lupine leaves, and cause plants to have depressed growth and seed production (Figure 1B). The herbivory by these insects is so intense that it greatly depresses the rate at which lupines can invade open habitat on Mount St. Helens [6].

Over a decade of research on the devastating effects of herbivory on lupine population dynamics has just come to fruition with a recent paper in the *American Naturalist* [9]. For this work, empirical and theoretical ecologists teamed up to create a mathematical model that is able to project the spread of lupines across the volcanic area. Their model included 18 empirically measured parameters which describe the ecology of the lupines and their enemies, including lupine seed dispersal distances and the spatial location of herbivory.

Lupine seeds can move long distances as a result of dispersal by small mammals, winter runoff and wind. The first lupine plant was found on Mount St. Helens in 1981, and to get there the seed dispersed over 2 km [10]. However, long-distance seed dispersal is a relatively rare event in these lupines. In contrast, their lepidopteran enemies are capable of frequent, long distance dispersal [9]. Lepidopteran herbivores preferentially consume lupines that are isolates, or individuals located on the edge of a cluster of plants [6–8]. This may result from the higher quality of nutrients they obtain for plants growing at low density [8], or because arthropod predators are more prevalent in large clusters of plants [10]. However, because these isolated individuals otherwise have the potential to contribute disproportionately to the spread of the population [11], lepidopteran herbivory greatly stunts the rate of lupine invasion.

The results of the model [9] show that, under the best estimates for all parameters, the lupine population is expected to spread by approximately 25 min per year. However, small perturbations in any of the parameter values can cause the spread of lupines to come to a halt. For example, a slight increase (5%) in the fertility rates of herbivores

would cause the lupine population to contract rather than expand. Their results also highlight the importance of chance events, such as the timing in which herbivores invade [9]. If lupines are able to colonize and establish 9 years or more before herbivores arrive, then herbivores will be able to slow, but not stop the spread of lupines. But if herbivores arrive earlier, they can drive the lupine population extinct. At Mount St. Helens, the first lupine arrived in 1981, and by 1991 over 1 million plants were present. It was not until after 1991 that lepidopteran herbivores established in strong numbers on the front of the lupine invasion.

The implications of these new results [9] extend well beyond how lupines and other lifeforms reassert themselves after a volcanic eruption. This research demonstrates that species interactions, such as interactions between plants and herbivores, will influence the recovery of vegetation after natural and anthropogenic disturbances. Further, the results are also applicable to the invasion of non-native pests. A take home message from these results is that biological control and other types of management will have the highest likelihood of success early on in the invasion process.

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Mate Choice: Female Relatives Share Sexual Partners in Bats

Groups of female greater horseshoe bats share more than just caves. A long-term study has revealed that female relatives share males as well, but the adaptive significance of this family-wide mate fidelity remains obscure.

Ido Pen and Gerald Kerth

For females, choosing the right sexual partner can be crucial, as mate choice may strongly affect their fitness, even if males provide nothing but genes [1]. A recent paper reporting a long-term study

[2] of the colonial greater horseshoe bat *Rhinolophus ferrumequinum* (Figure 1) provides a new twist to our understanding of female mate choice in social species. Combining data from 17 years of fieldwork with detailed genetic pedigree analyses, Rossiter

Figure 1. Picture of a roosting greater horseshoe bat (*Rhinolophus ferrumequinum*). Remarkable new aspects of mate choice unfold from a long-term study on the mating behaviour of greater horseshoe bats. (Photo ©www.fledermausschutz.ch.)

and colleagues [2] found evidence for remarkable mate fidelity within matrilineal groups of females. Not only are individual females faithful to the same mate for several years, but also they often share that mate with their female relatives. In fact, some females have the same mate as their mother and grandmothers. This kind of within-family polygyny strongly increases the degree of relatedness among females of the same matriline. For example, in several cases a female and her maternal half-aunt were also half-sisters on their father's side. At the same time, female bats rarely mate with blood relatives, such as their own father, thus largely avoiding potentially negative fitness consequences of inbreeding [3]. But how inbreeding is avoided in greater horseshoe bats remains unknown.

It has long been appreciated that female mating behaviour can

have a significant impact on the genetic structure of populations. For example, genetic diversity within social insect colonies is strongly determined by the queen's mating frequency [4]. In mammals, mating behaviour of females is often correlated with other life history traits that affect population structure. Inbreeding avoidance by females that mate and breed at their natal site can induce male dispersal, thereby decreasing genetic variation between geographic locations or social groups [5]. Moreover, it is not uncommon for female mammals to remain faithful to their mate for years on end, nor is it rare for female relatives to share the same mate. This happens all the time in lions and other species where groups of related females are monopolised by one or several dominant males [6]. However, the study by Rossiter *et al.* [2] is the

first to show that mate sharing between maternal relatives raises the level of kinship within matrilines in a social mammal where the sexes are segregated outside the mating season.

In greater horseshoe bats, as in all other European bat species, females form breeding colonies during summer to raise their young communally [2]. Breeding colonies of greater horseshoe bats consist of dozens of females that belong to several different matrilines. Males are solitary and disperse from their natal colony. In autumn and spring, away from the breeding sites, the sexes meet for mating in caves where they also hibernate [2,7]. Because the sexes are segregated during most of the year and female bats can store sperm for several months, individual males cannot easily monopolize females. This is a typical scenario for bats living in temperate zones, but it contrasts strongly with the standard dominant-male scenario found in many other social mammals [6,8]. As a result, female bats are probably able to choose their sexual partners more freely than mammals that live year round in stable mixed-sex groups with access to only a limited number of males. But as male greater horseshoe bats often occupy the same mating territory for years, mate fidelity could also be an artefact of females preferring certain caves rather than individual males. Rossiter *et al.* [2] cannot completely dismiss this possibility, but they show that some females stick to their mates even after the latter switched caves.

As a possible evolutionary implication of their findings, Rossiter *et al.* [2] argue that mate sharing between maternal relatives, while avoiding inbreeding at the same time, may stabilize social groups. Clearly, increased relatedness among group members may facilitate kin-selected cooperative behaviour [9]. But increased relatedness is a double-edged sword, as it also ensures that competition is more likely to occur among relatives, potentially negating the benefits of cooperation [10,11]. Recent theoretical models, however, indicate that certain life histories

and mating systems are more likely than others to tip the scales in favour of cooperation. In particular, both polygyny [12] and overlap between generations [13] tend to boost the evolution of altruistic behaviour. Indeed, these traits even allow for altruistic acts directed towards random group members, without a need for kin recognition. These results suggest that the lifestyle of the greater horseshoe bat may be especially conducive to cooperative behaviour based on kin selection. There is only one problem: there is, thus far, no evidence that greater horseshoe bats engage in such behaviour despite many years of research on this species.

In other bats, several cooperative behaviours have been described. They range from feeding starved colony members [14], to nursing foreign pups [15], to information transfer about food [16] and suitable roosts [17]. Remarkably, most of these cooperative behaviours are apparently not preferentially directed towards kin. Blood regurgitation in vampire bats is even one of the few possible cases of reciprocal altruism in wild animals. Moreover, in the few bat species for which relevant data are available, relatedness does not explain spatial associations of individual females within colonies [18]. In greater horseshoe bats, however, no cooperative behaviours have been described and the only kin-directed behaviour shown — daughters sharing foraging areas with their mothers [19] — cannot be used to explain benefits due to increased relatedness within matrilines. Therefore, our current knowledge of bat sociobiology does not suggest that kin selection is the most important factor for stabilizing bat colonies [20]. In fact, if entire colonies function as social units, higher relatedness within matrilines and hence greater genetic differentiation between matrilines, as observed in greater horseshoe bats [2], may even disrupt social groups when cooperation would be directed towards kin only.

To determine the importance of mate sharing between relatives for kin selected cooperation and group stability we have to look at mate choice in animals where females live in groups consisting of several matrilines and that show cooperation. The current lack of evidence for cooperation among horseshoe bats does ask for a closer look at the social behaviour of this species. However, it should be kept in mind that even in taxa with high levels of relatedness among group members, such as in clonal aphids or haplo-diploid insects, cooperation is the exception rather than the rule [4].

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Photosynthesis: The Processing of Redox Signals in Chloroplasts

Recent work identifies two kinases required for phosphorylation of proteins of chloroplast thylakoid membranes. One kinase, STN7, is required for phosphorylation of light-harvesting complex II; another, STN8, is required for phosphorylation of photosystem II. How do these kinases interact, what do they do, and what are they for?

John F. Allen

Phosphorylation of chloroplast proteins was first reported in 1977, and shown to be light-dependent [1]. The implications of this landmark discovery are still being worked out. Now that mutants are available for a protein kinase whose activity was first demonstrated by John Bennett [1], one story can be retold with increased confidence. But there are clearly multiple chloroplast kinases, with multiple substrates and multiple effects. This was forecast [2], but only recently has a second protein kinase been identified, putting the phenomenon of chloroplast protein phosphorylation on course for more complete biochemical