# The Great Basin Naturalist

PUBLISHED AT PROVO, UTAH, BY
BRIGHAM YOUNG UNIVERSITY

ISSN 0017-3614

VOLUME 56 30 APRIL 1996 NO. 2

Great Basin Naturalist 56(2), © 1996, pp. 95–118

# SELECTING WILDERNESS AREAS TO CONSERVE UTAH'S BIOLOGICAL DIVERSITY

Diane W. Davidson[1], William D. Newmark[2], Jack W. Sites, Jr.[3], Dennis K. Shiozawa[3],
Eric A. Rickart[2], Kimball T. Harper[4], and Robert B. Keiter[5]

ABSTRACT.—Congress is currently evaluating the wilderness status of Bureau of Land Management (BLM) public lands in Utah. Wilderness areas play many important roles, and one critical role is the conservation of biological diversity. We propose that objectives for conserving biodiversity on BLM lands in Utah be to (1) ensure the long-term population viability of native animal and plant species, (2) maintain the critical ecological and evolutionary processes upon which these species depend, and (3) preserve the full range of communities, successional stages, and environmental gradients. To achieve these objectives, wilderness areas should be selected so as to protect large, contiguous areas, augment existing protected areas, buffer wilderness areas with multiple-use public lands, interconnect existing protected areas with dispersal and movement corridors, conserve entire watersheds and elevational gradients, protect native communities from invasions of exotic species, protect sites of maximum species diversity, protect sites with rare and endemic species, and protect habitats of threatened and endangered species. We use a few comparatively well-studied taxa as examples to highlight the importance of particular BLM lands.

*Key words: wilderness, biodiversity, conservation, Utah, Bureau of Land Management, endemic species, exotic species, cryptobiotic soils, plants, bees, vertebrates.*

## THE WILDERNESS ACT AND BIODIVERSITY

In the Wilderness Act of 1964, Congress endorsed the preservation of federal land in its natural state (16 U.S. Code, Sections 1131–36). Congress plainly anticipated that ecological considerations were an important dimension of the wilderness concept, since the act provides that wilderness may contain "ecological" features of "scientific, educational, scenic, or historical value" (16 U.S. Code, § 1131 [c][4]). Ecological concerns have also figured prominently in several congressional wilderness bills for Bureau of Land Management (BLM) public lands. Both the Alaska National Interest Lands Conservation Act, 16 U.S. Code, § 3101 (b), and the California Desert Protection Act, 103 Public Law 433 Section 2 (b) (1) (B) (1994), expressly acknowledge that wilderness designation is intended to protect important ecological

---

[1] Department of Biology, University of Utah, Salt Lake City, UT 84112.
[2] Utah Museum of Natural History, University of Utah, Salt Lake City, UT 84112.
[3] Department of Zoology, Brigham Young University, Provo, UT 84602.
[4] Department of Botany, Brigham Young University, Provo, UT 84602.
[5] College of Law, University of Utah, Salt Lake City, UT 84112.

values. Among the significant ecological functions of wilderness areas is their role in conserving biological diversity (biodiversity).

In Utah, undeveloped public lands administered by the BLM (Fig. 1) can potentially play a key role in conserving the state's natural heritage. The BLM is now pursuing an ecosystem management policy designed to ensure sustainable ecological processes and biological diversity on lands under its jurisdiction (Department of the Interior 1994). By using these same criteria to designate wilderness areas, Congress could not only advance the BLM's ecosystem management goals but also reduce conflict over the agency's multiple-use lands (e.g., by diminishing the risk of future endangered species listings and the accompanying regulatory limitations). Over the long term, it is both cheaper and easier to protect species in aggregate in their intact, functioning ecosystems than to conserve them individually in fragmented and decimated populations under the Endangered Species Act.

In short, the use of biological and ecological criteria to designate BLM wilderness areas in Utah is consistent with the legal concept of wilderness and would help to avoid future conflicts over resource management.

## BIODIVERSITY DEFINED

Biological diversity—the variety of life in a given area—includes three hierarchical components: genetic diversity, species diversity, and ecosystem diversity (e.g., National Research Council 1978, Wilson 1988, Reid and Miller 1989, Raven 1992). Genetic diversity refers to the variety of genes within species. Depletion of genetic diversity during population bottlenecks, or because of inbreeding within fragmented and isolated populations, can threaten a species' survival by reducing the capacity of organisms to adapt to changing environments (Soulé and Wilcox 1980, Frankel and Soulé 1981). Species diversity, or the number of species within a region (species richness), can be divided into three major components (Whittaker 1972): alpha diversity ($\alpha$), the number of species in a homogeneous habitat; beta diversity ($\beta$), the rate of species-turnover across habitats; and gamma diversity ($\gamma$), the total number of species observed in all habitats within a region. Finally, ecosystem diversity consists of the variety of major ecological communities within areas that are heterogeneous in their physical attributes, for example, in elevation or soil type.

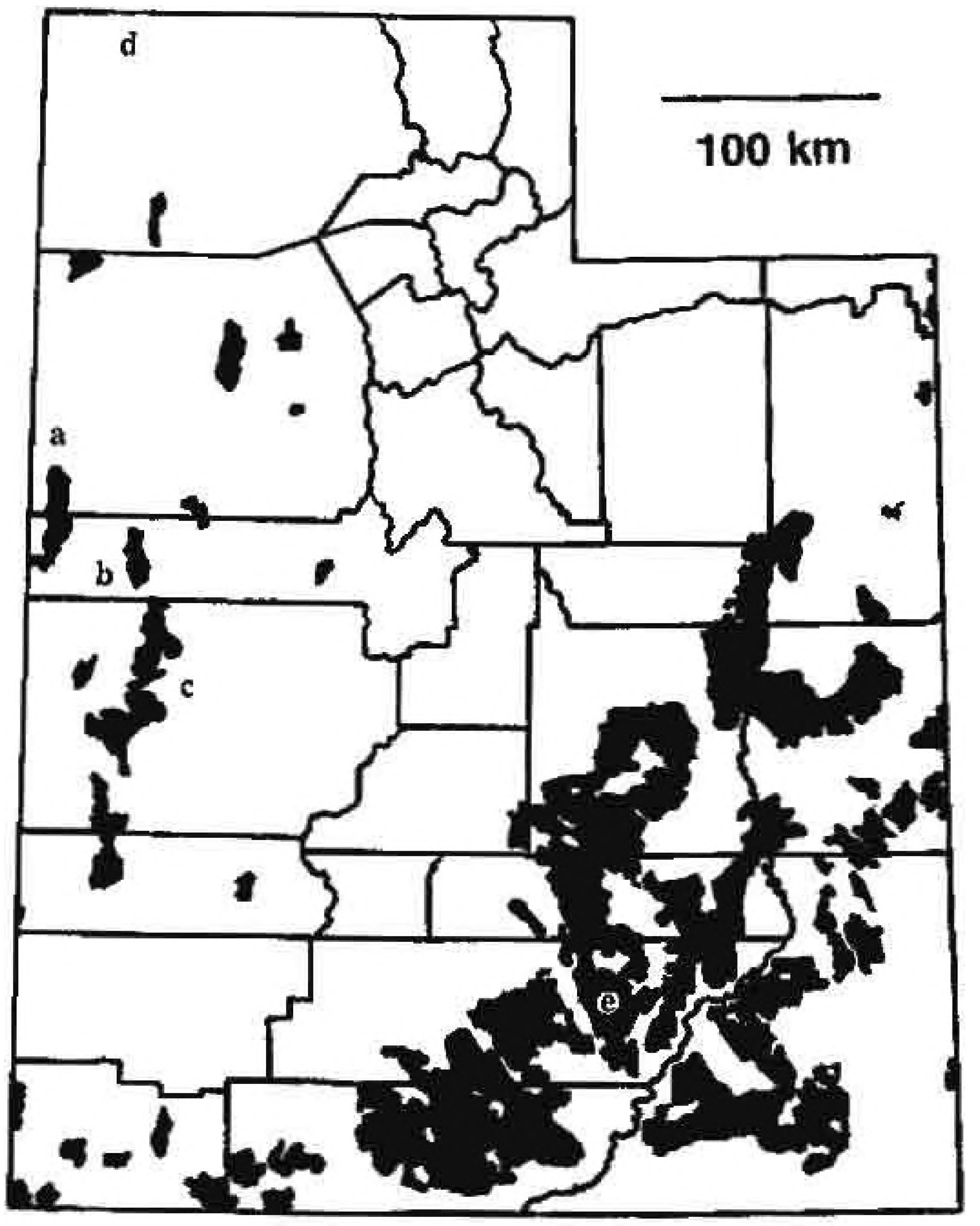

Fig. 1. Map of the state of Utah showing (in black) locations of all existing roadless areas proposed for BLM wilderness status. The BLM formally studied a subset of these areas and recommended a portion of studied lands for wilderness status. Data are from a Department of Interior map of BLM Wilderness Study Areas, BLM Proposed Wilderness, and the Utah Wilderness Coalition's BLM Wilderness Proposal. County boundaries also are shown. Isolated mountain ranges in Utah's western deserts are identified as follows: a = Deep Creek; b = Fish Springs; c = House range, and d = Newfoundland range (not formally proposed or studied for wilderness designation). On the Colorado Plateau, e = the Henry Mountains.

Genetic, species, and ecosystem diversity all result from both interactions between organisms and their environments, and interactions of organisms with one another. The physical environment sets limits on which species can inhabit an area, and interactions among those species determine which are most abundant. Strategies for preserving biodiversity must therefore take note of all living things in the landscape, and the linkages among them. Finally, since different species specialize on different stages of natural disturbance cycles, it is important to preserve a range of communities and ecosystems representing all stages in the disturbance cycle.

## OBJECTIVES

The success of conserving biological diversity within a system of protected areas can only be assessed in relationship to a series of selected objectives. We propose that the conservation of Utah's biological diversity depends on (1) ensuring the long-term viability of native plant and animal populations, (2) maintaining the critical ecological and evolutionary processes upon which these species depend, and (3) protecting the full range of communities, successional stages, and environmental gradients (e.g., IUCN 1978, MacKinnon et al. 1986, Noss 1992).

Both the size of the network of protected areas and the selection of individual wilderness areas should be guided by these 3 goals. Although it is possible to preserve a small subset of species and genotypes in zoological and botanical gardens, communities and species interactions must be conserved in situ. Large areas with minimal human intrusion, and with natural processes reasonably intact, are critical elements of an in situ conservation strategy; they provide protection for fragile habitats, such as easily eroded soils, and preserve habitat for reclusive species. Moreover, wilderness areas offer natural ecosystems some protection from the biological invasions that have devastated many communities, especially plant communities, across Utah.

Here we describe a strategy, based upon widely accepted principles of conservation biology (see e.g., Primack 1993, Meffe and Carroll 1994), for both selecting critical sites for wilderness designation and determining the amount of habitat that should be preserved as wilderness (see also Babbitt 1995).

## CRITERIA FOR SELECTION

### Viable Populations

Utah contains approximately 3000 indigenous plant species and varieties and about 584 vertebrate species. Viable populations for most of these plants and animals can be ensured by focusing, within ecological communities, on species for which the risk of extinction is greatest. Risk-prone species typically include those with small populations, large home range requirements, low reproductive potential, restricted geographic ranges, or large temporal variation in population size (Brown 1971, Willis 1974, Terborgh and Winter 1980, Diamond 1984, Pimm et al. 1988, Belovsky et al. 1994, Newmark 1995). Many top predators have several of these traits. On BLM lands in Utah, examples of such organisms are river otter (*Lutra canadensis*) and both Bald and Golden Eagles (*Haliaeetus leucocephalus* and *Aquila chrysaetos*). Risk-prone plants include Holmgren locoweed (*Astragalus holmgreniorum*) and Jones cycladenia (*Cycladenia humilis* var. *jonesii*), which have highly specific substrate requirements.

Viability of populations depends on both the level of risk one is willing to accept, and the time frame over which one wishes to conserve the population (Shaffer 1981, Schonewald-Cox 1983, Soulé 1987). In general, both survival time and the likelihood of population persistence increase with population size. A level of risk and persistence that is commonly proposed as a management goal is a 99% chance of survival for 1000 years (e.g., Belovsky 1987, Armbruster and Lande 1993).

For large carnivores, the minimum viable population necessary to ensure a 99% chance of survival for 1000 years is estimated to be approximately 10,000–100,000 individuals (Belovsky 1987). In habitat area, this is equivalent to 100,000–1,000,000 $\text{km}^2$, or 2.5–25 million acres. Although this area requirement may seem remarkably large, documented losses of mammalian species from among the largest of North American national parks (e.g., the 10,328-$\text{km}^2$ Yellowstone–Grand Teton park assemblage) during the last 90 years make clear the importance of protecting large areas (Newmark 1987, 1995).

### Maintenance of Ecological and Evolutionary Processes

In selecting wilderness areas, one must take care to ensure the maintenance of the ecological and evolutionary processes upon which all plant and animal species depend (Pickett and Thompson 1978, Kushlan 1979). Among the most important of these processes are natural disturbance and recovery cycles. Ideally, criteria for the selection of wilderness areas should include information on frequency, size, and longevity of natural disturbances. Protected areas should be large enough to contain minimum critical areas of the entire range of recovery stages for each community type (Pickett and Thompson 1978). In western North America, natural disturbance regimes can encompass tens of thousands to millions of acres, as witnessed by the recent and extensive wildfires in Yellowstone National Park (Christensen et al. 1989).

Two other critical ecological processes are migration and dispersal of terrestrial organisms across landscapes, and of aquatic species within watersheds. The selection of wilderness areas requires that attention be given to ensuring that migratory pathways are open to organisms migrating seasonally along elevational gradients. Of particular importance is the need to maintain winter ranges and migratory routes of large mammals such as mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and moose (*Alces alces*).

Interactions among competitors, and between predators and prey, are integral aspects of natural ecosystems and should be preserved. For example, in the southwestern deserts of the United States, the direct and indirect effects of seed predation on plant community structure have been documented in long-term experiments manipulating densities of rodent and ant granivores (Davidson et al. 1984, Samson et al. 1992). These effects include transformation of a shrubland into a grassland biome (Brown and Heske 1990). Special care must be taken to conserve populations of predators with large area requirements, because extinctions of these species can alter whole communities (e.g., by leading to outbreak densities of prey, which then overexploit their plant resources). Some of the strongest evidence for such "trophic cascades" comes from the Greater Yellowstone Ecosystem, where intensive browsing by elk has greatly altered many riparian zones by the removal of willows (genus *Salix*), and has eliminated aspen seedlings (*Populus tremuloides*) recruiting from seeds and rhizomes shortly after the extensive 1988 fires. Huge contemporary elk herds, numbering ~40,000 individuals in the park, and 20,000 in the northern herd alone, are likely the result of reductions in the full complement of large predators (Kay 1990, Wagner et al. 1995). Considerable evidence also suggests that deer and elk herds in Utah average significantly larger at present than during any extended period in the historical past (Durrant 1950, Julander 1962, Harper 1986).

## STRATEGIES FOR SELECTING WILDERNESS AREAS

### Landscape-wide Priorities

Given the large area requirements of many extinction-prone Utah species, it is important to protect large, contiguous land blocks. In designating wilderness areas, high priority should be given to lands whose selection would enlarge and connect existing protected areas (e.g., national parks, wildlife refuges, and Forest Service wilderness areas) and thus enhance the viability of animal and plant populations (Newmark 1985, Salwasser et al. 1987, Noss 1992, Grumbine 1994). By themselves, BLM wilderness areas in Utah clearly cannot satisfy the huge area requirements noted above as requisite for maintaining viable populations of large carnivores. However, when linked to other public lands (e.g., Utah's national parks, and wilderness areas in other states), BLM wilderness in Utah can be a key component of strategies for long-term preservation of biological diversity.

Other high-priority areas are those which, alone or together with other protected areas, encompass entire watersheds. In addition to affording direct benefits to humans, watershed protection is the most effective means of conserving the aquatic and riparian communities that account for a disproportionate fraction of both species diversity and endangered and threatened species in arid western North America (Miller 1961, Minckley and Deacon 1968, 1990, Holden et al. 1974, Johnson et al. 1977, Cross 1985, Knopf 1985, Moyle and Williams 1990). Moreover, since populations of riparian species are usually isolated from similar communities in other drainage systems, species losses from these environments are not easily remedied by natural recolonization.

A 3rd priority in selecting wilderness sites is land that forms or helps to complete the protection of entire elevational gradients, for example, in isolated mountain ranges of the Great Basin. Scant attention paid to conserving these gradients in the past is evident in the restriction of most national parks and wilderness areas in western North America to higher elevation sites. Designation of wilderness in comparatively low elevation BLM lands would afford protection to regions of greatest species richness for many organisms (e.g., mammals, birds, amphibians, insects, and trees) whose diversity generally declines with elevation throughout much of western North America (Harris 1984, Stevens 1992).

### Optimal Design Goals

If BLM wilderness areas are to contribute substantially to the preservation of biodiversity in Utah, then site selection must take into account the 3 general goals outlined above. Ideally, BLM wilderness lands should form an interconnected core zone of roadless lands when combined with other federal wilderness areas, national and state parks, and wildlife refuges (Fig. 2). Special attention should be given to linking roadless lands so as to preclude further fragmentation of natural habitat. Fragmentation, or the transformation of an unbroken block of natural habitat into a number of smaller patches separated by altered habitats, reduces population sizes, increases their isolation, and threatens their long-term viability. It is one of the greatest threats to biological diversity worldwide (Wilcox and Murphy 1985, Wilcove et al. 1986, Saunders et al. 1991). Across diverse habitats, there are numerous examples of species extinctions precipitated by both natural and human-induced habitat fragmentation (e.g., Brown 1971, Terborgh and Winter 1980, Diamond 1984, Heaney 1984, Patterson 1984, Newmark 1987, 1991, 1995, Case and Cody 1988, Soulé et al. 1988, Bolger et al. 1991).

Adjacent multiple-use lands can buffer human impacts on biological diversity within wilderness areas. Such lands can be expected to provide marginal habitat for the many species that are restricted primarily to more pristine wilderness regions. Thus, proposed wilderness areas surrounded by public lands should receive high priority for protection.

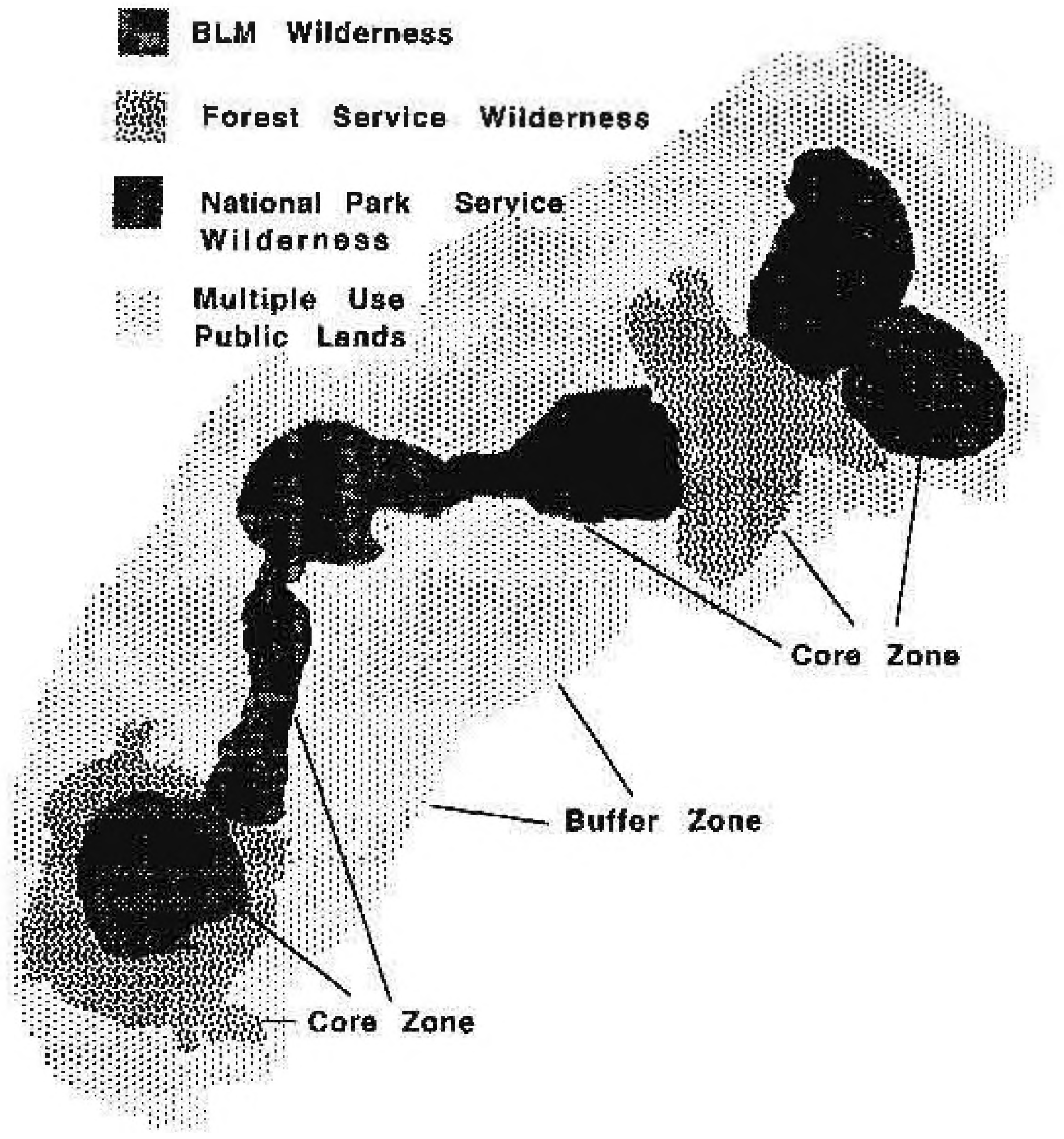

Fig. 2. An example of a preferred arrangement of wilderness and multiple-use federal and state lands to conserve biological diversity. Wilderness areas administered by the Bureau of Land Management, Forest Service, National Park Service, and Fish and Wildlife Service should form a contiguous core zone in which the most extinction-prone species in Utah can be protected. Multiple-use lands can effectively buffer this core zone and provide additional marginal habitat to species that are primarily restricted to roadless areas.

## Examples of Rare and Endemic Species

The design advocated above is based largely on conservation strategies for preserving wide-ranging vertebrate species. Although such strategies can help to ensure the long-term viability of most species within a given region, exclusive reliance on such approaches may well overlook and endanger many locally isolated, rare, and endemic plants and animals. We cannot give a comprehensive treatment of this subject here, but we discuss 3 taxonomic groups of organisms for which especially high rates of endemism or existing threats to isolated populations present particular management dilemmas that should be taken into account in wilderness decisions. In most cases, specific habitats must be protected to assure the preservation of these species.

### Plants of Special Concern

Unlike the wide-ranging animals discussed above, plants occupy fixed positions; they and their genes move about only through the processes of seed dispersal and pollen transport. Therefore, it is not surprising that many plants have narrowly restricted ranges, are locally adapted to conditions within those ranges, and are isolated, often by great distances, from other sites where similar conditions prevail. Although locally endemic plants can often be relatively abundant inside their ranges, their populations are easily jeopardized by habitat alteration (e.g., by all-terrain vehicles) within their narrow distributions. Of Utah's approximately 2600 plant species and 400 named varieties (Albee et al. 1988, Welsh et al. 1993), about 180 (or 7% of species) are currently classified by federal or state agencies as endangered, threatened, or sensitive. A majority of these (133, or ~74%) definitely or probably occur on BLM lands (Atwood et al. 1991), and a substantial subset of the classified species are narrow endemics.

Shultz (1993) provides a useful summary of endemism in the Utah flora. Approximately 240 species, or 10% of all Utah plant species, are endemic to the state. This rate of endemism, the percentage of the flora considered for listing as threatened or endangered, and the percentage of rare species in the flora are among the highest in the continental United States. The vast majority (86%) of Utah endemics reside in arid and semiarid regions of the state, and 90% are edaphically restricted to fine-textured and/or high pH substrates (limestone, clay, silt, mudstone, and shale) that magnify drought stress. Plant distributions generally appear to respond more to edaphic, topographic, and geologic features of the environment when drought is a factor (Stebbins 1952). Because most endemics live in close proximity to morphologically similar species (Albee et al. 1988), these species appear to be mainly neoendemics that have evolved since the last glacial maximum (18,000 yrs BP), or in the Bonneville basin during the past 10,000 yrs.

Geographically, endemism of Utah plants is highest in the Canyonlands Phytogeographic Section of the Colorado Plateau Division of the Intermountain Region (Cronquist et al. 1972, Fig. 3 modified from Shultz et al. 1987). An unusual diversity of substrates occurs here, and these substrates are more apt to be exposed, rather than covered with alluvium as in other areas of semiarid Utah (Welsh et al. 1993). Thus, fully 50% of Utah's 240 rare and endemic plant species occur on the Colorado Plateau, whereas just 15% occur in the Great Basin, 11% in the Mojave Desert, and 10% in the Uinta Desert (Welsh 1978, Shultz 1993). About half of Utah's endemics belong to just 5 genera that are both common and physiologically adapted to aridity (total Utah species and percent endemics, in parentheses): *Astragalus*, Fabaceae (114, 36.8%), *Penstemon*, Scrophulariaceae (106, 26.4%), *Cryptantha*, Boraginaceae (61, 36.1%), *Eriogonum*, Polygonaceae (60, 23.3%), and *Erigeron*, Asteraceae (54, 24.1%; Welsh et al. 1975, Welsh 1978, Shultz 1993).

Because most of the state's endemic plants are restricted to particular geologic formations, and because multiple endemics often occur on the same formation, groups of endemics generally can be protected simultaneously by safeguarding those soil formations and surrounding areas. Two regions where large numbers of endemics stand to benefit from wilderness protection of BLM lands are the Uinta Basin and the San Rafael Swell and surrounding San Rafael Desert (Fig. 3, Table 1; M. Windham personal communication). No fewer than 15 plant species are endemic to the region in and around the proposed wilderness area (PWA) near the White River south of Vernal (UWC 1990), and most of these are confined to the Parachute and Evacuation Creek members of the Green River Shale formation. Another dozen endemics occur in a diversity of habitats in and around the San Rafael Swell. Here the most important habitat is a beige (rather than red) Moenkopi formation, spatially isolated from other Moenkopi outcrops and unusual in its soil chemistry. A few endemics also occur on the younger Carmel and Summerville formations surrounding the core of the swell, especially between Muddy Creek and Crack Canyon (S. Welsh personal communication). Wilderness designation in these 2 regions (the San Rafael PWA and the White River PWA of the Uinta Basin [Fig. 3]; see UWC 1990) could afford significant protection to some of Utah's endemic plants. South and east of the San Rafael, in the Dirty Devil PWA (UWC 1990), are the distinctive flora of the Orange Cliffs region (Fig. 3) and some additional narrow endemics deserving protection in the Main and South forks of Happy Canyon (Shultz et al. 1987).

The Moenkopi formation is also important as a substrate for endemics elsewhere in semiarid Utah. Two federally listed endangered species, *Arctomecon humilis* (the dwarf bearclaw poppy) and *Pediocactus sileri* (a cactus), and several other species are endemic to particular Moenkopi outcrops in southwestern Utah. Wherever possible, the boundaries of wilderness areas and other protected areas should encompass these specialized habitats.

## Bees and Wasps in the San Rafael Desert

Because of their capacity for directed movements, animals are less likely than plants to exhibit high rates of endemism. Nevertheless, since insects often tend to be host- or habitat-specific (e.g., in pollinators, herbivores, or substrate-specific ground nesters), endemism can often be high in insect taxa. Bees and wasps (order Hymenoptera) are examples of such insects. Here, as elsewhere, bees and predatory wasps are especially diverse in arid regions (Michener 1979). The state supports a minimum of 950 species of native bees (roughly 25% of the total number of species known

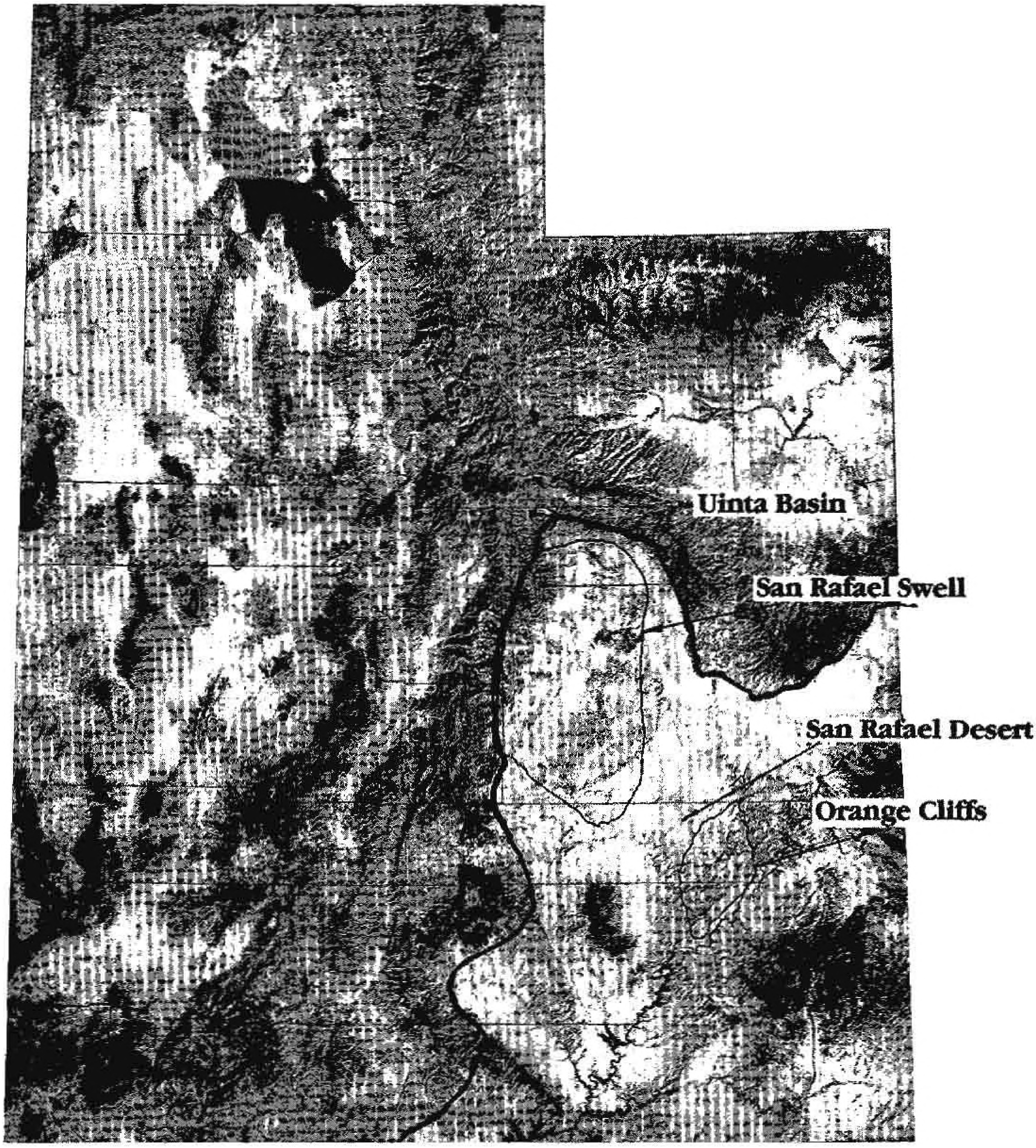

Fig. 3. Satellite image of Utah showing the positions of the San Rafael Swell, the San Rafael Desert, and the Orange Cliffs, all within the Canyonlands Phytogeographic Section, outlined in bold. The arrow in the Uinta Basin shows the approximate position of the White River PWA (Utah Wilderness Coalition 1990).

from America north of Mexico), and 50 of the Utah species are currently undescribed (T. Griswold, F. Parker, and V. Tepedino personal communication). Many areas, especially in the southern part of the state, have not been explored intensively and undoubtedly harbor many additional undescribed species.

Bees and plants often show comparable geographic patterns in diversity and endemism (Neff and Simpson 1993), and many of the areas currently under consideration for wilderness designation in Utah are centers of endemism for both groups. Although we lack extensive information on bees of the Canyonlands Section (Fig. 3), where endemism is highest for plants (see above), intensive collecting in that small part known as the San Rafael Desert has yielded a total of 316 species of bees, 42 of

TABLE 1. Plants endemic to the 2 areas with the highest endemism on Utah BLM lands.

| Endemics of the southern Uinta Basin | Endemics of the San Rafael Swell |
|---|---|
| *Aquilegia barnebyi* Munz (Ranunculaceae) | *Astragalus rafaelensis* Jones (Fabaceae) |
| *Astragalus equisolensis* Neese & Welsh (Fabaceae) | *Cryptantha creutzfeldii* Welsh (Boraginaceae) |
| *A. hamiltonii* C. Porter | *C. johnstonii* Higgins |
| *A. lutosus* Jones | *C. jonesiana* (Payson) Payson |
| *A. saurinus* Barneby | *Erigeron maquirei* Cronquist (Asteraceae) |
| *Cirsium barnebyi* Johnst. (Asteraceae) | *Lomatium junceum* Barneby & N. Holmgren (Apiaceae) |
| *Cryptantha barnebyi* Johnst. (Boraginaceae) | *Lygodesmia entrada* Welsh & Goodrich (Asteraceae) |
| *C. grahamii* Johnst. | *Pediocactus despainii* Welsh & Goodrich (Cactaceae) |
| *Cymopteris duchesnensis* Jones (Apiaceae) | *Penstemon marcusii* (Keck) N. Holmgren (Scrophulariaceae) |
| *Penstemon flowersii* Neese & Welsh (Scrophulariaceae) | *Schoencrambe barnebyi* (Welsh & Atwood) Rollins (Brassicaceae) |
| *P. goodrichii* N. Holmgren | *Talinum thompsonii* Atwood & Welsh (Portulacaceae) |
| *P. grahamii* Keck | *Townsendia aprica* Welsh & Reveal (Asteraceae) |
| *Schoencrambe argillacea* (Welsh & Atwood) Rollins (Brassicaceae) | |
| *S. suffrutescens* (Rollins) Welsh & Chatterly | |
| *Sclerocactus glaucus* (K. Schum.) L. Benson | |

which are presently undescribed (T. Griswold, F. Parker, and V. Tepedino personal communication). Thus, 33% of the state's total species count, and 84% of Utah's undescribed (but catalogued) species, are endemic to a region comprising just 2.0% of the state's land area. Furthermore, a significant portion of this fauna (24%) occurs only on the Colorado Plateau. The remainder of the Canyonlands Phytogeographic Section, in which the San Rafael Desert is embedded, is likely to be equally diverse and to have as many new species.

Other hymenopteran groups, such as the aculeate wasps, also are highly diverse in the San Rafael Desert (T. Griswold, F. Parker, and V. Tepedino personal communication). For example, with a total of 22 species there, the circumglobal genus *Philanthus* is more diverse in the San Rafael Desert than anywhere else in North America, and probably the world. These predatory "digger wasps" nest in the soil and may have diversified in response to the varied substrates present in this desert. Clearly, designation of wilderness in the San Rafael region (see UWC 1990) could afford significant protection to an area of very high endemism and diversity for the order Hymenoptera.

Bees and wasps are among the most beneficial insects. Predatory and parasitic wasps help to control populations of pest species (e.g., grasshoppers, aphids, etc.) below outbreak densities. An estimated 67% of flowering plants depend on insects (primarily bees) for pollen transfer and sexual reproduction (Axlerod 1960), and the welfare of many plant species in semiarid Utah assuredly depends on their relationships with bees. For example, a rare species of *Perdita*, found in Utah only at the BeeHive Dome site southeast of St. George, pollinates the rare and endangered dwarf bearclaw poppy (V. Tepedino personal communication). Bees that have specialized by collecting pollen only from flowers of a particular plant family, or even from a single genus within a family, are termed oligoleges. Such bees tend to be most common in arid regions (Neff and Simpson 1993) and generally are regarded as being closely adapted to the phenology and floral traits of the plants on which they specialize. Such adaptations tend to make them superior pollinators. Squash bees and squash flowers are examples of such a co-adapted pair in the Americas (Tepedino 1981). Some oligoleges may one day prove to be useful as crop pollinators. The legume specialist *Osmia sanrafaelae*, a native of the San Rafael Desert, has been investigated as a potential pollinator of alfalfa (*Medicago sativa* L.), an important forage crop (Parker 1985, 1986). Many of the species of the San Rafael Desert appear to be oligoleges. A brief list of some of the undescribed and recently described bee species and their host plants is provided in Table 2. These entries were chosen only to illustrate the variety of plant taxa upon which native bees specialize.

## Native and Endemic Fishes

Freshwater ecosystems are natural habitat "islands"; as such, their long-term isolation by

TABLE 2. Pollen preferences for representative oligolectic bees in the San Rafael Desert (data from T. Griswold, F. Parker and V. Tepedino personal communication).

| Plant family | Plant genus/species | Bee species |
|---|---|---|
| Asteraceae | *Helianthus anomolus* | *Perdita* nr. *laticincta** |
| | | *Hesperapis* sp.* |
| | *Wyethia scabra* | *Perdita bohartorum* |
| Boraginaceae | *Coldenia* | *Perdita (Heteroperdita)* sp.* |
| | *Stanleya* | *Perdita* nr. *zebrata** |
| Euphorbiaceae | *Euphorbia parryi* | *Perdita* nr. *labergei** |
| Fabaceae | *Astragalus* | *Ashmeadiella* nr. *micheneri** |
| Loasaceae | *Mentzelia multiflora* | *Perdita multiflorae* |
| Onagraceae | *Camissonia* | *Dufourea* sp.* |
| Papaveraceae | *Argemone* | *Perdita ute* |
| Polemoniaceae | *Gilia* | *Perdita* nr. *giliae** |
| | | *Perdita elongaticeps* |
| Scrophulariaceae | *Penstemon* | *Anthocopa* sp.* |

*Undescribed species

intervening terrestrial habitats, or by unsuitable aquatic habitats, often promotes local specialization, evolutionary diversification, and endemism in aquatic organisms. Seven centers of endemism are recognized for fishes of western North America (Miller 1959), and Utah includes substantial portions of 2 of these centers, the Bonneville Basin and the Colorado River Basin. Collectively, 28 fish species are native to these basins (Smith 1978), and 27 are extant.

Because of their limited distributions, endemic species are easily endangered by both habitat alterations and introductions of nonnative competitors and predators. Seven species and subspecies from the Bonneville and Colorado basins are now federally listed as endangered (U.S. Fish and Wildlife Service 1993). A further 11 species and subspecies are considered by fishery specialists to be endangered, threatened, or of special concern in Utah (Warren and Burr 1994). The decline of native fishes has been associated with both watershed development (e.g., reservoirs, irrigation diversions, channelization, floodplain drainage) and the introduction of alien species.

Conservation of endemic fish populations has been especially successful when much of the watershed has been protected (Williams 1991), but adherence to strict legal definitions of wilderness often precludes such widespread protection. In Utah, opportunities for protecting entire watersheds are limited to relatively small drainage systems extending from stream headwaters in mountain ranges of the Bonneville Basin to dry or saline lake beds at lower elevations. A particularly important case is in the Deep Creek Range, where the Bonneville cutthroat trout (*Oncorhynchus clarki utah*), once thought to be extinct (Behnke 1992), survives in populations in Trout Creek and Birch Creek within the Deep Creek PWA (UWC 1990).

Where protection of whole watersheds is not possible, wilderness that includes key habitats may help to stabilize declining populations of native fishes, preclude new listings and draftings of recovery plans, and promote recoveries and delistings. This should be the case most often for fishes living in headwater streams protected by natural and artificial downstream barriers from unintended invasions of alien cold-water species. For example, habitat in the upper Book Cliffs–Desolation Canyon PWA may support the Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*), considered the rarest of the cutthroat taxa (Behnke and Zarn 1976) and federally listed as a category 2 species (Kerchner 1995). Although the region has not been surveyed for this subspecies, native populations occur in streams entering the Duschesne River from the north (Shiozawa and Evans 1994) and have recently been found in streams of the western Book Cliffs, closer to Price and Soldier Summit (Shiozawa and Evans unpublished data). Given these observations, it is likely that streams flowing into the Book Cliffs–Desolation Canyon PWA will also contain this subspecies.

In relatively large downstream systems (secondary and tertiary streams), key habitats include floodplain wetlands, among the first habitats to be lost due to human activities. Although wetlands have been viewed traditionally either as breeding sources for insect pests or as waterfowl production sites, periodic or continuous connection to rivers renders them important appendages to lotic systems. Densities of aquatic invertebrates are significantly higher in wetlands than in main river channels, over 100-fold in some cases (Wolz and Shiozawa 1995, Mabey and Shiozawa unpublished data). Floodplain wetlands can therefore serve as important nursery grounds for larval and immature native fishes.

The loss of wetlands may be a significant factor endangering several native fishes in the Colorado River (Tyus and Karp 1989). Fishes native to the larger streams and rivers of the Colorado River Basin are predominantly minnows (Cyprinidae) and suckers (Catostomidae) that have evolved in isolation, are adapted to unique local conditions of this drainage (e.g., heavy silt loads and wide fluctuations in discharge and temperature), and are the most morphologically distinct fishes in North America (Hubbs 1940, 1941, Deacon and Minckley 1974, Minckley et al. 1986). Four of these native species, the Colorado squawfish (*Ptychocheilus lucius*), the humpback chub (*Gila cypha*), the bonytail chub (*Gila elegans*), and the razorback sucker (*Xyrauchen texanus*), are now federally listed as endangered. The decline of both the bluehead sucker (*Catostomus* [*Pantosteus*] *discobolus*) and the flannelmouth sucker (*Catostomus latipinnis*) within the main stems of the Colorado and Green rivers may result in their listings as threatened, especially if populations in tributary streams are not stabilized. Several of these species occur in areas under consideration for wilderness status. Both the Price River, in the Book Cliffs–Desolation Canyon PWA, and the San Rafael River, in the San Rafael PWA, have populations of roundtail chub, flannelmouth sucker, and bluehead sucker. Bluehead sucker are also known from the Dirty Devil and Muddy Creek drainages (Smith 1966), and both flannelmouth sucker and roundtail chub are likely to occur there. Wilderness designation could broaden the protected ranges of several of these species by stabilizing wetland habitats in the Dirty Devil, San Rafael, and Book Cliffs–Desolation Canyon PWAs.

Although the Virgin River drainage is also part of the Colorado River Basin, it has a unique fish fauna that appears to have evolved in isolation from populations in other parts of the basin. The Virgin River spinedace (*Lepidomeda mollispinus*), the woundfin (*Plagopterus argentissimus*), and the Virgin River chub (*Gila robusta seminuda*) are endemic to this system. Two additional species, the flannelmouth sucker and the desert sucker (*Catostomus clarki*), have evolved very slender caudal peduncles, possibly as a response to occasional high flows in the Virgin River (Smith 1966).

The health of this unique fish fauna already is cause for concern. Two of the endemics, the woundfin and the Virgin River chub, are federally listed as endangered. Although the desert sucker occurs in Arizona, Nevada, and New Mexico, this species merits special concern in Utah (Utah Division of Wildlife Resources [UDWR] 1992), where it is limited to the Virgin River drainage. Loss of either this species or the flannelmouth sucker from the Virgin River system would eliminate only a subset of their existing populations and is unlikely to move either species to endangered status. However, the uniqueness of these populations (Smith 1966) may warrant their designation as separate subspecies. This, together with the concern now evidenced for the flannelmouth sucker throughout its range, could easily translate into candidacy for listing if existing populations are not protected.

Concern for native fishes of the Virgin River drainage has already constrained water development in Washington County, Utah. Any actions that would help preserve the integrity of riparian habitat and stream channels would also reduce stress for these fishes. Since the integrity of riparian habitats is best maintained over large areas, wilderness designation in PWAs of the Beaver Dam slope and the greater Zion area would serve this purpose.

Finally, protection of Utah's rare and endangered fishes would likely also afford significant protection to other aquatic organisms, for example, Utah's diverse communities of aquatic insects. Reciprocally, the maintenance of high species diversity in stream insect communities is critical to assuring a continuous food supply to fishes in rivers with wide seasonal and annual fluctuations in flow rates. Mayflies (Ephemeroptera) are among the best-studied stream insects in Utah, and 16–18 genera (22–24 species) are known from warm water tributaries of the Colorado River system (G. Edmunds personal communication). Construction of reservoirs on these rivers has already inundated many river miles and altered flow rates, sediment loads, and downstream temperatures. Mayflies and other aquatic insects are highly sensitive to all these variables. Unnaturally constant temperatures in tailwaters beneath dams can lead to depauperate communities of mayflies and other stream insects, for example, below Flaming Gorge Reservoir (Edmunds 1994, 1995). (Four mayfly genera from this area of extremely high natural diversity have not been collected since the dam was built.) Habitats rich in mayflies and other aquatic insects, and most in need of protection from future impoundments, include the Green River from the Colorado border to Ouray, Utah, and the Colorado River from the Colorado border to Moab, Utah. Relatively warm sections of the Duchesne, Uintah, White, Escalante, Virgin, and Santa Clara rivers would also be sensitive to manipulations of stream flows.

## EXAMPLES OF BIOLOGICALLY IMPORTANT SITES ON BLM LANDS

The floras and faunas in different parts of Utah have unique evolutionary histories determined by the geography and topography of the lands they inhabit. In this section, we discuss 4 such sites in the context of important scientific criteria (outlined above) for wilderness site selection. We also review various scientific and educational values of these same sites.

### Book Cliffs and the Tavaputs Plateau

For several reasons, the Book Cliffs and Tavaputs Plateau areas, along both sides of the Green River, are critical for the long-term conservation of biological diversity in Utah. This region contains some of the largest remaining roadless areas on BLM lands in Utah (Fig. 1) and therefore provides important habitat for sensitive species with large area requirements. It includes broad elevational gradients with the potential to protect a wide range of natural communities and to maintain crucial routes for seasonal wildlife migration between high and low elevation. Furthermore, it constitutes a vital dispersal corridor linking the Uinta mountains to the north and the Colorado Plateau to the south.

Because of both the high habitat diversity and the central location of the Book Cliffs–Tavaputs region, the biota is unusually diverse and compositionally unique, and includes many species at their distributional limits. Among reptiles and amphibians, for example, the Great Basin spadefoot toad (*Scaphiopus intermontanus*), the western whiptail lizard (*Cnemidophorus tigris*), and possibly the rubber boa (*Charina bottae*) reach their eastern distributional limits here. Three additional species, the longnose leopard lizard (*Gambelia wislizenii*), the collared lizard (*Crotaphytus collaris*), and possibly the plateau striped whiptail (*Cnemidophorus velox*) are represented here by "edge" populations at the periphery of their respective ranges. Other species, such as the northern leopard frog (*Rana pipiens*), eastern fence lizard (*Sceloporus undulatus*), Great Plains ratsnake (*Elephe guttata*), and the Utah milk snake (*Lampropeltis triangulum*), have their westernmost limits in this region (Stebbins 1985, unpublished BYU museum records). While none of these species is federally listed as threatened or endangered, a few are so listed by the state (UDWR 1992). Moreover, geographically peripheral populations such as these are particularly important as dynamic foci of evolutionary change (e.g., Brown 1995, Lesica and Allendorf 1995).

The Book Cliffs–Tavaputs region also supports a rich mammalian fauna. Although our knowledge is far from complete, the area contains at least 62 native species, including a relatively stable population of black bear (*Ursus americanus*; H. Black personal communication). Recent fieldwork has resulted in records for 6 species previously unreported from the region (D. Rogers personal communication); these include Merriam's shrew (*Sorex merriami*), dwarf shrew (*S. nanus*), water shrew (*S. palustris*), big free-tailed bat (*Nyctinomops macrotis*), northern flying squirrel (*Glaucomys sabrinus*), and western jumping mouse (*Zapus princeps*). Of these species, *S. merriami, S. nanus,* and *N. macrotis* appear to be rare throughout their known distributions. More fieldwork is likely to produce additional records for this region.

### Isolated Desert Mountain Ranges

The isolated mountain ranges in Utah's Great Basin and Colorado Deserts are extremely important biologically because of their role in maintaining critical ecological and evolutionary processes. Because of their broad elevational gradients, extending from high peaks to desert valley floors, these ranges support a wider variety of habitats and a greater diversity of species than do areas of comparable size but less elevational relief. This characteristic also enables them to support the seasonal migrations of animals ranging from large ungulates to small passerine birds. Furthermore, these mountain ranges have outstanding scientific value because they represent cool and mesic habitat islands in an otherwise warm, arid landscape. Their natural communities have developed through intermittent periods of extreme isolation (Grayson 1993). Coupled with the great geological diversity of the region, this isolation has led to the formation of unique plant assemblages, often including rare local endemics (Albee et al. 1988, Welsh et al. 1993). By illustrating how populations and communities of habitat islands are modified through colonization and extinction, these mountain ranges have played a major role in the development of theories of geographical ecology and biogeography (Brown 1971, 1995, Grayson 1993, E. Rickart in preparation).

Portions of several isolated mountain ranges are represented within PWAs on BLM lands (UWC 1990). Such ranges include the Henry Mountains of the Colorado Plateau and the Deep Creek, Fish Springs, House, and Newfoundland ranges of Utah's west deserts (Fig. 1). As the most isolated range in Utah, the Newfoundland Mountains in Box Elder County are especially distinctive. At 2129 m above sea level, Desert Peak and a considerable area of surrounding uplands would have existed as an island throughout the history of ancient Lake Bonneville. Currently, the range forms a 154+ km$^2$ island of arid to semiarid vegetation immersed in a salt playa sea. No doubt salt marshes have covered the present salt flats periodically as the lake has advanced or receded in response to glacial and interglacial climates. The range has therefore been an ecological island throughout nearly 2 million years of Pleistocene and Quaternary time. Given such long isolation, these mountains have much to teach scientists about the persistence, local extinction, vagility, and evolutionary dynamics of a variety of animal and plant species that either live there now or have lived there in the past. In Utah and elsewhere in the intermountain region, knowledge of these topics will be important in the future as land managers try to anticipate plant and animal responses to the increasing fragmentation and isolation of natural habitats within the human-dominated landscape (Brown 1995).

## Mojave Desert in Southwestern Utah

Washington County includes Utah's only representative of the Mojave Desert, a warm desert commonly recognized by biogeographers as lying between the Great Basin Desert to the north and the Sonoran Desert to the south (Shreve 1942, Jaeger 1957, Rowlands et al. 1982, MacMahon 1986). The Mojave Desert is physically part of the Basin and Range Geological Province, but it is characterized by relatively low elevation over most of its area (600 to 1500 m above sea level) and by both limited precipitation (100–275 mm annually in most places) and warm summers (35°–40°C mean maxima for July; see MacMahon 1986). The uniqueness of the physical environment of the Mojave is reflected in its biota. Characteristic plants include the Joshua tree (*Yucca brevifolia*), creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), brittle bush (*Encelia farinosa*), and several species of saltbush (*Atriplex*). Of these, the Joshua tree can be considered endemic, and if the distribution of this species is used to define the boundaries of the Mojave Desert, then the desert covers a substantial portion of southeastern California, the southern cone of Nevada, the northwestern and west central parts of Arizona, and the extreme southwestern corner of Utah.

Judicious designation of new wilderness areas in this corner of the state could help to safeguard the many components of Utah's biological diversity that are endemic to the Mojave Desert and the associated Virgin Mountains of northwestern Arizona and adjacent Nevada. Figure 4 details land ownership in this region of Washington County. Because so much of this land is already in the public domain, there is opportunity for biodiversity conservation with minimal disruption of economic activity. Protected areas include Zion National Park, a substantial wilderness in the Pine Valley Mountains of the Dixie National Forest (no. 1 in Fig. 4), the Upper Virgin River Desert Wildlife Management Area (or DWMA, a reserve for the desert tortoise, *Gopherus agassizii*; nos. 2a and 2b in Fig. 4), the existing Beaver Dam wilderness areas that extend into Utah from Arizona (4), and the Lytle Ranch Preserve (5). Although all of these protected areas play important roles in conserving regional biodiversity, 2 of the largest areas, Zion National Park and designated Forest Service wilderness in the Pine Valley Mountains, are generally

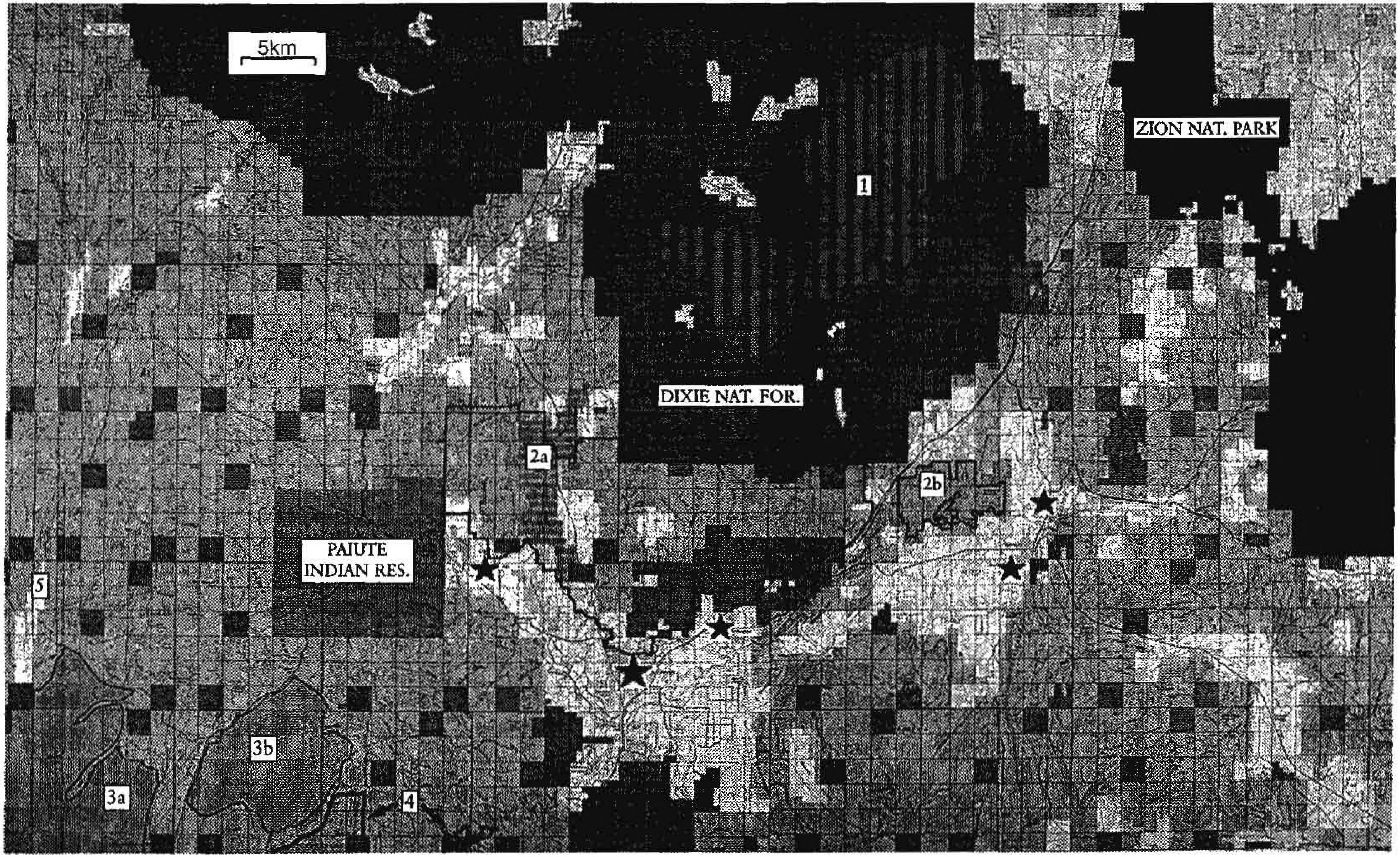

Fig. 4. Map of southwestern Utah (Washington County) showing patterns of land ownership and existing and proposed protected areas. Different shades identify privately held lands (white), BLM lands (lightest gray), and the checkerboard pattern of state lands interspersed within the BLM lands. Stars locate the major urban areas; from west to east these are Ivins, St. George (large star), Washington, Hurricane, and La Verkin. Current or proposed protected areas include Zion National Park, the Pine Valley Mountain wilderness area within the Dixie National Forest (1), Upper Virgin River DWMA (2), the proposed Beaver Dam Wash and Joshua Tree wilderness areas on BLM land (3a and 3b, respectively), the existing Beaver Dam Mountains wilderness on BLM land (4), and the Lytle Ranch Preserve (5).

too high in elevation and/or too far to the northeast to include many Mojave Desert species. The Upper Virgin River DWMA will protect lower elevation communities and will include some Mojave Desert taxa. However, many Mojave Desert species in Utah do not extend northeast of the Beaver Dam Mountains, and existing protected areas on the Beaver Dam slope are relatively small and isolated from each other (Fig. 4). By virtue of both size and location, 2 PWAs, the Beaver Dam Wash and Joshua Tree units (nos. 3a and 3b, respectively, in Fig. 4; see UWC 1990), could make important contributions to biodiversity conservation in Utah. Together these 2 units cover a range of elevations, include several distinctive plant communities not represented in the Upper Virgin River DWMA, and are close enough to one another and to the existing protected areas to serve as stepping stones for animal movement.

We illustrate the conservation value of these 2 PWAs through an example. The herpetofauna of the Mojave Desert includes 3 anurans, 1 tortoise, 16 lizards, 18 snakes, and about 28 additional species whose distributions are peripheral but extend into this desert along one of its edges (Stewart 1994). The portion of this fauna ranging into Utah includes 2 anurans, the turtle, and 13 squamates (5 lizards and 8 snakes). Their distributions across existing or proposed protected areas are summarized in Table 3. Of this total, the relict leopard frog (*Rana onca*) apparently is extinct in Utah (Platz 1984, Jennings and Hayes 1994) and therefore absent from all existing and proposed protected areas in Washington County. The other anuran confined to this part of Utah is the southwestern toad (*Bufo microscaphus*). It is known to exist with certainty in several areas and is likely widespread throughout the region where appropriate aquatic habitats exist (Table 3).

The desert tortoise (*Gopherus agassizii*) has been studied extensively over the past decade and intermittently for a much longer period of time (Woodbury and Hardy 1948, Bury and Germano 1994, Grover and DeFalco 1995). While Utah populations have apparently declined in the Beaver Dam slope area, they persist at high densities north of St. George (data summarized in Bury and Germano 1994) and are now protected in the Virgin River DWMA. Protection of the proposed Joshua Tree and Beaver Dam Wash wilderness areas would thus provide an economical way to augment conservation of tortoise populations confined to the south-facing slopes of the Beaver Dam Mountains.

Of the 13 squamate reptiles listed in Table 3, nine are confined to either the Mojave habitats proper (sites 3a, 3b, 4, and 5 in Fig. 4) or to these sites plus the Upper Virgin River DWMA (sites 2a and 2b in Fig. 4). Four species have more extensive distributions because they are also recorded from Zion National Park. Among the 9 squamates with restricted distributions, the lizards *Heloderma suspectum* and *Xantusia vigilis* and the snakes *Crotalus cerastes* and *Leptotyphlops humilis* may occur at all 5 Mojave sites, although this needs to be confirmed through additional fieldwork. *Xantusia vigilis* also occurs further east in isolated populations in Garfield and San Juan counties, and previous molecular studies by Bezy and Sites (1987) show deep genetic divisions among many isolated populations. Many of these isolates would qualify as full species, following the criteria of Davis and Nixon (1992), but the specific status of the isolated Utah populations remains unknown. The lizard *Callisaurus draconoides* occurs with certainty in the upper Virgin River DWMA (in Snow Canyon State Park), Beaver Dam Wash PWA, and Lytle Ranch Preserve (sites 2a, 3a, and 5 in Fig. 4). The iguana (*Dipsosaurus dorsalis*) is known confidently from only the lower Beaver Dam Wash PWA, although it may occur at low densities in the other 3 Mojave sites. Among the snakes, *Crotalus scutulatus* is confined to the 4 strict Mojave Desert areas, and *C. mitchellii* is known with certainty from only the higher elevation Mojave sites (3b and 4, although the other 2 locations are possible). Based on a new snake record for Utah, *Phyllorhynchus decurtatus* is known from a specimen (BYU 45605) taken on 11 July 1995, ca 1.5 mi N of the Utah-Arizona border along the Beaver Dam slope road. Based on this record, the species likely occurs in the Beaver Dam Wash and Joshua Tree areas (3a and 3b), which are similar in vegetative structure to the collecting site, and possibly at the other Mojave Desert sites as well. Regardless of exact distributions, all 9 squamate species with the most restricted distributions would benefit by wilderness designation of the proposed Beaver Dam Wash and Joshua Tree units (UWC 1990); and for 7 species (*C. draconoides*,

TABLE 3. Distribution of amphibians and reptiles restricted to southwestern Utah, relative to existing protected areas and Beaver Dam Wash and Joshua Tree units of proposed BLM wilderness included in H.R. 1500. The areas numbered are shown in Figure 4[a]. The proposed Red Mountain and Cottonwood Canyon wilderness areas (UWC 1990) are not illustrated because they are largely (Red Mountain) or entirely (Cottonwood Canyon) contained within the Upper Virgin River DWMA.

| Taxon | Zion National Park | Dixie N.F. Wilderness (1) | Upper Virgin River DWMA (2A, 2B) | Beaver Dam Wash Wilderness (3A) | Joshua Tree Wilderness (3B) | Beaver Dam Wilderness (4) | Lytle Ranch (5) |
|---|---|---|---|---|---|---|---|
| ANURA | | | | | | | |
| *Rana onca* | — | — | — | — | — | — | — |
| *Bufo microscaphus* | + | —(?) | —(?) | + | —(?) | —(?) | + |
| TESTUDINES | | | | | | | |
| *Gopherus agassizii* | — | — | + | + | + | + | + |
| SQUAMATA | | | | | | | |
| *Callisaurus draconoides* | — | — | + | + | ? | ? | + |
| *Coleonyx variegatus* | + | —(?) | + | + | +(?) | +(?) | +(?) |
| *Dipsosaurus dorsalis* | — | — | — | + | ? | ? | ? |
| *Heloderma suspectum* | — | — | + | + | ? | ? | + |
| *Xantusia vigilis* | — | — | +(?) | + | + | +(?) | + |
| *Crotalus cerastes* | — | — | + | + | + | +(?) | + |
| *Crotalus mitchellii* | — | — | — | ? | + | + | ? |
| *Crotalus scutulatus* | — | — | — | + | + | + | + |
| *Leptotyphlops humilis* | — | — | + | + | ? | ? | +(?) |
| *Masticophis flagellum* | + | —(?) | + | + | + | + | + |
| *Phyllorhynchus decurtatus* | — | — | — | +(?) | +(?) | +(?) | +(?) |
| *Sonora semiannulata* | + | —(?) | +(?) | + | +(?) | +(?) | +(?) |
| *Trimorphodon biscutatus* | + | —(?) | + | + | + | + | + |

[a] Distributions were inferred from locality records available in research collections of California Academy of Sciences; M. L. Bean Life Sciences Museum, Brigham Young University, Provo, Utah; Museum of Vertebrate Zoology, University of California, Berkeley; Utah Museum of Natural History, University of Utah, Salt Lake City. Species listed as present (+) if they (1) exist as museum voucher specimens, (2) have been documented photographically but not collected because of threatened or endangered status, or (3) have been collected near a protected area and are known to occupy the appropriate habitat. For example, Stewart (1994) summarized distributions of all Mojave Desert amphibians and reptiles on the basis of their occurrence in distinct habitat types, and we used these data as an indication of the likely presence of a species in an area if not actually documented. Doubts about any occurrences are indicated by (?).

*D. dorsalis*, the 3 species of *Crotalus*, *L. humilis*, and *P. decurtatus*), these 2 PWAs would constitute the largest blocks of protected area in the Utah portions of their distributions.

The biological significance of the Mojave Desert region could be illustrated with comparable examples involving native birds, small mammals, and vascular plants; literally scores of species are restricted to the low-elevation Joshua tree habitats on the southwestern slopes of the Beaver Dam Mountains (see Behle et al. 1985, Albee et al. 1988, and Zeveloff 1988 for recent species compilations). Although most are on the periphery of their ranges, it is increasingly apparent that such peripheral populations are critical to maintaining genetic diversity and to ensuring the long-term survival of species (Furlow and Armijo-Prewitt 1995, Lesica and Allendorf 1995, Lomolino and Channell 1995). Designation of the Beaver Dam Wash and Joshua Tree PWAs as wilderness would provide an extremely economical, proactive conservation strategy for many species.

## IMPACT OF ROADS ON PLANT AND ANIMAL COMMUNITIES

By definition under the 1964 Wilderness Act, wilderness areas must be large (at least 5000 acres) and roadless. Because even some remote and pristine areas contain primitive roads or tracks, roadlessness is often an issue in debates over wilderness designation. Environmentalists tend to argue that the existence of minor roads or dirt tracks is not contradictory to wilderness, but that no new roads should be built. Wilderness opponents respond that any road, no matter how primitive, disqualifies PWAs for wilderness status. Decision makers may be pressured to make exceptions to allow new roads and water development within wilderness boundaries. Here, we review the objective evidence bearing on the importance of roadlessness from a purely biological perspective. We deal with the effects of roads on animals and plants independently.

### Effects of Roads on Animals

Roads affect wildlife in many ways, both direct and indirect. Among the more commonly reported adverse impacts of roads on animal populations are road mortalities, animal avoidance of roads, isolation of populations by roads acting as barriers to animal movement, reductions in natural habitats, increased poaching, and elevated erosion leading to siltation of aquatic habitats. On Utah BLM lands, large mammals such as bighorn sheep (*Ovis canadensis*), black bear, and river otter are generally intolerant of human disturbance and activities. These and other mammals are known also to avoid habitat adjacent to roads (Oxley et al. 1974, Rost and Bailey 1979, Mader 1984, Witmer and Calesta 1985, Van Dyke et al. 1986) and can therefore be displaced by the presence of roads. Historically, humans in western North America have also persecuted a number of contemporary or former occupants of BLM lands; such species include Golden and Bald Eagles, gray wolf, and grizzly bear (Bortolotti 1984, Mech 1995). In Utah, the incidence of poaching is considerably higher in regions adjacent to roads than in roadless areas (W. Woody, UDWR, personal communication).

The negative effects of roads on wildlife can generally be ameliorated by closing the roads to traffic. Road mortality and the advance of habitat alteration along roads should stop entirely, and poaching should be sharply curtailed. For larger animals, roads would likely cease to act as barriers to animal movement and gene flow. However, this might not be true for some smaller species, whose movements are more restricted generally. Significant erosion and siltation of aquatic habitats might be reduced only slightly. Siltation can be an important consideration, for example, on the Aquarius Plateau, where reductions (by as much as 1/2) in the depths of some naturally shallow lakes have already increased winter fish kills. Finally, if efforts were made to reintroduce some of the large mammals considered above, these efforts might be greatly facilitated by the protection of large blocks of roadless lands that experience minimal human intrusion.

In summary, if travel on minor roads and tracks were to be permanently restricted, most but not all of the negative effects on wildlife would likely be ameliorated. Similar reasoning would suggest that the effects of any new unpaved minor roads or tracks might be minimal if the roads were used briefly and sporadically, e.g., to carry communications equipment.

### Effects of Roads on Plant Communities

The most compelling argument for large roadless areas is probably the protection of plant communities from disturbances that can eventually transform whole ecosystems. Through both direct and indirect effects, roads tend to disrupt native communities of both microphytes and macrophytes. Increased off-road vehicle traffic in roaded areas directly harms cryptobiotic soil crusts, which play a key role in maintaining healthy ecosystems in semiarid and arid lands, and kills or injures plants and perhaps soil-nesting insects like bees and wasps. Indirect effects include the introduction of nonnative pest plants, which have gradually replaced many native species and drastically altered features of certain habitats. The ecosystem-wide effects of these exotics are well illustrated by Asian tamarisk (*Tamarix chinensis*), which has channelized rivers and streams throughout the Colorado drainage and thereby altered the characteristics (flow regimes, temperatures, and sediment loads) of both aquatic and riparian habitats to the detriment of numerous native fishes, insects, birds, mammals, and plants (Loope et al. 1988, Sudbrock 1993). Below, we elaborate on the direct and indirect effects of roads on plant communities and on the maintenance of both biodiversity and natural networks of interactions in Utah's native ecosystems.

THREATS TO CRYPTOBIOTIC SOILS.—Across Utah's arid rangelands, a collection of cyanobacteria, algae, lichens, and mosses form microphytic or cryptobiotic crusts on soil surfaces. In pristine plant communities these crusts often account for at least as much soil surface cover as do vascular plants. The cryptophytes provide a number of valuable ecosystem services (reviewed in Harper and Marble 1988, West 1990, and Johansen 1993), including stabilization of soils against wind and water erosion, enhancement of water retention and infiltration (Brotherson and Rushforth 1983, Harper and St. Clair 1985, Harper and Marble 1988), and nitrogen fixation by autotrophic bacteria, including both free-living and symbiotic cyanobacteria (e.g., Snyder and Wullstein 1973, West and Skujins 1977, Klubek and Skujins 1980, Terry and Burns 1987). Their contribution to the nitrogen economy of these arid ecosystems is substantive. In southern Utah grasslands and cold deserts dominated by pinyon pine and juniper, nitrogen fixation by crusts is demonstrably the dominant source of nitrogen for vascular plants (Evans and Ehleringer 1993). The greater soil moisture and fertility associated with biotic crusts have been shown to result in higher tissue nutrient levels (Belnap and Harper 1995 and references therein), higher seedling survivorship in associated vascular plants (St. Clair et al. 1984, Harper and St. Clair 1985, Belnap 1994), and greater (α) floristic diversity (Kleiner and Harper 1972). Herbivores and other consumers may benefit indirectly from the enhanced nutrient status of these ecosystems (Harper and Pendleton 1993, Belnap and Harper 1995).

Growing recognition of the importance of cryptobiotic crusts to ecosystem processes has led to concern about the impact of disturbance by recreational users and nonnative grazers on such surfaces (Anderson et al. 1982, Johansen et al. 1984, Terry and Burns 1987, Cole 1991, Evans and Ehleringer 1993, Belnap et al. 1994, Belnap 1995). On most semiarid Utah lands, a single pass of an off-road vehicle will reduce nitrogen fixation by cyanobacteria and increase wind and water erosion of surface soils (Williams et al. 1995). Estimates of time to full recovery of disturbed biotic crusts (including nitrogen-fixing capacity) range up to 50 years in the Great Basin or 100 years on the Colorado Plateau (J. Belnap personal communication).

The full biological and economic consequences of disturbing biotic crusts remain to be quantified. However, in semiarid ecosystems where plant productivity is limited by availability of water and nitrogen, even small reductions in these resources can be expected to diminish primary productivity to the detriment of both the producers themselves and the many consumers depending directly or indirectly on these producers for food. Harper and Pendleton (1993) have suggested that destruction of soil crusts, and associated changes in forage quality, may be related to a decline in the health of desert tortoise populations in southwestern Utah (Grover and DeFalco 1995). If that suggestion is supported by empirical evidence in the future, then destruction of crusts may account in part for the ~$10 million cost (to date, T. Esque personal communication) of the Desert Tortoise Recovery Program.

ROADS AS CORRIDORS FOR INVASIONS OF INTRODUCED SPECIES.—Possibly the greatest adverse impact of roads on biological communities in Utah is the aggravation of invasions of aggressive weeds along road corridors, where disturbance from road construction has eliminated native competitors. These introduced plants now form the dominant cover on many arid and semiarid landscapes in western North America and are widespread in Utah (Mack 1981, Morrow and Stahlman 1984, Young et al. 1987, papers in McArthur et al. 1990 and Monsen and Kitchen 1994). Habitat degradation by nonnative, congregating grazers undoubtedly aided the initial spread of brome grasses (genus *Bromus*) and other European or Asian annuals into native habitats, including grasslands previously dominated by caespitose or tussock grasses (Young and Evans 1971, Loope 1976, Mack 1981, 1989, Billings 1990, 1994). Brome grasses (red brome [*B. rubens*], Japanese brome [*B. japonicus*], downy brome [*B. mollis*], ripgut brome [*B. diandrus*], and especially cheatgrass [*B. tectorum*]) have greatly increased fire frequency (from an average of 60–110 yr to <5 yr in sagebrush steppe), as well as altered the pattern and dynamics of fires (e.g., Whisenant 1990). Invaded lands suffer declining productivity (Stewart and Young 1939) and watershed damage (Buckhouse 1985) and become drastically depleted in both native plant species and cryptobiotic soil crusts (Young and Evans 1978, Whisenant 1990, Billings 1990, 1994, Rosentreter 1994; Fig. 5). Treatments to restore these lands often involve introductions of still other exotics (e.g., *Agropyron cristatum*, *Kochia prostrata*; see contributions to McArthur et al. 1990 and Monsen and Kitchen 1994).

The influx of invading weedy annuals has profound effects on genetic, species, and ecosystem diversity, although such effects remain poorly documented. In some parts of Utah,

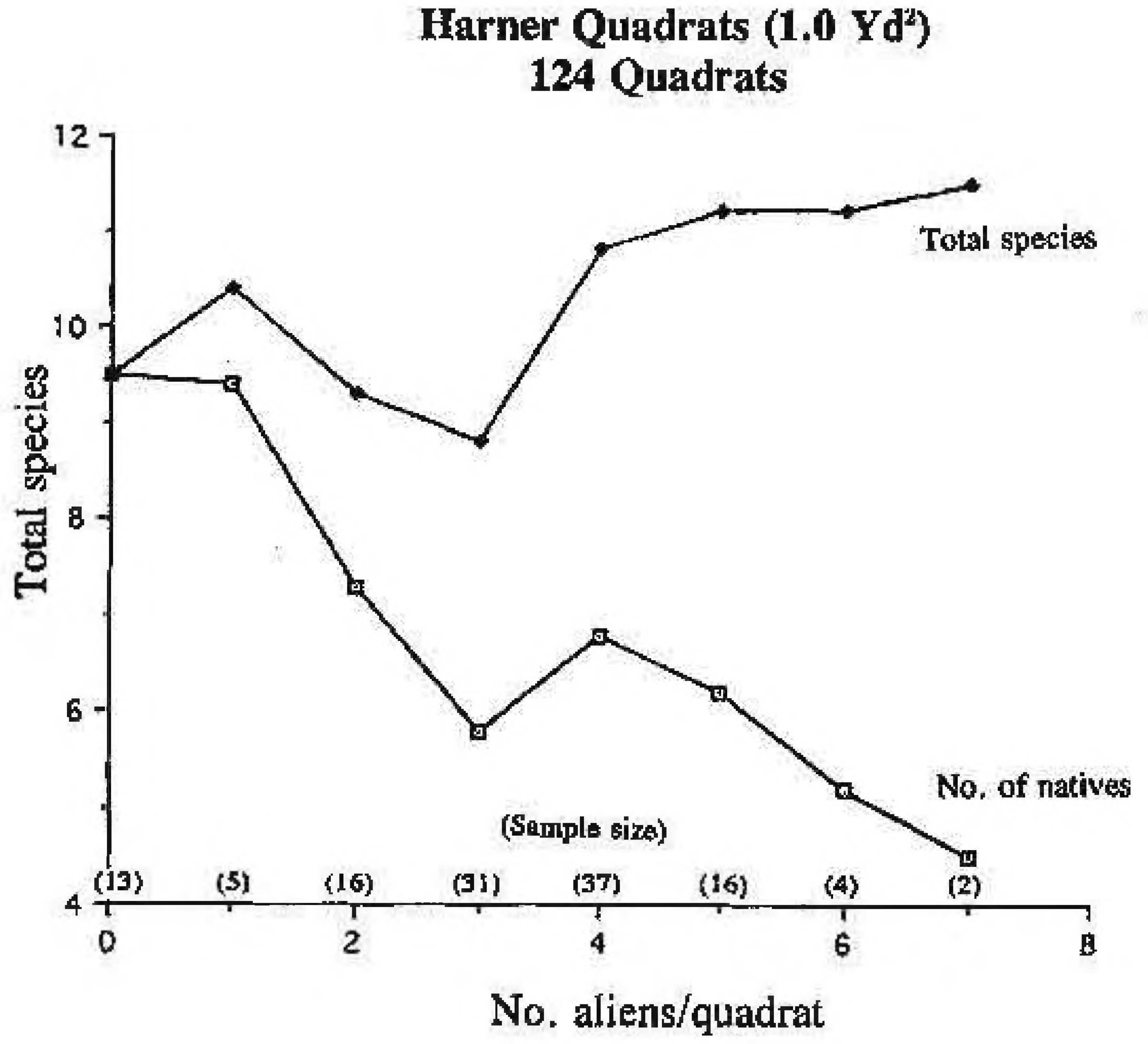

Fig. 5. Relationship of both total species richness, and numbers of native species per quadrat, to the number of individuals of introduced species per quadrat; plotted from raw data in Harner and Harper (1973). Data are from sagebrush-grasslands on private and BLM foothill lands in Salt Lake, Davis, and Tooele counties.

brome grasses form virtual monocultures, entirely replacing native communities, especially in wet years (e.g., Pellant and Hall 1994, and authors' observations). In other western states brome grass invasions threaten state or federally listed plant species (Rosentreter 1994, California Native Plant Society, personal communication). Effects of habitat conversion radiate upward through the food chain, and adverse effects have been documented on pronghorn (*Antilocapra americana*) and deer (Pellant 1990, Roberts 1994), small vertebrate prey of eagles and other raptors (Kochert and Pellant 1986, Nydegger and Smith 1986), native birds (Dobler 1994), and insects (Fielding and Brusven 1994). As summarized by Billings (1994), exotic annual grasses could constitute

> a genuine threat to the existence of large integrated ecosystems that have existed since the Pleistocene in the relatively arid lands between the Rocky Mountains and Sierra Nevada. These operational ecosystems could disappear over large areas of thousands of square kilometers.

A very high priority for future ecological work in Utah will be to determine the extent to which the remote BLM lands being considered for wilderness status might serve as refuges for native flora and fauna. Seeds of brome grass, dispersed by animal vectors, certainly travel over long distances and into wilderness areas. However, large roadless areas with low circumference-to-area ratios might protect arid and semiarid western ecosystems against wholesale habitat conversion. Exotic weeds tend to invade native plant communities mainly along roadsides, railroad right-of-ways, and other highly disturbed sites (Forcella and Harvey 1983, Hunter 1990, literature cited in Billings 1990 and 1994; see also Bergelson et al. 1993). Favorably wet drainage ditches provide inroads to new habitat, and invaders spread outward from the ditches during particularly wet years. Although systematic surveys of nonnatives do not presently exist for PWAs (and are sorely needed), there is evidence that invasions of exotic weeds may be prevented by restricting access on existing roads. Thus, of the replicate roadsides studied by Hunter (1990), introduced species (including not only brome grasses but *Erodium cicutarium*, *Salsola* spp., and *Sisymbrium altissimum*) dominated all but the one that had been closed to traffic and left undisturbed for many years prior to censusing.

The effects of roads on plant communities appear to differ importantly from those on animal communities. Construction of new roads, especially those with drainage ditches, may hasten long-term and permanent changes to local floras, and these changes may eventually have markedly adverse effects on whole ecosystems. Existing dirt tracks are probably less threatening to plant communities; although moisture conditions on the tracks may be as favorable here as in drainage ditches, soil compaction appears to retard growth of most plants.

Given the costliness of aggressive fire suppression (e.g., Vail 1994) and habitat restoration measures (see reports in McArthur et al. 1990 and Monsen and Kitchen 1994), the most economical strategy for preventing the spread of introduced grasses to areas that are still relatively pristine may be to maintain their roadless character. This also would provide opportunities for investigating the effects of roads (or lack thereof) on the advance of exotic plants on arid lands in Utah.

## CONCLUSIONS

Wilderness serves many purposes, and its designation involves many and varied considerations. The technical issues and evidence presented here demonstrate that BLM wilderness lands can play a major and perhaps predominant role in safeguarding genetic, species, and ecosystem diversity across much of arid

Utah. Over the long term, large, contiguous networks of wilderness and other protected lands can provide sanctuary for populations of animals with large area requirements, and can help maintain natural processes and interactions that sustain healthy biotic communities. In many situations, wilderness designation can provide low-cost protection for rare and endangered species. BLM lands in geographically diverse regions of Utah all offer unique ecological, scientific, and educational values. To an extent so far unmeasured, wilderness lands may protect native ecosystems from wholesale transformation by invasions of exotic species. Clearly, if biological considerations are taken into account in wilderness decisions, wilderness can play a critical role in the long-term preservation of Utah's biological heritage.

## ACKNOWLEDGMENTS

Jayne Belnap, Phyllis Coley, Donald Duff, Sharon Emerson, Donald Feener, Bruce Howlett, Thomas Kursar, and Samuel Rushforth contributed to an earlier, nontechnical version of this paper. In addition to these individuals and the authors, Patricia Berger, Lynn Bohs, Rex Cates, Steven Clark, Susan Fairbanks, Jerran Flinders, Sarah George, James Harris, Richard Hildreth, Carl Marti, Brian Maurer, Norman Negus, Duke Rogers, Jon Seger, John Sperry, Richard Tolman, Delbert Wiens, Michael Windham, and Samuel Zeveloff endorsed the earlier paper. Klancy de Nevers and Jon Seger rescued corrupted computer files. T. Griswold, F. Parker, and V. Tepedino allowed us to use their unpublished data (Table 2 and section on bees). J. Belnap and L. Shultz commented on a previous draft of the manuscript, and Carla Garrison helped us obtain BLM maps.

## LITERATURE CITED

Albee, B. J., L. M. Schultz, and S. Goodrich. 1988. Atlas of the vascular plants of Utah. Occasional Publications No. 7, Utah Museum of Natural History, University of Utah, Salt Lake City. 670 pp.

Anderson, D. C., K. T. Harper, and S. R. Rushforth. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Journal of Range Management 35: 355–359.

Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): How big should reserves be? Conservation Biology 7: 602–610.

Atwood, D., J. Holland, R. Bolander, B. Franklin, D. E. House, L. Armstrong, K. Thorne, and L. England. 1991. Utah threatened, endangered, and sensitive plant field guide.

Axlerod, D. I. 1960. The evolution of flowering plants. Pages 227–305 *in* S. Tax, editor, Evolution after Darwin. Volume 1, The evolution of life. University of Chicago Press, Chicago.

Babbitt, B. 1995. Science: opening the next chapter of conservation history. Science 267: 1954–1956.

Behle, W. H., E. D. Sorensen, and C. M. White. 1985. Utah birds: a revised checklist. Occasional Publications No. 4, Utah Museum of Natural History, University of Utah, Salt Lake City.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6. 275 pp.

Behnke R. J., and M. Zarn. 1976. Biology and management of threatened and endangered western trouts. USDA Forest Service, Technical Report RM-GTR-28. Fort Collins, CO.

Belnap, J. 1994. Potential value of cyanobacterial inoculation in revegetation efforts. Pages 179–185 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands. Report INT-GTR-313. Ogden, UT.

______. 1995. Soil surface disturbances: their role in accelerating desertification. Environmental Monitoring and Assessment 37: 1–17.

Belnap, J., and K. T. Harper. 1995. The influence of cryptobiotic soil crusts on elemental content of tissue in two desert seed plants. Arid Soil Research and Rehabilitation 9: 107–115.

Belnap, J., K. T. Harper, and S. D. Warren. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content, and chlorophyll degradation. Arid Soil Research and Rehabilitation 8: 1–8.

Belovsky, G. E. 1987. Extinction models and mammalian persistence. Pages 35–57 *in* M. E. Soulé, editor, Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Belovsky, G. E., J. A. Bissonette, R. D. Dueser, T. C. Edwards, Jr., C. M. Luecke, M. E. Ritchie, J. B. Slade, and F. H. Wagner. 1994. Management of small populations: concepts affecting the recovery of endangered species. Wildlife Society Bulletin 22: 307–316.

Bergelson, J., J. A. Newman, and E. M. Floresroux. 1993. Rates of weed spread in spatially heterogeneous environments. Ecology 74: 999–1011.

Bezy, R. L., and J. W. Sites, Jr. 1987. A preliminary study of allozyme evolution in the lizard family Xantusiidae (Reptilia, Sauria). Herpetologica 43: 280–292.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301–322 *in* G. M. Woodell, editor, The earth in transition: patterns and processes of biotic impoverishment. Cambridge University Press, Cambridge, UK.

______. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. Pages 22–30 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

BOLGER, D. T., A. C. ALBERTS, AND M. E. SOULÉ. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. American Naturalist 137: 155–166.

BORTOLOTTI, G. R. 1984. Trap and poison mortality of Golden and Bald Eagles. Journal of Wildlife Management 48: 1173–1179.

BROTHERSON, J. D., AND S. R. RUSHFORTH. 1983. Influence of cryptogamic crusts on moisture relationships of soils in Navajo National Monument, Arizona. Great Basin Naturalist 43: 73–78.

BROWN, J. H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist 105: 467–478.

______. 1995. Macroecology. University of Chicago Press, Chicago.

BROWN, J. H., AND E. J. HESKE. 1990. Control of a desert grassland transition by a keystone rodent guild. Science 250: 1705–1707.

BUCKHOUSE, J. C. 1985. Effects of fire on rangeland watersheds. Pages 58–60 *in* K. Sanders and J. Durham, editors, Proceedings of a Symposium: Rangeland Fire Effects. U.S. Department of the Interior, Bureau of Land Management, Boise, ID.

BURY, R. B., AND D. J. GERMANO, EDITORS. 1994. Biology of North American tortoises. USDI Fish and Wildlife Research Report ISSN 1040-2411, No. 13. 204 pp.

CASE, T. J., AND M. L. CODY. 1988. Testing theories of island biogeography. American Scientist 75: 402–411.

CHRISTENSEN, N. L., ET AL. 1989. Interpreting the Yellowstone fires of 1988. Bioscience 39: 678–685.

COLE, D. N. 1991. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. Great Basin Naturalist 50: 321–325.

CRONQUIST, A., A. H. HOLMGREN, N. H. HOLMGREN, AND J. L. REVEAL. 1972. Intermountain flora. Volume 1. Hafner Publishers, New York.

CROSS, S. P. 1985. Responses of small mammals to forest perturbations. Pages 269–275 *in* Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service, Technical Report RM-GTR-120. Fort Collins, CO.

DAVIDSON, D. W., R. S. INOUYE, AND J. H. BROWN. 1984. Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. Ecology 65: 1780–1786.

DAVIS, J. I., AND K. C. NIXON. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. Systematic Biology 41: 421–435.

DEACON, J. E., AND W. L. MINCKLEY. 1974. Desert fishes. Pages 385–488 *in* G. W. Brown, editor, Desert biology, Volume II. Academic Press, New York.

DEPARTMENT OF THE INTERIOR (BUREAU OF LAND MANAGEMENT). 1994. Ecosystem management in the BLM: from concept to commitment. U.S. Government Printing Office (573-183), Washington, DC. 16 pp.

DIAMOND, J. M. 1984. "Normal" extinctions of isolated populations. Pages 191–246 *in* M. H. Nitecki, editor, Extinctions. University of Chicago Press, Chicago.

DOBLER, F. C. 1994. Washington state shrub-steppe ecosystem studies with emphasis on the relationship between nongame birds and shrub and grass cover densities. Pages 149–161 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

DURRANT, S. D. 1950. Mammals of Utah: taxonomy and distribution. Museum of Natural History, University of Kansas Publications 6.

EDMUNDS, G. F. 1994. Tail water insects. The Landing Net (Summer): 6–7.

______. 1995. Tail water insects; revisited. The Landing Net (Fall): 4, 11.

EVANS, R. D., AND J. R. EHLERINGER. 1993. A break in the nitrogen cycle in aridlands? Evidence from $\delta^{15}N$ of soils. Oecologia 94: 314–317.

FIELDING, D. J., AND M. A. BRUSVEN. 1994. Grasshopper community responses to shrub loss, annual grasslands, and crested wheatgrass seedings: management implications. Pages 162–166 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

FORCELLA, F., AND S. J. HARVEY. 1983. Eurasian weed infestation in western Montana in relation to vegetation and disturbance. Madroño 30: 102–109.

FRANKEL, O. H., AND M. E. SOULÉ. 1981. Conservation and evolution. Cambridge University Press, Cambridge, UK.

FURLOW, F. B., AND T. ARMIJO-PREWITT. 1995. Peripheral populations and range collapse. Conservation Biology 9: 1345.

GRAYSON, D. K. 1993. The desert's past: a natural prehistory of the Great Basin. Smithsonian Institution Press, Washington, DC.

GROVER, M. C., AND L. A. DEFALCO. 1995. Desert tortoise (*Gopherus agassizii*): status-of-knowledge outline with references. USDA Forest Service, Technical Report INT-GTR-316. Ogden, UT. 134 pp.

GRUMBINE, R. E. 1994. What is ecosystem management? Conservation Biology 8: 27–38.

HARNER, R. F., AND K. T. HARPER. 1973. Mineral composition of grassland species of the eastern Great Basin in relation to stand productivity. Canadian Journal of Botany 51: 2037–2046.

HARPER, K. T. 1986. Historical environments. Pages 51–63 *in* W. L. D'Azevedo, editor, Handbook of North American Indians. Volume 11: Great Basin. Smithsonian Institution, Washington, DC.

HARPER, K. T., AND J. R. MARBLE. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. Pages 135–169 *in* P. T. Tueller, editor, Vegetation science applications for rangeland analysis and management. Kluwer Academic Publisher, Dordrecht.

HARPER, K. T., AND R. L. PENDLETON. 1993. Cyanobacteria and cyanolichens: Can they enhance availability of essential minerals for higher plants? Great Basin Naturalist 53: 59–72.

HARPER, K. T., AND L. L. ST. CLAIR. 1985. Cryptogamic soil crusts on arid and semiarid rangelands in Utah: effects on seedling establishment and soil stability. Final Report Bureau of Land Management, Utah State Office, Salt Lake City.

HARRIS, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago.

HEANEY, L. R. 1984. Mammalian species richness on islands on the Sunda Shelf, Southeast Asia. Oecologia (Berlin) 61: 11–17.

HOLDEN, P. B., R. STONE, W. WHITE, G. SOMERVILLE, D. DUFF, R. GERVAIS, AND S. GLOSS. 1974. Threatened fishes of Utah. Proceedings of the Utah Academy of Science, Arts, and Letters 51: 46–65.

HUBBS, C. L. 1940. Speciation of fishes. American Naturalist 74: 198–211.

______. 1941. The relation of hydrological conditions to speciation in fishes. Pages 182–195 *in* J. G. Needham, editor, A Symposium on Hydrobiology. University of Wisconsin Press, Madison.

HUNTER, R. 1990. Recent increases in *Bromus* on the Nevada Test Site. Pages 22–25 *in* E. D. McArthur, E. M. Romney, S. D. Smith, P. T. Tueller, editors, Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, USDA Forest Service, Technical Report INT-GTR-276. Ogden, UT.

IUCN. 1978. Categories, objectives and criteria for protected areas. Morges, Switzerland.

JAEGER, E. C. 1957. The North American deserts. Stanford University Press, Palo Alto, CA. 308 pp.

JENNINGS, M. R., AND M. P. HAYES. 1994. Decline of native ranid frogs in the desert Southwest. Pages 183–211 *in* P. R. Brown and J. W. Wright, editors, Herpetology of the North American deserts. Southwestern Herpetological Society Special Publication No. 5. Van Nuys, CA. 311 pp.

JOHANSEN, J. R. 1993. Cryptogamic crusts of semiarid and arid lands of North America. Journal of Phycology 29: 140–147.

JOHANSEN, J. R., L. L. ST. CLAIR, B. L. WEBB, AND G. T. NEBEKER. 1984. Recovery patterns of cryptogamic soil crusts in desert rangelands following fire disturbance. Bryologist 87: 238–243.

JOHNSON, R. R., L. T. HAIGHT, AND J. M. SIMPSON. 1977. Endangered species vs. endangered habitats: a concept. Pages 68–79 *in* Importance, preservation and management of riparian habitat. USDA Forest Service, Technical Report RM-GTR-43. Fort Collins, CO.

JULANDER, O. 1962. Range management in relation to mule deer habitat and herd productivity in Utah. Journal of Range Management 15: 278–281.

KAY, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural regulation" paradigm. Unpublished doctoral dissertation, Utah State University, Logan.

KERSHNER, J. L. 1995. Bonneville cutthroat trout. Pages 28–35 *in* M. K. Young, editor, Conservation assessment for inland cutthroat trout. USDA Forest Service, Technical Report RM-GTR-256. Fort Collins, CO.

KLEINER, E. F., AND K. T. HARPER. 1972. Environment and community organization in grasslands of Canyonlands National Park. Ecology 53: 299–309.

KLUBEK, B., AND J. SKUJINS. 1980. Heterotrophic nitrogen fixation in arid soils crusts. Soil Biology and Biochemistry 12: 229–236.

KNOPF, F. L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. Pages 105–111 *in* Riparian ecosystems and their management: reconciling conflicting uses. USDA Forest Service, Technical Report RM-GTR-120. Fort Collins, CO.

KOCHERT, M. N., AND M. PELLANT. 1986. Multiple use in the Snake River Birds of Prey Area. Rangelands 8: 217–220.

KUSHLAN, J. A. 1979. Design and management of continental wildlife reserves: lessons from the Everglades. Biological Conservation 15: 281–290.

LESICA, P., AND F. W. ALLENDORF. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9: 753–760.

LOMOLINO, M. V., AND R. CHANNELL. 1995. Splendid isolation: patterns of the geographic range collapse in endangered mammals. Journal of Mammalogy 76: 335–347.

LOOPE, L. L., P. G. SANCHEZ, P. W. TARR, W. L. LOOPE, AND R. L. ANDERSON. 1988. Biological invasions of arid land nature reserves. Biological Conservation 44: 95–118.

LOOPE, W. L. 1976. Relationships of vegetation to environment, Canyonlands National Park, Utah. Unpublished doctoral dissertation, Utah State University, Logan.

MACK, R. N. 1981. The invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agro-Ecosystems 7: 145–165

______. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. Pages 155–179 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors, Biological invasions. John Wiley and Sons, New York.

MACKINNON, J., K. MACKINNON, G. CHILD, AND J. THORSELL. 1986. Managing protected areas in the Tropics. IUCN, Gland, Switzerland.

MACMAHON, J. A. 1986. Deserts. Audubon Society Nature Guides. Alfred Knopf, New York. 638 pp.

MADER, H. J. 1984. Animal habitat isolation by roads and agricultural fields. Biological Conservation 29: 81–96.

MCARTHUR, E. D., E. M. ROMNEY, S. D. SMITH, P. T. TUELLER, EDITORS. 1990. Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management. USDA Forest Service, Technical Report INT-GTR-276. Ogden, UT.

MECH, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9: 270–274.

MEFFE, G. K., AND C. R. CARROLL. 1994. Principles of conservation biology. Sinauer, Sunderland, MA. 600 pp.

MICHENER, C. D. 1979. Biogeography of the bees. Annals of the Missouri Botanical Garden 66: 277–347.

MILLER, R. R. 1959. Origin and affinities of the freshwater fish fauna of western North America. Pages 187–222 *in* C. L. Hubbs, editor, Zoogeography. AAAS Publication 51.

______. 1961. Man and the changing fish fauna of the American Southwest. Papers, Michigan Academy of Science, Arts, and Letters 46: 365–404.

MINCKLEY, W. L., AND J. E. DEACON. 1968. Southwestern fishes and the enigma of "endangered species." Science 159: 1424–1432.

MINCKLEY, W. L. AND J. E. DEACON, EDITORS. 1990. Battles against extinction: native fish management in the American West. University of Arizona Press, Tucson.

MINCKLEY, W. L., D. A. HENDRICKSON, AND C. E. BOND. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. Pages 519–613 *in* C. H. Hocutt and E. O. Wiley, editors, The zoogeography of North American freshwater fishes. John Wiley & Sons, New York.

MONSEN, S. B., AND S. G. KITCHEN, EDITORS. 1994. Proceedings—Ecology and Management of Annual

Rangelands. USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

MORROW, L. A., AND P. W. STAHLMAN. 1984. The history and distribution of downy brome (*Bromus tectorum*) in North America. Weed Science 32 (Supplement 1): 2–7.

MOYLE, P. B., AND J. E. WILLIAMS. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4: 275–284.

NATIONAL RESEARCH COUNCIL. 1978. Conservation of germplasm resources: an imperative. National Academy of Sciences, Washington, DC.

NEFF, J. L., AND B. B. SIMPSON. 1993. Bees, pollination systems and plant diversity. Pages 143–167 *in* J. LaSalle and I. E. Gauld, editors, Hymenoptera and biodiversity. C.A.B. International, Wallingford, UK.

NEWMARK, W. D. 1985. Legal and biotic boundaries of western North American national parks: a problem of congruence. Biological Conservation 33: 197–208.

______. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature 325: 430–432.

______. 1991. Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. Conservation Biology 5: 67–78.

______. 1995. Extinction of mammal populations in western North American national parks. Conservation Biology 9: 512–526.

NOSS, R. F. 1992. The wildlands project: land conservation strategy. Pages 10–25 *in* The wildlands project. Wild Earth Special Issue, Cenozoic Society.

NYDEGGER, N. C., AND G. W. SMITH. 1986. Pages 152–156 *in* D. E. McArthur and B. L. Welch, editors, Proceedings—Symposium on the Biology of *Artemisia* and *Chrysothamnus*, USDA Forest Service, Technical Report INT-GTR-200. Ogden, UT.

OXLEY, D. J., M. B. FENTON, AND G. R. CARMODY. 1974. The effects of roads on populations of small mammals. Journal of Applied Ecology 11: 51–59.

PARKER, F. D. 1985. A candidate legume pollinator, *Osmia sanrafaelae* Parker. Journal of Apiculture Research 24: 132–136.

______. 1986. Field studies with *Osmia sanrafaelae* Parker, a pollinator of alfalfa (Hymenoptera: Megachilidae). Journal of Economic Entomology 79: 384–386.

PATTERSON, B. D. 1984. Mammalian extinction and biogeography in the southern Rocky Mountains. Pages 247–293 *in* M. H. Nitecki, editor, Extinctions. University of Chicago Press, Chicago.

PELLANT, M. 1990. The cheatgrass-wildfire cycle—are there any solutions? Pages 11–18 *in* E. D. McArthur, E. M. Romney, S. D. Smith, P. T. Tueller, editors, Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, USDA Forest Service, Technical Report INT-GTR-276. Ogden, UT.

PELLANT, M., AND C. HALL. 1994. Distribution of two exotic grasses on intermountain rangelands. Pages 109–112 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

PICKETT, S. T. A., AND J. N. THOMPSON. 1978. Patch dynamics and the design of nature reserves. Biological Conservation 13: 27–37.

PIMM, S. L., H. L. JONES, AND J. DIAMOND. 1988. On the risk of extinction. American Naturalist 132: 757–785.

PLATZ, J. 1984. Status report for *Rana onca* Cope. Prepared for Office of Endangered Species, U.S. Fish and Wildlife Service, Albuquerque, NM. 27 pp.

PRIMACK, R. B. 1993. Essentials of conservation biology. Sinauer, Sunderland, MA. 561 pp.

RAVEN, P. R. 1992. The nature and value of biodiversity. Pages 1–18 *in* Global biodiversity strategy: guidelines for action to save, study, and use earth's biotic wealth sustainably and equitably. WRI, IUCN, UNEP.

REID, W. V., AND K. R. MILLER. 1989. Keeping options alive: the scientific basis of conserving biodiversity. World Resources Institute, Washington, DC.

RICKART, E. A. In preparation. Elevational diversity gradients, biogeography, and the structure of montane mammal communities in the intermountain region. Journal of Biogeography: In preparation.

ROBERTS, T. C., JR. 1994. Resource impacts of cheatgrass and wildfires on public lands and livestock grazing. Pages 167–169 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

ROSENTRETER, R. 1994. Displacement of rare plants by exotic grasses. Pages 170–175 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

ROST, G. R., AND J. A. BAILEY. 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43: 634–641.

ROWLANDS, P., H. JOHNSON, E. RITTER, AND A. ENDO. 1982. The Mojave Desert. Pages 103–162 *in* G. L. Bender, editor, Reference handbook on the deserts of North America. Greenwood Press, Westwood, CT. 594 pp.

SALWASSER, H., C. SCHONEWALD-COX, AND R. BAKER. 1987. The role of interagency cooperation in managing viable populations. Pages 159–173 *in* M. E. Soulé, editor, Viable populations for conservation. Cambridge University Press, Cambridge, UK.

SAMSON, D. A., T. E. PHILIPPI, AND D. W. DAVIDSON. 1992. Granivory and competition as determinants of annual plant diversity in the Chihuahuan Desert. Oikos 65: 61–80.

SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5: 18–32.

SCHONEWALD-COX, C. M. 1983. Guidelines to management: a beginning attempt. Pages 414–445 *in* C. M. Schonewald, S. M. Chambers, B. MacBryde, and, L. Thomas, editors, Genetics and conservation. Benjamin Cummings, Menlo Park, CA.

SHAFFER, M. L. 1981. Minimum population size for species conservation. Bioscience 31: 131–134

SHIOZAWA, D. K., AND R. P. EVANS. 1994. The use of DNA to identify geographical isolation in trout stocks. Pages 125–131 *in* R. Barnhart, B. Shake, and R. H. Hamre, editors, Wild trout V: wild trout in the 21st century.

SHREVE, F. 1942. The desert vegetation of North America. Botanical Reviews 8: 195–246.

SHULTZ, L. M. 1993. Patterns of endemism in the Utah flora. Pages 249–263 *in* R. Sivinski and K. Lightfoot, editors, Southwestern rare and endangered plants. New Mexico Department of Forestry and Resources Conservation Division, Miscellaneous Publication No. 2. Santa Fe, NM.

Shultz, L. M., E. E. Neely, and J. S. Tuhy. 1987. Flora of the Orange Cliffs of Utah. Great Basin Naturalist 47: 287–298.

Smith, G. R. 1966. Distribution and evolution of the North American catostomid fishes of the subgenus *Pantosteus*, genus *Catostomus*. Miscellaneous Publications of the Museum of Zoology, University of Michigan, No. 129.

______. 1978. Biogeography of intermountain fishes. Intermountain Biogeography: a Symposium. Great Basin Naturalist Memoirs 2: 17–42.

Snyder, J. M., and L. H. Wullstein. 1973. The role of desert cryptogams in nitrogen fixation. American Midland Naturalist 90: 257–265.

Soulé, M. E., editor. 1987. Viable populations for conservation. Cambridge University Press, Cambridge, UK.

Soulé, M. E., D. T. Bolger, A. C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds on urban habitat islands. Conservation Biology 2: 75–92.

Soulé, M. E., and B. A. Wilcox. 1980. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, MA.

St. Clair, L. L., B. L. Webb, J. R. Johansen, and G. T. Nebeker. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. Reclamation and Revegetation Research 3: 129–136.

Stebbins, G. L., Jr. 1952. Aridity as a stimulus to plant evolution. American Naturalist 86: 33–44.

Stebbins, R. C. 1985. A field guide to western reptiles and amphibians. Houghton Mifflin Co., Boston, MA.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. American Naturalist 140: 893–911.

Stewart, G. R. 1994. An overview of the Mohave Desert and its herpetofauna. Pages 55–69 *in* P. R. Brown and J. W. Wright, editors, Herpetology of the North American deserts. Southwestern Herpetological Society Special Publication No. 5. Van Nuys, CA. 311 pp.

Stewart, G., and A. E. Young. 1939. The hazard of basing permanent grazing capacity on *Bromus tectorum*. American Society of Agronomy Journal 31: 1002–1015.

Sudbrock, A. 1993. Tamarisk control. I. Fighting back: an overview of the invasion, and a low-impact way of fighting it. Restoration and Management Notes 11: 31–34.

Tepedino, V. J. 1981. The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honeybee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). Journal of the Kansas Entomological Society 54: 359–377.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pages 119–134 *in* M. E. Soulé and B. A. Wilcox, editors, Conservation biology. Sinauer, Sunderland, MA.

Terry, R. E., and S. J. Burns. 1987. Nitrogen fixation in cryptogamic soil crusts as affected by disturbance. Pages 369–372 *in* Proceedings—Pinyon-Juniper Conference, USDA Forest Service, Technical Report INT-GTR-215. Ogden, UT.

Tyus, H. M., and C. A. Karp. 1989. Habitat use and streamflow needs of rare and endangered fishes, Yampa River, Colorado. U.S. Fish and Wildlife Service Biological Report 89(14). 27 pp.

U.S. Fish and Wildlife Service. 1993. Endangered and threatened wildlife and plants, 50 CFR 17.11 and 17.12, August 23, 1993. Division of Endangered Species, U.S. Fish and Wildlife Service, Washington, DC.

Utah Division of Wildlife Resources. 1992. Native Utah wildlife species of special concern. Draft document. Utah Division of Wildlife Resources, Salt Lake City. 31 pp.

Utah Wilderness Coalition (UWC). 1990. Wilderness at the edge. Peregrine Smith Books, Layton, UT.

Vail, D. 1994. Symposium introduction: management of semiarid rangelands—impacts of annual weeds on resource values. Pages 3–4 *in* S. B. Monsen and S. G. Kitchen, editors, Proceedings—Ecology and Management of Annual Rangelands, USDA Forest Service, Technical Report INT-GTR-313. Ogden, UT.

Van Dyke, F. G., R. H. Brocke, H. G. Shaw, B. B. Ackerman, T. P. Hemker, and F. G. Lindzey. 1986. Reactions of mountain lions to logging and human activity. Journal of Wildlife Management 50: 95–102.

Wagner, F. H., R. Foresta, R. B. Gill, D. R. McCullough, M. R. Pelton, W. F. Porter, and consultation on law and policy by J. L. Sax. 1995. Wildlife policies in the U.S. National Parks. Island Press. 242 pp.

Warren, M. L., and B. M. Burr. 1994. Status of freshwater fishes of the United States: overview of an imperiled fauna. Fisheries 19: 6–18.

Welsh, S. L. 1978. Endangered and threatened plants of Utah, a reevaluation. Great Basin Naturalist 38: 1–18.

Welsh, S. L., N. D. Atwood, S. Goodrich, and L. C. Higgins. 1993. A Utah flora. 2nd edition. Print Services, Brigham Young University, Provo, UT.

Welsh, S. L., N. D. Atwood, and J. L. Reveal. 1975. Endangered, threatened, extinct, endemic and rare or restricted Utah vascular plants. Great Basin Naturalist 35: 327–326.

West, N. E. 1990. Structure and function of microphytic soil crusts in wildland ecosystems of arid to semiarid regions. Advances in Ecological Research 20: 179–223.

West, N. E., and J. Skujins. 1977. The nitrogen cycle in North American cold-winter semi-desert ecosystems. Oecologia Plantarum 12: 45–53.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pages 4–10 *in* E. D. McArthur, E. M. Romney, S. D. Smith, P. T. Tueller, editors, Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, USDA Forest Service, Technical Report INT-GTR-276. Ogden, UT.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. Taxon 21: 213–251.

Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237–256 *in* M. E. Soulé, editor, Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125: 879–887.

WILLIAMS, J. D., J. P. DOBROWOLSKI, N. E. WEST, AND D. A. GILLETTE. 1995. Microphytic crust influence on wind erosion. Transactions of the American Society of Agricultural Engineers 38: 131–137.

WILLIAMS, J. E. 1991. Preserves and refuges for native western fishes: history and management. Pages 171–189 *in* W. L. Minckley and J. E. Deacon, editors, Battle against extinction, native fish management in the American West. University of Arizona Press, Tucson. 517 pp.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecological Monographs 44: 153–169.

WILSON, E. O. 1988. Biodiversity. National Academy Press, Washington, DC.

WITMER, G. W., AND D. S. CALESTA. 1985. Effect of forest roads on habitat use by Roosevelt elk. Northwest Science 59: 122–125.

WOLZ, E. R., AND D. K. SHIOZAWA. 1995. Soft sediment benthic macroinvertebrate communities of the Green River at the Ouray National Wildlife Refuge, Uinta County, Utah. Great Basin Naturalist 55: 213–224.

WOODBURY, A. M., AND R. HARDY. 1948. Studies on the desert tortoise, *Gopherus agassizii.* Ecological Monographs 18: 145–200.

YOUNG, J. A., AND R. A. EVANS. 1971. Invasion of medusahead into the Great Basin. Weed Science 18: 89–97.

______. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management 31: 283–289.

YOUNG, J. A., R. A. EVANS, AND B. L. KAY. 1987. Cheatgrass. Rangelands 9: 266–270.

ZEVELOFF, S. I. 1988. Mammals of the Intermountain West. University of Utah Press, Salt Lake City.

*Received 27 September 1995*
*Accepted 21 March 1996*