

Detectability, philopatry, and the distribution of dispersal distances in vertebrates

Walter D. Koenig
Dirk Van Vuren
Philip N. Hooge

Dispersal is of central importance to population biology, behavioral ecology and conservation. However, because field studies are based on finite study areas, nearly all dispersal distributions for vertebrates currently available are biased, often highly so. The inadequacy of dispersal data obtained directly by traditional methods using population studies of marked individuals is highlighted by comparing the resulting distributions with dispersal estimates obtained by radio-tracking and by using genetic estimates of gene flow.

Walter Koenig is at the Hastings Reservation, University of California, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924, USA;

Dirk Van Vuren is in the Dept of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, USA; Philip Hooge is with the National Biological Service, Glacier Bay Field Station, PO Box 140, Gustavus, AK 99826, USA.

Obtaining unbiased estimates of the distribution of animal dispersal distances in natural unbounded populations has long been known to be problematic. One approach has been to compare observed patterns against a particular dispersal model, of which many have been proposed¹⁻⁵. In general, these models are based on Murray's⁶ idea that dispersing animals in search of a breeding opportunity move to the first uncontested site they can find nearest their natal area. This approach generally yields an expected geometric distribution of dispersal distances that is highly skewed toward short-distance dispersers.

Unfortunately, the application of these models to data acquired from field studies has frequently been compromised by a failure to take into account the decreasing probability of detection with distance resulting from a finite study area⁷⁻¹¹. Although this bias has been recognized for some time, its significance remains underappreciated, misleading many workers into drawing unsound conclusions about the level of gene flow and the extent of population substructuring within their study populations. For example, consider the studies summarized by Zack¹² in a comparison of dispersal in cooperative and non-cooperative breeding birds. Of the 11 studies discussed that have been published since 1978, one effectively dealt with the problem by having an extraordinarily large study area and one applied Barrowclough's correction⁷ to the observed dispersal data. Three other studies at least mention the problem; one of these

looked for dispersers off the main study area by censusing and a second compared observed movements with those expected if birds randomly dispersed among potential nesting sites within the study area. This leaves six studies (over half) that fail to acknowledge the likelihood that long-distance dispersers are being missed. Our impression is that this proportion has not decreased significantly in recent years.

Here, we review the difficulties associated with determining dispersal distributions and present some examples of recent efforts made to obtain more accurate estimates than are available using traditional resighting or trapping methods. We also suggest a resolution to the paradox presented by the frequent disparity in gene flow estimates obtained from standard mark-recapture studies and genetic techniques. (Here, and in the literature, mark-recapture studies are usually referred to as 'direct' methods, and genetic techniques as 'indirect' methods; however, a strong case can be made for reversing these designations.)

The problem

Because study areas are finite in size, there is an unavoidable, systematic bias in the dispersal distributions obtained from studies using plot-based resighting or recapture data. The extent of the bias varies with the dispersal distance relative to the size of the study area. For the relatively simple case of a circular study area, Barrowclough⁷ derived a formula for the correction factors needed to adjust an

observed dispersal distribution for this bias. The formula entails numerical integration and its derivation is not critical for our purposes; few study areas approximate the shape of a circle and thus in most cases a more accurate correction can be obtained by computer simulation¹³. The important general result is that the probability of detecting dispersal events declines directly and dramatically with dispersal distance. For example, using an idealized circular study area (Fig. 1), the probability of detecting a disperser that moves the radius of the study area is about 45%. In contrast, 100% of philopatric individuals that inherit and breed in their natal territory are detected.

Correcting for this bias is an important step in obtaining better dispersal distributions. However, it is only a start, inasmuch as individuals dispersing farther than the diameter of the study area have a probability of detection of zero. With no observed values, it is impossible to 'correct' for the bias or compare observed values against expected distributions without making untestable assumptions about the frequency of more-distant dispersal events. This fact is seductively easy to forget when contemplating an observed dispersal distribution that has taken years of hard field work to collect and shows the frequency of dispersal dropping off nicely with distance, reaching zero at or near a distance corresponding to the diameter of the study area, an example of which is shown in Fig. 1. Unfortunately, such data do not constitute evidence for a lack of more distant dispersal. Rather, this pattern is exactly that predicted by taking into consideration the geometry of finite study areas even if dispersal is random with respect to distance.

Recognizing the limitations of dispersal data will not be easy, since such data are difficult to collect. More disturbingly, the problem cannot be solved simply by collecting more data: biased data do not improve in accuracy as larger sample sizes are obtained over longer periods of time. Biased data can provide valuable information that is relevant to specific questions⁹, including estimates of mortality risks associated with dispersal¹⁴. However, biased data do not generally exclude the possibility of long-distance dispersal, and thus cannot be used to estimate gene flow and population differentiation.

Case histories

Two general approaches can be used to circumvent the limitations imposed by a finite study area. The first is to increase the effective size of the study area that is monitored. Several ways to partially do this are mentioned below, but in general the only realistic method to accomplish

this is by radio-tracking¹⁰. One avian and one mammalian example from our own studies serve as good examples.

Both yellow-bellied marmots (*Marmota flaviventris*) in Colorado, USA and acorn woodpeckers (*Melanerpes formicivorus*) in California, USA have been the subject of long-term studies lasting over 20 years and involving the marking of thousands of individuals^{15,16}. More recently, D. Van Vuren (Ref. 17, and PhD Thesis, University of Kansas, USA, 1990) and P. Hooze (PhD Thesis, University of California, Berkeley, USA, 1995) have used radio-tracking specifically to obtain data on natal dispersal which they can use to compare dispersal distributions obtained from the long-term plot-based studies using marked individuals. Both studies demonstrate that overall long-distance dispersal is strikingly more frequent than had been suspected previously. For yellow-bellied marmots, it was possible to follow a large sample of young individuals until they dispersed and established a new home range. Comparing dispersal by the same individuals, based on intensive trapping and observations and by radio-tracking, yielded mean dispersal distances that increased by 332% for males from 0.77 to 2.56 km, and by 282% for females, from 0.51 to 1.44 km (Fig. 2). Equally important, a high proportion of dispersal events (65% of males and 42% of females) were detected only by radio-tracking and would have been completely missed by a study that was restricted to observations and/or trapping.

For acorn woodpeckers, birds could only be followed for several weeks until radios fell off, during which time only a small proportion of individuals actually established a new home range. Thus, it was necessary to omit non-dispersing individuals from the study in order to compare the distributions based on banding and radio-tracking data. As an index of potential dispersal, data were also acquired on the distance of forays, during which birds intruded into non-natal territories in search of reproductive vacancies. (Results are summarized in Fig. 3.) Based on the small sample of females that dispersed and set up new home ranges while being radio-tracked, mean dispersal distance increased by 904% from 0.67 to 6.06 km. Using the more extensive data from forays that occurred while birds were radio-tracked, mean dispersal distance increased by 504% for males from 0.49 to 2.47 km, and by 743% for females from 0.67 to 4.98 km. Similar results emerged for the root-mean-square dispersal distance, which is the value of direct relevance to gene flow¹⁸. For example, the root-mean-square dispersal distance (again excluding non-dispersers) for female acorn woodpeckers went from 0.59 km, using the banding

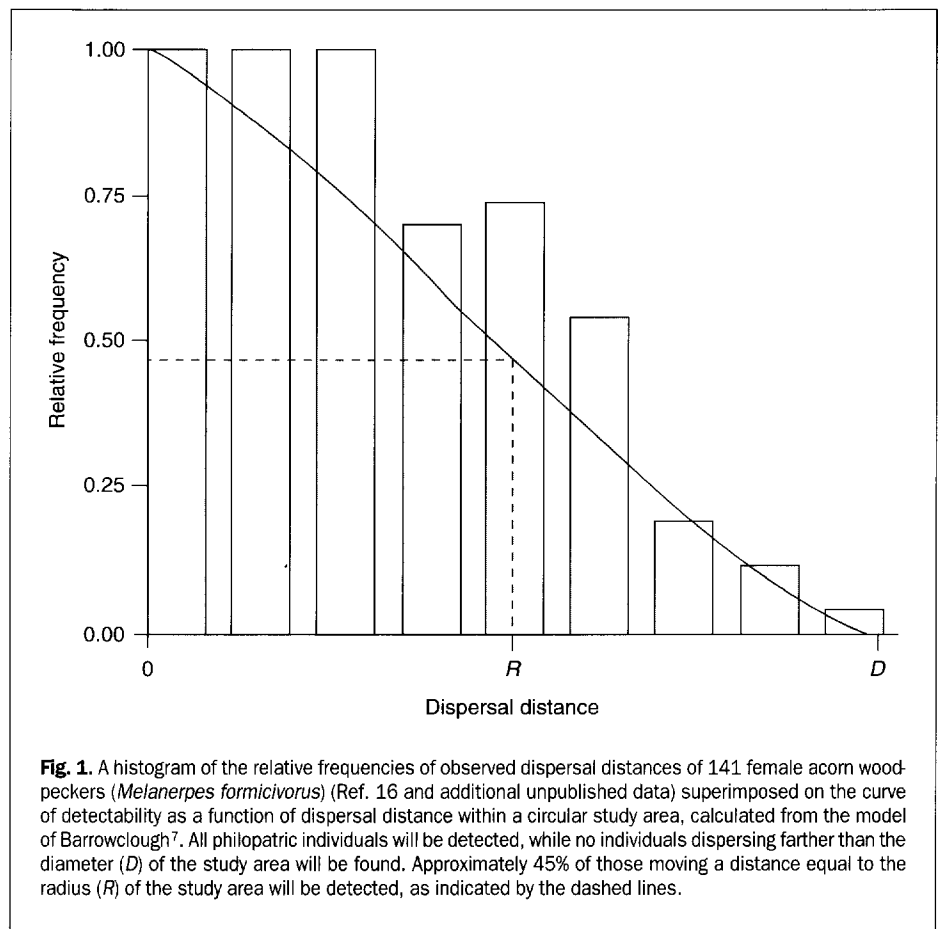


Fig. 1. A histogram of the relative frequencies of observed dispersal distances of 141 female acorn woodpeckers (*Melanerpes formicivorus*) (Ref. 16 and additional unpublished data) superimposed on the curve of detectability as a function of dispersal distance within a circular study area, calculated from the model of Barrowclough⁷. All philopatric individuals will be detected, while no individuals dispersing farther than the diameter (D) of the study area will be found. Approximately 45% of those moving a distance equal to the radius (R) of the study area will be detected, as indicated by the dashed lines.

data, to 5.37 km for the eight females that dispersed while being radio-tracked, and 4.79 km for forays, increases of 904% and 808%, respectively.

These examples demonstrate the shortcomings of estimating dispersal distributions of birds and mammals based on traditional marking and resighting or trapping data. Although radio-tracking has been used before to detect dispersal events (for example, Ref. 19 and D.F. Hackett, PhD Thesis, University of Alberta, Edmonton, Canada, 1987), we know of no published studies that provide the data needed to determine the bias associated with observational methods of estimating dispersal distributions. Thus, the available evidence suggests that dispersal distances based on traditional plot-based methods may underestimate actual mean dispersal values in many vertebrates by a factor of at least three to nine.

Genetic estimates

The second general method of circumventing the limitations of banding data as a means of determining dispersal distributions is to measure dispersal and gene flow indirectly using genetic markers. Such methods yield estimates of the relative degree of population differentiation (F_{ST} values) that can then be used, with appropriate assumptions, to determine rates of gene flow between population

subunits measured in individuals per generation²⁰.

The results from such efforts are often strikingly at odds with data derived by direct observational techniques. Consider the commonly held view that highly social, cooperatively-breeding birds are highly philopatric and disperse over relatively short distances, which is a conclusion supported by field data from many of the longest and most exhaustive field studies ever conducted¹². Edwards²¹ tested this hypothesis by comparing mitochondrial DNA sequences from cooperatively breeding grey-crowned babblers (*Pomatostomus temporalis*) collected from 12 populations distributed throughout this species' extensive distribution in Australia and New Guinea. In contrast to a pattern of philopatry expected from traditional field studies of other cooperative breeders, Edwards was able to detect evidence for migration events between populations separated by up to 1390 km. Such findings confirm that both the mean and variance of dispersal distances are likely to be much larger than would ever be suspected based on directly observed dispersal data²¹.

This hypothesis is reinforced by studies in which direct and indirect measures of dispersal have been made on the same or comparable populations. Waser and Elliott²², for example, examined local population structure of bannertailed kangaroo

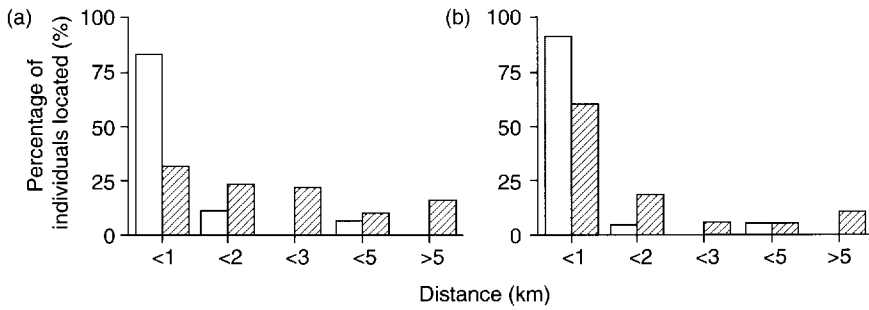


Fig. 2. Dispersal distributions for the same individual yellow-bellied marmots (*Marmota flaviventris*) based on intensive observation/trapping methods (shaded bars) versus radio-tracking (hatched bars). Individuals that had not yet established a new home range were excluded. (a) Males ($N=18$ trapped, 52 radio-tracked). (b) Females ($N=22$ trapped, 38 radio-tracked). Mean dispersal distances: males 0.77 km (trapped), 2.56 km (radio-tracked); females 0.51 km (trapped), 1.44 km (radio-tracked). Note that 34 out of 52 males (65%) and 16 out of 38 females (42%) that dispersed and were detected by radio-tracking were not relocated by intensive observation/trapping efforts.

rats (*Dipodomys spectabilis*) using allozyme data and found no evidence for spatial clustering of alleles up to 1 km apart, despite extensive long-term trapping data indicating that virtually all individuals disperse less than 400 m. They reconciled these opposing estimates by hypothesizing considerable 'gamete dispersal' by which males, although resident near their birth sites, move significant, generally undetected, distances in order to mate with more distant females in the population.

A second example of direct and indirect dispersal data similarly at odds is work by Dobson²³, who calculated F_{ST} values for six populations of Columbian ground squirrel (*Spermophilus columbianus*) populations that were spread out over 183 km in southern Alberta, Canada. F_{ST} values averaged 0.026, corresponding to little population differentiation over

this relatively wide area despite data from field studies that suggested that the maximum dispersal distance in this species is 8.5 km and that most dispersal events are less than 2 km (Ref. 24 and D.F. Hackett, PhD Thesis, University of Alberta, Canada, 1987). Dobson explained the discrepancy by hypothesizing that short distance dispersal was indeed the norm, leading to small, genetically effective population sizes, but that short distance dispersal was so frequent that it was able to homogenize allele frequencies among relatively distant populations, leading to larger 'ecological' population sizes.

These are not the only explanations for disparate direct and indirect measures of gene flow. One difficulty is that the scales over which dispersal is measured by the two approaches are very different in both timescale and number of individuals. Direct measures based on field studies look

at dispersal by dozens to hundreds of individuals measured over a period of, at most, a few generations. In contrast, indirect measures based on genetic estimates infer rates of effective dispersal by a larger number of individuals (corresponding to the long-term effective population size) averaged over hundreds or thousands of generations. Consequently, low F_{ST} values may be the result of past rather than current dispersal and gene flow²⁵.

Estimates of gene flow based on indirect measures may frequently turn out to be markedly greater than those based on direct field estimates, as in the kangaroo rat and ground squirrel studies cited above. However, the primary, if not exclusive, reason for this disparity may be the bias inherent in dispersal estimates based on traditional plot-based studies. That is, long-distance dispersal is occurring undetected in the population, as demonstrated by the radio-tracking studies discussed earlier. It is unfortunate, but we believe true, that the vast majority of intensive field studies conducted thus far on birds and mammals provide data on dispersal that are highly biased and virtually useless in determining either the true distribution of dispersal distances in the population or the extent of gene flow.

The future

What can be done to mitigate this situation and ultimately arrive at a better understanding of vertebrate dispersal? Most importantly, workers should acknowledge the bias inherent in plot-based studies and correct for the bias as much as possible. The proportion of individuals dispersing off a site should be estimated, thereby providing information on the potential number of long-distance dispersers even if the distance they move remains unknown. This can be done either by comparing the number of new individuals entering the study with those leaving, or by using an area-ratio method²⁶.

Beyond this, there are at least four ways to reduce the bias imposed by a finite study area, depending on the taxon. One is to survey very large areas relative to dispersal distances, an approach that is feasible in a few cases²⁷. For some birds, ringing recovery data can provide insights into long-distance dispersal events that could never be detected within a typical study area a few kilometers in diameter²⁸. In other cases, nearby sites can be monitored and the number of individuals dispersing between disjunct study areas can be determined^{29,30}. If appropriately adjusted for the size of the disjunct site and the distance from the primary site, such data can provide a useful estimate of the number of individuals dispersing moderately long distances²⁹.

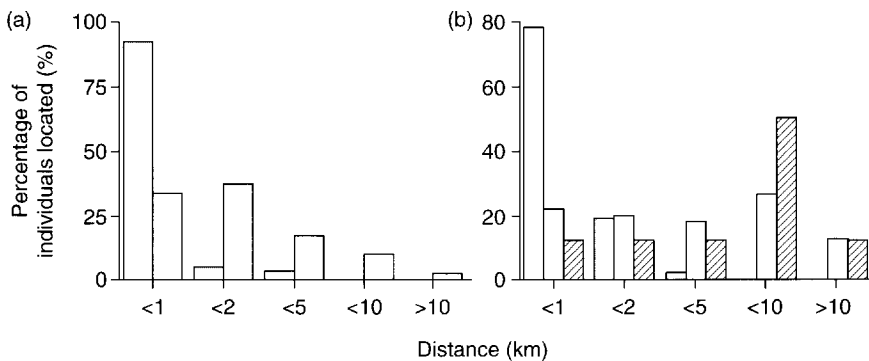


Fig. 3. Dispersal distributions for acorn woodpeckers (*Melanerpes formicivorus*) based on intensive observation/banding methods versus radio-tracking methods. Studies overlapped in time and space but data based on resightings were collected over a longer time. The radio-tracking (hatched bars) dispersal events include eight females that established new home ranges while being monitored; forays (unshaded bars) include all trips made off the natal territory by 13 male and 28 female nonbreeders. In all cases, including the banding (shaded bars) data, individuals remaining on their natal territory were excluded. (a) Males ($N=121$ banded, 163 radio-tracked forays). (b) Females ($N=119$ banded, 563 radio-tracked forays, 8 radio-tracked dispersal events). Mean distances: males 0.49 km (banded), 2.47 km (radio-tracked forays); females 0.67 km (banded), 4.98 km (radio-tracked forays), 6.06 km (radio-tracked dispersal events).

Generally, however, the only satisfactory approach currently available is radio-tracking. Unfortunately, even this technique has serious limitations. The acorn woodpecker study discussed earlier, for example, was conducted in rugged terrain where radio signals could only be detected over a distance of 1–2 km and birds had to be followed closely in order to detect long-distance movements. Any bird foraging or moving much farther than the maximum observed distance of 19 km is unlikely to have been detected. This emphasizes that although current radio-tracking technology can significantly extend the observable dispersal distances, it is still unlikely to pick up very long-distance dispersal events unless satellite tracking or air searches are made, thus in general this method offers no guarantee of providing a truly unbiased estimate of dispersal distributions.

New technologies may change this in the relatively near future. Already satellite tracking can and has been used to track movements of large birds and mammals over extensive distances^{31,32}. Use of Global Positioning Receivers³³ is a technology that provides even more frequent and accurate location fixes.

Currently available options for small animals are still quite limited, although significant improvements are on the horizon. The use of Doppler shift effects with signals from the new, low, Earth orbit satellites may enable the use of relatively small positioning receivers³⁴. The size of such tags could be further reduced by storing locational information within the tag rather than by transmitting the information (although the necessity of retrieving tags would limit their use in many cases).

Even more promising are passive integrated transponders (PIT tags), which are small enough to use with all but the tiniest of vertebrates and have unlimited life. PIT tags are already being used to mark a variety of small vertebrates including fish, lizards, and ground-dwelling mammals. Unfortunately, PIT tags can only be detected by hand-held readers a short distance away (about 10 cm). Consequently, the individual must either be recaptured or return to sites close to a detector. With luck, advancing technology in the future will offer similarly small tags that are detectable from a significant distance. Ultimately, the day that small PIT-like tags can be tracked by satellite will be the day we are finally able to obtain unbiased direct estimates of dispersal distributions in vertebrates.

Of course, unbiased data on long-distance dispersal fail to address the issue of how successful dispersers are at establishing themselves and breeding. That is,

dispersers may be more or less successful at subsequent breeding than philopatric individuals, thereby contributing a relatively greater or lesser amount to gene flow in the population. A comprehensive understanding of the demographic and evolutionary consequences of dispersal will therefore continue to require extensive long-term demographic studies in conjunction with new technologies for minimizing the biases associated with dispersal data.

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