

High connectivity despite high fragmentation: iterated dispersal in a vertebrate metapopulation

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32.1 Introduction

A dispersal strategy is defined by the frequency and triggers of emigration, the characteristics of movement trajectories during the transience phase (step length, degree of correlation of dispersal paths, and perceptual ranges), and the influence of conspecifics on immigration. Identifying the selective pressures on each of those traits is the topic of a sustained research effort (e.g. Barton *et al.* 2009). Dispersal strategies and the context dependency of dispersal decisions remain poorly characterized for most systems. In order to understand the costs and benefits of dispersal, the empirical challenges include 1) the requirement for sufficiently large study areas to encompass the whole distribution of realized movements, 2) the difficulty in observing the transience phase, and 3) the characterization of the landscape experienced by dispersers, especially with respect to the distribution of relatives present in the natal area, as well as more distant patches. Because of these obstacles, empirical evidence lags behind theoretical developments, and too many theories remain unchallenged by data.

Whilst experimental approaches are clearly best suited for testing the relevance of mechanisms putatively causing dispersal (Chapters 3, 4, 13, 14, 23, 33), these are by necessity performed over small, tractable scales. Descriptive studies of patterns and correlates of dispersal at more ecologically relevant scales are thus paramount, because small-scale processes do not necessarily predict large-scale pat-

terns. Indeed, studies of dispersal that have checked the consistency of pattern emerging at behavioural, individual, and population scale are rare or altogether lacking.

In this chapter, we review published and unpublished studies on dispersal by water voles (see Figure 32.1) inhabiting fragmented habitats and organized as metapopulations. We describe how we have drawn inferences from exceptionally large-scale, but largely descriptive, studies of dispersal through the use of molecular markers, combined with small-scale individual-level experiments. These studies reveal a high degree of connectivity through dispersal between geographically isolated water vole colonies, and experiments with 'enforced dispersers' show how water vole behaviour during the transience phase of dispersal might bring this about, if dispersal takes place over a long time through multiple stepping-stone movements.

32.2 Study system

Water voles are large rodents (200–300 g) which, in the UK, occupy margins of slow-flowing stretches of waterways with high grass coverage (Woodroffe *et al.* 2008). Individuals construct burrows in the plant rooting zone and residents do not normally move more than a few meters away from water. Both sexes mark range boundaries with latrines, and consequently the absence of latrines makes vacant sites easily identifiable. Voles born in the preceding year (overwintered adults) produce most



Figure 32.1 Water voles are large rodents up to 300 g that are semi-aquatic and restricted to riparian habitats in the UK. They form small colonies in grass-rich sections of waterways with slow flowing water. They show a colour polymorphism, with black, brown, or black-brown coloration. Photo Alexandre Millon.

of the young (Telfer *et al.* 2003). Some juveniles from the first litter of the year tend to mature in the year of birth in lowland areas, and typically disappear from their natal range when they reach 80 to 130 g, equivalent to 1–2 months old. Juveniles from later litters in the lowland, and virtually all juveniles born in upland areas where the growing season is shorter, do not reproduce in the year of birth, and their dispersal takes place over a more protracted period. Only a small fraction of adults survive to breed in two successive years, such that, except for the rare early maturing individuals, generations are nearly non-overlapping at the breeding stage.

Water vole populations described in Scotland closely conform to a metapopulation structure (reviewed in Lambin *et al.* 2004). In the Scottish uplands, suitable sections of waterways (habitat patches hereafter) are imbedded in a matrix of unsuitable habitat dominated by prostrate dwarf heath, sedge and rush, moss heaths, and bogs in which they never settle. These suitable stretches are typically 505 m apart (range: 201 m–1507 m) and amount to 11% of the 860 km of waterways in the study area. They are separated by fast-flowing water, rocky or heather margined sections. Discrete breeding colonies use sections of riverbank typically 200 m long (range 10 m–1845 m). In lowland Scotland, the matrix consists of arable land and pastures. Because of overall higher productivity, a

greater fraction of the waterway network is suitable for occupancy. Upland colonies typically include a single breeding female and her progeny. Thus, in the absence of dispersal, there would be a high potential for kin competition and close inbreeding between siblings, but virtually none between parents and offspring.

Our approach has been to study the demography, dispersal, and spatial dynamics of water voles over an exceptionally large spatial scale (140 km²) relative to the size of the organism and that which is normally attempted with microtine rodents. We aimed to census all individuals once per year. Thus all patches ever identified as potentially suitable for occupancy are visited in summer, and where voles are present, live trapping is conducted over 3–5 days. While such snapshot sampling yields information on the status and composition of colonies at a given time, rich additional information on individual breeding success and dispersal can be derived through genotyping of all trapped water voles (details in Aars *et al.* 2006; Stewart *et al.* 1998; Telfer *et al.* 2003).

32.3 High connectivity between fragmented populations

The limitations of classical population genetics approaches to make inferences about dispersal in populations are well known (Lowe and Allendorf 2010) but, critically, such approaches do not require exhaustive sampling over a large area to reveal large-scale dispersal (Ehrlich *et al.* 2001). In our empirical studies addressing the theory that genetic diversity should become eroded in fragmented populations (Aars *et al.* 2006), evidence of the mixing power of dispersal at the largest scale in our upland water vole metapopulation is somewhat indirect, but nevertheless compelling. Aars *et al.* (2006) reported that temporal genetic drift (whether measured by the slope of the relationship between F_{st} or G'_{st} estimates derived from 12 microsatellite loci and time between sampling occasion) amongst groups of water vole colonies occurred at similar rates at different spatial scales up to 20 km (Oliver *et al.* 2009). By inference, dispersal must take place at a sufficient rate and frequency to achieve effective panmixia over a few generations, and

preclude any divergence between sub-groups of colonies due to independent drift up to at least such a distance. The lack of any evidence of isolation by distance at the scale of metapopulation networks covering > 100s km² was also indicative of frequent dispersal up to a few kilometres. As with any inference drawn from population genetics data, a degree of care must be exercised when interpreting these strands of evidence (Lowe and Allendorf 2010). Firstly, high degrees of genetic cohesiveness may arise from cumulative smaller scale dispersal movements by multiple individuals or less frequent long-distance dispersal (Ehrich *et al.* 2001). Second, the degree of fragmentation, frequency of extinction, and fluctuations in abundance of populations may interact in complex ways with dispersal strategies in shaping the emerging genetic structure. Thus, while it might seem reasonable to assume that the dispersal ability of a given species is invariant, it is striking that similar analyses to those we performed, but conducted on the fossorial form and cyclically fluctuating populations of the same vole species, revealed clear genetic discontinuities between areas with contrasting density (Berthier *et al.* 2005). Similarly, two studies with *Microtus arvalis*, a related vole species, both in agricultural habitats, revealed a persistent overall genetic structure among populations separated by 0.4–2.5 km in one instance (Schweizer *et al.* 2007), and a single genetic unit covering the entire 500 km² area in the other instance where the focal population experienced multi-annual cycles (Gauffre *et al.* 2008). Thus, differences observed in the genetic patterns of populations of a given species must be attributed to variation in demographic processes and flexible dispersal strategies rather than to differences in inherent dispersal abilities.

Aars *et al.* (2006) used population genetics approaches to draw inferences on the age-specific prevalence of dispersal by water voles over ecological timescales using the distinctive age structure visible in water vole colonies as they are sampled after the emergence, but typically before the dispersal of juveniles from the first annual litter. F_{IS} values among juveniles sampled in the year of birth were negative, reflecting heterozygosity in excess of Hardy Weinberg equilibrium, whereas they clus-

tered around zero among adults born in previous years. F_{ST} values among colonies were high for juveniles, but moderate and often insignificant for parents. The excess heterozygosity seen within colonies was taken to reflect the few individuals dispersing from beyond the range of the closest neighbour patch to form discrete breeding colonies. Thus rapid reproduction and the formation of local family groups apparently cause an increase in differentiation, but this is cancelled by subsequent dispersal.

Comparisons of F_{IS} between years at the metapopulation level show that excess heterozygosity (across both adults and juveniles) increases with the average level of isolation between colonies (Oliver *et al.* 2009). This illustrates a situation where individuals dispersing from distant colonies, characterized by different genetic frequencies, locate mates in a sparsely occupied landscape. The resulting mixing of genotypes sourced from distant colonies (with intervening colonies having gone extinct) results in levels of heterozygosity in excess of Hardy Weinberg equilibrium. Interestingly this demonstrates how excess heterozygosity, which may mistakenly be attributed to the action of selection or inbreeding avoidance, both of which would be expected to lead to a general excess of heterozygosity, rather than one that correlates specifically with increasing isolation, can be generated purely by metapopulation effects combined with long-distance dispersal events.

32.4 Natal dispersal of individuals linking populations

In addition to making inferences from population genetic parameters, genetic information can also be used to infer dispersal through the identification of genealogically related individuals. Here, we present an example where we infer the connectivity between patches by reconstructing pedigree relationships between pairs of water voles using the software KINSHIP 1.3.1 (Goodnight and Queller 1999). Other softwares (e.g. COLONY Jones and Wang 2010) can similarly be used, although computational requirements can vary substantially. KINSHIP calculates the genetic relatedness, r , between pairs of individuals which, when combined with likelihood tests

on competing relatedness hypotheses (e.g. parent offspring versus non-related), can be used to assign full sibling or parent offspring pairs without requiring any other prior information. Including age data can help improve discrimination between parent offspring and full sibling pairs. Using this method, dispersers are those individuals who are located in a different patch from that where their putative close relatives are located. Identifying such individuals was facilitated by the very high proportion of related individuals present in the study area being sampled. Note, however, that in those instances where two close relatives both left their natal patch, dispersal distance may be under- or overestimated.

Water voles disperse over exceptionally long distances. Of 1498 individuals assigned and who survived to reproduce, 757 (51%) dispersed and the mean dispersal distance was 3.5 km (STD 4.7, max 23.9 km). The average dispersal distance was at least four times higher than predicted from allometric relationships based on other studies of mammalian dispersal (Sutherland *et al.* 2000), and substantially further than estimated using similar techniques for raccoon, which are at least tenfold larger (Cullingham *et al.* 2008). Dispersal in water voles shows no evidence of sex bias in either distance or frequency of dispersal (Telfer *et al.* 2003; Aars *et al.* 2006).

Dispersal movement binds water vole colonies in a highly connected network (Figure 32.2), the structure of which approaches randomness with very little dependency of connectivity on distance. Median dispersal distance doubled from within (1.02 km) to between year (1.97 km) timescales. When considering natal dispersal and resulting networks, connectedness markedly increased with time such that by the spring following birth, even patches on either side of major topographical obstacles were connected. Contrasting Figure 32.2A and 32.1B implies that water voles are sufficiently mobile to bypass obstacles, such that if considering the ecologically relevant annual timescale, the impact of intervening topographical obstacles on connectedness between patches would not be apparent. In such circumstances, least-cost surface distances would not outperform Euclidean distances as predictors of dispersal, reflecting the mismatch between

observations at short (behavioural) and ecological (annual) timescales. Network statistics indicate that some patches, including those bounded by topographical obstacles, have high centrality, especially those used as transit patches in the year of birth.

32.5 Short-term experiments and the behaviour of transient water voles

While our study is otherwise wholly descriptive, we used simulated dispersal experiments of sub-adults fitted with small VHF radio-transmitters attached to collars to assess disperser's ability to immigrate to occupied or presently vacant but previously occupied sites (Fisher *et al.* 2009). Sub-adults aged 1.5–2 months that would often naturally disperse were used to minimize any bias arising from forced dispersal or behavioural differences in hormonally primed or motivated dispersal. Individuals were located hourly during daytime for the first three days and at least daily thereafter. Performing such experiments is challenging owing to the number of sites required, the care needed in selecting appropriate candidates for enforced dispersal, and the large scale of movements taking place relative to the limited range of radio-transmitters when dealing with a partly fossorial organism. Despite achieving only modest levels of replication (ten and seven voles moved to different occupied and vacant sites respectively, and three newly mated females radio-tracked but not translocated), we learned a great deal about how the behaviour of voles during the transient phase might translate into the extremely long movements observed in the uplands. The salient points are summarized here, though more details are available in Fisher *et al.* (2009).

The fate of the sub-adult voles that survived a few days post-movement (three were immediately predated) varied according to the context of their release. Of the six surviving voles translocated to a suitable but vacant patch, all rejected the site and dispersed; a vacant site where a young male was released was colonized by a natural (non-experimental) opposite-sex disperser and both settled there, and, half of those voles translocated to occupied sites settled ($n = 8$ non-predated). Dispersing voles also rejected all vacant sites they encountered



Figure 32.2 Network of dispersal movements by first-degree relative water voles detected through parentage assignment. Lines connect patches linked by dispersal movements that took place (a) in the first three months of life of the youngest vole in the pair; (b) up to 11 months after the birth of the youngest vole. The size of each circle reflects the centrality of a patch (number of connections to other patches). Solid grey areas represent areas above 400 and 600 m, including cliff faces and sparsely vegetated stony ground. Dark stippled areas represent water bodies (sea to the north) and lochs in the study area. The area where all patches are monitored yearly is delineated by the black line. Annual patch occupancy and colony extinction probability both average 35% but no account is taken of occupancy or population size in these network representations. C and D. Frequency distribution of dispersal distances for 873 and 625 individuals assigned pairs within year and between years respectively.

after leaving their release patch and often followed a 'stepping-stone' dispersal trajectory. Dispersing voles remained in the transient phase of dispersal for up to 16 days. Dispersers stayed for up to ten days at sites that were considered suitable (previously occupied) and contained no other water voles but, with the exception of two instances when they were joined by an individual of the opposite sex, they eventually abandoned vacant sites and moved on. There was some evidence of density dependent immigration; vole density at the sites where translocated voles settled (0.88 adult/100 m) was substantially and significantly lower than the density at the four occupied sites rejected by the translocated voles (2.35 adults/100 m).

Voles that rejected their release sites for settlement dispersed out of their own volition either along waterways ($n = 4$) or overland ($n = 5$). Thus, they readily entered the assumed matrix of unsuitable habitats where no vole ever settles. On four occasions voles were recorded as having dug a burrow in a transit area. Of these, one transient individual dug a substantial burrow in a field well away from water, and remained in this shelter for one night before resuming its exploration. Thus not only are these herbivorous rodents able to sustain themselves in a relatively permeable matrix, but they might also be able to reduce the cost of transience by creating temporary refuges. They do, however, suffer an elevated mortality risk relative to non-dispersers, estimated previously by comparing daily mortality risk to predation between translocated individual and the disappearance rate of individuals from the same juvenile spring cohort followed by capture recapture in their natal patches, to be fourfold higher for sub-adults of the same age and general area (Lambin *et al.* 2004). This predation cost rather than any depletion of energetic resources is also believed to account for the death of failed dispersal in Vancouver marmot (Brashares *et al.* 2010). Whereas one contributing factor to elevated marmot mortality during dispersal is their use of inadequate shelters such as fallen trees instead of burrows when away from colonies, the ability of water voles to create effective temporary shelters during dispersal is a likely contributory factor to their success as a species inhabiting highly fragmented habitats.

The collection of anecdotes reported above demonstrates that water voles occasionally leave their normal habitat, and embark on one-way dispersal movements. Each movement bout displaces them by some hundreds of meters per day; for example, we observed an individual moving 1800 m over 13 days. Such stepping-stone movements may be repeated multiple times and are seemingly interrupted by either an encounter with an opposite sex conspecific in a suitable site or the death of the disperser. Whereas early-maturing spring-born voles tracked by Fisher *et al.* (2009) may lose valuable breeding time in the year of birth if they fail to encounter a mate rapidly, later cohorts in the lowlands and probably all juveniles in upland areas do not face this time constraint. Instead, they have the option of dispersing over many months between adolescence and their first breeding opportunity in the spring following their birth. If they followed the iterated dispersal strategy described above, they would have the opportunity to sample a large number of habitat patches sequentially, hence to optimize patch or mate choice.

Using an iterated dispersal strategy between habitat patches, including waiting for the arrival of an opposite-sex conspecific seems effective for encountering a potential mate despite very low conspecific density, although little existing theory tackles this aspect of dispersal. Indeed, population genetic evidence (Oliver *et al.* 2009) suggests that pairs are formed by individuals of distant provenance at low density. However, whereas dispersal of the spring cohort that was the focus of Fisher *et al.*'s (2009) work is mostly synchronized, coinciding with sexual maturation, dispersal over the summer and autumn is probably more asynchronous, reducing the likelihood of encountering a mate during dispersal.

While there is no evidence of mating limitation amongst water voles (dispersers or not) that survived until the spring (Aars *et al.* 2006), failure to encounter an opposite-sex conspecific may amount to a depensatory process at low conspecific density, such as on the edge of a species range where the transience phase may be protracted (Chapter 26). A greater perceptual range of dispersers and higher ability to detect both habitat patches and the

presence of conspecifics would obviously increase their success in dispersal.

32.6 Conclusions

We presented evidence, collected at daily, monthly, and annual scales that reveal a water vole patch network highly connected by dispersal despite long inter-patch distances. Individuals performed multiple stepping-stone dispersal movements over many days in search of opposite sex conspecifics. Multiple individuals dispersed between patches, mostly irrespective of the intervening distance, and colonies were thus genetically homogeneous over extended distances being formed by individuals originating from larger areas at low density. We conclude that in water voles, but also probably in many other species for which dispersal may take place over time through repeated stepping-stone movements, between-patch connectivity in a network brought about by dispersal may be higher than expected from properties of single dispersal events.

The pattern of movement employed by voles appears to be in contrast to the foray search pattern described for some butterflies (Conradt *et al.* 2003), but its effective straightness is not dissimilar to that predicted for species inhabiting sparsely populated environments (Barton *et al.* 2009; Heinz and Strand 2006; Zollner and Lima 2005). Here the effective displacement achieved by an individual employing such a 'move and wait' strategy should reflect its dispersal lifespan, which for water voles able to access food resources while transient, should in turn be influenced by the mortality risk during dispersal (Chapter 16). While pikas (*Ochotona princeps*) have a similar size and probably similar intrinsic mobility as water voles, their effective vagility is constrained, especially at low altitudes, by the need to have completed the process of dispersal in time for collecting the hay stores on which they rely in winter, and their inability to tolerate high diurnal temperature. These constraints limit the dispersal lifespan and contribute to a relatively low vagility of this species (Smith 1974). Dispersal lifespan is much shorter for butterflies living in appropriate climatic conditions for only a few days and relying on on-board energy stores (Chapter 18), though is much

longer for species with delayed maturation able to acquire information from direct sampling of patches. While the patterns observed at the individual and population scales imply that water vole dispersal behaviour is protracted and probably spans many weeks or months, our observation that one individual achieved the median natal dispersal distance in only 13 days and the substantial mean dispersal of individuals sampled in their year of birth indicate that mobility *per se* might not be a constraint. Crucially, the information gleaned by dispersers concerning their environment and conspecifics is acquired up to breeding. As such, in contrast to common lizards making dispersal decisions based on maternal quality in the first days of life but years before they reproduce (Case Study I), the reliability of the information gleaned by dispersers should not be severely eroded by changing circumstances such as conspecific mortality.

The lack of clear theoretical predictions for how the behaviour of transients translates into overall effective dispersal stands in contrast with the plethora of predictions of the evolution of emigration (Chapter 10). Informing theory with relevant empirical data such as those presented here is likely to be a fruitful endeavor.

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