the way they represent visual information [16] or their particular patterns of connectivity [17], may be better than others in allowing artificial activity to seep into consciousness. Murphey and Maunsell [13] addressed this possibility by measuring thresholds from five different areas in the visual cortex. These ranged from the primary visual cortex, which is the first cortical way station for information arriving from the retina, to inferotemporal cortex, thought to be the highest stage of processing relevant to object recognition. As a group, these areas span the breadth of almost every measure one might consider relevant to this question, predicting a broad range of threshold sensitivities. In fact, just the opposite was observed: threshold current increased by only a factor of two as increasingly higher visual areas were stimulated. If the threshold current is treated as a stand-in for the number of neurons that must be stimulated for the animal to be aware of the microstimulation [18], these results argue strongly that the visual cortex is surprisingly egalitarian in the way it accords access to awareness.

Of course, we don't know what this awareness might have looked or felt like. While Murphey and Maunsell's [13] results do not hint at the subjective dimensions of the effect, future experiments might. If microstimulation effectively reproduces normal visual experience, as might be expected in the early visual areas, it should be possible to study the visual qualities of the percept with psychophysical approaches that have been successfully used to understand illusory perception. For example, stimulation of directionally selective neurons in visual area MT (or V5) might generate a perception of motion, whose direction could be estimated objectively by a nulling procedure [3,19]. Especially as higher-tier brain areas are stimulated, however, the possibility exists that the evoked percept is wholly unlike anything that the animal has ever experienced [20], in which case these approaches will fail. This would represent a fundamental limit on what the scientific (third-person) approach is able to tell us about a subjective (first-person) experience. Maybe we will need to teach monkeys how to talk after all.

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Dispersal Ecology: Where Have All the Seeds Gone?

How effective are different animals at dispersing seeds? A new study has traced seeds sampled in faeces to their mother of origin and concluded that carnivorous mammals can be better dispersers than birds.

John R. Pannell

The ecological and evolutionary success of any species ultimately depends on its ability to disperse and spread its genes. Most animals do it by moving around, but dispersal poses a serious challenge to sessile plants. Of course, plants have risen to the challenge by co-opting vectors such as wind or animals to carry their seeds and pollen. The mechanics of how they do it has long fascinated biologists, but describing the precise paths taken has been exceedingly difficult, not least because it is the rare events of successful long-distance dispersal that are both the most elusive to track down and the most biologically far-reaching [1,2]. Most seeds and pollen are dispersed close to their parent plant [3], but a few of them reach long distances, and these allow the spread of adaptations to distant populations, the colonisation of new available habitat, or species replacement after a previous extinction.

Genetic markers have for some time allowed biologists to determine the successful paths taken by pollen grains [4–6], but tracking seed dispersal has been harder to pin down because seeds carry the scrambled genomes of two parents rather than one. Now, Jordano *et al.* [7] have managed to assign mothers to dispersed seeds on the basis of the genotype of maternally derived tissue in the seed coat of the European Mahaleb cherry, *Prunus mahaleb*. Their study is particularly revealing because it highlights not only the distribution of distances over which seeds are dispersed — the so-called 'dispersal kernel' — but also the complexities of dispersal by different animals and into different types of habitat.

Jordano *et al.* [7] studied an isolated population of *P. mahaleb* in the southern Spanish mountains of Cazorla (Figure 1A). This small tree produces single-seeded fruits that attract a range of frugivorous birds and mammals during a short window in summer (Figure 1B). The researchers determined the genotype of all of the 196 fruiting trees in the 26 hectare study area, and they carried out extensive observations of fruit removal from these trees by various bird and mammal frugivores; this enabled them to determine the fruit-removal rate by each animal visitor. They then collected faeces and regurgitation pellets, recorded their species and the habitat in which they were found, and returned to the laboratory to remove the cherry stones they contained. Finally, they extracted the DNA from the seed coat of a sample of seeds and determined their genotypes at a number of highly variable genetic ('microsatellite') loci.

Because the seed coat is composed of maternal tissue, Jordano *et al.* [7] could match the genotypes of their seeds with the mother of origin and could thus determine how far each seed had come. Seeds that did not match the genotype of any of the fruit-producing trees in the population were obviously immigrants that had come from populations further afield. Not only was it thus possible to characterize the dispersal kernel within this particular plant population, but the authors also determined the rate of seed immigration and the relative contributions made to within- and between-population dispersal by the different frugivores [7,8].

Figure 1. Dispersal of the European Mahaleb cherry.
(A) The study species, *Prunus mahaleb*, in its habitat in the Cazorla mountains in Spain (tree in central middle-ground). (B) Fruits of *P. mahaleb* prior to dispersal. Images kindly supplied by P. Jordano.

Characterization of seed dispersal kernels has been something of a cottage industry in plant ecology and evolution, and for good reason. Plants typically produce a profusion of seeds, but unless they can be effectively dispersed, the investment is potentially wasted. Seeds that fail to disperse from their mother face intense competition with their siblings to replace their mother when she dies [9], or they may succumb to the pests and diseases concentrated around their mother [10]. Thus, despite the enormous potential risks of death during dispersal, the successful establishment of progeny away from their mother promises rich rewards by escaping these hazards.

Researchers have used a variety of methods to track the dispersal trajectories of seeds, combining, for example, the use of seed traps and phenomenological models to characterize the dispersal curves [3,11]. However, the focus has necessarily been on the large majority of seeds that disperse over relatively short distances [2]. Short-distance seed dispersal is likely to represent a major contribution to a mother's fitness, but it is often insufficient to account for the often rapid geographical spread of species during range expansion [12,13] and the genetic signatures it leaves [14], a process likely driven by infrequent long-distance events [15].

Similarly, while successful dispersal of progeny within populations reduces the chance that they will compete or mate with closely related neighbours [9], dispersal between different populations can provide a critical source of genetic variation that might rescue small and inbred populations from genetic drift and extinction [16]. Long-distance dispersal also governs the extent to which populations are held together by gene flow or are allowed to diverge from one another genetically. Thus both short- and long-distance dispersal are important processes, about which still far too little is known.

Jordano *et al.* [7] found that small passerine birds were responsible for removing a large majority of the fruits harvested from individuals of *P. mahaleb*, with larger birds and mammals removing substantially fewer fruits. However, these potential dispersers of *P. mahaleb* seeds differed, not only in the quantity of seed removed, but also in the distance they travelled before defecating or disgorging them. More than half of the seeds eaten by small passerines, such as warblers, redstarts and robbins, were dispersed within about 50 metres of their maternal parent. In contrast, two larger species of bird, mistle thrushes and carrion crows, dispersed most seeds consumed more than 110 metres, while foxes, stone martens and badgers dispersed the majority over distances of more than 0.5 kilometres; indeed, 70% of the seeds inferred to have immigrated from outside the population were due to mammal dispersal. Thus, while small birds removed most of the fruits, mammals took the seeds they had eaten much further. The research not only succeeds for the first time in quantifying the long tail of a plant's dispersal kernel, but it also indicates that the kernel shape is a compound function of interactions with several quite different frugivore contributors.

Interestingly, while mammals disperse seeds further, they also tend to deposit them on rockier, more open ground than do passerines. Because *P. mahaleb* establishes and grows better under the protection of shrubs than at open sites, the many long-distance dispersal events therefore do not necessarily promise successful recruitment. It does not seem possible yet to be precise about how much the poorer recruitment from fox scats should reduce inter-population gene flow through seeds, but we might bear in mind that genetic cohesion amongst population requires only one successful immigrant per generation, and genetic rescue of inbred populations may require even fewer. Given the small contribution to immigration caused by warblers and other small birds, the genetic integrity of *P. mahaleb* through seed dispersal probably relies heavily on the persistence of a population of foxes — and this has palpable conservation implications.

Genes of course are transmitted through pollen, too, so it is interesting to reflect that a previous study [17], also conducted in the Cazorla mountains on a species of lavender, inferred that butterflies dispersed pollen further, and therefore more effectively, than did large bees. The paper now published by Jordano *et al.* [7] based on research done in the same Natural Park thus provides yet another example of the importance of decomposing the contributions made by animals to plant dispersal and gene flow (see also [8]). Such studies of course also throw light on the paths taken by animals during their foraging sprees. The birds and bees may do it for plants, but they appear to do it less well than foxes or butterflies.

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