III.5 The Reproductive Biology of Rare Rangeland Plants and Their Vulnerability to Insecticides

Vincent J. Tepedino

NOTE: Acephate is no longer approved by EPA for rangeland grasshopper control.

The Western United States is an area of high plant and animal diversity. Many of the plants on this vast expanse of mountain, plain, and desert occur nowhere else in the world (Cronquist et al. 1972, Barbour and Billings 1988). Currently about 150 of these plant species are so rare that they have been listed under the Endangered Species Act as either threatened or endangered. Four are shown in figure III.5–1 (a–d). Most of these rare plants have been found on public rangelands (fig. III.5–2).

Figure III.5–1—Rare rangeland plants. A = Blowout penstemon (Nebraska), B = Dwarf bear-poppy (Utah), C = Dudley Bluffs twinpod (Colorado), D = San Rafael cactus (Utah).

Preserving rare plant species means removing or reducing threats to existing individuals and ensuring that those individuals can reproduce. Plants reproduce both asexually and sexually. For example, the rare plants *Cycladenia humilis* var. *jonesii* in Utah and *Mirabilis macfarlaneii* in Idaho and Oregon both reproduce sexually by seeds and asexually by the production of rhizomes. However, in seed plants, sexual reproduction is the predominant method. All rare plants that my associates and I studied and described in this chapter reproduce sexually. Sexual reproduction is particularly important because it enables plants to generate and maintain in their offspring the genetic variability necessary to cope with unusual circumstances. In contrast, asexual reproduction produces only copies of the parent plant, not variations on the theme.

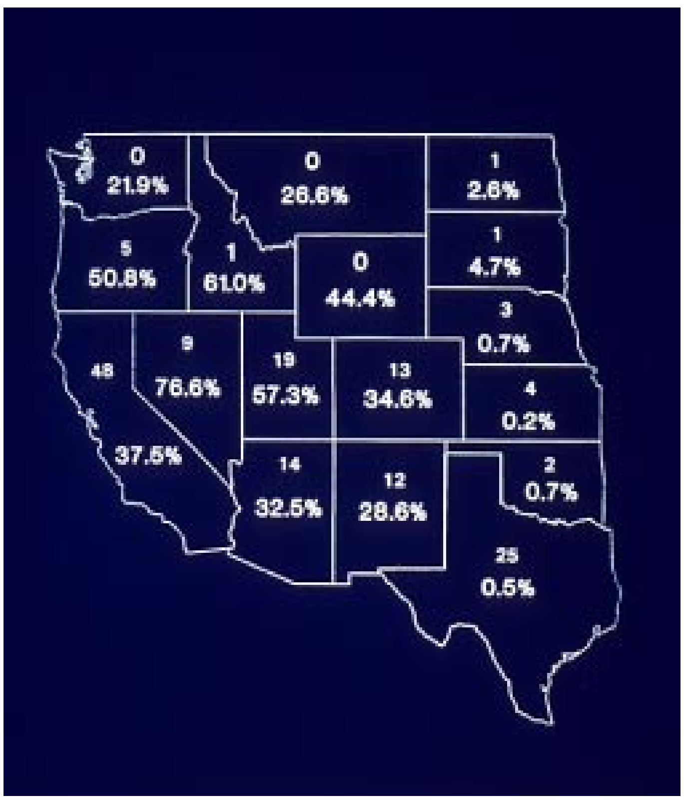

Figure III.5–2—Number of threatened and endangered plant species listed under the Endangered Species Act as of August 1993 (U.S. Fish and Wildlife Service 1993, upper figure) and percent total area administered by the Bureau of Land Management and Forest Service (lower figure), by State, in the West.

In seed plants, sexual reproduction depends on the movement of mature pollen from the anthers to a receptive stigma (pollination). To complete the process, pollen grains must germinate and send pollen tubes down the style to fertilize one or more ovules in the ovary (fertilization). Sexual reproduction may take place between individuals, or individuals may fertilize themselves if they are self-compatible, meaning their stigmas are receptive to their own pollen.

Because plants are immobile, they require “go-betweens” to move pollen from anthers to stigma. Such assistance comes mostly from insects–although wind, water, gravity, and other animals may occasionally be agents of pollination for some species. Although butterflies, moths, flies, ants, and beetles may pollinate flowers as they visit them to eat pollen and/or nectar, the truly essential pollinators for North American flowering plants are bees.

The bees to which we refer are not honeybees, which are of Eurasian origin, but native bees, which have evolved in North America. The North American bee fauna is quite diverse. In the State of Wyoming alone, there are more than 600 species (Lavigne and Tepedino 1976). In the Western United States, there are well over 2,500 species. Many of these bees are quite specialized in the plants that they visit and pollinate. For example, *Perdita meconis*, an uncommon bee that pollinates the endangered dwarf bearclaw poppy, *Arctomecon humillis*, visits only plants in the genera *Arctomecon* and *Argemone* for pollen.

Most bees that visit rare plants are solitary rather than social (the familiar honeybee). Like social bees, solitary bee females care for their offspring. Individual females carefully construct nests without the aid of workers, usually in the ground (fig. III.5–3) or in dead wood (fig. III.5–4). These nests will hold and protect the young bees and the food provided for them. The nesting material varies from species to species and may be quite specific. For example, for certain species, the ground must have a certain slope or soil moisture content or texture (Cane 1991).

Figure III.5–3—Entrance/exit holes at a nest-site of a ground-nesting bee.

Bees provision these nests with pollen and nectar molded into a loaf (fig. III.5–4) for the young to eat. Adults also eat nectar and pollen while foraging. In addition, bees may forage for water or other extraneous materials needed to construct the nest, such as leaf pieces (fig. III.5–5), resin, mud, etc., (Stephen et al. 1969). Adult females must launch many foraging expeditions from their nest-sites to obtain these resources. Frequently the best nesting substrate is not in the same area as food or other necessities, and bees must travel some distance to obtain nest materials.

Unfortunately, bees are generally vulnerable to most commonly used insecticides, including those that are approved for use to control grasshoppers on Federal rangelands: acephate, carbaryl, and malathion (Johansen et al. 1983). Bees that are forced to travel widely to gather their resources are most vulnerable because they must forage over larger areas and are therefore more likely to encounter a spray area. If bees are vulnerable, so may be the plants that depend on them for pollination services. Because of the potential vulnerability of both bees and plants, the U.S. Department of the Interior's U.S. Fish and Wildlife Service (FWS) and the U.S. Department of Agriculture's (USDA) Animal and Plant Health Inspection Service must hold joint consultations before aerially treating rangelands with insecticides. Usually, insecticide-free safety zones called buffers must be left around rare plant populations to reduce effects on both plant and pollinators.

Figure III.5–4—The nest of a twig-nesting bee, split open to expose feeding larvae, their food provisions, and the partitions between cells.

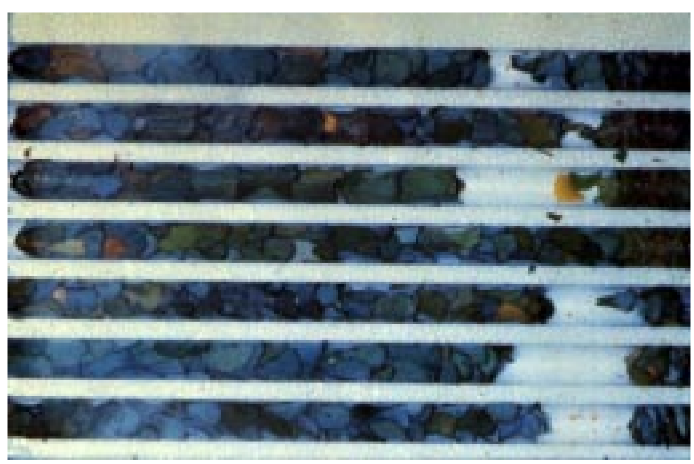

Figure III.5–5—Several leafcutter bee nests in an artificial domicile, exposed to show the numerous cells enfolded in leaves.

Questions about optimal buffer zone size and vulnerability of rare plant reproduction to insecticides are important. If flowers normally self-fertilize automatically, then grasshopper spraying programs are unlikely to be of consequence because pollinators will not be necessary for reproduction. Thus, scientists first must determine whether the flowers of the plant species in question are capable of self-fertilization, and, second, if self-fertilization is automatic. We also must determine whether fruit and seed set are improved by cross-pollination and identify the agents of pollination. When this is accomplished, we will have described the breeding system of the plant and will have some idea about the life history of its pollinators.

The size of the buffer zone that should be left around rare plant populations that rely exclusively on insect pollination depends on how far bees fly to obtain their resources. Presently, a buffer zone of 3 miles is being left around rare plant populations, but this is provisional in that it is based on best guesses rather than accurate estimates. By experimentation, we can help resolve questions about the value of buffer zones and whether they should be expanded or contracted in size.

Conducting a Study

To uncover general patterns in the reproductive biology of rare plants on western rangelands, I elected to study the breeding systems and pollinators of a large number of species rather than to conduct very detailed studies on a few species.

I gave study priority to rare plant species on actively grazed public rangelands (fig. III.5–6) in counties with high probabilities of having large numbers of grasshoppers, and thus of being sprayed. The approximate locations of the species studied are shown in figure III.5–7. With two exceptions *(Penstemon harringtonii* in Colorado and *Castilleja aquariensis* in Utah), all are listed as threatened or endangered under the Federal Endangered Species Act.

To describe the plant breeding system, we conducted a series of experiments using mesh bags or cages to prevent insects from visiting the flowers. Individual flowers, entire inflorescences (flower clusters), or entire

Figure III.5–6—Cattle grazing at a Brady pincushion cactus site (Arizona).

plants (where necessary) were bagged or caged just prior to the onset of flowering (fig. III.5–8). Each of the following treatments was applied to a different flower: for self-pollination, flowers were hand-pollinated with the pollen of another flower on the same plant; for cross-pollination, flowers were hand-pollinated with pollen from a flower on a distant plant; to test for automatic self-pollination, flowers were left untreated; and, as a control, some flowers were left unbagged (open-pollinated). My associates and I carried out a complete series of treatments, one of each, on each of 15 to 25 experimental plants. Treatments were randomized on each plant to remove any effects of order or position on fruit or seed set.

We observed and collected naturally occurring pollinators as they visited the flowers during several time periods each week. Insects were pinned and identified later using the insect collections at the USDA, Agricultural Research Service, Bee Biology and Sytematics Laboratory in Utah, and the collection at Utah State University.

Estimating the distances a bee typically flies on its foraging trips proved very difficult because of its size, the speed at which it moves, and the size of the area to be monitored. Because native bees are too small to track with radio collars or electronic chips, as many mammals and birds can be, other methods were necessary. We used both direct (A below) and indirect (B, C, D) methods:

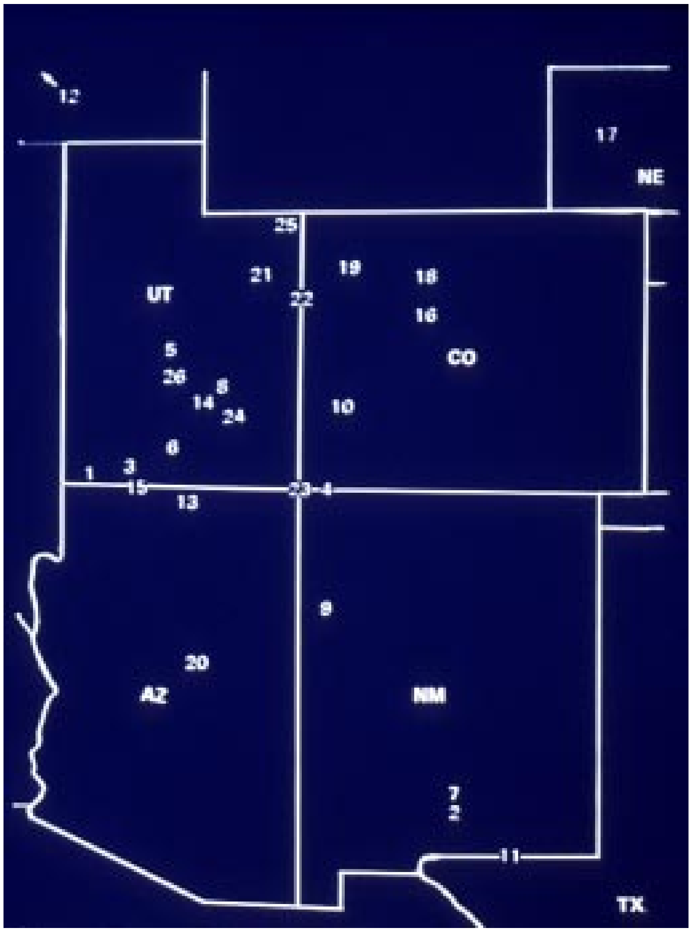

Figure III.5–7—Locations of specific threatened and endangered plants studied from 1988 to 1993. 1 = dwarf bear-poppy, 2 = Sacramento prickly-poppy, 3 = Welsh's milkweed, 4 = Mancos milkvetch, 5 = Heliotrope milk-vetch, 6 = Aquarius paintbrush, 7 = Sacramento Mountains thistle, 8 = Jones' cycladenia, 9 = Zuni fleabane, 10 = clay-loving wild-buckwheat, 11 = McKittrick pennyroyal, 12 = McFarlane's four-o'clock, 13 = Brady pincushion cactus, 14 = San Rafael cactus, 15 = Siler pincushion cactus, 16 = Harrington beard-tongue, 17 = blowout penstemon, 18 = Penland beard-tongue, 19 = Dudley Bluffs twinpod, 20 = Arizona cliffrose, 21 = shrubby reed-mustard, 22 = Uinta Basin hookless cactus, 23 = Mesa Verde cactus, 24 = Wright fishhook cactus, 25 = Ute ladies'-tresses, 26 = last chance townsendia.

(A) Foraging bees were captured, marked on the thorax with a dot of water-resistant paint that was nontoxic to plants and insects, released, and then searched for on subsequent days at other plant populations at set distances from the marking site (fig. III.5–9 and 10).

(B) Nontoxic fluorescent powders (pollen analogs or imitators) were placed in "donor" flowers, where they would be picked up and spread by foraging bees, and were searched for in the evening with a black light in other flowers at different distances from the donors.

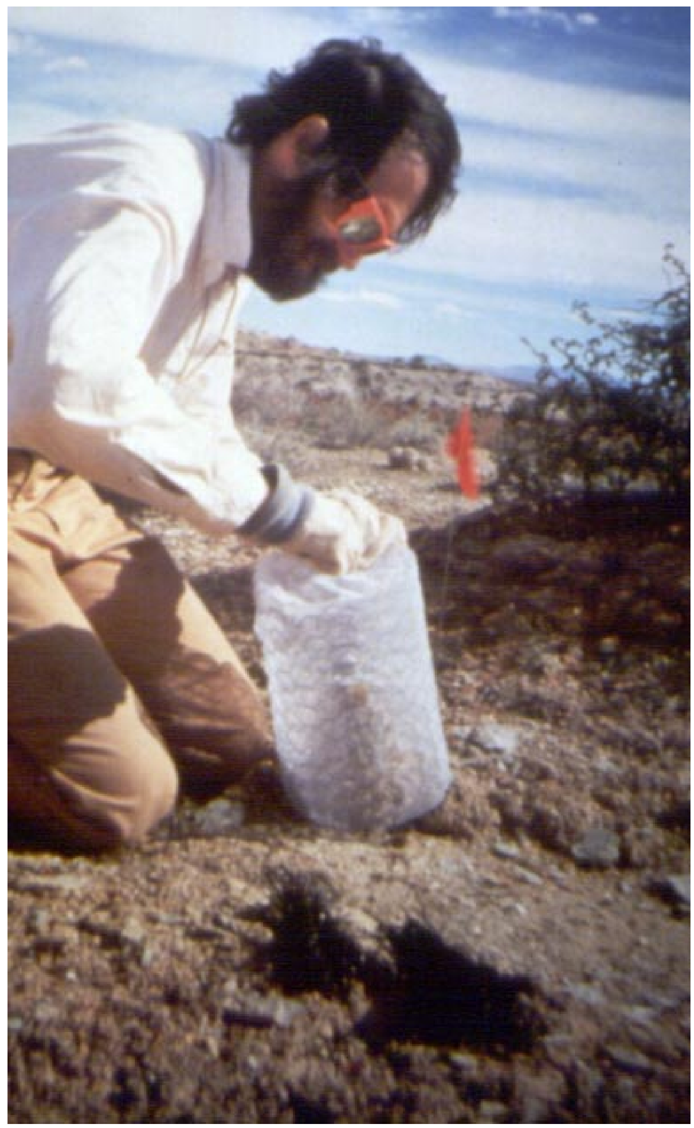

Figure III.5–8—Fitting a cage over a cactus plant to exclude insects.

Figure III.5–9—Coaxing a bee into a marking tube.

Figure III.5–10—The coaxed bee marked on the thorax.

Figure III.5–11—An artificial bee "condominium" offers bees cheap housing.

(C) Trap-nests (artificial nests that bees will use, figure III.5–11) were placed at different distances from donor flowers, and the provisions of the cells made therein were examined for fluorescent powder.

(D) A "mobile garden," a pickup truck with a bed full of blooming potted plants, was used to attract marked bees that had earlier foraged on flowers dusted with fluorescent powders (see above) (fig. III.5–12). The "mobile garden" was parked at different distances from areas where bees had been marked and flowers had been dusted. My associates and I then recorded marked bees visiting plants in the garden or any flowers with fluorescent powder deposited on them.

Figure III.5–12—The oldest floating "mobile garden" in Arizona.

Study Results

Three clear patterns were evident from the data. First, rare plants do not tend to be automatic self-fertilizers. Indeed, just the opposite is the case. With the exception of two species *(Astragalus montii* in central Utah and *Schoencrambe suffrutescens* in eastern Utah), all species are primarily outcrossing (table III.5–1). Many are also self-compatible, meaning pollen moved from one flower to another on the same plant will sometimes cause fertilization, but in most cases the fruits and seeds produced are inferior either in number or size to those produced as a result of cross-pollination. In any case, pollinators also are needed to cause this type of self-pollination, which is not automatic.

The second pattern is that the most abundant visitors to the flowers of these plants are almost always native bees (table III.5–1). In some cases, bee pollination is supplemented by other animals. For example, in New Mexico the Sacramento Mountains thistle *(Cirsium vinaceum)* also is pollinated by several species of hummingbirds, flies, and butterflies.

Table III.5–1—Summary of the reproductive characteristics of 26 species of rare plants

Common name	Species name	Status	State	BrSys	I	Pollinators	L
Dwarf bear-poppy	*Arctomecon humilis*	E	UT	CR SI	Y	Bees, many	N
Sacramento prickly-poppy	*Argemone pleiacantha pinnatisecta*	E	NM	CR PS	Y	*Dialictus*	?
Welsh's milkweed	*Asclepias welshii*	T	UT	?	Y	Bees, wasps	?
Mancos milk-vetch	*Astragalus humillimus*	E	CO NM	CR SC	Y	Bees, many	N
Heliotrope milk-vetch	*Astragalus montii**	T	UT	AS SC	?	*Osmia*	N
Aquarius paintbrush	*Castilleja aquariensis**		UT	CR SI	Y	*Bombus*	?
Sacramento Mountains thistle	*Cirsium vinaceum*	T	NM	CR PS	Y	Various	?
Jones cycladenia	*Cycladenia humilis* var. *jonesii**	T	UT	CR SI	Y	Bees, many	?
Zuni fleabane	*Erigeron rhizomatus*	T	NM	CR PS	Y	Various	N
Clay-loving wild-buckwheat	*Eriogonum pelinophilum*	E	CO	CR SC	Y	Various	?
McKittrick pennyroyal	*Hedeoma apiculatum*	T	NM TX	CR SC	Y	Halictidae	N
MacFarlane's four-o'clock	*Mirabilis macfarlanei**	E	ID OR	CR PS	Y	Bees, many	?
Brady pincushion cactus	*Pediocactus bradyi*	E	AZ	CR SI	Y	*Dialictus*	N
San Rafael cactus	*Pediocactus despainii*	E	UT	CR SI	Y	Bees, many	N
Siler pincushion cactus	*Pediocactus sileri*	E	AZ UT	CR SI	Y	Bees, many	N
Harrington beardtongue	*Penstemon harringtonii*		CO	CR PS	Y	Bbees, many	?
Blowout penstemon	*Penstemon haydenii*	E	NE	CR PS	Y	Bees, many	N
Penland beardtongue	*Penstemon penlandii*	E	CO	CR SC	Y	Bees, many	N
Dudley Bluffs twinpod	*Physaria obcordata*	T	CO	CR SI	Y	Bees, many	N
Arizona cliffrose	*Purshia subintegra*	E	AZ	CR PS	Y	Bees, many	Y
Shrubby reed-mustard	*Schoencrambe suffrutescens**	E	UT	AS SC	?	Halictidae	N
Uinta Basin hookless cactus	*Sclerocactus glaucus**	T	CO UT	CR SI	Y	Bees, many	Y
Mesa Verde cactus	*Sclerocactus mesae-verdae**	T	CO NM	CR PS	Y	Halictidae	N
Wright fishhook cactus	*Sclerocactus wrightiae*	E	UT	CR SI	Y	Halictidae	N
Ute ladies'-tresses	*Spiranthes diluvialis**	T	CO UT	CR SC	Y	*Bombus*	N
Last chance townsendia	*Townsendia aprica*	T	UT	CR PS	Y	*Osmia*	N

T = threatened, E = endangered. BrSys describes the plant's breeding system: CR = cross-pollinated, AS = automatic self-pollination, SI = self-incompatible, SC = self-compatible; PS = partially self-compatible. I = insect pollinated, Y = yes. Pollinators: genus or family of bee given when possible, many = several bee taxa, various = several animal taxa. L = evidence that fruit or seed set is being limited by inadequate pollination, N = no, Y = yes; * = uncommonly visited species.

The third pattern is that the flowers of about one-third of the plant species studied received few visits (table III.5–1). For several species, insect visitation was so low that we were forced to abandon the original pollinator observation and collection schedules. In these cases insects were simply captured whenever possible. Such low numbers of flower visitors are of concern, especially for rare plants that can produce seeds only when visited by pollinators.

These experiments also can be used to indicate species that may be producing fewer than the highest number of seeds, perhaps because of insufficient pollinator visits. Species whose seed production is low are of special concern because they may not be producing enough new individuals to replace those that are dying. Fortunately, only *Purshia subintegra* in central Arizona and *Sclerocactus glaucus* in eastern Utah gave any indication of underpollination. Because these two species set significantly fewer seeds in open-pollinated treatments than in cross-pollinated treatments, these plants should be studied further to determine if underpollination is common.

My results in estimating distances traveled by foraging bees were surprising. While it was easy to recapture bees in the general vicinity in which they were marked, or to detect fluorescent powders in flowers in the general area of the donor flowers, it was very difficult to find either marked bees or fluorescent particles at distances beyond a few dozen yards from the marking point. The record for distance moved was about a quarter mile (400 m) from a donor flower in a study of *Pediocactus sileri* in northern Arizona (Peach et al. 1993).

Implications for Chemical Sprays

To say that most plants reproduce sexually and that most depend on insects to pollinate them does not necessarily mean that rare plants do so. Indeed, prior to this study, there were reasons to suspect that rare plants were more likely than common plants to automatically self-pollinate and less likely to require insect visitors to achieve sexual reproduction (Tepedino 1979, Karron 1991). If this were true, then insecticide spraying for grasshoppers would have little effect on reproduction by rare plants, and land managers would not need to be concerned about the potential effects on the plants' pollinators.

The results obtained in this study show that rare plants on rangelands do not commonly self-pollinate. Almost all species studied set seed only when native bees visit their flowers. Because these bees are likely susceptible to liquid insecticide sprays, land managers should consider the implications of some reduction in pollinators as a result of spraying. Significant reduction of pollinators is likely to reduce the seed production of rare plants.

In addition, land managers should consider that many of the insect pollinators may be vulnerable to insecticides at any time of the year. Unless there is a perfectly synchronized, one-generation-per-year specialist pollinator for a plant, and my associates and I found none of those, the conservative approach—until more is known—is to avoid spraying within the buffer zone around each rare plant population at any time. However, if the plan is to use carbaryl bran bait (2 percent active ingredient), a nonliquid treatment, no buffer zones are needed (see III.4).

Overall, the pollinator situation on Federal rangelands may not be as perilous as some scientists had feared. Despite past spraying history, there is little indication that rare plants on rangelands are currently producing fewer seeds than they are capable of producing. While this is a conclusion that cries out for additional corroboration, it is also encouraging to find that seed production of open-pollinated flowers of rare plants do not seem to be pollinator limited. In most cases, visitation rates of bees to flowers, and by implication, bee numbers, appear to be sufficient to support maximum seed production. It is probable that bee numbers and seed production of native forbs have not been impacted because large-scale insecticide spray programs to control or suppress populations of grasshoppers on rangeland are not usually applied in the same areas in successive years. This policy must continue if rangeland pollinators are to have ample time to recover from spray episodes. Other researchers working in Canadian forests have shown that bee numbers will usually return to prespray levels in 1 to 3 years, depending upon the species of bee and the insecticide used (Plowright and Thaler 1979, Kevan and LaBerge 1979, Wood 1979, Miliczky and Osgood 1979). Recovery times and patterns for rangeland pollinators also should be studied.

Scientists regard the absence of evidence for long-distance movement of pollen grain analogues (fluorescent powders) less as evidence that native bees do not move long distances than as an indication of a logistical problem in testing. It is simply impossible for one or two people effectively to cover the area that must be censused. A complicating factor is that every study to look at pollen dispersal has reported drastic reductions in pollen deposition with distance (Handel 1983). By the time one samples flowers more than 33 ft (10 m) from the source, the number of pollen grains deposited is minimal. Again, this does not mean that pollen flows only over very short distances but that investigators are faced with detecting a very small needle in a very large haystack.

Other studies of bee movement and gene flow are of little help because they are invariably conducted over relatively short distances (Handel 1983). Pollen can, however, move long distances. Kernick (cited in Levin 1984) noted that several species of crop plants must be isolated by as much as 1.24 miles (2 km) to maintain varietal purity. Several other studies have examined the homing ability of solitary species of bees. They have shown that bees are capable of returning to their nests from distances of up to 5 miles (Fabre 1925, Rau 1929 and 1931; reviews by Packer 1970 unpubl. and Roubik 1989). While such experiments in no way tell us the distance that a bee normally flies on a typical foraging trip, they help to put an upper bound on bees' movements.

Conclusions

Although much valuable information has been obtained on both plants and their pollinators, much remains to be done. There are four areas in which additional research should be encouraged. First, the pollination biology of other plant species listed under the Endangered Species Act must be studied. The Grasshopper Integrated Pest Management Project has supported studies of 26 species in 13 families (see table III.5–1) or roughly 17 percent of the plant taxa in the Intermountain West which are listed under the Endangered Species Act. Thus, we feel confident in concluding that, in general, the flowers of rare plants must be pollinated by native bees to produce seeds. However, unless administrators and land managers are willing to assume that all rare plants must be managed as if they required bee pollinators, the reproductive biology of the remaining species must be studied.

Second, to make informed recommendations about the size of buffer zones to be left around rare plant populations, better information is needed on the distances pollinators and/or pollen travel. Laboratory methods that demonstrate genetic differences between the enzymes produced by different plants can be used, together with theoretical population genetic models, to provide information on gene flow between plant populations separated by a range of distances and on the genetic isolation of selected plant populations (Slatkin 1985 and 1993, Slatkin and Barton 1989). Long-distance pollinator movement can be documented by showing that certain forms of particular enzymes, which are primarily or exclusively restricted to one population, have moved to other populations. Indeed, these techniques can be used to give a rough approximation of the average number of individual plants per generation that are the result of pollen migration between populations.

Third, information is needed on the toxic effects to native bees of the liquid insecticides commonly used to treat rangeland grasshoppers. Current knowledge has been obtained from studies of the honey bee and the alfalfa leafcutter bee (both introduced species) and the alkali bee because they are cultured for crop pollination and are easily obtainable. Little is known about how susceptible the 2,500-plus species of rangeland bees are to insecticides because their populations are too small, or too difficult to obtain, to yield adequate sample sizes for experimentation of this kind. Prior to studying the toxicology to native species, it will be necessary to build up their populations to a sufficient size for experimentation by raising them in large field cages or greenhouses.

Fourth, decisionmakers must be advised when it is safe to spray. As noted earlier in this chapter, such decisions cannot be made by simply using flowering phenology records for the rare plant species because its pollinators may be active at other times of the year. Information must be available on the flight times of adult pollinators and on their activity patterns for the potential season of spraying. Thus far, activity patterns for pollinators of only one rare plant species have been studied (Peach et al. 1993).

References Cited

Barbour, M. G.; Billings, W. D., eds. 1988. North American terrestrial vegetation. New York: Cambridge University Press. 434 p.

Cane, J. H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. Journal of the Kansas Entomological Society 64: 406-413.

Cronquist, A.; Holmgren, A. H.; Holmgren, N. H.; Reveal, J. L. 1972. Intermountain flora, vol. 1. New York: Hafner Publishing Co. 270 p.

Fabre, J. H. 1925. The mason bees. Garden City, NY: Garden City Publishing Co. 315 p.

Handel, S. N. 1983. Pollination ecology, plant population structure, and gene flow. In: Real, L., ed. Pollination biology. New York: Academic Press: 163–211.

Johansen, C. A.; Mayer, D. F.; Eves, J. D.; Kious, C. W. 1983. Pesticides and bees. Environmental Entomology 12: 1513–1518.

Karron, J. D. 1991. Patterns of genetic variation and breeding systems in rare plant species. In: Falk, D. A.; Holsinger, K. E., eds. Genetics and conservation of rare plants. New York: Oxford University Press: 87–98.

Kevan, P. G.; LaBerge, W. E. 1979. Demise and recovery of native pollinator populations through pesticide use and some economic implications. In: Caron, D. M., ed. Proceedings of the fourth international symposium on pollination. Misc. Publ. 1. College Park, MD: Maryland Agricultural Experiment Station: 489–508.

Lavigne, R.; Tepedino, V. J. 1976. Checklist of the insects in Wyoming. I. Hymenoptera. Agric. Exp. Stn. Resour. Jour. 106. Laramie, WY: University of Wyoming. 61 p.

Levin, D. A. 1984. Immigration in plants: an exercise in the subjunctive. In: Dirzo, R.; Sarukahn, J., eds. Perspectives on plant population ecology. Sunderland, MA: Sinauer Associates: 242–260.

Miliczky, E. R.; Osgood, E. A. 1979. The effects of spraying with Sevin-4-oil® on insect pollinators and pollination in a spruce–fir forest. Tech. Bull. 90. Orono, ME: University of Maine and Maine Agricultural Experiment Station: 1–21.

Peach, M. L.; Tepedino, V. J.; Alston, D. G.; Griswold, T. L. 1993. Insecticide treatments for rangeland grasshoppers: potential effects on the reproduction of *Pediocactus sileri*(Englem.) Benson (Cactaceae). In: R. Sivinski; Lightfoot, K., eds. Proceedings of the southwestern rare and endangered plant conference. Misc. Pub. 2. Santa Fe, NM: New Mexico Forestry and Resources Conservation Division: 309–319.

Plowright, R. C.; Thaler, G. R. 1979. The effect of biocides on forest pollination in New Brunswick. In: Caron, D. M., ed. Proceedings of the fourth international symposium on pollination. Misc. Publ. 1. College Park, MD: Maryland Agricultural Experiment Station: 483–487.

Rau, P. 1929. Experimental studies in the homing of carpenter and mining bees. Journal of Comparative Psychology 9: 35–70.

Rau, P. 1931. Additional experiments on the homing of carpenter-and mining-bees. Journal of Comparative Psychology 12: 257–261.

Roubik, D. W. 1989. Ecology and natural history of tropical bees. New York: Cambridge University Press. 514 p.

Slatkin, M. 1985. Rare alleles as indicators of gene flow. Evolution 39: 53–65.

Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. Evolution 47: 264–279.

Slatkin, M; Barton, N. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43: 1349–1368.

Stephen, W. P.; Bohart, G. E.; Torchio, P. F. 1969. The biology and external morphology of bees. Corvallis, OR: Oregon State University and Oregon Agricultural Experiment Station. 140 p.

Tepedino, V. J. 1979. The importance of bees and other insect pollinators in maintaining floral species composition. Great Basin Naturalist Memoirs 3: 139–150.

U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants. U.S. Fish and Wildlife Service. 50 CFR 17.11 and 17.12. Washington, DC: U.S. Government Printing Office: 1993-342-447/94033. 40 p.

Wood, G. W. 1979. Recuperation of native bee populations in blueberry fields exposed to drift of fenitrothion from forest spray operations in New Brunswick. Journal of Economic Entomology 72: 36–39.

Reference Cited—Unpublished

Packer, J. S. 1970. The flight and foraging behavior of the alkali bee *Nomia melanderi* (Ckll.) and the alfalfa leafcutter bee *Megachile rotundata* (F.). Ph.D. dissertation. Logan, UT: Utah State University. 119 p.