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Methods for estimating long-distance dispersal

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Long-distance dispersal (LDD) includes events in which propagules arrive, but do not necessarily establish, at a site far removed from their origin. Although important in a variety of ecological contexts, the system-specific nature of LDD makes "far removed" difficult to quantify, partly, but not exclusively, because of inherent uncertainty typically involved with the highly stochastic LDD processes. We critically review the main methods employed in studies of dispersal, in order to facilitate the evaluation of their pertinence to specific aspects of LDD research. Using a novel classification framework, we identify six main methodological groups: biogeographical; Eulerian and Lagrangian movement/redistributional; short-term and long-term genetic analyses; and modeling. We briefly discuss the strengths and weaknesses of the most promising methods available for estimation of LDD, illustrating them with examples from current studies.

The rarity of LDD events will continue to make collecting, analyzing, and interpreting the necessary data difficult, and a simple and comprehensive definition of LDD will remain elusive. However, considerable advances have been made in some methodological areas, such as miniaturization of tracking devices, elaboration of stable isotope and genetic analyses, and refinement of mechanistic models. Combinations of methods are increasingly used to provide improved insight on LDD from multiple angles. However, human activities substantially increase the variety of long-distance transport avenues, making the estimation of LDD even more challenging.

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Dispersal is the movement of individuals away from their source. Some of these movements, typically termed "migration," are part of a cyclical dispersal process in which individuals or populations regularly translocate among sites. In other cases, the process is unidirectional. A "dispersal curve," the frequency distribution of the distances traveled by all individuals in a population, is often used to numerically characterize unidirectional dispersal. The scale and fine details of this curve vary considerably among populations, taxa and regions. However, its general shape is almost universally regular: at one end of the distribution there is an abundance of relatively short dispersal distances, whereas at the other end there is a scarcity of relatively long-distance dispersal (LDD) events (Harper 1977, Dingle 1996, Kot et al. 1996, Cain et al. 2000, Nathan 2001b). Migration, in comparison, typically involves a mass movement to a distant location, resulting in very different pattern. We focus here on LDD but many of the same methodological issues also pertain to migration.

Short-distance dispersal events help to determine resource use, recruitment patterns, small-scale metapopulation dynamics, and species co-existence (Hurtt and

Pacala 1995, Hanski 1999, Nathan and Muller-Landau 2000). LDD events have impacts at larger (regional-global) scales, directly affecting spatial spread and colonization rates. Thus, LDD affects both ecology (resource use, species co-existence, and large-scale metapopulation dynamics) and evolutionary trajectory (gene flow, genetic structure and species diversity) (Kot et al. 1996, Turchin 1998, Ouborg et al. 1999, Cain et al. 2000, Nathan 2001b, Webster et al. 2002). Difficulty in observing and quantifying rare LDD events has been a major obstacle hindering its study (Nathan 2001b, Akesson 2002, Webster et al. 2002). Consequently, a clear understanding of the mechanisms, influencing factors and magnitude of LDD is still lacking.

Numerous methods currently exist for estimating dispersal (recently reviewed by Dingle 1996, Turchin 1998, Southwood and Henderson 2000, Clobert et al. 2001, Bullock et al. 2002), but few are appropriate for estimating LDD. Recent discussions of specific methods for estimating LDD have focused on the use of genetic analyses in estimating LDD in plants (Cain et al. 2000), and the use of satellite telemetry, genetic analyses and stable isotope chemistry in estimating long-distance migration in birds (Webster et al. 2002). Since methodological problems encountered when studying dispersal and migration have many common grounds, we wish to extend the scope of these valuable reviews by integrating elements from both plant and animal studies, and by broadening the scope to other methodological approaches. Towards this end, we first identify the specific difficulties involved with the study of LDD: we discuss the questions of interest, break the methodological challenge into its basic components, and classify the most important methods currently available. In the main body of this paper we illustrate these major methodological approaches, and highlight their merits and limitations. We conclude with general methodological recommendations, along with an emphasis on difficulties still not addressed, some promising new methods, and avenues for future research.

The questions

Two broad types of questions have been asked in ecological and evolutionary studies of LDD. First, what are the circumstances that select for LDD? More specifically, what are the internal (e.g. morphological, physiological and behavioral) and external (e.g. dispersal agents of sessile organisms, resource availability) factors leading to LDD and determining its success at ecological and evolutionary scales? Second, how does LDD affect key ecological and evolutionary processes? Providing a complete answer to these questions for a given species would require detailed knowledge of its biology: interactions with its immediate environment;

conditions prevailing in areas that it might disperse to and through; and its ability to face these conditions. Rarely is our knowledge sufficient for such a task, and even documenting an LDD event in detail is often an accomplishment. We therefore focus here on the methodological challenge of quantifying those rare events at the tail end of the dispersal curve. Many of these also pertain to the difficulty in predicting the final location of a migrating individual or population.

Components of the methodological challenge

Attempts to estimate LDD must begin with recognition that due to the inherent uncertainty typically associated with LDD processes (Clark et al. 2001), highly accurate estimates of LDD will often be difficult to obtain. Even perfect information on the dispersal distance of all individuals in a population would not provide more than a case-specific documentation of LDD: because LDD processes are highly stochastic, LDD is likely to be different when the same population is examined at another time. However, the level of inherent uncertainty is essentially unknown, and its existence does not prevent us from gleaning important information from dispersal data. Moreover, it should not discourage our efforts to reduce those uncertainties that are not inherent but are reducible by better methods for estimating LDD; at the extreme, those uncertainties can be reduced to zero with perfect methods that provide perfect information on LDD. Thus, it is essential to improve our methods for estimating LDD to (a) reduce the level of uncertainty in LDD data, (b) examine the consequences of different levels of uncertainties, and (c) facilitate the formation of well-founded generalizations about LDD. Efforts to develop better methods for estimating LDD are complicated by difficulties in defining LDD, collecting and analyzing data, and interpreting the results. We discuss each of these difficulties in turn.

Definition

The basic problem is that how far is "far enough" to be considered LDD depends on the scale of inquiry. In a biogeographical study, this could easily be thousands of kilometers, accounting for movements within and between continents (Carlquist 1974, Briggs 1995, Nathan 2001b). By contrast, the dispersal of agricultural pests among farms (Aylor 1999), or seed dispersal by ants to a few tens of meters (Cain et al. 1998), may be considered LDD at much smaller scales. Any threshold chosen must therefore be case-specific and in most cases arbitrary (though in the section Mechanistic models we point to a unique example in which such a threshold can be set quantitatively). The LDD threshold should

be chosen judiciously, and be based on the dispersal attributes, the spatial structure, and the spatial scale of the system being studied. As an operational threshold, researchers often apply a round distance that is considerably higher than the typical (e.g. mean or median) dispersal distance in their system, e.g. 100 or 1000 m. A more quantitative approach ascribes the LDD threshold as a function of a measurable trait known to determine the dispersal distance. For example, a study measuring dispersal up to 80 m from a 50-cm tall wind-dispersed shrub (Bullock and Clarke 2000), may set an LDD threshold of 50-m (100 times plant height). However, use of a single trait to set an LDD threshold can be misleading, since dispersal is influenced by multiple factors. In the above example, seed aerodynamics and wind conditions also play a major role.

One way to construct the dispersal curve is to plot the frequency distribution of dispersal distances (Fig. 1, Nathan and Muller-Landau 2000). If reliable estimates of dispersal distances in a population are available, a threshold for LDD can be set as a high percentile (e.g. 95th or 99th) of the specific cumulative probability. In Fig. 1 we demonstrate the sensitivity of percentile-based LDD thresholds to factors influencing dispersal, which amplifies the problems associated with setting a "round" number as LDD threshold. A conceptual problem with a percentile-based definition of LDD is whether dispersal beyond some LDD threshold distance

has ecological and evolutionary consequences that differ from those for dispersal below this threshold. For example, Nathan et al. (2002a) found that the 99th percentile threshold for seeds dispersed by wind from 10-m tall trees can vary from < 3 m to 200 m, depending on the landscape structure. Is a seed deposited just 3 m from the point of release, and thus within the immediate influence of the parent tree, ecologically equivalent to a seed traveling 200 m and perhaps reaching a new habitat type? Similarly, is a songbird moving 100 km experiencing the same type of dispersal event, as would a large raptor that covered the same distance?

Identifying what constitutes the dispersal unit, and when and where a dispersal event ends, may also involve difficulties. Dispersal may be mediated by various agents acting at different spatial scales, which may be difficult to distinguish (Higgins et al. 2003). Terrestrial plants and animals, for example, sometimes cross large water bodies in the absence of adaptation for over-water dispersal, by being transported on a floating island (Nathan 2001b).

Finally, it is important to distinguish between dispersal per se and subsequent stages of establishment (Nathan 2001b). By itself, dispersal is meaningless to population dynamics. Many LDD researchers therefore focus on effective dispersal events, that is, dispersal followed by establishment. However, without direct data on dispersal, neither the efficiency of LDD (i.e., how many attempts were needed to yield this successful colonization), nor its relative role compared to establishment (what makes a colonization event successful) can be assessed. In most systems, LDD is probably more frequent than previously thought (Silvertown 1991), but difficulties in establishment and identification far from the parent location dictate low rates of colonization and detection.
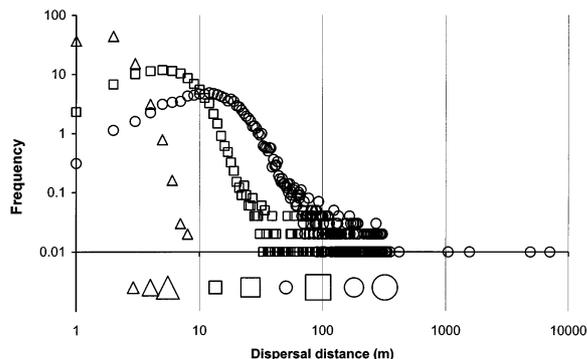

Fig. 1. Simulated dispersal curves for red maple (*Acer rubrum*) seeds dispersed from a height of 20 m in a 33 m high deciduous forest, in three different wind conditions (characterized by the friction velocity u_*). The three wind conditions represent calm ($u_* = 0.1$ m/s; triangles), moderate ($u_* = 0.5$ m/s; squares) and strong stormy ($u_* = 2.0$ m/s; circles) winds. The percentile-based thresholds for long-distance dispersal are marked by the corresponding symbols just below the abscissa for the 95.0th, 99.0th and 99.9th percentiles (small, medium and large symbols, respectively). The vertical lines provide some "round" thresholds for comparison. Simulations are generated by a wind dispersal model (Nathan et al. 2002b), calibrated for a site at Duke Forest from local measurements of the vertical profile of the leaf area density, with a leaf area index of 2.8. Each dispersal curve is based on 10000 dispersal events. Seed terminal velocity is randomly selected from a normal distribution (mean ± SD: 0.66 ± 0.12 m/s; Green 1980).

Collection

The main difficulty in data collection is the rarity of LDD events. Tracking short-distance movements of a few individuals, or documenting redistribution of individuals near their source, are often feasible. In contrast, long-distance movements and documentation of redistribution of individuals over extended areas are often impossible (Akesson 2002, Webster et al. 2002). Even when millions of birds have already been marked, recapture rates are very low (Webster et al. 2002). In addition, documenting arrival of an individual organism to a remote habitat only provides partial evidence of LDD. Source strength (the number of propagules dispersed) and source location typically remain unknown. Overall, difficulties associated with documenting LDD cause both the frequency and magnitude of LDD to be under-estimated (Koenig et al. 1996).

Analysis and interpretation

The rarity of LDD events, exacerbated by the difficulties in data collection, yield data sets that are often anecdotal, typically incomplete, and potentially biased. Thus, statistical analysis of such data is always problematic, as is the interpretation of the results (Turchin 1998, Southwood and Henderson 2000, Clobert et al. 2001, Bullock et al. 2002).

Classification of methods

To help organize our understanding of the methods appropriate for estimating LDD, we develop a classification framework based on seven criteria (Table 1). In the following section, we discuss promising methods listed in Table 1, and illustrate their application to the study of LDD with selected case studies.

Major methodological approaches

Biogeographical methods

Use of biogeographical data to infer dispersal precedes Darwin (reviewed in Darlington 1957). Because LDD events are required to explain the existence of biota on remote islands, much work has since centered on island distributions. Following the example of Darwin and Wallace, Darlington (1957) devoted a major portion of his work to the use of distributional data for inferring dispersal among islands. For example, the fresh-water fish genus *Aplocheilus* is found on several geographically disparate islands. It is known to be salt-tolerant, leading Darlington (p. 51) to state "there can be little doubt that *Aplocheilus* has dispersed partly through the sea." The colonization of organisms in newly created locations, such as the resettlement of Krakatau following the 1883 explosion which annihilated the island's entire biota (reviewed in Thornton 1996) provides dramatic evidence for LDD. However, such data sets typically document effective dispersal, rather than dispersal per se. Moreover, they lack information on both location and strength of the propagule source, and thus are insufficient for quantifying LDD.

A disjunct distribution can also emerge from vicariance (splitting) events driven by plate tectonics or other forces (Briggs 1995, Nathan 2001b). For example, the finding that lizard faunas on the tiny islets surrounding Guam are subsets of species on the "mainland" does not provide evidence for LDD: these islets became separated from Guam only recently (Perry et al. 1998).

Modern phylogenetic methods using increasingly detailed and diverse molecular markers are powerful recent additions to the biogeographic tool kit. For example, Kim et al. (1998) used molecular phylogenetic analyses to conclude that the Hawaiian plant *Hesperomannia* most likely represents an LDD event originating in Africa. In another example, Raxworthy et al. (2002) studied chameleon phylogeny, based on multiple morphological and molecular markers. The relationships they obtained could not be reconciled with vicariance-based explanations of present-day distributions. Instead, the data suggest that chameleons arose on Madagascar, and repeatedly dispersed, presumably over water, to locations such as Africa and the Seychelles (Raxworthy et al. 2002).

Drawing inference from observed distributions remains the cornerstone of the biogeographical approach to estimating LDD. Use of multiple tools has given rise to our understanding of modern horse distribution (MacFadden 1992) and of the dispersal of a variety of taxa across Central America (Briggs 1995). However, such studies do not allow important ecological elements, such as dispersal method and source strength, to be identified. Consequently, although biogeographical approaches often provide the foundation upon which other approaches (see below) can be built, they cannot provide a full understanding of LDD.

Movement/redistribution methods

There is a rich tradition of quantifying the pattern, rate and range of dispersal of plant and animal propagules by tracking individual movements and population redistribution. "Mark-recapture/resighting" techniques (Southwood and Henderson 2000) are most frequently applied to animals, and techniques using unmarked individuals are most frequently applied to plants. Following Turchin (1998, p. 36), we divide movement/redistribution methods into two empirical approaches. The Eulerian approach (Table 1) emphasizes the population and involves recording the redistribution of large numbers of marked or unmarked individuals at specific points in space. In contrast, the Lagrangian approach (Table 1) involves the characterization of the magnitude (spatial extent), speed and directionality of movements of individuals. These two terms have been originated and widely used in fluid mechanics to describe two basic ways to investigate motion; their application to ecology (Okubo 1980, Turchin 1998) would facilitate interdisciplinary research integrating biology and fluid mechanic principles (Cowen et al. 2000, Nathan et al. 2002b). Each approach holds both merits and limitations for estimating LDD. Eulerian methods are in general much more feasible (Okubo 1980), but require great source strength to raise the likelihood of detecting rare LDD events; they also lack information about events between the source and the recovery site. Lagrangian methods can provide more detailed information on long-distance individual movements, but are difficult to carry out and are limited to a small number

Table 1. Classification of the major methods used to estimate long-distance dispersal. We used seven main criteria to categorize the methods: (1) Type of evidence, upon which the data is derived: distributional (dispersal inferred from geographical distribution); occurrence (observing individual movement or population redistribution to sites previously unoccupied); movement (observing dispersal directly); genetic (genetic markers); theoretical (predicted by models). (2) Process. The method uses data on movement per se (dispersal) or on its consequences (effective dispersal), and then dispersal is inferred indirectly. (3) Identity of dispersers. The data describe movements of specific individuals or many nonspecific individuals (mass). (4) Knowledge of the source. Both source strength (number of individuals dispersed) and location are known; both are unknown. (5) Organisms. The major taxa for which the method is usually or most effectively applied. (6) LDD data. The method can provide data for: estimating the frequency, magnitude (spatial extent), presence, or just the potential for LDD. (7) Popularity. The frequency with which the method is used: high, moderate or low.

Methodological group	Specific methods	Type of evidence	Process	Identity of dispersers	Knowledge on source	Organisms	LDD data	Popularity	Case studies	Reviews
Biogeography	Comparison of species composition; Analysis of current distribution; Colonization in remote/virgin habitats; range expansion	Distributional	Effective dispersal	Mass	Usually unknown	All	Presence (sometimes only potential)	High (historically. Currently common in conjunction with genetic methods)	Darlington 1957, Thornton 1996, Kim et al. 1998, Raxworthy et al. 2002	Nathan 2001b
Eulerian movement/redistribution methods	Color markers; Radioactive and elemental tracers; Stable isotopes	Occurrence	Mostly dispersal	Mass	Usually known or assumed	Color markers: mostly invertebrates and plants; elements: mostly vertebrates	Frequency and rough estimates of magnitude	High (increasing)	Jones et al. 1999, Schneider 1999, Bullock and Clarke 2000, Rubenstein et al. 2002	Southwood and Henderson 2000, Webster et al. 2002
Lagrangian movement/redistribution methods	Direct observation; Radar and satellite telemetry	Movement	Mostly dispersal	Individual	Known	Vertebrates	Magnitude	Moderate (sharply increasing)	Van Vuren 1990, Block et al. 2001, Weimerskirch et al. 2002	Gillespie 2001, Webster et al. 2002
Short-term genetic analysis	Paternity analysis; Assignment tests; Multilocus MLE	Genetic	Mostly effective dispersal	Individual	Unknown	All	Presence	High-Moderate	Meagher and Thompson 1987, Prodohl et al. 1998, Schnabel et al. 1998	Cain et al. 2000, Webster et al. 2002
Long-term genetic analysis	F_{ST}; Coalescence	Genetic	Effective dispersal	Mass	Unknown	All	Presence	Moderate-Low	Tufto et al. 1998, Spong and Creel 2001	Cain et al. 2000, Webster et al. 2002
Modeling	Mechanistic models; Phenomenological models	Theoretical	Mostly dispersal	Mass	Known (assumed)	Mostly plants	Magnitude and frequency (predicted)	Moderate-Low	Clark et al. 1999, Nathan et al. 2002b	Cain et al. 2003

of individuals at a time, and usually for species with relatively large body size.

The Eulerian approach. To increase the likelihood of detecting LDD events, Eulerian methods emphasize increasing source strength. For example, Bullock and Clarke (2000) studied seed dispersal from a shrub with an estimated annual reproductive output of $\sim 1.6 \times 10^6$ seeds; plants were transplanted in open isolated fields, thus avoiding the problem of unknown source location. When such practice is infeasible, mark/recapture methods such as mist-netting and banding of birds, radio-isotope labeling of insects, or otolith (ear bones) dyeing in fish can be applied to mark individuals en masse (recently reviewed by Southwood and Henderson 2000, Hagler and Jackson 2001). Schneider (1999), for example, marked with an internal dye $\sim 7 \times 10^6$ moths (*Heliothis virescens*), and discovered through trapping that adult males moved a typical distance of 10 km from the release site. Several traits or morphological structures in some taxa may act as natural tags, and hence provide unique opportunities to carry out extensive mark-recapture studies. For example, Jones et al. (1999) marked the otoliths of over 10^7 damselfish (*Pomacentrus amboinensis*), and found that pelagic larvae often return to their birth site.

New methods now allow analyses of stable isotopes – of elements such as hydrogen and carbon – in animal tissues. These reflect the local environment in which those tissues were grown (reviewed by Hobson et al. 1999). These are attractive to LDD studies because all individuals in a population are ''self-marked'', bearing a signature of the site of their origin (e.g. place of birth, wintering area). This method helped reveal unknown patterns of leapfrog migration in Wilson's warbler (*Wilsonia pusilla*) (Kelly et al. 2002), and the existence of two distinct migratory strategies in the black-throated blue warbler (*Dendroica caerulescens*) (Rubenstein et al. 2002). It also revealed that two subspecies of willow warbler (*Phylloscopus trochilus*) breeding in Sweden have different wintering grounds in Africa (Chamberlain et al. 2000), while widespread North American monarch butterfly (*Danaus plexippus*) populations converge to winter in a limited region in Central Mexico (Wassenaar and Hobson 1998). This promising technique, however, has been applied to study movement only at large (continental) scales, because element concentrations change rather slowly and gradually in space. Multiple isotopic analyses combining other elements, along with improved mapping of their geographical gradients, are expected to improve the spatial resolution of stable isotope analyses and their applicability to LDD studies at ecological scales (Hobson 2002).

Two methodological problems are associated with the quantification of LDD by Eulerian methods. First, designs using a spatial array of traps, nest boxes or observation points typically under-sample LDD events (Porter and Dooley 1993, Koenig et al. 1996). To properly estimate LDD, the spatial scale of the study area should correspond to the scale of LDD events (Koenig et al. 1996). Unfortunately, keeping the probability of disperser recovery roughly constant across large spatial scales requires an often-impracticable sampling effort at more distant locations. The problem may still hold even if sampling efforts are intensive and spatially extensive (Hansson et al. 2002). This difficulty can be addressed by using a distance-weighted correction (Turchin and Thoeny 1993, Baker et al. 1995). Second, the inability to discern the cause for losses of individuals from the sampling area forms another methodological problem. Few empirical studies have attempted to quantify or exclude sources of loss in Eulerian studies (but see Turchin 1998); this information, however, is required to properly estimate the tail of the dispersal curve (Turchin 1998).

The Lagrangian approach. When applicable, the Lagrangian method can be much more precise and informative regarding the LDD of organisms than the Eulerian method. Van Vuren's (1990) study of yellow-bellied marmots (*Marmota flaviventris*) illustrates the advantages of telemetry over conventional mark/recapture methods. Two hundred juvenile marmots were implanted with radio transmitters and their dispersal behavior monitored at 1–3 day intervals. Marmots dispersed as far as 15.5 km to establish a new home range (Van Vuren 1990). Observational and trapping information produced estimates of mean dispersal distance of about a third of the estimates from radio tracking (Koenig et al. 1996). Similar differences were found when comparing dispersal distances of acorn woodpeckers (*Melanerpes formicivorus*) based on radio-telemetry versus observations of leg-banded individuals (Koenig et al. 2000). Radio-tracking also showed that dispersers engaged in LDD (> 500 m) had higher mortality than those moving shorter distances, and ruled out the possibility that individual loss from the study area was due to emigration (Van Vuren 1990).

Satellite tracking provides various advantages over radio tracking in estimating LDD, especially the ability to collect data on inter-continental scales over relatively long periods (Gillespie 2001, Akesson 2002, Webster et al. 2002). The ARGOS system, involving transmitters sending periodic signals to NOAA satellites, is most often utilized; the signal is then translated to determine the location of the organism. The technique is being used in both terrestrial (Webster et al. 2002) and marine (Akesson 2002) organisms, and has already revolutionized our understanding of several animal migratory and foraging pathways (Akesson 2002, Webster et al. 2002). For example, we now know that Atlantic bluefin tuna (*Thunnus thynnus*) exhibit complex migratory behavior and that some travel as far as the central Mediterranean Sea, implying that western and eastern tuna populations are well mixed (Block et al. 2001). We also

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know that white-chinned petrels (*Procellaria aequinoctialis*) fly over 8355 km, on average, in a single two-week foraging bout, and that similar flying speeds of roughly 23 km h^{-1} are attained during both day and night (Weimerskirch et al. 1999). Uncertainties involved with the accuracy of spatial location recorded in such systems (Hays et al. 2001), can be neglected if the movement occurs over such a large spatial scale, but can be consequential if an animal is moving slowly or has a restricted range. The spatial accuracy of Global Positioning System (GPS) records is considerably better, and data on long-distance movements can be recorded in extremely fine detail. For example, tagging wandering albatrosses (*Diomedea exulans*) with miniature GPS tags enabled multi-scale analysis of their flight patterns at both small and oceanic scales (Weimerskirch et al. 2002). Such unique detailed data required recapturing of the tagged animal hence this method cannot easily be applied to many species.

Historically, the purview of Lagrangian methods has been large vertebrates. However, new advances in telemetry and GPS have reduced by orders of magnitude the size of an organism that can carry an electronic tag. For example, harmonic radar tags weighing a few milligrams were used to track flights of bumblebees from distances of up to 1 km (Riley et al. 1996, J. Riley pers. comm.). Miniaturization of satellite-telemetry tags to total unit weight of under 30 g (Britten et al. 1999, Webster et al. 2002) now enables dispersal studies of medium sized animals (> 600 g), but the application of these techniques is still fairly expensive (Webster et al. 2002). With new tracking technology, however, the Lagrangian approach holds great promise for estimating LDD (Koenig et al. 1996, Turchin 1998, Akesson 2002, Webster et al. 2002).

Genetic methods

Genetic methods are often thought to provide otherwise hard-to-collect data on LDD. This suggestion has proven controversial, in part because commonly used genetic approaches suffer from well-known limitations (Whitlock and McCauley 1999, Cain et al. 2000, Webster et al. 2002). In general, genetic methods estimate effective dispersal, rather than dispersal per se (but see Godoy and Jordano 2001). Here, we discuss the general issues associated with the use of genetic markers to estimate LDD and detail two approaches that focus upon effective dispersal among natural populations at different time scales (Table 1).

General considerations. A rich variety of techniques can be used to obtain genetic markers for the study of dispersal, each with its own advantages and disadvantages (reviewed by Wolfe and Liston 1998, Ouborg et al. 1999, Webster et al. 2002). Besides differing in the means by which they are obtained, genetic markers also vary in how they are inherited. Cytoplasmic markers (i.e. chloroplasts, mitochondria) usually have uniparental inheritance, unlike the biparental inheritance of nuclear genome. Comparison between the two inheritance classes allows the dispersal of different life-history components to be estimated. For example, chloroplast markers allow seed dispersal to be estimated, separate from dispersal of pollen. Comparison of mitochondrial and nuclear DNA in animals can also yield estimates of male dispersal (Petit et al. 2001). A comparison of mitochondrial to Y-chromosome DNA may allow a more detailed separation of female and male dispersal in those species where males are the heterogametic sex (Petit et al. 2002).

Genetic markers can also provide evidence of LDD at multiple time scales. Within a generation, markers can be used to document the movement of individuals (Prodohl et al. 1998). At the scale of one to many generations, the configuration of multilocus genotypes can provide information on rates of movement among populations (Waser and Strobeck 1998).

Short-term genetic analysis. If all potential parents in a population are genotyped using frequency-based markers, and the number of alleles present at each locus is large, parentage can be assigned using a simple exclusion procedure. If many individuals share alleles, maximum-likelihood estimators can be used to rank potential parents (Roeder et al. 1989). Effective dispersal can be evaluated using estimation of paternity, maternity, or dual parentage. Paternity analysis has long been used in plant populations to characterize long-distance pollen movement (Ellstrand and Marshall 1985), but it has also been used to characterize extra-population male movements in animal populations (Burland et al. 2001). Dual parentage analyses can be particularly useful for characterizing actual dispersal curves. For example, in a parentage analysis of naturally established seedlings in the plant *Chamaelirium luteum*, Meagher and Thompson (1987) used allozyme data and maximum-likelihood to assign both parents to individual seedlings, and to estimate fine-scaled effective dispersal curves. Prodohl et al. (1998) used microsatellite genotypes and a similar approach to estimate dispersal distances of armadillos within a single generation. Information regarding lactation status was used to choose between mothers whose genetic likelihood of producing a particular offspring was similar. In a maternity analysis used to estimate effective seed dispersal curves in *Gleditsia triacanthos*, Schnabel et al. (1998) reduced the number of parameters estimated by treating the paternal contribution as a single randomly mixed pollen pool and focusing on likely maternal sources. Of the three effective dispersal curves estimated in the studies described in this paragraph, two were leptokurtic (*C. luteum* and one *G. triacanthos* site) and one appeared normally distributed (the other *G. triacanthos* site). Godoy and Jordano (2001) also

estimated a right-skewed, leptokurtic dispersal curve, but because they genotyped seeds, not seedlings, the resulting curve was a true seed dispersal curve. In this pioneering study, each of the 182 reproductive *Prunus mahaleb* trees in an isolated stand has a unique multilocus genotype. Analysis of DNA microsatellites of the maternally-inherited endocarp of 95 seeds collected from traps revealed that 17 of them (18%) must have been dispersed, probably by birds, from trees located at least 3 km away from this stand.

Clearly, parentage methods can be extremely powerful. However, such analyses make three important assumptions: Mendelian inheritance of diploid loci; undetectable mutation rates; and complete genotyping of parent pools. In most organisms, the last assumption is problematic, as it requires a prodigious amount of genotyping. Because they rely on sub-samples within populations, assignment methods could obviate this problem (Cain et al. 2000). However, these methods are based on some restrictive assumptions, such as Hardy-Weinberg equilibrium, which may be inappropriate in many natural populations. Such methods have yet to be used to estimate effective dispersal curves.

Long-term genetic analysis. Long-term average rates of effective dispersal influence both the distribution of alleles within and among populations and the frequency of inter-population coalescent events. The most common long-term frequency-based approach is estimating numbers of migrants in an island population structure from F_{ST}. Because it has been extensively reviewed, and possesses potentially serious limitations for the estimation of LDD (Whitlock and McCauley 1999, Cain et al. 2000), we do not discuss this method here.

An alternative set of approaches that still utilize patterns of differentiation among populations to estimate dispersal parameters are methods based upon the observation that dispersal frequencies drop as distance increases (Wright 1943, Slatkin 1993). Typically, estimates of Nm derived from $1/4 ((1/F_{ST}) - 1)$ between pairs of populations are obtained and plotted against a measure of spatial separation, although other measures of genetic similarity could be utilized. For example, Spong and Creel (2001) attempted to take advantage of this relationship to estimate male dispersal in lions by calibrating a dispersal curve based upon average pairwise relatedness estimates within and among pride members. Because males are known to disperse from natal prides, they reasoned that a pairwise relatedness estimate between a male and the females in the pride can be used to determine male dispersal distances. Although this approach appears promising, the behavior of relatedness estimators is not well characterized and will require further statistical evaluation.

Tufto et al. (1996) developed a maximum-likelihood method for estimating migration among populations based upon observed mean allele frequencies, and treating the (unknown) equilibrium allele frequency as a nuisance parameter. The primary advantage of this method is that, unlike the island population structure assumed in F_{ST}-based methods, the estimator can be used for a rich variety of population structures. Moreover, because each combination of structure and migration rate yields a likelihood score, it is possible to compare the fit yielded by alternative population structures using likelihood ratio tests. Utilizing this feature, Tufto et al. (1998) studied RFLP marker variation in 21 sub-populations of the plant *Beta vulgaris* along a 1-km linear transect. The authors were unable to reject the null hypothesis that this system was isolated from external input. Furthermore, they were able to show that seed dispersal distances were exponentially distributed.

Genealogical approaches that take into account coalescent events among alleles, both within and among populations (Beerli and Felsenstein 1999), also have the potential to resolve LDD (Cain et al. 2000). To our knowledge, however, these methods have not actually been used to estimate LDD.

Models

Because any estimation involves statistics, all the above approaches for estimating LDD assume some type of underlying dispersal model. In this section, we focus on those models that describe or predict individual movements and population redistribution (Table 1). Attempts to improve predictions of LDD must recognize the existence of inherent uncertainty (see Components of the methodological challenge), and act to reduce uncertainties in the model structure and parameter estimation (Clark et al. 2001).

Two complementary approaches have been used to mathematically model LDD. Phenomenological models fit a functional form to observed or hypothesized dispersal data describing the dispersal patterns while ignoring the details of the dispersal process. Mechanistic models use data on factors affecting dispersal, and describe their effects mathematically; the dispersal curve is then predicted independently of the dispersal data. Mechanistic models are usually more difficult to construct than phenomenological models, in part because they typically incorporate many more parameters, which may be difficult to estimate. They also tend to be computationally expensive; hence their application to date is mostly limited to local scales, whereas phenomenological models are often applied to simulate spatial spread at large scales (Clark et al. 1998). Although lacking this important advantage, mechanistic models can provide insights into the role of landscape structure (Nathan et al. 2002a) and other influencing factors that phenomenological models disregard. This attribute of mechanistic models is very important for estimating LDD, since processes that affect LDD may

be different from those determining local dispersal (Higgins et al. 2003). In addition, mechanistic models that appropriately incorporate LDD processes can predict LDD independently of the observed data, whereas phenomenological models rely on observed data – which rarely include LDD – for their calibration.

Phenomenological models. Studies that examine the fit of dispersal curves to observed data traditionally have used particular leptokurtic distributions, such as the negative exponential and the inverse power law (see references in Kot et al. 1996). A rather long and fat tail, implying high levels of LDD, often characterizes these fitted dispersal curves, also called dispersal kernels (Nathan and Muller-Landau 2000). Formally, "fat-tailed" dispersal kernels are defined as those having tails that drop off with distance less rapidly than the negative exponential function. A more inclusive approach has been taken more recently, using a general functional form with a shape parameter accounting for specific functions as special cases (Portnoy and Willson 1993, Turchin 1998). For example, Clark et al. (1998) described the one-dimensional dispersal kernel

$$f(x) = \frac{c}{2\alpha\Gamma(1/c)} \exp\left(-\left|\frac{x}{\alpha}\right|^c\right) \tag{1}$$

where c and α are the shape and distance parameters, respectively and $\Gamma(\ )$ is the gamma function. The negative exponential ($c = 1$) and the Gaussian ($c = 2$) are special cases of this formula, and $c < 1$ is considered a fat-tailed kernel. Clark (1998) examined how kernels with different shape parameters matched the patterns of post-glacial tree expansions, and showed better fits of fat-tailed kernels. An earlier study (Veit and Lewis 1996) fit this dispersal kernel for the banded-recaptured data of the house finch (*Carpodacus mexicanus*), and found $c = 0.47$ and $\alpha = 41$ km for juveniles, and $c = 0.86$ and $\alpha = 77$ km for adults. These fat-tailed kernels are consistent with the rapid invasion of this species in eastern North America.

Another phenomenological modeling approach uses mixed-kernels, where one functional form describes population short-distance dispersal and another describes LDD (Tufto et al. 1997, Higgins and Richardson 1999, Cronin et al. 2000). This approach, also called "stratified diffusion" (Turchin 1998), is attractive because it allows estimation of the frequency of LDD, as well as consideration of short- and long-distance dispersal as two distinct modes (Higgins et al. 2003). An interesting approach using extreme-value statistics to model LDD and likely to be more powerful than curve fitting was suggested by Portnoy and Willson (1993) and Turchin (1998). However, it requires considerable data from the tail of the dispersal curve, which are rarely available.

Mechanistic models. Mechanistic models of seed dispersal by wind, using relatively few and easily measur-able parameters, have been shown to provide reliable predictions of short-distance dispersal, as well as better understanding of dispersal processes (reviewed by Nathan et al. 2001). It has long been suggested that uplifting by vertical wind updrafts provides the key mechanism for LDD of seeds (Ridley 1930), but only recently has this process been successfully incorporated in wind dispersal models. For example, a model coupling seed release and aerodynamics with turbulent transport processes reliably predicted the vertical distribution of dispersed seeds of five tree species in an Eastern US deciduous forest (Nathan et al. 2002b). This verified model revealed that uplifting is necessary and sufficient for LDD. Consequently, LDD can be quantitatively, rather than arbitrarily, defined in wind-dispersed trees.

Passive dispersal of animals by wind-driven sea current can also be modeled using a mechanistic approach. Cowen et al. (2000) presented two mechanistic models of larval fish passive dispersal in the eastern Caribbean: a Eulerian two-dimensional flow model and a Lagrangian three-dimensional General Circulation Model. Influencing factors were the horizontal speed of currents, their turbulence, and larval mortality. The models revealed very low frequency of LDD, thus questioning the characterization of marine populations as "open", i.e. easily connected via LDD. However, as discussed by Cowen et al. (2000), their models are likely to underestimate LDD because they do not account for such factors as rapid transport by hurricanes and active swimming of fish at the end of their larval period. Clearly, such models need further refinement before they can be of general utility to study animal dispersal.

Holbrook and Smith (2000) provided a relatively rare example of a mechanistic modeling approach applied to study LDD of a sessile organism by a biotic dispersal agent. They used radio-tracking methods and seed gut-passage trials to estimate the seed shadows of trees dispersed by two species of hornbills in Cameroon. Predicted dispersal distances were about two orders of magnitude larger than those found in most empirical studies, with maximum estimated dispersal distances of up to 7 km. Similar approaches are increasingly applied in studies of frugivory and seed dispersal (Higgins et al. 2003). We anticipate development of comprehensive mechanistic models of seed dispersal by animals, taking into account the complexities involved with animal behavior, attraction to seed sources, and motivations for long-distance movements, in the near future.

Conclusions

In this final section, we concentrate on two questions: first, what is the current state of methods for studying LDD (and, to a lesser extent, migration)? second, what

are the crucial methodological improvements we still need to accomplish in order to obtain better estimates of LDD, and how soon will these improvements become available? We then briefly address the main new challenges in LDD research that we foresee developing in the coming years.

The selective survey above suggests both bad and good news. The bad news is that we still have a long way to go. Some popular genetic methods make assumptions that are unrealistic, particularly for evaluating LDD. The need to genotype all potential parents remains a major limitation in other genetic studies. Phenomenological models remain limited because they cannot validly be extrapolated beyond the limited range of observations. Mechanistic models offer great promise, but are difficult to implement in complex systems, and, to date, are poorly validated. The basic limitations outlined at the opening of this article, regarding data acquisition, analysis, and interpretation, remain partially unresolved. A simple and comprehensive definition of LDD that is applicable at multiple scales remains beyond reach. Above all, it is important to recognize that even with perfect methods, our estimations of LDD will always be less than perfect due to the typical inherent uncertainty involved with the stochastic LDD processes; the level of this inherent uncertainty, however, is essentially unknown.

The good news comes from two quarters. First, a wide range of methods is already available, and more sophisticated ones are being developed. Mature methods are available for both biogeographical studies and those of movement/redistribution. Clearly LDD is a Lagrangian process, which has long been estimated mostly by the more feasible Eulerian methods. However, emerging advances in technology, primarily miniaturization of marking aids (e.g. harmonic radar tags and satellite-tracking devices) – which promise to improve their utility even further – enable direct estimation of LDD using Lagrangian methods. Lagrangian methods are also promising in genetics. Nevertheless, Eulerian methods also have been advanced by new technology such as stable isotopes, and by creative ways to look at known traits (e.g. marks in fish otoliths). Improved models that use genetic or ecological data are also on the horizon. Recent development of tools designed to use phylogeny in biogeographic context promises even greater refinement (Nathan 2001b). Free software is now available for conducting such analyses (http://www.nceas.ucsb.edu/papers/geneflow/software/index.html).

Second, studies are becoming more sophisticated in combining the results from a variety of methods. Indeed, not all combinations of methods are feasible: for example, large vertebrates are suitable for satellite telemetry, but are difficult to be marked en masse; on the contrary, many other organisms can efficiently be marked, but they are too small to carry a tag for satellite tracking. Some other methods such as otolith chemistry in fish are unique to specific taxa. Yet, some combinations seem to be particularly appealing. For example, a very promising way to assemble an interdisciplinary effort for estimating LDD is to combine empirical methods, e.g., stable isotope analysis or GPS tracking, with predictive mechanistic models that can describe this process based on features of the dispersal system, independently of the movement per se.

Such an integration of methods is most apparent in studies of human dispersal, as exemplified by a recent series of articles in Science (291:1721–1752, 2001). Biogeographical methods, often based on analyses of fossils and artifacts, have traditionally dominated studies of human distribution. Another traditional approach, using linguistic similarities to deduce the relatedness of cultures, and therefore patterns of human dispersal, dates back to the late 18th century (Jones 1992). A variety of molecular techniques has been used to study human origins and dispersal, including plotting of blood groups, and DNA, mtDNA and Y chromosome sequencing. Model-based approaches are also now being used. Combined, these methods paint a much more complete picture of hominid dispersal than each provides separately. Although we doubt that a similar concentration of efforts is likely to occur, we believe that combined approaches will increasingly provide greater insight into LDD in other taxa as well.

In concluding, we would like to point out one challenge and two opportunities for future work on LDD. The greatest emerging challenge we see is related to the rapidly increasing homogenization of biotas by human-mediated dispersal (Mack et al. 2000, Nathan 2001b, Suarez et al. 2001). The "Lessepsian migration" of marine species from the Red Sea to the Mediterranean, following the construction of the Suez Canal, offers an example (Nathan 2001b). Even more extensive information, including dispersal method (Fritts et al. 1999) and estimates of source strength (Vice and Engeman 2000), is available for harmful invasives such as the brown treesnake (*Boiga irregularis*). As species become increasingly more widespread, it will become more difficult to ascertain the source of a particular population: an introduction event, natural spread via LDD, or natural spread of a previously introduced population. Thus, an important challenge is to develop methods for estimating human-mediated LDD, in alignment with methods focusing on natural processes.

We believe that a better understanding of the individual behaviors underlying dispersal can offer exciting new insights, and, especially, can lead to better mechanistic models of LDD. More broadly, however, we believe that our ability to analyze LDD events and even predict them will improve markedly as our ability to identify and follow dispersing individuals continues to improve. A second, and related opportunity, involves a better understanding of the consequences of dispersal.

Arguably, it is effective dispersal, rather than dispersal per se, which is of greatest ecological impact. Once it is possible to quantify LDD and track dispersers, the next challenge we see is better quantifying the establishment process that follows LDD events (Nathan 2001a). These methodological advances are expected to produce a predictive ability of actual and effective dispersal curves. This would be a major contribution to our understanding of prominent global processes, such as the spread of invasive species, and species response to climate changes, habitat fragmentation and various other human-induced environmental changes.

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