

Causes and Consequences of Dispersal in Plants and Animals

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What is dispersal? The type and extent of dispersal impacts organisms at the individual, population, and species level.



Dispersal is an ecological process that involves the movement of an individual or multiple individuals away from the population in which they were born to another location, or population, where they will settle and reproduce. The two most common forms of dispersal are: natal or dispersal. Natal dispersal is the first movement of an organism from its birth site to the site in which it first attempts to reproduce. Adult dispersal entails changing location in space after reaching

reproductive maturity, usually involving movement from one habitat patch to another. Another type of dispersal that does not fall into these two categories is gamete dispersal, which is especially common for non-motile adult individuals, such as plants. Relocation to a new site is a usual part of the life cycle of many plants and animals and is viewed as an adaptive trait in life history.

Active and Passive Dispersal

Individuals can disperse either actively or passively. Active dispersal involves movement of the entire organism through its own ability and is common in both adult and juvenile animals. The degree of adult and/or juvenile dispersal will vary among species depending on a variety of factors, including (in part) the social structure. For example, social systems that rely on a single adult male for reproduction (e.g., a harem breeding system) force juvenile males born into a particular unit to disperse. Active dispersal, in general, is thought to be a density-dependent process in that its magnitude depends on local population size, resource competition, and habitat quality and size. However, evidence supporting the connection between density-dependence and active dispersal is equivocal (reviewed by Matthysen 2005). Nevertheless, local population conditions may affect juveniles and adults differently, resulting in varying degrees of dispersal between different age groups.

Animals that are highly vagile are considered to be the most efficient at active dispersal. Highly vagile animals include many species of birds, bats, and large insects. The Monarch butterfly (*Danaus plexippus*) is a notable example of a highly vagile insect capable of flying hundreds to thousands of kilometers. Other animals, which cannot fly, are also considered highly vagile. Large aquatic animals are effective dispersers, and some terrestrial animals can disperse large distances on foot. As a result, highly vagile organisms have the greatest capacity for long-distance dispersal. Despite the intrinsic vagility of a species, the extent of dispersal is linked to restrictions imposed by the habitat. Flying animals are less affected by habitat changes because they can bypass barriers by flying over or around them. Additionally, there are fewer barriers in the ocean than on land, so large aquatic species can disperse large distances unimpeded (Figure 1). Dispersal by terrestrial animals is generally considered less effective or energy-efficient because individuals are forced to travel through unfavorable habitats, and contend with potential geographic barriers.

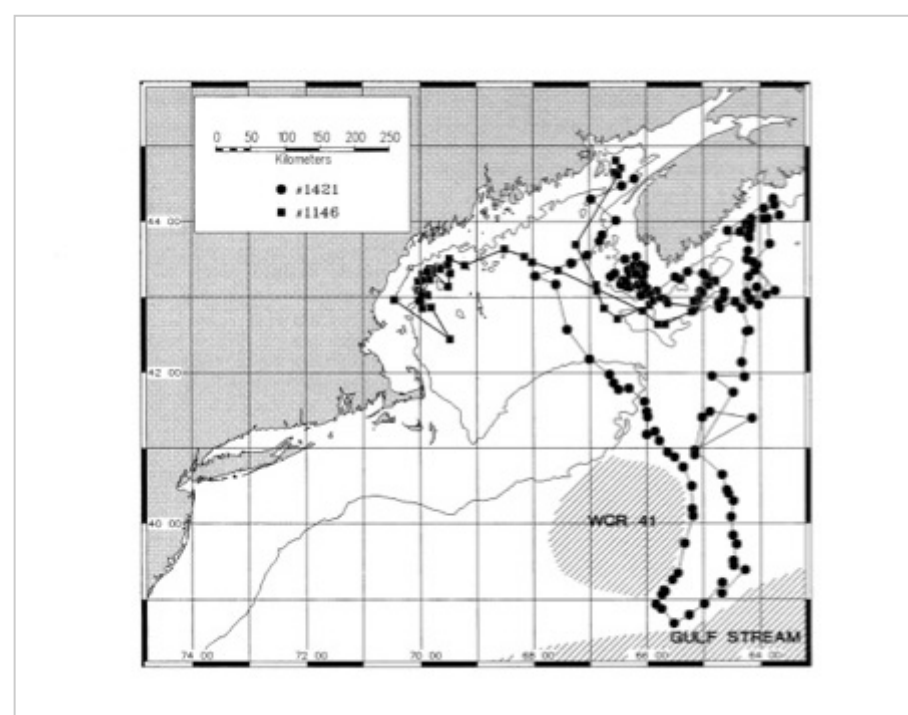


Figure 1: Satellite monitored movements of two male northern right whales (*Eubalaena glacialis*; #1421 and #1146) showing their ability to disperse large distances unimpeded

Individual #1421 moved 3,056 km over 42 tag days and #1146 1,523 km over 24 tag days.

Both individuals were radiotagged in the Bay of Fundy with the purpose to investigate habitat use patterns (see Mate et al. 1997). WCR = warm core ring.

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Passive dispersal involves both plants and animals that cannot themselves move but use dispersal units called disseminules to aid in reproduction or the exploitation of new habitats. Many disseminules are adapted for movement by specific dispersal agents available in the environment, like wind, water, or another animal capable of active dispersal, or species may have a motile larval stage. Sessile adult animals that utilize passive dispersal include marine invertebrates like sponges and corals. Their disseminules are typically specialized buds or cells used in reproduction. For example, most corals sexually reproduce by releasing gametes directly into the water. The male gametes are generally motile, and eggs are moved passively via ocean currents. Other sessile animals exemplify natal dispersal in that they have a free-living, aquatic juvenile stage, wherein larvae drift near the surface and are passively carried by water currents to other locations.

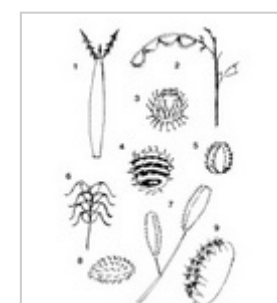


 Figure 2

In plants, disseminules include seeds, spores, and fruits, all of which have modifications for movement away from the parent plant via available environmental kinetic energy. Distance traveled by a disseminule is a result of the velocity and direction of movement by the

dispersal agent. Winds, flying animals, or water currents are some of the most successful agents of long-distance passive dispersal. Seeds and fruits that have wings, hairs, or inflated processes are carried efficiently by wind. For example, modifications in *Hypochoeris radicata* (Asteraceae) seeds have allowed it to successfully disperse in a fragmented landscape in the Netherlands and counteract the negative effects of population isolation with substantial levels of gene flow (Mix *et al.* 2006). Furthermore, some plants have sticky or barbed seeds, or fruits, that adhere to the feathers or fur of mobile animals (Figure 2). Some disseminules are explosively released over short distances whereas others fall to the ground at the base of the parent plant. On the ground, invertebrates, mammals, and birds compete for fallen seeds and fruits. Seeds and fruits are scattered during feeding and after ingestion are distributed in feces. These seeds are adapted to resist digestive juices and, consequently, can pass through the digestive tract while remaining viable. The distance a disseminule travels by animal transportation, either via ingestion or attachment, is indefinite and depends on the dispersal behavior of their host. For example, some animals may follow a nomadic or brief dispersal trajectory, resulting in variance in the distances traveled.

Why Disperse? Why Not?

Multiple processes influence juvenile and adult dispersal. Proximate causes vary but include local population conditions such as crowding and food availability. Environmental stochasticity (e.g., weather, species interactions) also contributes to substandard conditions in the local environment and may affect changes in both dispersal and general behavior (e.g., aspects of phenology including migration and breeding). Individuals that emigrate as a result of environmental conditions may experience more favorable conditions in the new location. Additionally, climate change will impact dispersal. Since climate typically influences the distributions of species, the general warming trend that will occur as a result of global climate change will cause species' ranges to shift. As a result, many areas outside of current distributions may become climatically suitable. However, these areas may be beyond the dispersal capacity of many species. If species cannot adapt to the range changes and/or cannot disperse to more favorable conditions, then those populations may face extinction (see Walther *et al.* 2002 for a review of effect of climate change on species ecology).

Ultimate causes of dispersal can be explained by avoidance of inbreeding and inbreeding depression. Small, isolated populations can become inbred and result in decreased fitness, but dispersal can counteract these negative effects. Additionally, dispersal can reduce competition for resources and mates, thereby increasing individual fitness. At local scales, dispersal can be reinforced through inclusive fitness benefits by decreasing competition among kin (Hamilton & May 1977). In some situations, these ultimate causes will result in sex-biased dispersal. For example, mammals typically exhibit male-biased dispersal, and birds typically exhibit female-biased dispersal. These dispersal strategies result mostly from males attempting to increase their access to females (male-biased dispersal) and in female-biased dispersal systems in birds from male resource defense (female-biased dispersal in birds results) (Greenwood 1980).

Despite the perceived benefits of dispersal, there can be costs. First and foremost, there is a greater mortality risk during dispersal due to increased energy expenditure, unfamiliar habitat, or predation risk (e.g., Johnson *et al.* 2009). Second, dispersers may suffer reduced survival or reproductive success because of unfamiliarity with the new environment and the inability to acquire sufficient resources, resulting in decreased adaptive ability to the new habitat.

The Effects of Dispersal on Individuals, Populations and Species

Dispersal affects organisms at individual, population, and species levels. Survival, growth, and reproduction at the level of individuals are intimately tied to both the distance and frequency of dispersal, factors which are typically mediated by aspects of local resource availability. At the population level, patterns of emigration and immigration within and among habitat patches associated with local population density, among other factors, drive temporal and spatial cycles of colonization and extinction. The form of such movements, such as stepping-stone versus one-way migration, ultimately determines the genetic structure of populations, wherein genetic differentiation is directly proportional to the amount of gene flow among populations. For populations exhibiting frequent dispersal, ongoing gene flow within and among populations results in those populations becoming genetically similar to one another and ultimately evolving as a single unit. Finally, over evolutionary time frames, a lack of dispersal among populations impacts organisms at the species level. If dispersal between populations ceases, these newly isolated populations accumulate novel genetic attributes via genetic drift or natural selection potentially leading to local adaptation. Insurmountable landscape features, such as mountains and rivers, typically drive such processes, and in cases where genetic differentiation persists even after dispersal between formerly isolated populations could resume, such entities can then be designated as separate species (Figure 3).

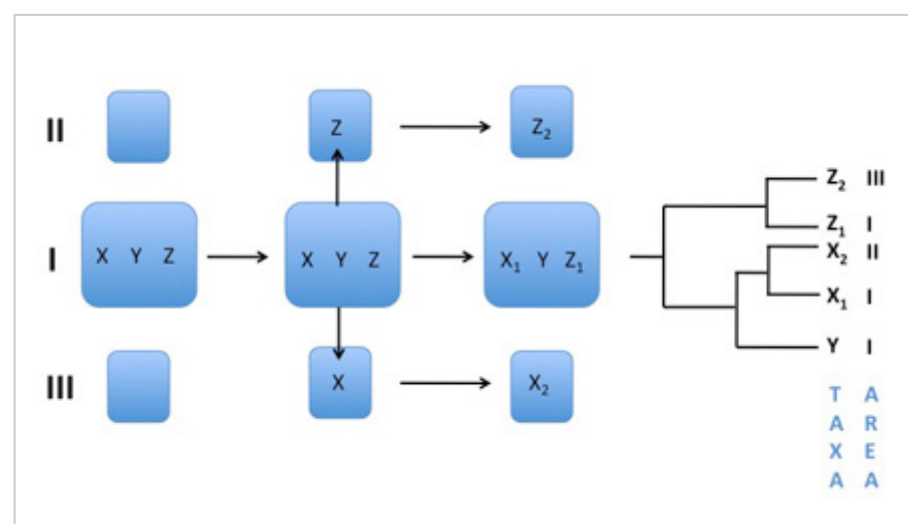


Figure 3: Phylogenetic relationships of hypothetical populations that became isolated via dispersal

Uppercase letters represent taxa, roman numerals represent geographic areas, black arrows represent dispersal events.

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Limits To Dispersal

Species exhibit geographic distributions that are constrained by a range of environmental variables — outside of which individuals may experience reduced survival and reproduction due to physical and physiological constraints. For example, species are often accustomed to particular temperature ranges, and dispersal to regions with temperatures outside those ranges reduces fitness. Additionally, resources necessary for population persistence may be insufficient at range edges and outside the range. Physical barriers to dispersal consist of landscape features that prevent organisms from relocating. Mountains, rivers, and lakes are examples of physical barriers that can limit a species' distribution. Anthropogenic barriers, like roads, farming, and river dams, also function as impediments to movement.

It has been suggested that anthropogenic barriers are the most serious threats to dispersal. These barriers can effectively divide up a species' range into isolated fragments, and dispersal from one habitat patch to another can prove difficult. Creating dispersal corridors has been suggested as a means to maintain connectivity between habitat patches. For example, Banff National Park in Alberta, Canada, contains 22 underpasses and 2 overpasses to facilitate wildlife dispersal within the park across a busy four-lane highway (the Trans-Canada Highway). Similarly, wildlife crossings, specifically designed for Florida panthers, were constructed along a forty-mile stretch of Interstate 75 in Florida. Corridors are not just for large mammals either: Salamanders have also benefited from miniature underpasses to facilitate

dispersal. Additionally, recent research has focused on using modeling techniques to analyze available habitat to designate potential dispersal pathways for species whose ranges have been fragmented (Figure 4).

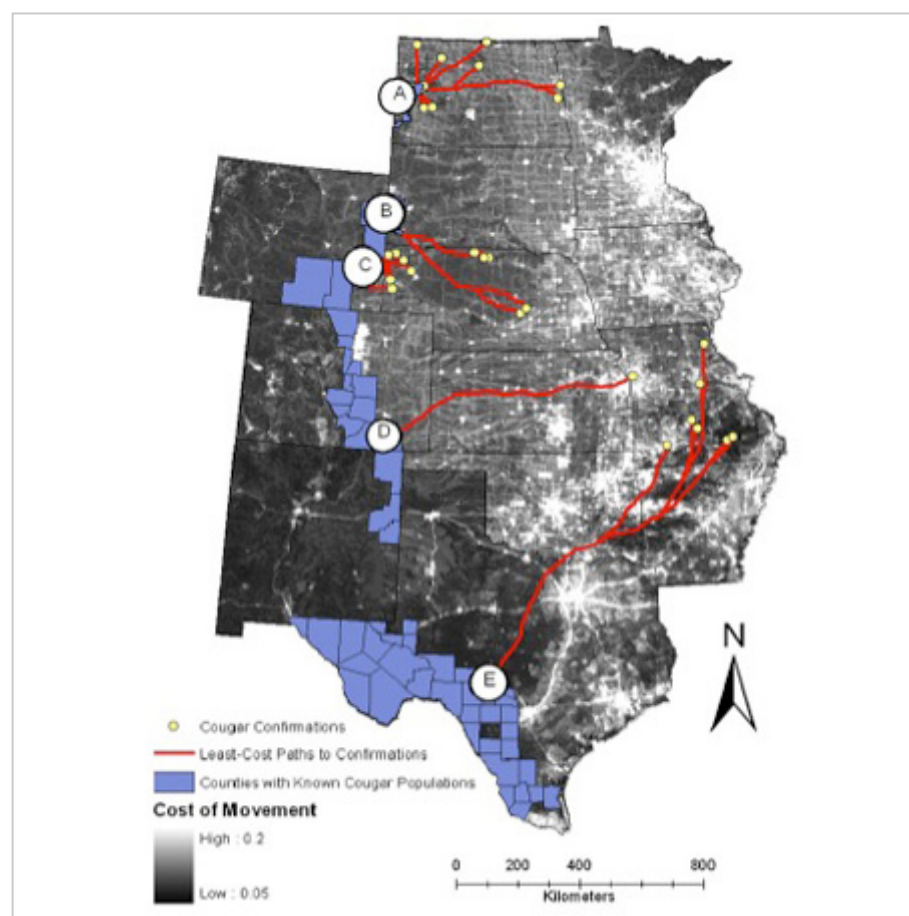


Figure 4: Potential cougar dispersal corridors modeled via least-cost paths analysis (see Larue & Nielsen 2008) from source populations in the West to confirmed cougar sighting locations in the Midwest observed from 1990 to 2006

Least-cost paths models the relative cost for an animal to move between two areas of suitable habitat, and is based on how the movement path of an animal may be affected by characteristics of the landscape, like land cover, human density, roads, or slope (Penrod et al. 2006). Source populations in the West were as follows: A. Badlands, ND; B. Black Hills, SD; C. Platte and Nobrara Counties, WY; D. Las Animas County, CO; E. Kimble County, TX.


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Quantifying Dispersal

Two approaches can be used to estimate dispersal in wild populations: direct or indirect methods. Direct methods consist of mark-recapture (or capture-mark-recapture) using live trapping, individual marking techniques, and/or radio-tracking devices. Direct methods can be somewhat easier to use in larger animals simply because tracking the smallest organisms (e.g., insects) can sometimes be impracticable. However, tracking devices are becoming increasingly more advanced and useful in small organisms (Figure 5). Interpretation of results from direct measurement can sometimes prove difficult though. Low accuracy of spatial position, disproportionate mortality of marked individuals, labor intensity, and high costs are all deterrents to using direct measurement methods.

In contrast to direct methods, indirect methods infer the degree of dispersal without actually having to observe the dispersal movement. Typically, indirect methods involve utilizing molecular markers to measure gene flow and deduce dispersal patterns based on within and among population genetic differences. Specifically, the differences in allele or genotype frequencies resulting from gene flow between populations reveal patterns and levels of dispersal. Indirect methods are increasingly being used to infer dispersal because of the difficulties involved with direct measurement. Genetic methods, while expensive, can provide larger sample sizes to infer dispersal patterns and are usually less labor intensive (Whitlock & McCauley 1999).



 **Figure 5**

Human Effects on Dispersal

Human activities have facilitated and impeded dispersal in many ways. As stated previously, anthropogenic barriers in the form of human development have disrupted natural dispersal patterns in a variety of species. Conversely, humans have also facilitated dispersal, both deliberately and accidentally. A common inadvertent way organisms have been dispersed is through their transport in the ballast water of ships. Ships emptying ballast water may release foreign organisms. For example, zebra mussels, a freshwater mollusk native to the lakes of southeast Russia, were accidentally introduced into the Great Lakes of North America where they have caused major economic problems by clogging water treatment and power plants through ballast water discharge. As a result of the potential for introduction of non-native organisms via ballast water, new standards have been proposed for ballast tank cleaning. Humans have also transported organisms to areas outside their native ranges for deliberate reasons. The seeds of attractive plants native to areas outside North America are routinely used in gardens and have the capacity to disperse to wild areas if conditions are suitable (e.g., purple loosestrife). Also, bighead and silver carp originating from China were introduced to catfish farm ponds in the United States to control algal growth. Fish accidentally escaped from these ponds and have subsequently colonized the Mississippi, Missouri, Illinois and Ohio rivers where they have had significant negative impact on the native fauna (Figure 6).

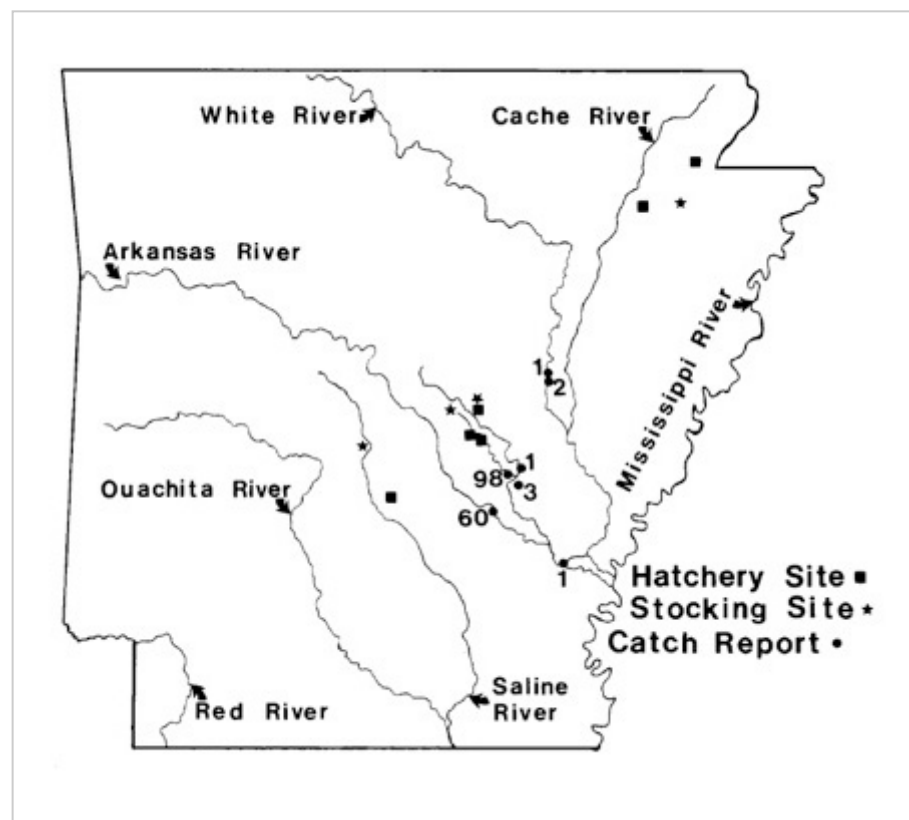


Figure 6: Location of known stocking sites and hatcheries of bighead carp (*Aristichthys nobilis*) and/or silver carp (*Hypophthalmichthys molitrix*) in Arkansas, which may be the centers of distribution for escaped fish

Numbers indicate number of silver carp reported from January 1980 to September 1981 (see Freeze & Henderson 1982).

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Summary

Dispersal is a common process undertaken by individuals at different stages of the life cycle and in response to various factors. Morphological adaptations make dispersal achievable but with varying degrees of success due to anthropogenic and natural barriers. These barriers modify the level of dispersal and consequently exert effects on population dynamics and genetic structure. As environments are altered, through stochastic events and global climate change, it will become increasingly important to assess how such changes will affect dispersal at the individual, population, and species levels.

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