcting for detectability within the maximum observable distance are the first steps toward achieving a realistic estimate of dispersal distributions. Unfortunately, there is generally no objective way to determine the fates of birds not accounted for by these procedures, much less estimating the distances they may have moved. Estimated mean and root-mean-square dispersal distances range from 0.22–2.90 km for males and 0.53–9.57 km for females depending on what assumptions and corrections are made. Three field methods used to help correct for bias beyond the limits of normal study areas include surveying alternative study sites, expanding the study site (super study sites), and radio-tracking dispersers within a population. All of these methods have their limitations or can only be used in special cases. New technologies may help alleviate this problem in the near future. Until then, we urge caution in interpreting observed dispersal data from all but the most isolated of avian populations.

Key words: Acorn Woodpecker, demography, dispersal, *Melanerpes formicivorus*, radio-tracking.

INTRODUCTION

Three processes determine population growth: birth rate, mortality rate, and dispersal, the latter of which is often divided into immigration and emigration. Extensive data are available on birth rates in birds; indeed, there may be no demographic parameter that has been studied in more detail than avian clutch size and nesting success. In contrast, relatively little is known about the other two phenomena. However, there is a significant difference between our knowledge of avian mortality and avian dispersal. Mortality of adult birds is rarely observed due to their relative mobility, large home range size, and the fragility of their remains. Thus, although estimates of survivorship are available for many species, little is known about specific causes of adult mortality in most populations of wild birds.

In contrast, both immigration and emigration are frequently observed in studies involving marked individuals. Nonetheless, two difficulties conspire to make the specifics of dispersal as difficult to obtain as those of mortality. First, because physical evidence of death is rarely obtained, emigration is invariably confounded with mortality. Second, because study areas are finite in size, dispersal distributions are subject to systematic bias. Unfortunately, both the distribution and frequency of dispersal are critical parameters in estimates of gene flow and effective population size. How much confidence can we place in estimates given to these parameters?

We contend that considerably less is known about dispersal distributions of birds than much of the literature suggests. Here we discuss several issues relating to the problem of, and partial solutions to, obtaining unbiased dispersal distributions using data from our long-term study of Acorn Woodpeckers (*Melanerpes formicivorus*) in central coastal California.

DISPERSAL DISTRIBUTIONS: THE DATA

Acorn Woodpeckers are cooperative breeders and offspring frequently remain in their natal

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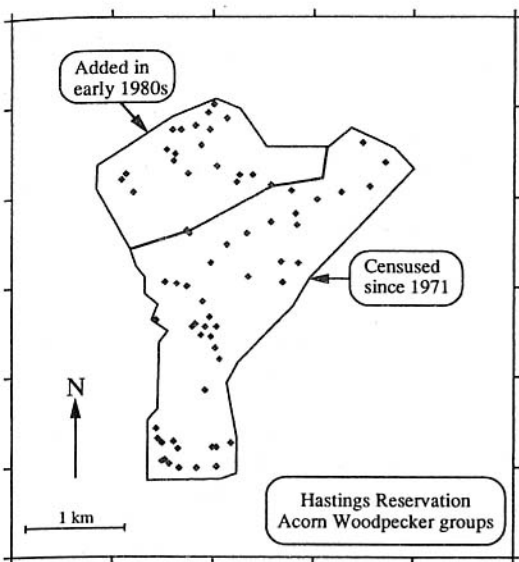


FIGURE 1. Map of the study area, located in upper Carmel Valley, central coastal California. Locations of the study areas and the primary granaries of Acorn Woodpecker groups followed starting in 1971 and starting around 1981 are marked. Tick marks are at 1-km intervals and the maximum distance between granaries within the study area is 4.3 km.

groups for up to several years after fledging as nonbreeding "helpers at the nest" (Koenig and Mumme 1987). Offspring can eventually become breeders either by inheriting breeding status within their natal group following the death of breeders of the opposite sex or by dispersing and filling reproductive vacancies elsewhere in the population. The latter is often accomplished by sibling units, and two sisters or up to four brothers may jointly fill a vacancy and subsequently cobreed together in the group. Similarly, birds inheriting breeding status often join older siblings or parents as breeders. Groups thus consist of a variable number of cobreeding males that are close relatives and joint-nesting females that are sisters or a mother and her daughter, along with offspring from prior years.

We followed 25 to 40 social groups between 1972–1998 over an irregular area of approximately 424 ha (to 1981) and 625 ha (1982–1998) (Fig. 1). In all, we determined the fates of 1,059 offspring (577 males, 482 females) that survived to their first February following fledging, the earliest date at which young have been observed to disperse (Koenig and Mumme 1987). We recorded birds as having become

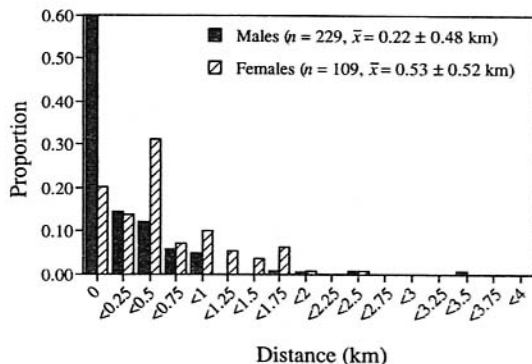


FIGURE 2. Natal dispersal distributions of male and female Acorn Woodpeckers observed at Hastings Reservation between 1972 and 1998 grouped into non-cumulative 0.25-km (approximately the diameter of a territory) categories (that is, the "< 0.5 km" category encompasses dispersal events that were > 0.25 and < 0.5 km). Means ($\pm$ SD) and sample sizes are listed.

breeders when they fulfilled two criteria: (1) they attained breeder status, either by inheriting their natal territory following the disappearance of breeders of the opposite sex (Koenig et al. 1998), or by dispersing and filling a vacancy elsewhere, either by themselves or with siblings, and (2) they had the opportunity to breed, defined as having attained breeder status in a group for at least 60 days, 30 of which were during the primary breeding season (April through June, inclusive).

Out of 1,059 offspring, 338 (229 males, 109 females) qualified as having attained breeding status in the population. Of these, 159 (137 males, 22 females) were birds that inherited their natal territories, whereas the remainder dispersed and became breeders elsewhere within the study area. The distribution of dispersal distances based on these events (Fig. 2) indicate mean ($\pm$ SD) dispersal distances of 0.22 ± 0.48 km for males and 0.53 ± 0.52 km for females, a highly significant difference (Mann-Whitney *U*-test, $z = 7.4$, $P < 0.001$). If birds that inherit their natal territories are omitted (dispersal distance = 0), mean dispersal distances are 0.54 ± 0.63 km for males and 0.66 ± 0.50 km for females, still a significant, albeit much smaller, difference (Mann-Whitney *U*-test, $z = 2.7$, $P < 0.01$). Thus, the usual avian pattern of greater dispersal by females (Greenwood 1980) holds for Acorn Woodpeckers, both overall and among birds dispersing within the study area. The reasons that males inherit their natal territory more frequent-

ly (23.7% of males vs. 4.6% of females) are largely demographic: because cobreeding is more frequent among males than females, there are almost always fewer breeder females than breeder males in groups. As a result, female vacancies, which subsequently allow male offspring to inherit and breed in their natal territory (Koenig et al. 1998), are more common than male vacancies allowing females to inherit.

What proportion of all dispersal events do these figures represent or, equivalently, what proportion of the population emigrates (Waser et al. 1994)? We addressed this question by counting the number of nonbreeding helpers disappearing from our study area and comparing it to the number of unbanded immigrants entering into the population and attaining breeder status by the criteria listed above. That is, they remained in the group into which they immigrated for at least 60 days, 30 of which were during the April to June breeding season. As before, juveniles were included, but only if they survived through the February following fledging. Care was taken to consider only groups in which essentially all birds were banded and that we censused sufficiently regularly to be confident that any immigrants were detected.

Assuming that immigration equals emigration over the long run, our results suggest that approximately one-third (35.7%) of nonbreeders that disappeared attained breeding status outside the study area and that slightly over half (56.3%) of all nonbreeders attained breeding status some-

where (Table 1). The percentage of nonbreeders successfully dispersing that attained breeder status within the study area was estimated as 71.8% of males and 41.3% of females. Thus, the values graphed in Figure 2 represent nearly three-fourths of all males and slightly less than half of all females that become breeders in the population.

Based on these data, the observed dispersal distributions are highly skewed toward short distances (Fig. 2), suggesting that few individuals disperse farther than the 4.3 km separating the two most distant groups surveyed during the study (Fig. 1). Furthermore, the proportion of all birds estimated to have attained breeder status that we were able to detect was reasonably high (58.0%; Table 1), and many of the individuals that disappeared probably died or dispersed only a short distance to territories just outside the study area. Are the values graphed in Figure 2 therefore likely to be reasonable approximations of the true dispersal distributions exhibited by birds in the population?

There are at least two reasons why we believe the answer is no. First, there is a strong bias in these data toward the detection of short-distance dispersal events. Second, it is impossible to detect dispersal events longer than the relatively short maximum distance (4.3 km) between territories within the study area. In combination, these factors preclude the detection of long-distance dispersal events that could alter consider-

TABLE 1. Estimation of the percent of nonbreeders that disperse and breed. Criteria for dispersal is that the bird left its natal group for at least 60 days, at least 30 of which were during the breeding season. Numbers in lower section of the table refer to line numbers in the upper section.

	Males	Females	Total
1. <i>n</i> nonbreeding helpers	577	482	1,059
2. <i>n</i> known dead (%)	7 (1.2)	4 (0.8)	11 (1.0)
3. <i>n</i> known emigrants within study area (%)	92 (15.9)	87 (18.0)	179 (16.9)
4. <i>n</i> inheriting natal territory (%)	137 (23.7)	22 (4.6)	159 (15.0)
5. <i>n</i> disappearing or leaving study area (%)	323 (57.8)	363 (76.1)	686 (66.2)
6. Still a nonbreeding helper	18 (3.1)	5 (1.0)	23 (2.2)
7. <i>n</i> immigrants entering study area	90	155	245
Estimates (%)			
Nonbreeders disappearing that attain breeder status (7/5)	27.9	42.7	35.7
Nonbreeders attaining breeder status $((3 + 4 + 7)/(1 - 6))$	57.1	55.3	56.3
Successfully dispersing nonbreeders attaining breeder status within the study area $((3 + 4)/(3 + 4 + 7))$	71.8	41.3	58.0

ably the distributions graphed in Figure 2. We expand on these issues below.

DISPERSAL DISTRIBUTIONS: CORRECTING THE DATA

The first step in mitigating the problems associated with finite study areas is to estimate the proportion of dispersers that were detected (Table 1), thereby setting an upper limit to the number of birds that may have dispersed but were not detected. For our study, this is 28.2% of males and 58.7% of females. These proportions are relatively low because Acorn Woodpeckers are highly social and many offspring remain in or near their natal territories their entire lives; in most species that are less social, few offspring are seen after achievement of independence.

The next step is to correct observed dispersal distributions for the probability of detection, defined as the probability of a disperser ending up in a patch where it is likely to be found by the researcher. This then allows estimation of the proportion of individuals dispersing as far as the maximum detectable dispersal distance as opposed to within the study area itself. Various techniques have been proposed to do this. We contend that methods based on *a priori* assumptions concerning the form of the dispersal distributions, such as Wetzler and Risch's (1984) assumption of a normal distribution, Caley's (1991) null models, or Murray's (1967) assumptions that dispersing individuals will generally move to the first uncontested site they can find nearest their natal territory, are unsatisfactory: too few data on complete dispersal distributions are available to know whether the assumptions of such models are met.

At least two methods have been proposed that do not rely on such assumptions. Barrowclough (1978) proposed a geometric model based on a circular study area within which the expected proportion of dispersal events of a given distance falling within the study site can be calculated. More recently, Baker et al. (1995) proposed a method in which the probability of detecting dispersal events of a given distance is estimated by means of simulations in which the average proportion of dispersers ending up within the study area (and thus detected) is estimated from a large number of hypothetical dispersal events of a given distance starting from a random point within the study area and moving in a random direction. This method allows for

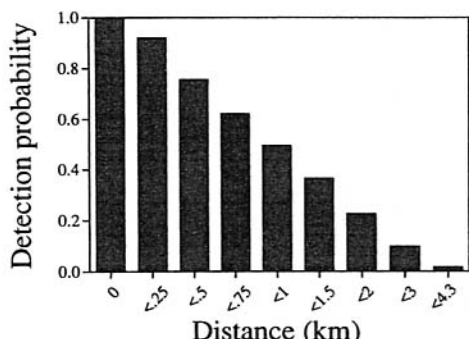


FIGURE 3. Detection probabilities based on the Baker et al. (1995) technique using the Acorn Woodpecker study area at Hastings Reservation. Categories are noncumulative, and some distance categories used in Figure 2 were combined to minimize errors associated with small sample sizes. All birds inheriting their natal territory are detected whereas less than half of birds dispersing 1 km are detected.

study areas of any shape and, with minor modifications, can even accommodate study areas that change in size and shape during the study period such as is the case here. It also adjusts values for potential areas of unsuitable habitat in or near the study area, thereby permitting a more realistic and general estimate than that provided by Barrowclough's (1978) technique.

We used Baker et al.'s (1995) method to calculate estimated probabilities of detection of dispersal events up to the 4.3 km maximum dispersal distance within the Hastings Reservation study area. Detection probabilities averaged over the study area, taking into account the area added in the early 1980s (Fig. 1), are graphed in Figure 3, while Figure 4 compares the observed and the adjusted dispersal distributions, the latter based on the observed number of dispersal events within a given distance category divided by the detection probability for that distance.

The results (Fig. 4) raise two issues. First, the low estimated detection probability for long-distance dispersal events can inflate the adjusted number of dispersers to an unrealistic degree. This problem occurs in the case of males because of the two individuals that were observed to disperse farther than 3 km (Fig. 2). The estimated detection probability for birds dispersing 3–4.3 km is 0.0165, which yields an estimated 121 males dispersing this distance. Because only 34 males are unaccounted for after correcting for dispersal up to 3 km (Table 2, line 3 and line 4a), this is clearly unrealistic.

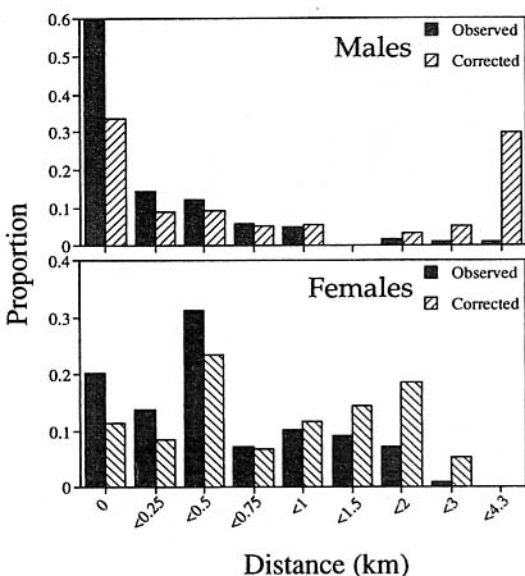


FIGURE 4. Frequency distributions of dispersal distances for male and female Acorn Woodpeckers as observed (from Figure 2) and after adjusting for the detection probabilities graphed in Figure 3. Distance categories are noncumulative.

One solution to this problem is to assume that the low probability of detection renders it inappropriate to correct for detectability beyond some distance shorter than the maximum detectable dispersal distance. For example, if we correct for detectability only up to 3 km, we are left with 34 males, 32 of which are unaccounted for after subtracting the 2 that were known to have dispersed between 3 and 4.5 km (Table 2). Using these values, 89.3% of nonbreeder males

dispersed < 3 km (Table 2) and only 10.0% are unaccounted for after adding the two birds that are known to have dispersed farther. Because no females were observed to have dispersed farther than 3 km, their values are unchanged by correcting for detectability up to 3 km (rather than to 4.3 km), and 29.2% are unaccounted for in either case (Table 2).

The second issue is that the dispersal distribution adjusted for detectability is much less skewed than the original distribution (Fig. 4). For males, skew ($\pm$ SE) based on the categories in Figure 4 decreases 65% from 4.46 ± 0.16 to 1.57 ± 0.14 , whereas for females it decreases 53% from 1.27 ± 0.23 to 0.60 ± 0.18 . This considerably reduces the strength of the argument that few individuals are likely to have dispersed more than the maximum detectable dispersal distance because of the highly skewed distribution of observed dispersal events.

At this stage it is possible to estimate mean dispersal parameters (Table 3), including mean dispersal distances and root-mean-square (RMS) dispersal values, the latter of which puts more weight on long-distance dispersal events and better reflects the evolutionary consequences of gene flow (Haldane 1948, Fisher 1950). Using the observed distributions (Table 3, line 1) is tantamount to assuming that no birds successfully disperse beyond the limits of the study area and thus provides (unrealistic) minimum estimates for mean and RMS values. Using the adjusted distributions increases values considerably, depending on whether the two males that dispersed farther than 3 km are adjusted for de-

TABLE 2. Estimation of the percent of nonbreeders that disperse and breed beyond the maximum detectable dispersal distance (4.3 km). Numbers in lower section refer to line numbers in the upper section.

	Males	Females	Total
1. <i>n</i> nonbreeding helpers	577	482	1,059
2. Total number of observed dispersal/inheritance events	229	109	338
3. Total number of inferred dispersal events ^a	319	264	583
4a. Total number of dispersal events <3.0 km, adjusted for detectability	285	187	472
b. Total number of dispersal events <4.3 km, adjusted for detectability	319 ^b	187	506
Estimates (%)			
Nonbreeders dispersing <3.0 km (4a/3)	89.3	70.8	81.0
Nonbreeders dispersing <4.3 km (4b/3)	100.0	70.8	86.8

^a Estimated as the total number of observed dispersal events (line 2) plus the number of inferred dispersal events as estimated by the number of immigrants entering the study area (Table 1, line 7).

^b Estimate capped at the total number of inferred dispersal events.

TABLE 3. Estimates of mean and root-mean-square (RMS) dispersal distances (in km) for Acorn Woodpeckers at Hastings Reservation using different assumptions and based on dispersal by radio-tracked individuals ($n = 8$ females; data from Koenig et al. 1996).

	Males		Females	
	Mean	RMS	Mean	RMS
1. Using observed distribution; remaining birds assumed dead	0.22	0.37	0.53	0.52
2. Using adjusted distribution (to 4.3 km)	0.73	0.94	0.84	0.76
3. Using adjusted distribution (to 3 km only)				
a. Remaining birds assumed dead	0.44	0.59	0.84	0.76
b. Remaining birds disperse 5 km	0.90	1.25	2.05	2.01
c. Remaining birds disperse 10 km	1.40	2.31	3.51	3.87
d. Remaining birds disperse 25 km	2.90	5.63	7.89	9.57
4. Forays by radio-tracked individuals	—	—	6.06	5.37

tectability (line 2) or not (line 3). Correcting for dispersal as far as 3 km and assuming the unaccounted birds die (line 3a) provides a plausible lower estimate of dispersal; the resulting values increase mean dispersal distance by 100% for males and 58% for females over the observed distribution (Table 3, line 1).

There remains the vexing problem of the birds that are unaccounted for even after correcting for dispersal up to the maximum detectable dispersal distance. Unfortunately, the adjusted data provide a poor objective basis for a judgment as to how far such birds may have moved. The fact that a high proportion of individuals (approximately 81%) are estimated to have dispersed < 3 km (Table 2) does not justify the conclusion that the remaining 19% of birds dispersed only a bit farther than 3 km. If the unlikely assumption that all males unaccounted for dispersed between 3 and 4.3 km is adopted, the proportion of birds unaccounted for drops to 13.2% (Table 2).

The adjusted distributions graphed in Figure 4 include a large proportion of dispersers and thus would appear to provide a good representation of philopatry and dispersal as experienced by most birds in the population. However, the fraction of birds unaccounted for, although relatively small, may still have a disproportionately large effect on overall estimates of dispersal (Table 3). If we assume that all birds that are unaccounted for disperse exactly 5 km (line 3b), then RMS dispersal distances are over twice the values obtained if we assume that these individuals die (line 3a); if we assume that they disperse exactly 25 km (line 3d), values are 9.5 to

12.5 times the values obtained by assuming that birds unaccounted for all die.

Data from radio-tracking suggests that these upper estimates are plausible. Although Acorn Woodpeckers are highly social and many birds are philopatric, radio-tracking has confirmed that nonbreeding helpers can foray 10 km or more on a daily basis (Hooze 1995, Koenig et al. 1996; see below). Furthermore, Acorn Woodpeckers are good colonizers as evidenced by frequent reports of individuals sighted up to 200 km away from known populations, by colonizations of several offshore islands, and by their having crossed the Sierra Nevada Mountains in northeastern California, all apparently in recent decades (Koenig et al. 1995). Indeed, populations in the southwestern United States may even depend on frequent long-distance dispersal between populations for their long-term viability (Stacey and Taper 1992). Thus, dispersal on the order of 10 to 25 km is probably not uncommon, and occasional dispersal events of 100 km or more clearly occur.

Unfortunately, there is no objective way to determine how far the individuals unaccounted for in Table 2 actually dispersed. Banding returns can in some cases be useful (Payne 1990, van Noordwijk 1995), but in general the probability of birds being recovered is so low that returns are unlikely to yield more than anecdotal evidence regarding long-distance dispersal events. In our case, for example, we have yet to receive an outside banding return after having banded over 3,000 individuals over a period of 27 years. More disturbingly, this problem cannot be eliminated or even reduced by acquiring

more data over a longer period of time, because larger sample sizes can improve the precision of our estimates but cannot resolve the bias associated with those estimates. Thus, our ability to estimate mean dispersal parameters is unlikely to improve even if we continue to study the population for another 20 years. Indeed, there is no *a priori* reason to consider the dispersal distributions resulting from our 27-year in-depth study to be more accurate than those obtained during a relatively short, 3-year preliminary study. Deriving meaningful estimates of dispersal is a problem that cannot be resolved by brute force alone.

However, at least three activities can mitigate the problem of determining how far dispersers go that cannot be accounted for either by observation or inference. These include sampling secondary study sites, measuring dispersal in very large study sites, and radio-tracking. We will briefly discuss each in turn.

USE OF SECONDARY STUDY SITES

One method that has frequently been used to address the problem of long-distance dispersers has been to count the number of individuals observed to disperse between a primary study site and one or more secondary study sites. Often such data have been used to support the contention that few individuals disperse long distances (Zack 1990, Rabenold et al. 1991, Waser and Elliott 1991).

Unfortunately, data from secondary sites are not always adjusted for detectability. Correction is readily achieved using an approach similar to that used above for correcting observed dispersal distributions for the size and shape of the study area. Consider two circular study sites: one, the primary site, is 1 km² in size and the other, the secondary site, is either 100%, 50%, or 25% as large. Next, let the distance between the edges of the two sites vary between 0 and 5 km. The resulting probabilities of detecting dispersers as a function of the distance of dispersal, calculated using the Baker et al. (1995) technique, are plotted in Figure 5.

Detection probabilities vary depending on the relative size and distance separating the study areas and the actual distance of dispersal. However, the probability of observing an individual dispersing from a primary study site to a secondary study site is generally low, often only a few percent, for individuals dispersing a given

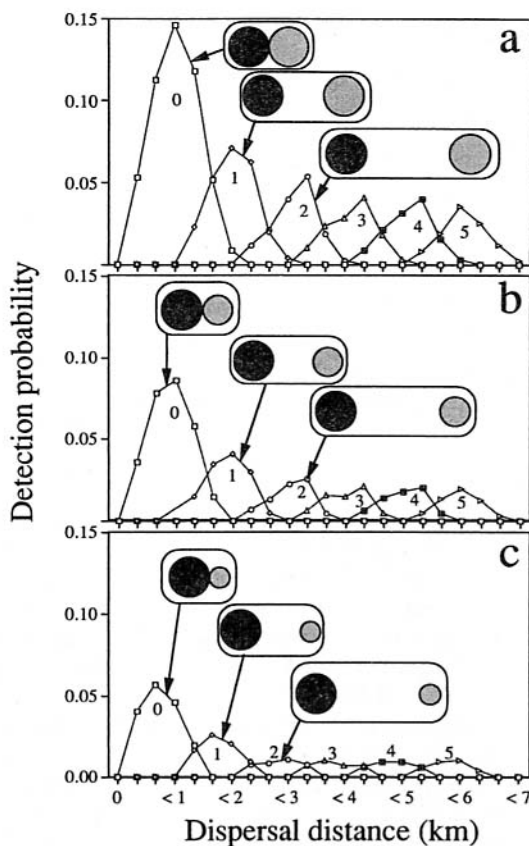


FIGURE 5. Probability of detecting individuals dispersing from a primary (black) to a secondary (gray) circular study site as a function of dispersal distance, the relative size of the secondary site, and the distance separating the two sites. (a) Both sites are 1 km² in size and separated by 0 to 5 km. The distances between the sites are written within the distribution curves; only those separated by 0, 1, and 2 km are depicted graphically. (b) Primary site 1 km², secondary site 0.5 km², separated by 0 to 5 km. (c) Primary site 1 km², secondary site 0.25 km², separated by 0 to 5 km.

distance. For example, the probability of observing an individual dispersing between 2 and 4 km from a study site 1 km² in area to a secondary study site 0.5 km² in area separated by 2 km from the primary site (Fig. 5b) is about 0.012. Thus, for every individual found in the secondary site, 1/0.012 or 83 individuals presumably dispersed between 2 and 4 km, assuming suitable habitat is evenly distributed. Under many realistic circumstances this is a conservative estimate. Because secondary study sites are unlikely to be searched as thoroughly as primary sites, some of those few individuals that disperse

to a secondary site are likely to be missed. This makes it even more difficult to accurately assess the frequency of long-distance dispersal from censuses of secondary sites.

With such low probabilities of detection, corrections based on observed dispersal to secondary study sites is usually of limited value. In general, if a dispersal event is recorded in a secondary site, one can use it as evidence for long-distance dispersal. However, little can be concluded if no dispersal events are recorded.

DETECTABILITY AND SUPER STUDY SITES

From the standpoint of detecting long-distance dispersal, most studies involving marked individuals, including our study of Acorn Woodpeckers, cover too small an area to avoid potentially large biases in observed dispersal distributions even for distances of only a few kilometers. There are generally good reasons for such relatively small study areas. In our case, the 40 or so groups of Acorn Woodpeckers covering 6.25 km² is as much as can be monitored without a small army of full-time assistants censusing birds. Furthermore, even this small area extends beyond the borders of Hastings Reservation on three sides. Both political problems of obtaining permission to survey private lands and logistical difficulties in searching areas of difficult terrain make it virtually impossible to monitor a significantly larger area. Similar challenges face any researcher trying to balance an interest in dispersal with limitations of time and funding, hazards associated with remote study sites, and the desire to obtain data on other topics that demand focused study of fewer individuals.

Nonetheless, at least two studies have succeeded in partially resolving the biases associated with a finite study site by monitoring such a large area that all but the longest-distance dispersers can be found. An excellent example of this approach is that of Walters and his colleagues studying the cooperatively breeding Red-cockaded Woodpecker (*Picoides borealis*) (Walters 1990, Reed et al. 1993, Daniels and Walters 2000). Their study site in the North Carolina Sandhills encompasses approximately 225 social groups and covers a breathtaking area of 1,100 km². Although super study sites of this magnitude do not necessarily eliminate biases in dispersal data, they significantly reduce the bias

associated with dispersal events that generally would be considered extremely long. For example, assuming a circular study area, just under half of all individuals that disperse a distance equal to the radius of a 1,100 km² study area (18.7 km) would be detectable (Koenig et al. 1996) and dispersal events as far as 37 km could be observed at least occasionally. In fact, Red-cockaded Woodpeckers are endangered and a large amount of time and effort has gone into surveying their currently limited populations beyond the Sandhills region, resulting in several records of long-distance dispersal even farther than 37 km, such as a 90-km dispersal event by a female in 1986 (Walters et al. 1988).

A second study that has effectively used the super study site approach is that of the Florida Scrub-Jay (*Aphelocoma coerulescens*) (Stith et al. 1996). Like the Red-cockaded Woodpecker, this species has very specific habitat requirements and is of conservation interest. Consequently, considerable effort has been expended on monitoring jays throughout their relatively limited range. Two conclusions emerge: many jays disperse only relatively short distances, but long-distance dispersal events up to at least 35 km occur. Given the relatively tameness of Florida Scrub-Jays, their tendency to respond to playbacks and to use exposed perches to watch for territorial intruders and predators, and the relatively large amount of public attention given to this threatened species, these data perhaps come as close as any available to representing the true, unbiased dispersal distribution of a wild bird species.

RADIO-TRACKING DISPERSAL EVENTS

A third approach to mitigating the bias of dispersal distributions is to use radio-tracking to follow individuals (Porter and Dooley 1993, Koenig et al. 1996). Hooge (1995) has used this technique in Acorn Woodpeckers to demonstrate that nonbreeding helpers are regularly searching for vacancies several kilometers away from their natal groups. Estimates of mean dispersal distances using data from radio-tracked individuals confirm the bias of the observational data and suggest that the mean distances calculated from the latter underestimate the true values by factors of 5 to 10 (Koenig et al. 1996). For example, mean dispersal distance by eight females that set up new home ranges while being radio-tracked was 6.06 km. This approaches the mean

dispersal distance estimate obtained by correcting the observed distribution to 3 km and assuming that all remaining birds disperse 25 km (Table 3).

These results provide dramatic evidence of the shortcomings of behavioral data and have important implications for the relationship between dispersal distances and cooperative breeding (Zack 1990, Hooze 1995). However, even radio-tracking suffers from limitations. As anyone who has conducted a radio-tracking study can attest, the technique is expensive and highly labor intensive. Consequently, sample sizes are invariably small. Moreover, batteries in the radios that most birds are able to carry last only a few weeks, whereas natal dispersal in most species is a once-in-a-lifetime event that may occur at any time during a period of months or even years. As a result, it is difficult to follow actual dispersal events. For example, Hooze (1995) radio-tracked 240 Acorn Woodpeckers, of which 8 successfully dispersed while their radios were active (Table 3).

Radio-tracking reduces the bias associated with measuring dispersal primarily by increasing the area over which dispersing individuals can be detected and is thus similar to the "super study site" approach discussed earlier. However, depending on the terrain and the methods used to follow individuals, radio-tracking does not guarantee that dispersal events will be detected and thus may still entail significant bias toward short-distance dispersers. For example, our Acorn Woodpecker study site at Hastings Reservation is located in foothills with moderately rough terrain varying over an elevational range of several hundred meters. Moreover, birds were followed only from the ground using either Yagi or a null-peak antenna. As a result, it was difficult to follow radio signals once birds flew more than a few kilometers, and thus it is likely that these data remain biased against long-distance forays of more than a few kilometers.

Using aircraft to search for radio-tagged dispersers can minimize this problem (Martin et al. 1999), but the investment of time and funds necessary to make this feasible is beyond most studies. Satellite tracking can also be of use in particular cases (Jouventin and Weimerskirch 1990, Sagar and Weimerskirch 1996), although the current size of satellite transmitters limits their use to large birds and the relatively coarse resolution of current satellite fixes means that only

very long-distance movements can be reliably measured.

These limitations ensure that radio-tracking is unlikely to resolve the difficulties associated with obtaining unbiased dispersal data on a large number of avian species until it is feasible to acquire data in a significantly different way than is currently the case. For example, advances in computer technology may soon make it possible to set up a large number of receiving stations across the landscape that can automatically search for and record the direction of signals emanating from narrow-band, low-power transmitters fitted on marked individuals, whose positions could then later be triangulated based on simultaneous records from multiple stations (D. W. Winkler, pers. comm.). Such techniques verge on those already being used in a few studies (Irons 1998). Alternatively, it may at some point be possible to tag at least some birds with small global positioning devices capable of either storing or transmitting their positions to a local base station (Ginati et al. 1995, Koenig et al. 1996).

WHAT CAN WE CONCLUDE ABOUT DISPERSAL IN ACORN WOODPECKERS?

The dispersal distributions obtained from our observational data are clearly biased toward birds that inherit their natal territories or disperse short distances. After correcting for birds that apparently dispersed only a short distance but nonetheless left the study area, we can account for a high proportion (about 81%) of individuals that we estimate attained breeder status. This is a sufficiently large proportion that the adjusted distributions (Fig. 4) surely approximate the correct shape. In other words, we have a good idea about what to expect from a particular individual: a male will most likely either inherit its natal territory or breed within 1 km of where it was born. A female is unlikely to inherit its natal territory, but still has a high probability of breeding within 3 km of where it fledged.

However, we do not know where the remaining individuals go and we can only speculate about the effect of those missing individuals on the mean dispersal distances of this population. The best we can do at the moment is to place some boundaries on plausible values (Table 3). The lowest values are obtained by assuming that the observed distribution is unbiased, which yields mean and root-mean-square dispersal dis-

tances of 0.53 km or less (Table 3, line 1). If we use the values adjusted for dispersal distances up to 3 km and assume that the remaining individuals otherwise unaccounted for disperse 25 km, the mean and RMS values are 13 to 18 times greater than the lowest figures (Table 3, line 3d). The truth lies between these extremes. However, until advances in technology allow us to determine the fate of a higher proportion of birds regardless of how far they disperse, better precision is not possible.

CONCLUSION

Obtaining unbiased dispersal data is central to many problems in contemporary avian biology, including the importance of demographic rescue and metapopulation structure to population viability (Stacey and Taper 1992, Martin et al. 2000). Unfortunately, few (if any) unbiased data sets exist. However, the problem is actually far worse due to the misconception that the avian dispersal data are generally good. The reasons for this are in part psychological. A vast amount of time and effort has been spent on observational studies of dispersal and it may be difficult to accept that the resulting data are nonetheless biased. Perhaps more importantly, we suspect that the strongly skewed dispersal distributions that emerge from many observational studies (Fig. 2) seduce many researchers into believing that their data are not biased and that the number of individuals that disperse long distances actually declines to insignificance as distances approach the limits of their study area. Unfortunately, skewed distributions such as those in Figure 2 are exactly what are predicted by the declining probability of detection with distance (Fig. 3) even if no actual decline in the frequency of dispersal with distance occurs.

We therefore urge caution in interpreting dispersal distributions that look similar to those graphed in Figure 2. Even when a serious attempt is made to locate dispersing individuals, we suspect that a relatively large proportion of birds that disappear are missed. Even more importantly, the missed fraction, however small, will always be biased toward long-distance dispersers, which have a disproportionate influence on the measures of dispersal relevant to many ecological and evolutionary questions. Additional data acquired by means other than direct observation, for example using genetic signatures to detect interpopulation dispersal (Waser and

Strobeck 1998), are almost always desirable to provide an independent means of evaluating data from banding studies.

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