

Innate and Environmental Dispersal of Individual Vertebrates

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Little is known about the rates of dispersal of the young of wild populations of vertebrates, because it is difficult to recover marked individuals after they have dispersed to breed elsewhere. Nevertheless, growing evidence suggests that the observed dispersal patterns may be governed by the laws of heredity as well as being influenced by population pressure.

Dispersal of an individual vertebrate is the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. The significant role of an individual's dispersal is the greatest distance its genetic characteristics are transmitted, rather than the greatest distance the animal may have migrated or otherwise traveled away from the place where it was conceived, hatched or born. Most, but not all vertebrate animals make some sort of a dispersal movement at about the time they attain puberty, regardless of their actual age. Individuals that make innate dispersals, as defined by the hypothesis advanced herein, are predisposed at birth to disperse beyond the confines of their parental home range. They ignore available and suitable niches and voluntarily disperse into strange and sometimes even unfavorable habitats (Fig. 1). In contrast, environmental dispersal is defined as the movement an animal makes away from its birthplace in response to crowded conditions (mate selection, territoriality, lack of suitable homesites, or parental ejection). Environmental dispersers are assumed to have inherited a homing tendency. Environmental dispersal is a density-dependent factor, whereas innate dispersal is independent of density, but both are presumed to be inherited traits.

Even though the hypothesis that vertebrates are predisposed at birth to make either innate or environmental dispersal movements still needs to be substantiated, it seems worth while and desirable to present this concept at this time as a stimulus to further research on this neglected aspect of population ecology. In the literature there are many statements implying that vertebrates disperse because of population pressure factors, but there are relatively few that support the innate dispersal hypothesis.

Burt (1949) wrote, in regard to rodents and other mammals, "If . . . there is an inherent desire to wander, it most certainly is not developed to the same degree in all individuals of a species." Blair (1953) theorized that the dispersal of rodents may result from either population pressure or "an inherent tendency to disperse, stimulated by physiologic changes as the animal becomes sexually active." Dice

and Howard (1951) provide some support for an innate and an environmental dispersal trait, for they found that dispersal distances of prairie deer mice (*Peromyscus maniculatus*) are nonrandom — that apparently there is an innate stimulus which might motivate certain individuals but not others to leave the vicinity of their birthplaces. Johnston (1956) similarly found that salt-marsh song sparrows did not have a random dispersal pattern. As with the deer mice, too many birds aggregated close by, too few moved intermediate distance (350 to 650 meters), and too many moved beyond 650 meters. He says that both his data and those of Mrs. Nice (Ohio song sparrow) have dispersal curves that differ from the expected significantly at the one percent level.

In an intensive study of valley quail by Howard and Emlen (1942), the birds were marked individually with colored bands, and practically every bird in three of six coveys studied was readily observed each day from an automobile. In this quail population there was an interchange of a few members between coveys prior to the spring nesting. At this time, additional, unmarked birds appeared from more distant coveys, and some resident birds disappeared. In every case when a strange bird attempted to merge with a new covey, it was repeatedly attacked for about a month, and ostracized by the members of the same sex in the covey. These ostracized birds had not been driven from their original coveys; they left voluntarily, and patiently awaited acceptance into a different covey. At that time of the year the birds were pairing,

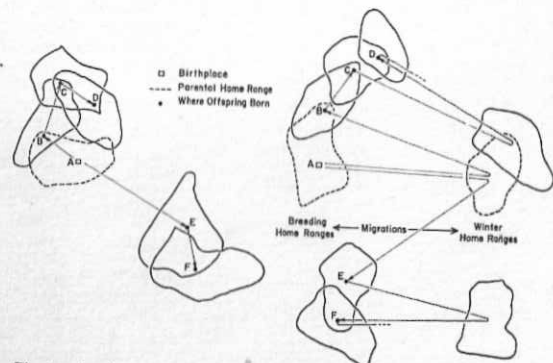


Fig. 1.—A schematic drawing illustrating distance of innate dispersal movements (shortest line between A-E) and of environmental dispersal changes of home ranges (the shortest distance between A-B, B-C, C-D, and E-F) for non-migratory (left) and migratory (right) animals.

although still in covey formation. Individuals of both sexes made dispersal movements, even though there were unpaired members of the opposite sex in the coveys they left. Perhaps "shuffling" in bobwhite quail is a similar phenomenon and is also composed of innate dispersers.

Von Haartman (1951) made a study in Finland of the tendency of pied flycatchers to return to their birthplaces. According to a review of von Haartman's article by Huntington (1951), about three times as many young females as young males did not return to their birthplaces. Many of these probably made innate dispersals. Of the birds that returned the second and following years after banding, the percentage was about the same for both sexes. Von Haartman considers the homing, or philopatric, quality to be hereditary rather than due to greater success in competition for territory, because combat is unusual in the females, and unsuccessful attempts to settle were much more common in males than in females. Furthermore, the dates of arrival and egg-laying of philopatric females were not significantly earlier than those of others. Apparently the nonphilopatric adult females lack a genetically controlled factor that makes their home-loving sisters try to settle in a familiar place. If that is so, then the nonphilopatric individuals may likewise possess a genetically controlled factor for innate dispersal. Of course, innate dispersal and philopatry may not be the hereditary consequence of each other, but von Haartman does consider the differences, *i.e.*, the variation in dispersal distance, to be inherited. He suggests that philopatry may be a recessive character, because six (3%) offspring of 196 banded philopatric females returned to the area, whereas only three (0.5%) offspring of 632 nonphilopatric females returned. This information is too meager to permit drawing any definite conclusions, but it provides some support for the hypothesis that philopatry, hence, also innate and environmental dispersal, are genetically determined.

There are numerous examples indicating that a certain percentage of both males and females (it will vary with species) is likely to make extensive dispersal movements. Only one case will be cited here. In Fitch's (1948) careful investigation of ground squirrels on an 80-acre plot, he found that 40.9 percent of young females survived to maturity, whereas only 31.1 percent of the males survived. He attributes this difference to an "extensive movement of young males off the area rather than actual mortality."

Introduced animals, like the English sparrow and starling in North America and rabbits in Australia and New Zealand, spread their range far more rapidly than population pressure factors could have demanded. It seems more likely that certain young individuals inherit an instinct to disperse considerable distances, and that is why the range of introduced species is often greatly extended by the time the earlier occupied habitats become crowded.

In 1905, three female and two male muskrats were released in two small natural ponds in Dobrisch, 40 km southwest of Prague.

Nine years later the resulting population in Bohemia was estimated at two million (Mohr, 1933). It takes very little calculation to realize that such a large population could not have resulted if young muskrats had not dispersed until population pressure in each favorable habitat caused them to disperse to the next available homesite. On the contrary, as the result of the presumed innate dispersal urge, there must have been a rapid spreading of individuals into new areas long before the populations they left behind had become very large. By the time the populations in the earlier occupied habitats approached overcrowding, which also probably resulted in increased mortality and decreased fecundity, the range of the species had probably already been extended many miles.

Beer and Meyer (1951) report on muskrats as follows: "The bulk of the reports on movements in the Madison area are received in March with a few in February and quite a few in April. This agrees with the period of increasing gonadotropic activity of the pituitary and the rapid development of the gonads. We believe that these early spring movements may be induced by an increased irritability of the animals or to an urge within the animal to move and that the latter is probably the closest to being correct, since the animals found in the early part of the spring movement have few, if any, wounds from fighting. The group that is found moving from April through July are usually severely wounded from fighting. These movements should be classified as force-out movements induced by population pressures."

Davenport (1915) stated that the nomadic impulse in man is an instinct that is sex-linked. Even though there seems to be little doubt that the dispersal trait is subject to the laws of heredity, additional evidence is necessary before one can be certain that the innate dispersal impulse is sex-linked, sex-modified, recessive, polygenic, or just how it operates.

At the San Joaquin Experimental Range, California, the author captured dispersing rodents in seven funnel traps located along drift fences of hardware cloth (patterned after traps used by Imler, 1945). With the nine species of rodents concerned, results indicate that the dispersal trait might be sex-linked, for about two males were captured for each female. Out of 766 trapped individuals that were carefully sexed, an average of 63 percent were males. It is interesting to note how close all these species independently approached this average. The percentage of male rodents captured between June, 1949, and July, 1952, is as follows (total number of individuals appears in parentheses): *Citellus beecheyi* 71% (7 individuals); *Thomomys bottae* 62% (158); *Perognathus inornatus* 68% (71); *Dipodomys heermanni* 61% (18); *Reithrodontomys megalotis* 63% (65); *Peromyscus maniculatus* 63% (51); *Peromyscus boyleyi* and *P. truei* 62% (26); and *Microtus californicus* 63% (370). If no locally established rodents or environmental dispersers had been captured, the figure might have been even closer to two males for each female. The traps were examined almost daily for four years and, at that time, it was obvious that nearly all the individuals captured were virgins in the act of dispersing.

In an attempt to measure the degree of dispersal among prairie deer mice (*Peromyscus maniculatus*) living on 300 acres of grassland, the birthplace, distance of dispersal, and subsequent breeding site were learned for 155 (77 males and 78 females) of the young deer mice (Howard, 1949). An arbitrary figure of 500 feet, which is beyond the boundary of most parental home ranges, is used to separate innate dispersal from environmental dispersal.

The over-all pattern of dispersal observed in the deer mice seemed to indicate that: 1) the availability of surplus home sites (at least artificial ones) had little influence on degree of dispersal; 2) virgin mice made their extensive dispersal, if they ever made one, when they attained puberty, regardless of whether at 4.5 weeks or 25 weeks old (reflecting the season when born); 3) even though various proportions of the sexes were found in the same nest during the breeding season (up to two pairs were present together in the same nest boxes), there was no tendency for deer mice to aggregate in the presumably more favorable habitats; 4) there was apparently very little trial and error searching for suitable niches, for dispersers were never found at intermediate points, suggesting that the dispersal urge for each individual was satisfied in a day or two; 5) individuals did not make more than one extensive dispersal, even if they later lost their mate, although there were minor shifts of nest sites, usually with each new

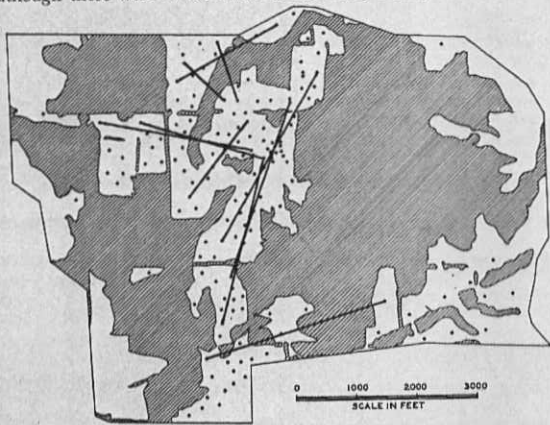


Fig. 2.—The lines indicate ten examples of extensive, innate dispersal movements made by prairie deer mice on the Edwin S. George Reserve, Michigan. The grassland areas are unshaded and locations of nest boxes buried in field are marked by dots. (From Howard, 1949.)

litter; 6) when no suitable mates were present, some dispersers remained unmated for several months during the breeding season without moving, and adults did not move whenever an uneven sex ratio developed; and, 7) there was no evidence suggesting that the parents forced the young to disperse, for quite frequently the mother would merely abandon the young and seek a new nest when a new litter was due.

With regard to the 36 deer mice (out of the 155 that survived to breed) that made "innate" dispersals of 550 to 3300 feet into unfamiliar territory (Fig. 2), the following deductions have been drawn: 1) twenty-four (31%) of the males and 12 (15%) of the females made the extensive dispersals; 2) some individuals traveled through unfavorable habitats (woodland) even though their home range areas were largely surrounded by favorable grasslands; 3) only one animal (a male) was known to return to its birthplace a short time after dispersing (2050 feet); and 4) mice that dispersed the greatest distance did not have time to explore the areas adjacent to their birthplaces or the availability of the habitats through which they passed.

DISCUSSION

If we assume that an innate dispersal trait exists, we can speculate on how the trait may be of value to a species: 1) it would bring about wide outbreeding; 2) it would help reduce the likelihood of too close inbreeding; 3) it would further the spread of new genes; 4) it would rapidly extend the range of the species as favorable habitats become available; 5) it would enable a species to reinvade areas depopulated by catastrophes, such as disease, fire, flood, abnormal weather, or man's activities, without having to start repopulating just at the edges and gradually overflow inward; 6) it would tend to reduce intraspecific conflict and bring about a more efficient utilization of habitat resources; and 7) it might spread a reservoir of characters of possible future value (not adaptive in the new situation yet not selected against, which might help explain why closely related species often differ by characters that are not adaptive).

Domestication probably favors the "homing" or environmental dispersal trait. If such is the case, domesticated animals introduced and released in foreign lands should spread their range more slowly than would be the case with their undomesticated relatives. There is some evidence that this is what happened with many of the introductions in New Zealand and with rabbits in Australia. Perhaps "wildness" is related to the adolescent wanderlust resulting from inheritance of the innate dispersal trait.

For the well-being of migratory species it is not only necessary that some individuals make extensive innate dispersal movements, but it is equally important that all other individuals return to the vicinity where raised. What would happen if most individuals of migratory populations did not tend to return to the home range? Chaos would

develop, for every individual would then be expected to return to the more preferred habitats in the breeding range of the species. There would be so much time and energy spent in establishing individual breeding territories that only a fraction of the total population would be able to breed, if the local food supply were not completely exhausted first. As it is, when the entire breeding range of a migratory bird, fish, or mammal is taken into consideration, there is a far more orderly establishment of the individual breeding ranges and territories than could possibly happen by chance, and natural selection has probably been important in the evolution of this pattern. Territoriality and environmental dispersals are of local importance rather than of geographic significance.

Since such a high proportion of the individuals making up mass emigrations are juveniles (Lack, 1954), it seems highly possible that they may also be responding to the innate dispersal trait. The higher the population density, the greater the number of innate dispersers. Such animals often pass up areas of abundant food supply, and the movements sometimes actually begin before there is any shortage of food. It seems possible that some emigrations, such as an occasional influx of snowy owls into northeastern United States, are merely an increased number of innate dispersers, brought about by an increase in population density rather than by an extensive shift in the home range of older adults. The age of this type of disperser needs to be determined to see if there are any old adults included, *i.e.*, individuals that have bred at least once before making the extensive dispersal. We also need to know if the distance of dispersal is any greater when population density is high.

If animals freely disperse in response to population pressure, then localized epidemics, or "outbreaks," should not occur. On the other hand, even though the direction of dispersal is probably inherently random, the direction of actual dispersal movements are probably greatly modified by many environmental factors. Consequently, there would be a greater tendency—for environmental dispersal movements in particular—toward the more densely populated regions of a species' range, where the more preferred habitats are to be found.

Howell (1922) put many of the factors to be considered in the dispersal of life into chart form. It seems quite plausible that the trigger mechanism initiating dispersals in many vertebrates is associated with the maturing of sex organs, as metabolic processes are speeded up by the activity of reproductive hormones. Lashley (1938) said that the "evidence points to the conclusion that the neural mechanism is already laid down before the action of the hormone, and that the latter is only an activator, increasing the excitability of a mechanism already present." Slonaker (1924 and 1927) recorded the rate of activity of albino rats in a revolving wheel, and noted that there was a marked increase in voluntary activity for males at puberty and for females during each estrus. It would be interesting to see if individuals

possessing the presumed innate dispersal trait had larger adrenals than the environmental dispersers.

Instinctive behavior does not necessarily have to be advantageous to the individual in a social species, but rather it may benefit the group by serving to maintain and spread the species (Tinbergen, 1951: 157). And, as pointed out by Tinbergen, homologous behavior elements may shift their position within the pattern and come to serve different functions in different species, or in some species become lost completely.

Many basic phenomena of animal behavior are not well understood, because they are difficult to investigate. It is particularly hard to analyze the inheritance of behavior patterns. The phenomenon of dispersal alone is a broad subject that will require the participation of many investigators. Much more information is needed about 1) the frequency with which different kinds of animals disperse various distances with population density at different levels; 2) the randomness of the distances of dispersal; 3) the sex ratio of the animals making extensive dispersals in relation to the current sex ratio of the local population; 4) the time relationships of the movements, and whether dispersals are always made at puberty; 5) the motivating and terminating forces, whether physiological or ecological; and 6) the genetic explanations of the variability observed in dispersal distances (field and laboratory experiments). Even if the innate concept should prove to be sound, much information will still be required to learn the various ways in which this behavior is expressed in different animal populations under different situations.

SUMMARY

Dispersal is the movement an organism makes away from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate. For the most part, the major dispersal movements are made by virgins about the time they attain puberty.

Possession of the innate dispersal trait implies that such an animal is predisposed at birth to leave home at puberty and make one dispersal into surroundings beyond the confines of its parental home range. Such density-independent individuals have inherited an urge to leave home voluntarily. They often pass up available and suitable niches and venture into unfavorable habitats.

Animals that make an innate dispersal movement are obsessed with a dispersal instinct. The "purposiveness" of the innate concept is not for the individual's welfare; rather, in spite of the high rate of mortality of innate dispersers, it has distinct survival value for the species. Innate dispersers are particularly important to a species because they, 1) increase the spread of new genes, 2) create wide outbreeding, 3) enable a species to spread its range rapidly as favorable habitats are created, 4) permit the species to have a discontinuous distribution,

and 5) help the species quickly reinvade areas that may have been depopulated by catastrophes, such as floods, fires, or man's activities.

Points that appear more or less to favor the existence of an innate dispersal concept include: 1) the distances of dispersal are, at least sometimes, significantly not random; 2) some introduced species spread their range too rapidly to be the result of population pressure factors; 3) reinvansion of a depopulated area does not commence at the edge and gradually overflow inward, but, instead, the density of the species builds up almost simultaneously over all of the area that is within the maximum limits of innate dispersals; 4) the rate at which innate dispersals are made seems to be density-independent; 5) the movements are made instinctively without any prior experience or instructions to imitate; 6) innate dispersers frequently cross or attempt to cross regions of unfavorable habitat, regardless of the availability of adjacent suitable habitats; and 7) the stimulus is of short duration, apparently being expressed only once, when the animal becomes sexually active for the first time.

The presence of the environmental dispersal trait implies that the individual will remain where born or, by means of trial and error, eventually select a new home range usually within the confines of its parental home range. It will have a strong homing tendency and move only as far as forced by population pressure factors (intraspecific competition or density-dependent factors) such as parental ejection of young, voluntary avoidance of crowded areas, mating and territoriality, availability of food and homesites, or the presence of other organisms including predators. Minor shifts of homesites result in a dispersal, but these are all called environmental dispersals, even though a series of them by one individual might eventually result in a total dispersal distance that is quite extensive, even exceeding that of some innate dispersal movements. Environmental dispersal has only local significance, whereas innate dispersal is of geographic importance.

To verify or refute the existence of an innate dispersal trait, the assistance of other investigators is urgently solicited, for findings of many workers will be necessary before we can thoroughly understand the dispersal behaviorism and dispersal pattern in different species.

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