

# The Burrowing Owl (*Athene cunicularia*): A Technical Conservation Assessment



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## COVER PHOTO CREDIT

The burrowing owl (*Athene cunicularia*). Photograph by Masaki Watanabe, NHK — Japan Broadcasting Company, Tokyo, Japan, used with his permission.

# SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE BURROWING OWL

## *Status*

The USDA Forest Service (USFS) Rocky Mountain Region (Region 2) considers the burrowing owl (*Athene cunicularia*) to be a Regional sensitive species in furtherance of its legal responsibilities to maintain biodiversity of National Forest System lands, as required by the National Forest Management Act. The U.S. Fish and Wildlife Service lists the burrowing owl as a National Bird of Conservation Concern and designates high-priority conservation status to the species in five Bird Conservation Regions relevant to USFS Region 2 (BCR 9, 11, 16, 17, 18). The Colorado Division of Wildlife lists the burrowing owl as threatened, and the state wildlife agencies within Wyoming, South Dakota, Nebraska, and Kansas list the burrowing owl as a Species of Concern.

The status of burrowing owls in Region 2 is closely tied to that of prairie dogs (*Cynomys* spp.), because of the owls' requirement for mammal-excavated burrows. Continued loss of prairie dog colonies through active eradication, habitat loss, or disease will negatively impact burrowing owl population viability. Although declines of burrowing owls in most of Region 2 are not yet as dramatic as at the limits of its range (e.g., in Canada), most of the states in Region 2 have tentative evidence for recent and ongoing declines. Recent genetic studies, however, suggest that burrowing owls are panmictic (genetically connected by extensive dispersal) and do not yet show evidence of genetic isolation among populations. Strong dispersal ability means that reversal of unfavorable conditions should result in re-establishment of burrowing owls in suitable habitat via dispersal. Very little is still known about migratory patterns, except a general "leapfrog" pattern whereby the most northerly populations, such as those in Canada, tend to move furthest south to wintering grounds in Mexico. More southerly populations, such as those in Colorado, appear to engage in partial migration, with some individuals staying on the breeding grounds through most or all of some winters. Little is known about threats on the wintering grounds outside Region 2. Matrix-based demographic analyses suggest that the survival rate of adult females is a key element in the population dynamics of burrowing owls. Standardized surveys and ongoing research should provide the basis for improved assessment of the status of burrowing owls in the region.

## *Primary Threats*

Recognized threats to the persistence of burrowing owls in Region 2 include:

- ❖ Habitat Loss and Fragmentation. Because of their close association with prairie dogs, loss of burrowing owl habitat can generally be equated with loss of active prairie dog colonies through eradication programs, agricultural and urban conversion, and sylvatic plague (*Yersinia pestis*). Habitat fragmentation caused by urbanization and agricultural conversion may increase road densities, and thus may increase burrowing owl mortality from vehicular collisions. Fragmentation may also increase negative edge effects on burrowing owls, such as susceptibility to predation and interspecific competition.
- ❖ Anthropogenic Sources of Mortality. Vehicular traffic, pesticides, domestic animals, and recreational shooting of prairie dogs can negatively impact burrowing owl populations directly through mortality or indirectly through their effect on reproductive success or food supply of owls.
- ❖ Losses on the Wintering Grounds. Little is known of the wintering range of burrowing owls that breed in Region 2, but many may overwinter largely in Mexico. Because matrix-based demographic analyses suggest that the population dynamics of burrowing owls are particularly sensitive to changes in "adult" and first-year survival, these threats may have even greater impact on the wintering grounds. Return rates of yearling and experienced breeders from the wintering grounds are critical to the persistence of healthy populations and represent an inherent biological vulnerability stemming from the life history

## ***Primary Conservation Elements, Management Implications, and Considerations***

Threats to burrowing owls in Region 2 include habitat loss, indirect losses due to decline of prairie dogs, and direct losses to predators, toxins, and incidental shooting. Because of their strong dependence on active prairie dog colonies for breeding habitat, long term persistence of well-connected, large, active prairie dog colonies is critical to the persistence of burrowing owls. Prairie dog persistence, in turn, is threatened by land conversion for urban and agricultural uses, sylvatic plague, and control measures that include poisoning and shooting. Poisoning of prairie dogs can also have direct effects on the owls, resulting in mortality or decreased fitness. Shooting of prairie dogs can result in direct incidental mortality of owls, as well as the risk of poisoning through ingestion of lead. Matrix-based demographic analyses suggest that adult survival rates are the key to population dynamics. Small decrements in adult survivorship, or even an increase in the variability of survival rates, may be more detrimental than larger and more obvious declines in reproductive output. In summary, any discussion of threats to burrowing owls must clearly be linked to threats to the persistence of prairie dogs.

The most significant burrowing owl population losses have occurred at the periphery of the species' distribution, but there is some evidence for population declines within Region 2 as well. A regular, systematic survey for burrowing owls is required to understand population trends in Region 2. Standardized population surveys for burrowing owls have been developed and implemented in Wyoming (as well as Washington and Arizona), and the method is included in the "Tools and practices" section of this assessment. While demographic parameters have been estimated in Colorado, Nebraska, and Wyoming, a lack of standardization among methods of estimation has precluded comparisons among populations. Conservation of the species elsewhere has focused on identification and preservation of historic nesting sites, maintenance of primary burrower populations (e.g., prairie dogs and ground squirrels), regulation of pesticides near burrowing owl nests, reintroduction in areas of extirpation or extreme decline, and public education to mitigate human impacts

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## INTRODUCTION

This assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). The burrowing owl (*Athene cunicularia*) (**Figure 1**) is the focus of an assessment because it is listed as sensitive species in Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance or in habitat capability that would reduce its distribution (FSM 2670.5). Because a sensitive species may require special management, knowledge of its biology and ecology is critical. This assessment addresses the biology of the burrowing owl throughout its range in Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

## *Goal of Assessment*

Species conservation assessments produced as part of the Species Conservation Project are designed to provide forest managers, biologists, other agencies, and the public with a thorough discussion of the biology, ecology, conservation, and management of certain species based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, to discussion of broad implications of that knowledge, and to outlines of information needs. The assessment does not seek to develop specific management prescriptions, but provides the ecological and conservation background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). It cites management recommendations proposed elsewhere and when those have been implemented, this assessment examines the success of their implementation.



**Figure 1.** Western burrowing owl, male on the left, female on the right. Burrowing owls are relatively small, weighing approximately 150 g. Sexual dimorphic males have noticeably lighter plumage and are slightly larger than females, but size differences are rarely detectable in the field. Photograph by Masaki Watanabe, NHK – Japan Broadcasting Company, Tokyo, Japan, used with his permission

### ***Scope of Assessment***

This assessment examines the biology, ecology, conservation, and management of the burrowing owl, with specific reference to the geographic and ecological characteristics of the USFS Rocky Mountain Region. Although some of the literature on this species originates from field investigations outside of Region 2 (namely California and Florida), this assessment places that literature in the ecological and social context of the area contained within Region 2: Colorado, Wyoming, South Dakota, Nebraska, and Kansas. Similarly, this assessment is concerned with the reproductive behavior, population dynamics, and other characteristics of burrowing owls in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is considered in conducting the synthesis, but is placed in a current context.

In producing this assessment, we reviewed refereed literature, as well as non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on burrowing owls are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications or reports were regarded with greater skepticism and were used primarily when this was the best available information for a specific topic. Unpublished data (e.g., National Heritage Program records) were important in estimating the species' current geographic distribution. These data required special attention because of the diversity of persons and methods used to collect the data.

### ***Treatment of Uncertainty***

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches used for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence

for particular ideas, and we describe alternative explanations when appropriate.

### ***Publication of Assessment on the World Wide Web***

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and those of other organizations, as well as the public, more rapidly than publishing them as reports. More importantly, it facilitates their revision, which will be accomplished based on guidelines established in Region 2.

### ***Peer Review***

Assessments developed for the Species Conservation Project have been peer reviewed prior to release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, employing two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

## **MANAGEMENT STATUS AND NATURAL HISTORY**

### ***Management Status***

The western burrowing owl is a neotropical migrant protected under the Migratory Bird Treaty Act (1918), and the Convention on International Trade in Endangered Species (CITES, <http://www.natureserve.org/explorer>). Burrowing owls have been listed as "declining" on the Audubon Society's Blue List since 1972, which is intended to provide early warning that a species is experiencing a range contraction or population decline (Tate 1986). Under purveyance of the National Forest Management Act, Region 2 considers the burrowing owl to be a sensitive species and prioritizes its conservation to promote biodiversity. Burrowing owls are not federally listed as threatened or endangered by the U.S. Fish and Wildlife Service (USFWS) (<http://endangered.fws.gov/wildlife.html>, Oct. 12, 2002), nor have they been petitioned for listing. From 1994 to 1996 the burrowing owl was designated by the USFWS as a Category 2 candidate for consideration to be listed as a threatened or endangered species. However, in 1996 the Category 2 designation was discontinued, and the species was

never listed. Currently, the burrowing owl is a National Bird of Conservation Concern for the USFWS (Office of Migratory Bird Management 1995), and it is of conservation concern in USFWS Regions 1 (Pacific Region, mainland only), 2 (Southwest Region), and 6 (Mountain-Prairie Region) (Klute et al. 2003). It is also listed with regional conservation priority (Tier II, <http://www.rmbo.org/pif/jsp/BCRbmap.jsp>) in nine Bird Conservation Regions (BCR) throughout North America. BCRs with burrowing owl conservation priority within USFS Region 2 include 9 (Great Basin), 11 (Prairie Potholes), 16 (Southern Rockies/Colorado Plateau), 17 (Badlands and Prairies), 18 (Shortgrass Prairie), and 19 (Central Mixed Grass Prairie) (Klute et al. 2003).

The burrowing owl was designated in 1995 as an endangered species in Canada by the Committee on the Status of Endangered Wildlife in Canada (Haug and Wellicome 1995), and was listed as endangered in the provinces of Manitoba, Saskatchewan, Alberta, and British Columbia. The species has a federal listing of “threatened” in Mexico (Sheffield 1997a).

The global Heritage status rank for burrowing owls is G4, meaning that the species is apparently secure, although it may be rare in portions of its range such as the periphery. The global Heritage trinomial rank, which refers to the rangewide status of the western subspecies, is TU, meaning the subspecies is possibly in peril, but the status is uncertain (<http://www.natureserve.org> Aug. 31, 2002). In Wyoming, burrowing owls have a heritage rank of S3, meaning they are rare or local throughout their range or found locally in a restricted range (<http://www.uwadmweb.uwyo.edu/wyndd/> Aug. 31, 2002). The Colorado Natural Heritage Program designates the burrowing owl as an S4 species, meaning the species is apparently secure, although rare in parts of its range, particularly at the periphery (<http://www.cnhp.colostate.edu/index.html> Aug. 31, 2002). In Kansas and Nebraska, burrowing owls are listed as S3 (<http://www.kbs.ukans.edu/>, <http://www.natureserve.org> Aug. 31, 2002) and in South Dakota they are given a dual S3/S4 status ([http://www.state.sd.uw/gfp/Diversity/Aug. 31, 2002](http://www.state.sd.uw/gfp/Diversity/Aug.31,2002)).

Such designations have prompted many western states to consider the burrowing owl a Species of Special Concern. Within Region 2, the Colorado Division of Wildlife has listed the burrowing owl as threatened (VerCauteren et al. 2001). In addition, state wildlife agencies in Wyoming, South Dakota, Kansas, and Nebraska list the burrowing owl as a Species of

Special Concern (Sheffield 1997a). In Wyoming, this designation refers to species with wide distribution throughout the state but very little information on status and population trend (Luce et al. 1999).

The Wyoming Partners in Flight state conservation plan lists the burrowing owl as a Level I species, meaning that the species clearly needs conservation action (Nicholoff 2003). Colorado Partners in Flight lists it as a priority species in physiographic area 36, central shortgrass prairie-grassland. While Nebraska, Kansas, and South Dakota do not have formal Partners in Flight working groups, the states are given consideration by the North American Bird Conservation Initiative, which gives the burrowing owl high priority conservation status within BCR’s 17 (Badlands and Prairies) and 19 (Central Mixed Grass Prairie) within those states

### ***Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies***

Within Region 2, the burrowing owl is considered a sensitive species. The Secretary of Agriculture’s Policy on Fish and Wildlife, Section 2670.32 on sensitive species (FSM 2600 1995), states that the USFS should:

1. Assist states in achieving their goals for conservation
2. As part of the National Environmental Policy Act process, review programs and activities, through a biological evaluation, to determine their potential effect on sensitive species
3. Avoid or minimize impacts to species whose livability has been identified as a concern
4. If impacts cannot be avoided, analyze the significance of potential adverse effects on the population or its habitat within the area of concern and on the species as a whole
5. Establish management objectives in cooperation with the States when projects on National Forest System lands may have a significant effect on sensitive species’ population numbers or distributions.

In 1992, Canada issued a National Recovery Plan for Burrowing Owls (Haug et al. 1992), which contained seven main strategies that may help to guide

management actions in other portions of the species' range. As listed in Hjertaas (1997a), these strategies with specific guidelines for implementation are:

1. Reduce mortality on the breeding grounds through
  - ❖ Elimination of the effects of pesticides, particularly carbofuran for grasshopper control. A label restriction now prohibits carbofuran application within 250 m of burrowing owl burrows
  - ❖ Reduction of collision with vehicles
  - ❖ Enforcement to prevent shooting
  - ❖ Development of policy to minimize owl-human conflicts.
2. Increase productivity through
  - ❖ Research on nest predators, food supply, and causes of differential productivity among areas
  - ❖ Identification of habitats where food supplies are limiting.
3. Protect and manage nesting habitat through
  - ❖ Promotion of landowner contact programs such as Operation Burrowing Owls, which create an awareness of burrowing owls on private lands
  - ❖ Modification of provincial and federal agricultural policies that subsidize conversion of grasslands to cultivation
  - ❖ Increased emphasis on habitat management for important burrowing owl life history needs, as opposed to just habitat protection.
4. Monitor populations through trend, mortality, and productivity, rather than absolute counts, which are expensive and infeasible.
5. Manage migration and wintering areas through
  - ❖ Determination of burrowing owl winter distribution

- ❖ Identification of limiting factors for burrowing owls during migration and winter

- ❖ Cooperative research and management among Canadian, American, and Mexican scientists.

6. Establish breeding populations through reintroduction in areas where populations are very low.

7. Develop public support through education to avoid human-caused mortality of burrowing owls nesting in farmed, urban, or other human landscapes.

A component of the Canadian Recovery Plan is Operation Burrowing Owl (OBO), a stewardship program initiated in 1987 to protect burrowing owls on private lands (Hjertaas 1997b). The objective of OBO is to protect known nesting locations through a volunteer contract with landowners who agree not to cultivate a defined nesting area for a five-year term. Landowners are also asked to report numbers of nesting pairs to OBO. In return, landowners receive an OBO sign to be placed at the entrance of the farm, as well as an annual newsletter. In the first five years of the project, 499 landowners enrolled 16,000 ha of private land in the OBO program. Over 85 percent of landowners who were contacted by OBO, agreed to enroll some land in the program (Hjertaas 1997b). Only 1.9 percent of landowners in the OBO program cultivated enrolled lands. Although the program was highly successful in creating landowner awareness of burrowing owls, the number of owls from OBO sites continued to decline (Hjertaas 1997b). Between 1988 and 2000, there was a 95 percent decline in estimated burrowing owl pairs in the OBO project, representing an annual decline of 21.5 percent (Skeel et al. 2001).

Captive breeding and reintroductions have been attempted in areas where burrowing owl populations are extremely small or have been extirpated. Captive breeding efforts in British Columbia have been quite successful and are capable of producing 100 juveniles each year (Leupin and Low 2001). Maintenance of a successful breeding population through reintroductions has been less successful (Leupin and Low 2001). A total of 106 owls were released at eight different sites in British Columbia, with 95 percent remaining at the release sites. Predation was the main source of mortality, which averaged 34 percent per year. During the release period, there were 12 nesting attempts, with 28 young

produced (Leupin and Low 2001). Since 1993, only two released owls have returned to their release sites. Because productivity and mortality rates in reintroduced owls are similar to those observed in other declining populations, the current effort in British Columbia is on habitat management and restoration. Reintroduction has also been attempted in Minnesota, but it was abandoned for lack of success (Martell et al. 2001).

Specific management recommendations have been offered by a range of agencies and organizations. The following management recommendations were provided by the U.S. Geological Survey's, Northern Prairie Wildlife Research Center (Dechant et al. 1999):

- ❖ Graze taller grasses to attract primary burrowers, e.g., ground squirrels and prairie dogs
- ❖ Mechanically control vegetation in mid-March to avoid disturbing nests
- ❖ Preserve historic nesting sites, as burrowing owls often show fidelity to these sites over the years
- ❖ Preserve rights-of-way, haylands, and uncultivated areas within 600 m of nests for foraging
- ❖ Maintain an adequate supply of holes and burrows by maintaining habitat for burrowing mammals
- ❖ Install artificial nest burrows if natural burrows are limiting
- ❖ Reintroduce owls from other areas when populations are low
- ❖ Educate the public, including private landowners, about burrowing owl status and conservation. Enlist landowner help in protecting nesting habitat
- ❖ Do not spray pesticides within 400 to 600 m of nest burrows. Choose insecticides with lowest toxicity to non-target organisms
- ❖ When controlling burrowing mammals, relocate them instead of using pesticides. Do not use traps or poisoned meat or grain when burrowing owls are present. Do not completely eliminate burrowing mammals

In addition to the management recommendations given above, the Rocky Mountain Bird Observatory in Colorado (Gillihan et al. 2001) suggests the following:

- ❖ Retain grasshopper, beetle, and cricket populations at levels compatible with economic practices on the land, avoiding insecticides when possible
- ❖ Retain populations of prairie dogs at levels compatible with economic practices on the land, consider non-lethal control (barrier fences)
- ❖ If poisoning prairie dogs is necessary, avoid poisoning known owl nest burrows and fumigate prior to burrowing owl arrival in the spring or after their departure in the fall
- ❖ Leave inactive burrows open as future nest sites for burrowing owls
- ❖ Educate recreational prairie dog shooters on burrowing owl identification to avoid incidental shooting of owls perched outside of burrow entrances
- ❖ Drive slowly by prairie dog colonies and known owl nests to avoid vehicular collisions with owls when they fly low over roads searching for prey

In the Wyoming Partners in Flight "Wyoming Bird Conservation Plan" (Nicholoff 2003), burrowing owls are given Level I conservation status, needing conservation action and monitoring. Per designation, the following management objectives are listed to supplement those given above:

- ❖ Determine statewide population trend data
- ❖ Maintain burrowing owls in the 22 Breeding Bird Survey routes from which they have been observed from 1968 through 2002
- ❖ Maintain prairie dog colonies where burrowing owls are present via conservation easements and voluntary agreements with landowners, and habitat management plans with land managers
- ❖ Leave dirt berms at the edge of cultivated fields

## ***Biology and Ecology***

Burrowing owls have been the focus of extensive study in the last twenty years, owing to their conspicuous and charismatic nature as well as troubling population declines across much of their range. These declines and population extirpations have lent a sense of urgency to understanding the biology of the species and have resulted in a wealth of publications. Two burrowing owl symposia held in conjunction with annual Raptor Research Foundation meetings have been especially important in promoting research on the species and in identifying gaps in understanding. The first symposium was held in Seattle, Washington in 1992 (Lincer and Steenhof 1997), and the second was held in Ogden, Utah in 1997 (Holroyd et al. 2001). Both symposia culminated in published proceedings that contain many of the papers referenced in this assessment. Given that some of the most serious population declines have occurred in western Canada, many of the papers discussed here originated in that region, and these results are extrapolated to Region 2 populations where appropriate.

### Systematics

The systematic classification of burrowing owls is:

Phylum: Chordata

Class: Aves

Order: Strigiformes

Family: Strigidae

Genus: *Athene*

Species: *Athene cucularia*

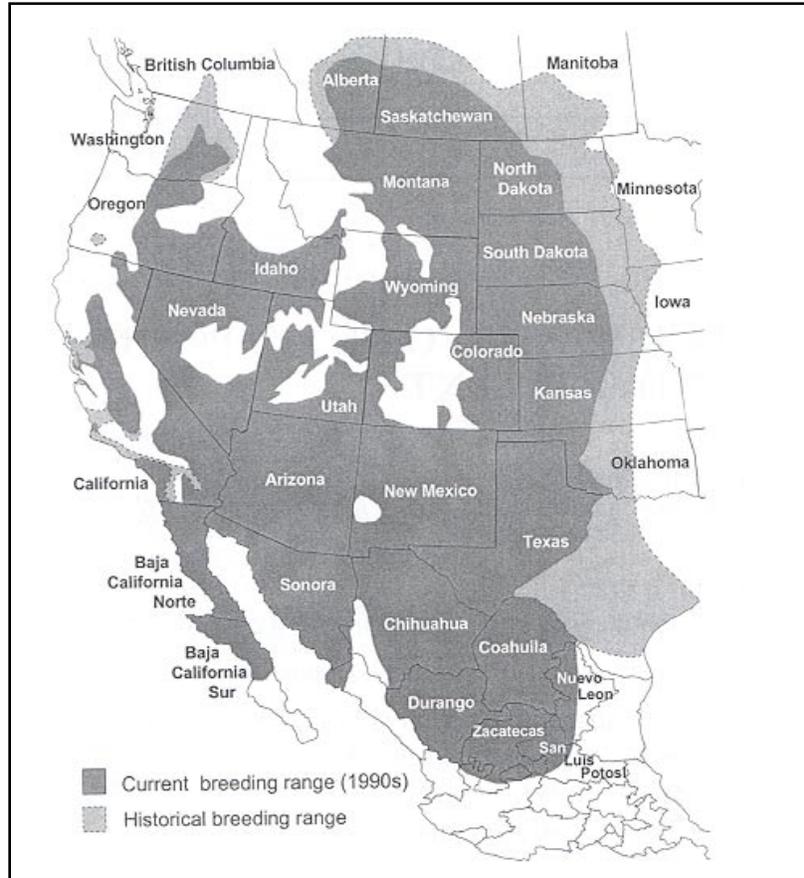
Burrowing owls have been variously assigned to genus *Athene* or genus *Speotyto*. After a long history of separating burrowing owls in the monotypic genus *Speotyto*, the American Ornithologists' Union (AOU) first included the species in the genus *Athene* in 1983 (American Ornithologists' Union 1983), making it a congener of the Old World little owl (*Athene noctua*). The AOU returned the species to the monotypic genus *Speotyto* in 1991 when DNA-DNA hybridization and karyotype data showed little relationship with other *Athene* owls (American Ornithologists' Union 1991). In 1997 burrowing owls were once again placed in the genus *Athene* (American Ornithologists' Union 1997), which it shares with *A. noctua* (little owl), *A. brama* (little spotted owl), and *A. blewitti* (forest owl),

none of which occur in North America. Placement in the genus *Athene* is probably partially due to similar vocalizations among burrowing owls and the other *Athene* species (Scherzinger 1988). Burrowing owls are thought to be descended from *S. megalopeza*, an extinct species whose fossils have been found in Kansas and which resembled a "more robustly built" burrowing owl (Ford 1966). The species name *cucularia* means "little miner," an appropriate name for this underground-nesting owl (Green 1988). Other common names include ground owl, prairie dog owl, rattlesnake owl, howdy owl, cuckoo owl, tunnel owl, gopher owl, and hill owl.

Eighteen subspecies of burrowing owl are currently recognized and are distinguished by plumage and size differences (Peters 1940, Clark et al. 1978, Haug et al. 1993). [Note, however, that the current American Ornithologists' Union (1998) checklist does not specify subspecies]. In North America, there are two subspecies, the western burrowing owl (*Athene cucularia hypugaea*) and the Florida burrowing owl (*A. cucularia floridana*). The range of the western burrowing owl (hereafter referred to as burrowing owl) extends from Canada to Panama and west from the Great Plains (**Figure 2**). There is strong genetic evidence to support the subspecific split of western and Florida subspecies (Desmond et al. 2001, Korfanta 2001), in addition to distinct behavioral differences. Importantly, burrowing owls of the Florida subspecies excavate their own burrows and are thus less tied to burrowing mammal populations than are western burrowing owls, which do not dig their own burrows.

In addition to *Athene cucularia hypugaea* and *A. cucularia floridana*, there are five other burrowing owl subspecies in North and Central America. These include:

- ❖ *A. cucularia rostrata* on Isla Clarion off the west coast of Mexico;
- ❖ *A. cucularia brachyptera* on Isla de Margarita, Venezuela;
- ❖ *A. cucularia troglodytes* on Hispaniola;
- ❖ *A. cucularia guadeloupensis* on Guadeloupe, Lesser Antilles;
- ❖ *A. cucularia amaura* on Nevis and Antigua, Lesser Antilles (Ridgway 1914, Clark et al. 1978).



**Figure 2.** Distribution of the western burrowing owl in western North and Central America (Wellicome and Holroyd 2001). Significant range contractions have occurred at the northern and eastern edges of the burrowing owl's range.

### General species description

Burrowing owls are unique in appearance and are not easily confused with other owl species (**Figure 1**). Their most distinctive feature is their very long legs, which are lightly feathered below the tibiotarsal joint. Total length for adult males is 19.5 to 25.0 cm, and for females it is 19.0 to 25.0 cm (Haug et al. 1993). Mass is approximately 150 g for both males and females, but males are slightly but significantly larger than females in other linear measurements such as rectrix length, wing chord, and tarsometatarsus length (Plumpton and Lutz 1994). This is significant because the burrowing owl is the only North American owl that does not exhibit reversed sexual size dimorphism, in which females are larger than males (Earhart and Johnson 1970). In the field, size difference is not a reliable means of distinguishing males and females, but difference in plumage coloration can sometimes be used. Because females tend to spend more time in the nest burrow during the breeding season, while males spend most of

their time outside of burrows, females often have darker plumage than the sun-bleached males during this time (Martin 1973a).

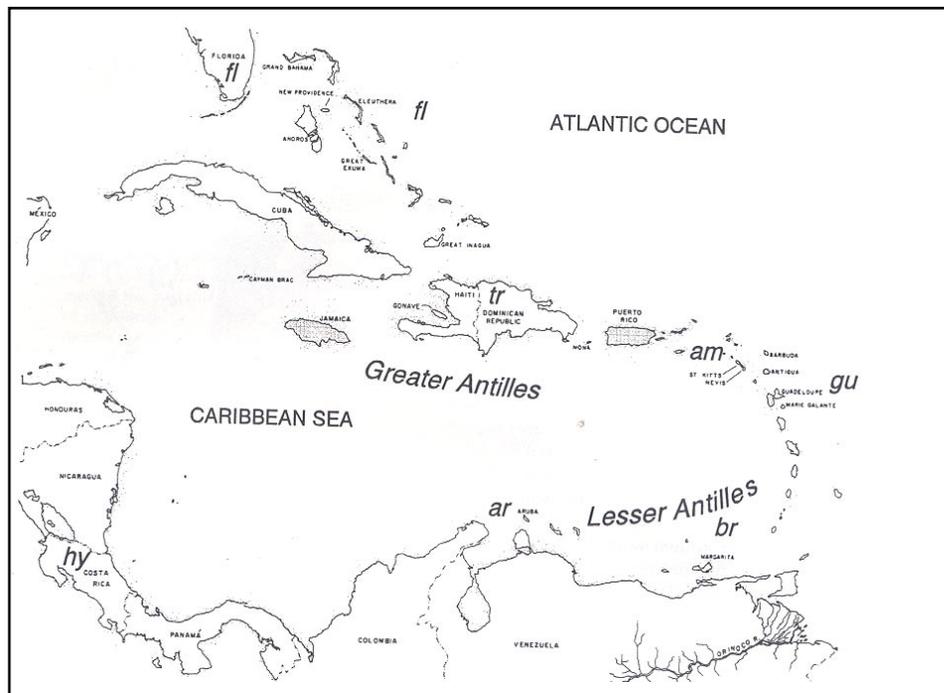
Other physical characteristics include a round head without ear tufts, lemon yellow irises, a prominent white chin stripe, and a buff-colored eyebrow-to-malar stripe, which is often exposed during territorial displays and prior to copulation (Haug et al. 1993). Wings are rounded and relatively long, with 10 brown and buff-colored primaries (Haug et al. 1993). The tail is quite short, with 12 brown and buff striped rectrices (Haug et al. 1993). The back and top of the head are dark brown with buffy-white spots. In adults, the breast is buffy-white with brown barring, which is generally more pronounced in males than females. Juveniles often have a clear breast until they molt into adult plumage during their first summer (Priest 1997). Further descriptions can be found in the *Birds of North America* account for burrowing owls (Haug et al. 1993).

## Current and historical distribution and abundance

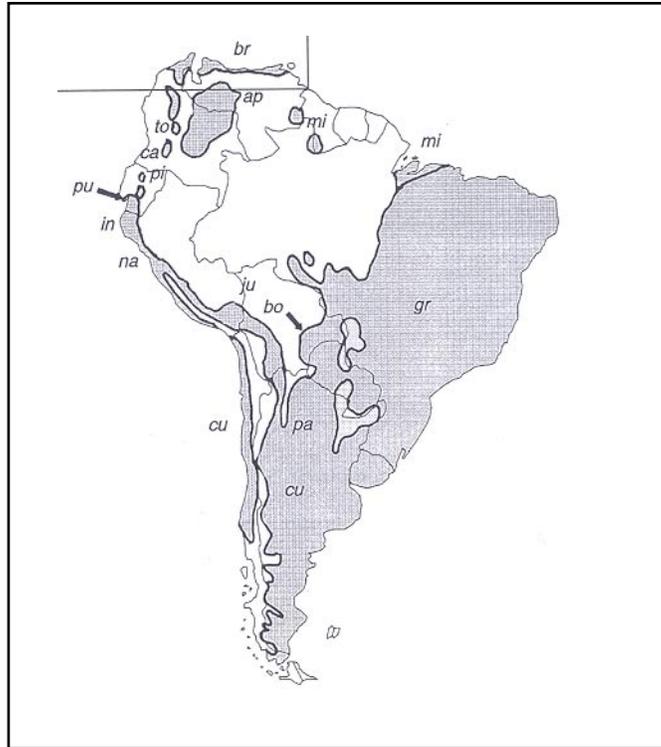
### *Global distribution – current and historical*

The earliest fossil evidence of a burrowing owl ancestor (*Speotyto megalopeza*) in North America dates back to the Pliocene, while the earliest fossil records of burrowing owls in South America date back to the more recent Pleistocene. This provides tentative evidence that burrowing owls originated in North America and subsequently spread via the isthmian land bridge to South America, where climatic fluctuations produced isolated habitat patches and a diversity of burrowing owl subspecies (Desmond et al. 2001). The fossil record may, however, simply be incomplete and may not represent the true sequence of events. Evidence from a mitochondrial DNA study showed large sequence divergence in the cytochrome b region between North and South American populations, suggesting a possible species split rather than the current subspecies designation (Desmond et al. 2001). Within North America, the western and Florida subspecies are currently geographically disjunct, with molecular studies supporting a subspecies split (Desmond et al. 2001, Korfanta 2001).

In the eastern parts of their range, burrowing owls inhabit Florida, Cuba, Hispaniola, the northern Lesser Antilles, and the Bahaman Islands (**Figure 3**). Burrowing owls are also distributed throughout western North America, south from central Alberta to Tierra del Fuego in South America (**Figure 4**). Range contractions have occurred at the edges of the western distribution. In particular, burrowing owls have been extirpated from British Columbia and Manitoba, Canada, with concurrent southerly range contraction in Alberta and Saskatchewan (**Figure 2**; Wellicome and Holroyd 2001). A population model predicts that burrowing owls will be extirpated from Saskatchewan within 20 years (James et al. 1997). In recent years, westerly range contractions have occurred in all U.S. states at the eastern edge of the species' distribution, including extirpation of the Minnesota populations. At the western edge of its range, burrowing owl distribution has contracted eastward, with coastal populations disappearing in California (DeSante et al. 1997). The burrowing owl has been extirpated from Tierra del Fuego since the early 1920's, possibly due to the introduction of widespread sheep grazing to the island (Humphrey et al. 1970). Conversely, a recent range expansion has been reported in Florida, where populations are expanding northward, possibly due to increased habitat from forest clearing and swamp draining for urban and agricultural development (Clark 1997).



**Figure 3.** Distribution of subspecies of *Athene cucularia* including *A. cucularia troglodytes* (tr), *A. cucularia amaura* (am) (extinct), *A. cucularia guadeloupensis* (gu) (extinct), *A. cucularia brachyptera* (br), and *A. cucularia arubensis* (ar) (Clark 1997).



**Figure 4.** Distributional range of subspecies of *Athene cucularia* in South America (Clark 1997).

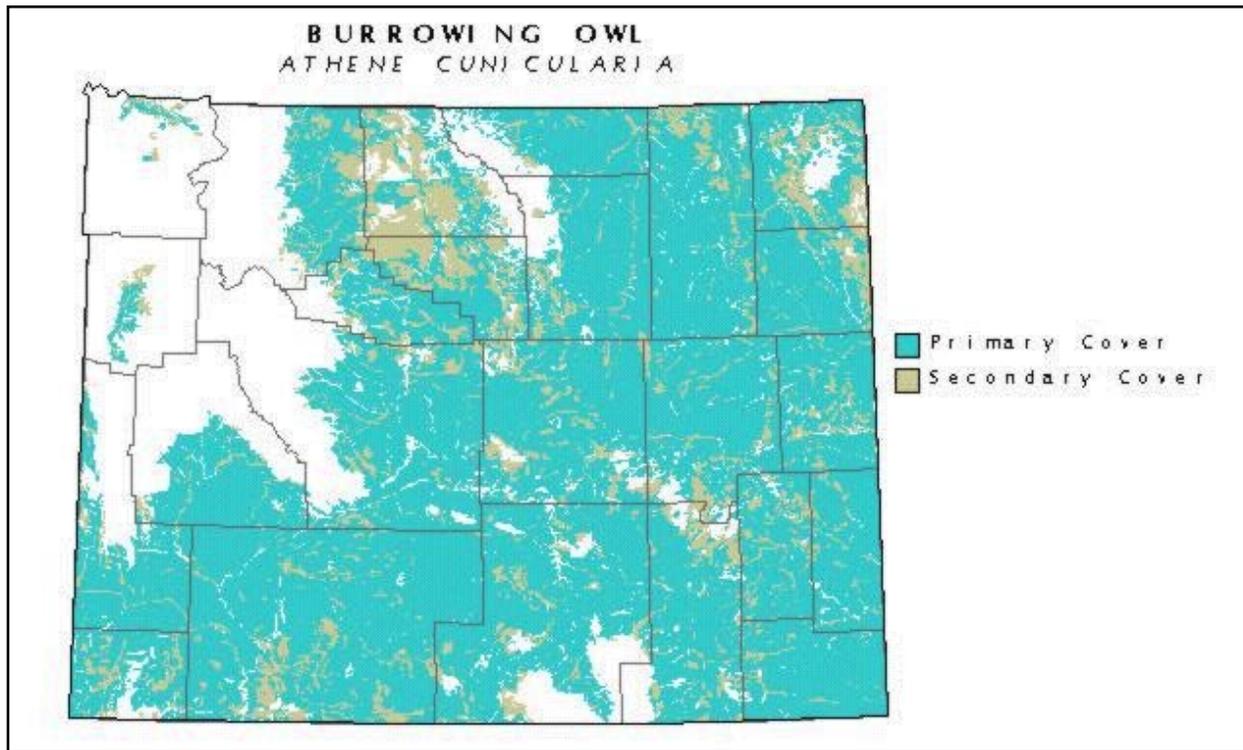
#### *Regional distribution – current and historical*

GAP data, which model potential habitat from species-specific habitat criteria, have been used to create maps of suitable burrowing owl habitat in Wyoming (**Figure 5**), Colorado (**Figure 6**), and South Dakota (**Figure 7**). GAP maps were not available for Kansas or Nebraska at the time this report was written. GAP models incorporate information from point locality records, range maps, and habitat conditions to generate maps of potential habitat, but it is important to note that the maps do not necessarily represent the current distribution of burrowing owls. In general, actual burrowing owl distribution is much more limited than the potential habitat depicted on the GAP maps. This may be partially due to the fact that the GAP models do not explicitly incorporate the presence of prairie dog or other primary burrower populations into the criteria for burrowing owl habitat.

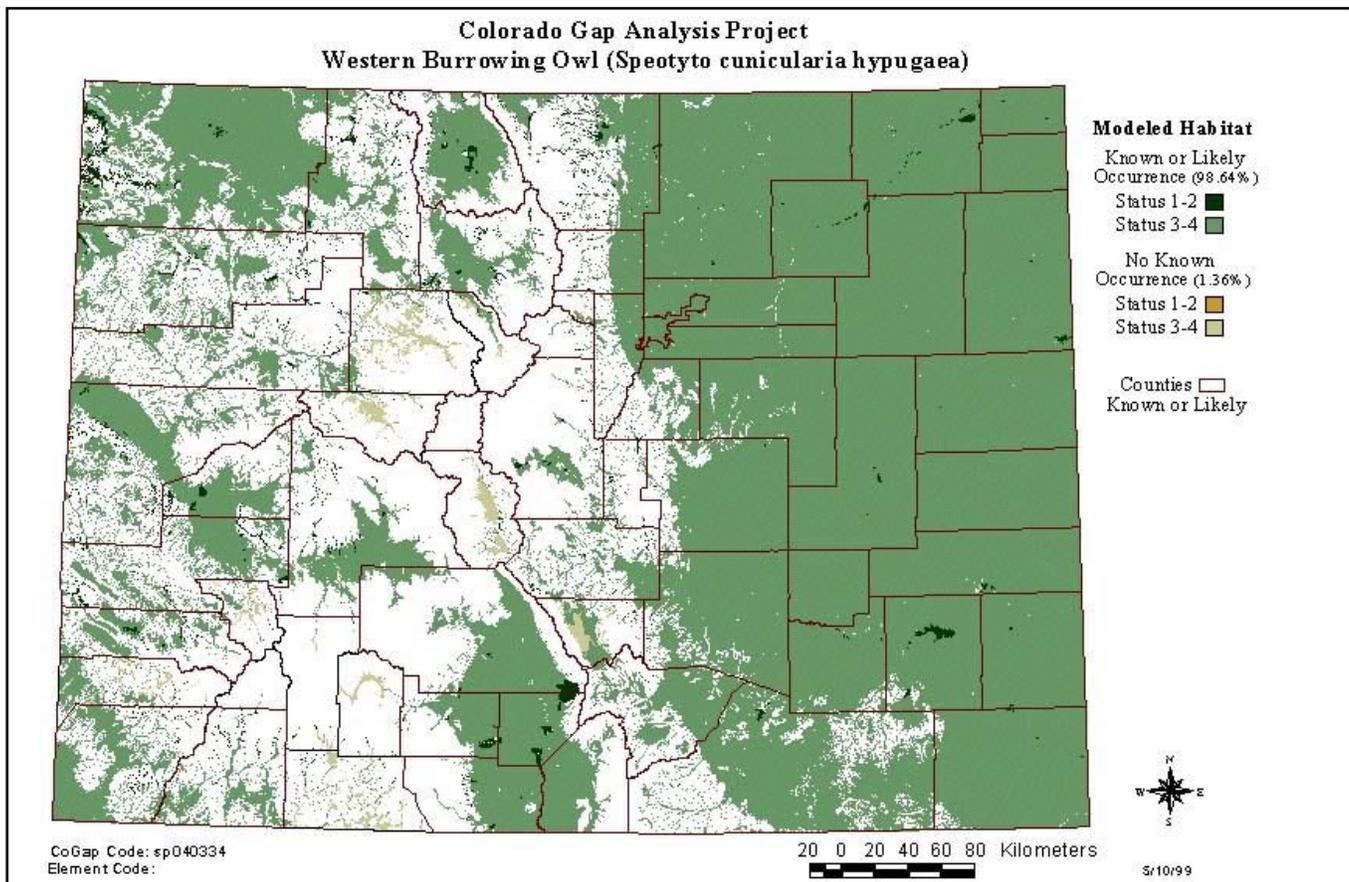
In addition to the GAP habitat modeling, several studies have mapped actual burrowing owl locations in the Rocky Mountain Region. VerCauteren et al. (2001) surveyed for burrowing owls in eastern Colorado and found a majority of owls nesting on private lands (**Figure 8**). In Wyoming, records from the Wyoming

Game and Fish Wildlife Observation (WOS) database show burrowing owl sightings throughout most of the state except for the northwest corner where prairie gives way to mountainous landscapes (**Figure 9**; Korfanta et al. 2001).

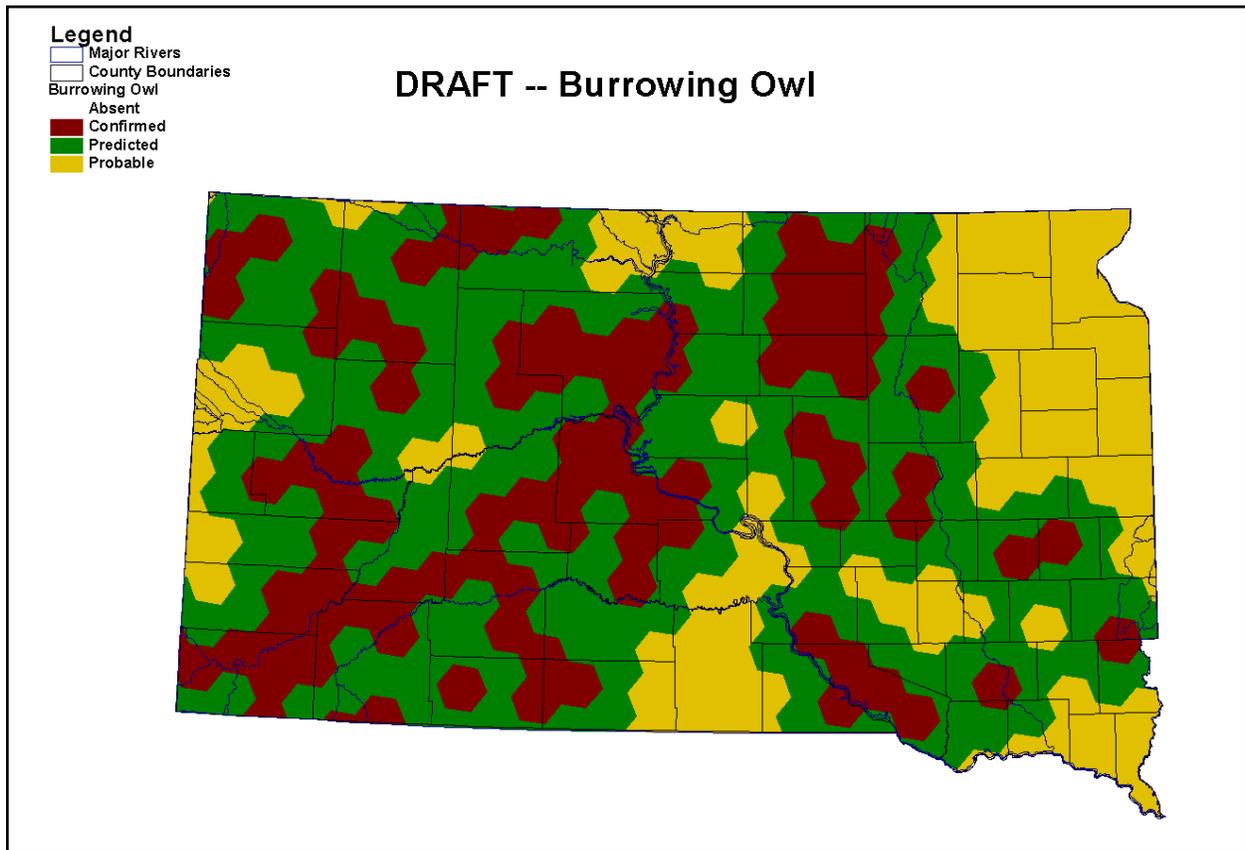
A problem with the WOS and other similar databases is that reported sightings do not represent a systematic sampling effort and are often biased in distribution. For instance, easy to access areas around urban centers may be better represented in the database. However, a systematic survey of potential burrowing owl habitat, comprising 85 townships in eastern Wyoming, resulted in only one burrowing owl sighting, emphasizing the importance of historical nesting locations and association with small mammals to create suitable nesting habitat (Korfanta et al. 2001). The Breeding Bird Survey represents another form of systematic survey effort, but again, it tends to miss burrowing owls due to their geographically clumped nesting distribution (Korfanta et al. 2001). In recent years, there have been efforts to standardize burrowing owl survey methods to maximize sightings and to minimize the temporal and spatial biases that characterize many data sets (DeSante et al. 1997, Martell et al. 1993, Conway and Simon 2003).



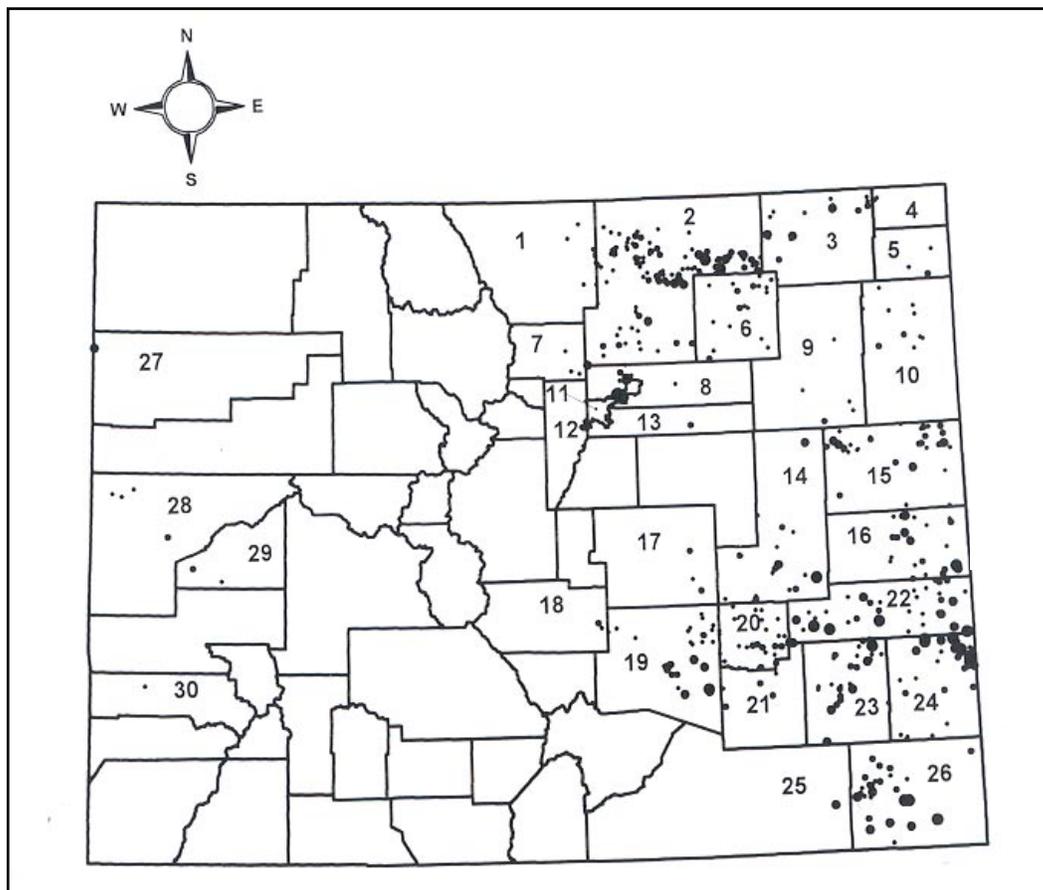
**Figure 5.** GAP habitat map for burrowing owls in Wyoming (<http://www.gap.uidaho.edu/Projects/States/>, October 14, 2002). Primary cover refers to the predicted presence of burrowing owls on the primary land cover type, which occupies the largest proportion of the area of each polygon of the habitat polygon. The tan color represents the predicted presence of the species based on the secondary land cover, which is the land cover occupying the second largest proportion of the area of each polygon.



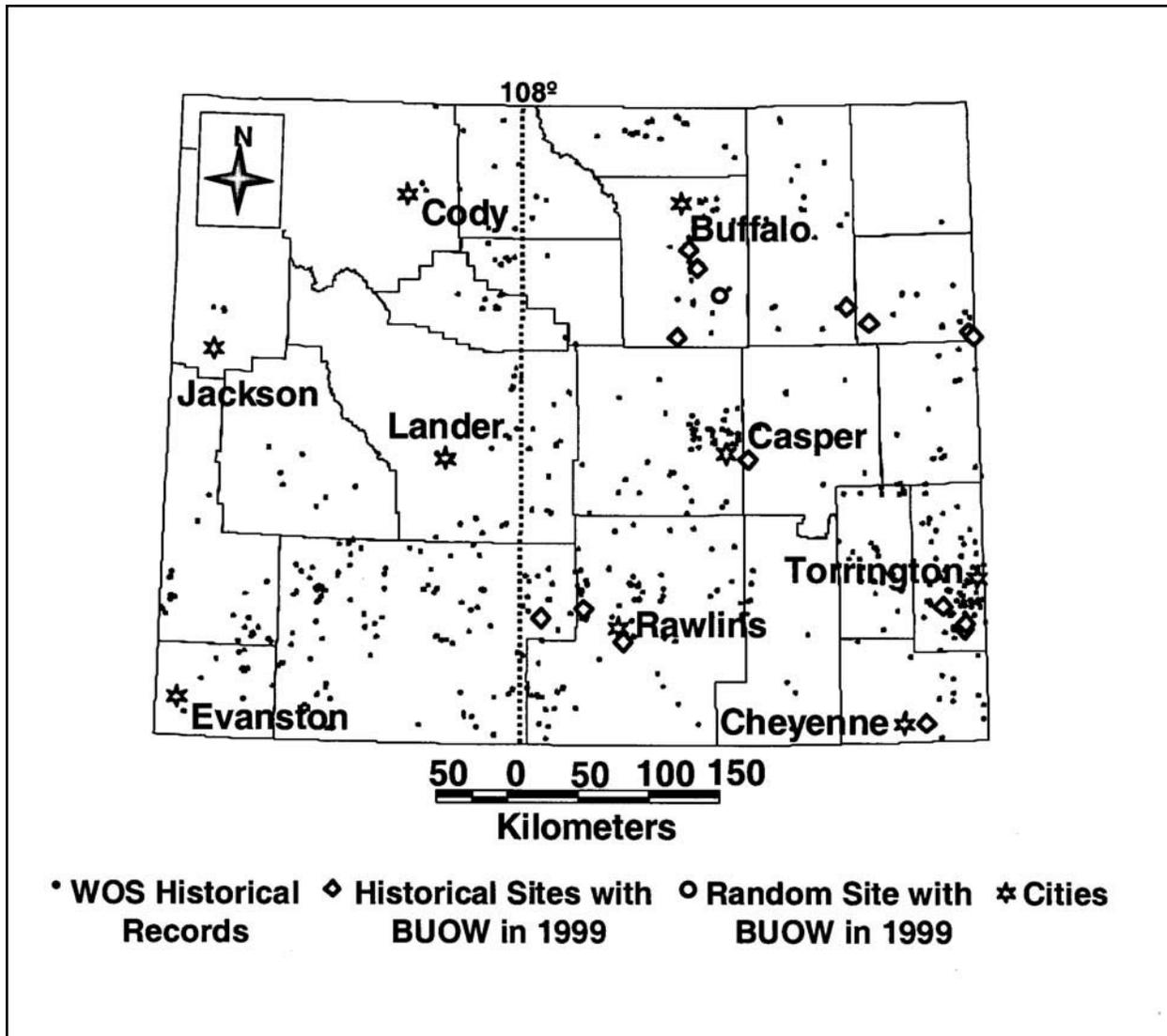
**Figure 6.** GAP habitat map for burrowing owls in Colorado (<http://www.gap.uidaho.edu/Projects/States/>, October 14, 2002). Status areas 1-2 include those areas that have some permanent form of protection from conversion of natural land cover as well as a mandated management plan to protect habitat. Status areas 3-4 do not have permanent habitat protection and may be subject to extractive uses.



**Figure 7.** GAP data for South Dakota (<http://www.gap.uidaho.edu/Projects/States/>, October 14, 2002).



**Figure 8.** Burrowing owl distribution and abundance in eastern Colorado from a 1999 survey (VerCauteren et al. 2001). Larger dots represent greater relative abundance of burrowing owls.



**Figure 9.** Burrowing owl sightings in Wyoming including Wyoming Game and Fish Wildlife Observation System records and results from a 1999 survey of historical nesting sites and random sites designated as preferred burrowing owl habitat (Korfanta et al. 2001).

*Global and regional abundance*

Historical abundance of burrowing owls in western North America is not well documented, but there is some evidence that they have existed in higher densities in the past. Anecdotal evidence of historically high burrowing owl abundance in Wyoming comes from Knight (1902), who characterized the owl as abundant in the late 1800's and early 1900's. In 1937, McCreary described Wyoming burrowing owls as a moderately common summer resident in appropriate habitat (McCreary 1937), but by 1982 burrowing owls were listed as uncommon in the *Wyoming Avian Atlas* (Wyoming Game and Fish Commission 1982).

Whether trends in the use of subjective terms represent a real trend in burrowing owl abundance is unclear, but they do appear to correspond with declining population trends in other parts of the region.

With recent suspected burrowing owl population declines, there has been an increased effort to survey populations to establish baseline information and to document changes in abundance. Many of these studies have resulted in population trend estimates rather than abundance estimates. An important exception to this is a burrowing owl census study conducted in central California in 1991 (DeSante et al. 1997). While California densities are not directly relevant to

Region 2, the technique for estimation is relevant for consideration. Researchers surveyed a 43,425-km<sup>2</sup> area including 16 counties and three broad biogeographic regions during the burrowing owl breeding season. Researchers found 336 pairs in the total census area and used two methods to obtain a population estimate of 873 pairs for the entire central California census area. Most of these owls were found in the Central Valley region, an area of intensive agriculture and rural open spaces. If it is assumed that the Central Valley was roughly 2/3 of the total census area, then density of owls in that region was roughly two pairs per 100 km<sup>2</sup>. However, this statistic does not give a sense of the spatial patchiness of burrowing owls, which tend to exist in clumps or colonies of breeding pairs.

A 1992 survey of North American wildlife agencies also provides rough estimates of burrowing

owl population sizes. Agencies were asked to estimate the size of the burrowing owl population in their state or province to the nearest order of magnitude (**Table 1**; James and Espie 1997). Within the Rocky Mountain Region, Wyoming and Colorado are estimated to have populations ranging from 1,000 to 10,000 pairs, while South Dakota, Nebraska, and Kansas are estimated to have roughly between 100 and 1,000 pairs. In general, populations are estimated to be largest at the center of the species' range, with smaller populations at the periphery.

Several burrowing owl surveys have been conducted within Region 2 in recent years. Historically in Colorado, burrowing owls were reported as locally common (Bailey and Niedrach 1965). The *Colorado Breeding Bird Atlas*, a summary of block surveys conducted throughout Colorado from 1987 through

**Table 1.** Results of a 1992 survey of state and provincial wildlife agencies. Biologists were asked to roughly estimate population sizes, trends, and contributing factors to population declines (adapted from James and Espie 1997).

Jurisdiction	Population size <sup>a</sup>	Trend <sup>b</sup>	Factors contributing to decline <sup>c</sup>	Special status
Alberta	Low 4	D/S	H, Ps	Yes
Arizona	3	D	H, Ps, B	No
British Columbia	1	D	H, Pr, B	Yes
California	4	D	H, Ps, Pr, Pe, B, V	Yes
Colorado	4	D	H, Ps, B	No
Florida	4	S	H, Pr, V	Yes
Idaho	Low 4	S	H	Yes
Kansas	3	D	B	No
Manitoba	2	D	Ps, Pr, Pe, V	Yes
Minnesota	1	S	B, V	Yes
Montana	3	S	?	Yes
Nebraska	3	D	H, Ps	No
Nevada	4	D	H, B, Ps	No
New Mexico	4	S	H, Ps	No
North Dakota	3	S	H, B, Ps	No
Oklahoma	3	S	H, B	Yes
Oregon	Low 4	S	H, B	Yes
Saskatchewan	Low 4	D	H, Ps, F	Yes
South Dakota	3	S	H, B	Yes
Texas	Low 5	S	H, B	No
Utah	Low 4	D	H	Yes
Washington	3	D	H	Yes
Wyoming	Low 4	S	H	Yes

<sup>a</sup>1 = 1-10 pairs, 2 = 10-100 pairs, 3 = 100-1,000 pairs, 4 = 1,000-10,000, 5 = 10,000-100,000 pairs

<sup>b</sup>D = decreasing, S = stable

<sup>c</sup>H = habitat loss, Ps = pesticides, B = reduced burrow availability, Pr = predators, Pe = persecution, V = vehicle collisions, F = food availability.

1994, documented burrowing owls in 40 percent of the priority blocks surveyed (Jones 1998). Evidence of breeding burrowing owls was reported in 259 (15 percent) of the 1745 priority blocks. In a more recent Colorado study, VerCauteren et al. (2001) revealed 423 burrowing owl locations in eastern Colorado, the large majority of which were on private lands. Each burrowing owl location represented one to many burrowing owls; thus, the number of locations is much lower than the actual burrowing owl population size in eastern Colorado.

Historical abundance of burrowing owls in Wyoming is not well-documented, although the Wyoming Game and Fish Department's Wildlife Observation System database provides some data on burrowing owl sightings in the state. A maximum of 139 burrowing owl sightings in one year was reported for 1981, with progressively fewer sightings in subsequent years (Korfanta et al. 2001). In a 1999 survey in Wyoming, 16 of 188 townships surveyed contained a total of 37 owls. Of 103 historical nesting sites, 17.5 percent were reoccupied in 1999 (Korfanta et al. 2001). Oliver Scott, in *A Birder's Guide to Wyoming* (1993), describes burrowing owls as "uncommon". In recent years, burrowing owl surveys have been conducted within the Thunder Basin National Grasslands in northeastern Wyoming (Conway and Hughes 2001, Conway and Lantz 2002, Conway and Lantz 2003). In 2002, 73 prairie dog colonies were surveyed, revealing 106 burrowing owl detections and 54 nest burrows (Conway and Lantz 2002). In 2003, the same 73 prairie dog colonies were surveyed, and 137 burrowing owls were detected, with 65 nests located (Conway and Lantz 2003). Of the 73 prairie dog colonies surveyed, 40 percent of the colonies were occupied by burrowing owls in both 2002 and 2003.

In 1998 an extensive survey for burrowing owls was conducted in active and inactive black-tailed prairie dog (*Cynomys ludovicianus*) colonies on national grasslands within Region 2. Of the 582 prairie dog colonies surveyed, burrowing owls were found at 322 (55 percent) of these; 69 percent of the active prairie dog colonies had burrowing owls, while 11 percent of the inactive colonies had owls (Sidle et al. 2001).

Although there are no published studies of recent statewide burrowing owl surveys in South Dakota, there have been recent surveys in North Dakota. Murphy et al. (2001) surveyed historical nesting sites throughout the state from 1994 to 1999, and they noted a maximum observed density of 3.2 pairs/100 km<sup>2</sup> in the northwestern part of the state, with 3 percent of

historical nesting areas occupied during the survey period. In the 1980's the species was considered common in north-central North Dakota (G. Berkey and R. Martin personal communication), but none was found during the 1994 to 1999 survey.

The North American Breeding Bird Survey (BBS; Sauer et al. 2001) provides another relative estimate of bird abundance. **Table 1** shows the number of burrowing owls per survey route, or relative abundance, in each of the Rocky Mountain Region states. Colorado has the greatest average number of burrowing owls per survey route at 2.63 per route, and Wyoming has the lowest average number at 0.09 per route. An important caveat to these data is that they have low credibility as characterized by Sauer et al. (2001) because of low encounter rates with the species. This may be because the species is of very low density in the state or because the survey routes have a low probability of detecting the species. This latter possibility is very likely since survey routes that do not intersect active prairie dog colonies are unlikely to encounter burrowing owls (Korfanta et al. 2001).

#### *Changes to distribution and abundance*

A well-documented range contraction has occurred at the edges of the western burrowing owl's distribution, particularly in the provinces of Alberta, Saskatchewan, and Manitoba, as well as the states of North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas, Washington and California (**Figure 2**; Wellicome and Holroyd 2001). In Canada, burrowing owls have been extirpated from British Columbia and Manitoba, and in the U.S. populations have been extirpated from Minnesota.

Although historical abundance data are largely lacking, it is likely that as some fossorial mammal populations have declined, nesting habitat has limited burrowing owl numbers. Many studies have documented a positive relationship between small mammal populations that provide burrows and burrowing owl numbers (Haug et al. 1993). For instance, in a survey of prairie dog colonies on national grasslands, burrowing owl occupancy was consistently higher on active than on inactive prairie dog colonies (although some national grasslands had many burrows but few owls, suggesting that appropriate habitat is necessary but not sufficient; Sidle et al. 2001). In addition, burrowing owl fledging success is higher in areas with greater numbers of prairie dogs (Desmond and Savidge 1996). In Wyoming, burrowing owl presence was shown to be a positive function of prairie dog presence (Korfanta et

al. 2001), and in California, burrowing owl reoccupancy of historical nesting sites was highly correlated with the presence of ground squirrels (DeSante et al. 1993).

Given that western burrowing owls rely on other species to excavate nest burrows, their populations are inextricably tied to small mammal species. However, these species have been actively persecuted in many areas, and this practice threatens to further limit burrowing owl populations. Reduced burrow availability was cited as a source of burrowing owl population declines by many states, including Colorado, Kansas, and South Dakota within Region 2. Black-tailed prairie dogs, which are a major source of burrowing owl nesting sites within Region 2, are estimated to have experienced an overall population decline of 98 percent (Coppock et al. 1983, Miller et al. 1994), largely attributable to widespread eradication campaigns. Whereas very large prairie dog complexes were once relatively common in the Great Plains, they are now rare, and they no longer occur in many states. For instance, Merriam (1902) discussed a prairie dog complex in Texas that covered approximately 65,000 km<sup>2</sup>. Sylvatic plague, which quickly decimates prairie dog colonies, also contributes to regional prairie dog population declines (Restani 2002). Ground squirrels, another important supplier of owl nesting burrows, have also been subject to population control.

The prairies of the Great Plains have been termed the “most endangered ecosystem in North America” (Samson and Knopf 1994), and the loss of this habitat has also likely reduced burrowing owl numbers. Grassland bird species are declining faster than any other avian guild (Askins 1993), and habitat loss due to urban and agricultural development is cited as a major factor contributing to burrowing owl population declines. The degree to which habitat loss has impacted burrowing owls varies throughout their range, but even in the relatively rural states of Wyoming, South Dakota, Nebraska, and Colorado, habitat loss is considered an important source of burrowing owl population declines (**Table 1**; James and Espie 1997).

#### *Population connectivity and degree of isolation*

With loss of habitat through human encroachment and reductions in small mammal populations, burrowing owl habitat has necessarily become less continuous than it was historically. Burrowing owls are thought to be philopatric (Plumpton and Lutz 1993) and tend to return to historical nesting sites, often in spite of declining habitat quality. Increasingly, burrowing owls are beginning to occupy patches or islands of habitat,

particularly near urban centers and at the periphery of their range.

Nevertheless, burrowing owls are highly mobile, and it is not clear whether the level of habitat fragmentation to date is sufficient to isolate populations. Evidence for high population connectivity derives from banding studies and a population genetic study. Adult and juvenile dispersal is not well understood in burrowing owls, with different studies providing very different estimates of dispersal distances. For instance, in resident Florida populations, natal dispersal distances averaged 1,116 m and 414 m for females and males, respectively (Millsap and Bear 1997). But in migratory populations in Canada, young returned the following year up to 30 km from natal sites (Haug et al. 1993). A recent radio collar study of burrowing owls in California documented several long distance dispersal events of over 53 km (Rosenberg personal communication 2003). Traditional mark-recapture and radio collar studies tend to miss infrequent, long-distance dispersal events when individuals leave the study area, and these missing individuals are commonly treated as mortalities rather than emigrants under most mark-recapture models (e.g., Nicholas and Kaiser 1999). These hard-to-detect dispersal events likely play a critical role in maintaining burrowing owl population connectivity.

A population genetics study of migratory and resident burrowing owl populations further supports population connectivity. Among 15 populations from the western and Florida subspecies, genetic differentiation of populations was minimal, and populations within subspecies were essentially panmictic, meaning that no evidence exists for genetic substructuring (Korfanta 2001). Included in this study were four Wyoming populations, which showed low genetic distances and high outbreeding levels. Even in the more fragmented habitats of California and Florida, there was no evidence of genetic isolation of populations. This suggests that geographic isolation of populations has not yet had discernible genetic consequences. Given that genetic data reflect the accumulated patterns of historical events and may not respond instantaneously to a lack of contemporary gene flow, it is difficult to reject the hypothesis that current gene flow remains similar to that found in the past.

Conflicting evidence comes from a separate population genetic study in a declining central California population. That population, which went locally extinct soon after the study, showed a homozygote excess, suggesting inbreeding as a result of small deme size (Johnson 1997a). Thus, geographic

isolation may be an issue in extreme cases and may lead to genetic inbreeding.

Within Region 2, habitat discontinuity and population isolation are probably less limiting factors than in other parts of the burrowing owl's range that are more subject to extensive human development. Even in Region 2, however, urban development (Zarn 1974) and fragmentation of prairie dog habitat (Butts 1973, Zarn 1974) may begin to isolate populations. In Colorado, it is estimated that black-tailed prairie dogs once occupied 1,860,000 ha of land, but currently they occupy an estimated 36,000 ha (W. Van Pelt public communication). Fragmentation of prairie dog colonies is extensive (Flath and Clark 1986), and most remaining colonies are isolated and ~40 ha in size (Sidle et al. 2001). Population isolation may also be a concern at the eastern edges of the burrowing owl's range in states like South Dakota, Nebraska, and Kansas, but this has not been documented. For now, it appears that the high vagility of burrowing owls prevents most populations from extreme isolation.

#### Population trend

There is strong evidence for a widespread, persistent decline in western burrowing owl numbers (Sheffield 1997a). Most long-term population trend analysis comes from the BBS and the Christmas Bird Count (CBC). BBS data have the advantage of standardized search effort for over 34 years. BBS data for the period 1966 to 2000 show an overall decline of 1.6 percent per year in burrowing owl numbers (Sauer et al. 2001); this estimate was not, however, statistically significantly different from 0 percent change ( $P = 0.54$ ). Trend estimates are shown for all Region 2 states in **Table 1**. Each of these states shows a negative population trend for the 1966 to 2000 time period. However, none of these trends is statistically significant and data from all states are considered to have low credibility because of very small sample sizes (Sauer et al. 2001). CBC data since the mid-1970's show a significant decline of 0.6 percent per year in burrowing owl numbers in those states that host wintering populations (e.g., Arizona, California, Louisiana, New Mexico, and Texas; Sauer et al. 1996).

Population trend data also come from a survey of state wildlife agencies (**Table 1**; James and Espie 1997). Over half of jurisdictions responding to the survey in 1992 reported declining populations, and no jurisdictions reported increasing populations. South Dakota and Wyoming reported stable populations while Nebraska, Kansas, and Colorado reported declining

populations (James and Espie 1997). In Colorado, no long-term surveys (other than the BBS) have been conducted to determine population trends; however, the Rocky Mountain Bird Observatory has completed a thorough initial survey of burrowing owls in the state to establish baseline data and distributional information (VerCauteren et al. 2001). Although the survey will need to be repeated to gain trend information, it is clear at this point that populations have already been extirpated from the heavily developed eastern aspect of the Front Range (Niedrach and Rockwell 1939).

In Wyoming, there is also no extensive, statewide survey effort aside from the BBS. There is however, the Wyoming Game and Fish Department's Wildlife Observation System (WOS) database, comprising wildlife sightings within the state, voluntarily reported by state and federal biologists, researchers, Audubon Society members, and interested members of the general public. The WOS database is extensive, containing 713 records of burrowing owl sightings between 1974, when the program began, and 1997. Korfanta et al. (2001) analyzed the WOS data to assess trends in burrowing owl sightings and found a significant, negative, linear relationship ( $P = 0.002$ ,  $r^2 = 0.64$ ) between numbers of burrowing owl sightings and year for the 1986 to 1997 subset of the data. During the same time period, however, WOS records also declined significantly for red-tailed hawk (*Buteo jamaicensis*), bald eagle (*Haliaeetus leucocephalus*), and American kestrel (*Falco sparverius*), three species whose populations have been stable or increasing in the region (Sauer et al. 2001). Thus it is difficult to tease apart trends of interest in the database, which may introduce a bias, from real population trends. Korfanta et al. (2001) recommended a standardized search effort that would address the sample size problems inherent in BBS data and the biases present in WOS data. Currently, standardized surveys are conducted within the Thunder Basin National Grasslands in northeastern Wyoming (Conway and Lantz 2003, Conway and Simon 2003; see "Tools and practices" section). However, statewide estimates will require more extensive survey coverage within Wyoming.

#### Activity patterns and movement

##### *Circadian patterns*

Among the traits that set burrowing owls apart from other Nearctic Strigiformes is their unusual daily time budget. Burrowing owls exhibit a range of daily activity patterns depending on season and temperature, and they are variously described as diurnal, crepuscular,

and nocturnal. Several researchers have described intensive crepuscular foraging activity by males during the breeding season (e.g., Coulombe 1971, Sissons et al. 2001), but foraging at all times of day is also common (Thomsen 1971, Marti 1974, Thompson and Anderson 1988). Coulombe (1971) identified four types of daily activity patterns: those that occur during winter, the incubation period, fledging, and the post-breeding period. In a resident California population, pair bonds were sometimes maintained year round, and males and females were often seen together outside the burrow in the mornings and evenings of winter months. During the daytime, one individual would remain outside the burrow while the other individual roosted in the burrow. Attachment to a primary burrow during this time was low, and pairs were observed to move readily to a new burrow if disturbed. During the incubation period, the female typically remains belowground for long stretches of time while the male remains close to, but rarely enters the burrow. During fledging, the male again keeps sentry over the nest burrow throughout the day, but the female begins to emerge for longer periods, especially during the morning and late afternoon. After fledging and when temperatures are usually the warmest, burrowing owls become less active during the midday and are often observed foraging along roads and elsewhere at night in family groups (Korfanta personal communication 2003). Several studies report primarily nocturnal behavior outside of the breeding season (Coulombe 1971, Butts 1973, Martin 1973a).

### *Migration*

Although most western North American burrowing owl populations migrate in winter months, the specifics of burrowing owl migration are poorly understood. There is some regional variability in the time that burrowing owls arrive on the breeding grounds although most reports show burrowing owls migrating north in March and April (Haug et al. 1993). Burrowing owls breeding in Saskatchewan may not arrive on breeding grounds until the first week of May (Haug et al. 1993), and Wyoming burrowing owls typically arrive on breeding grounds during the third week of April (Scott 1993). Burrowing owls may arrive on breeding grounds singly or paired (Martin 1973a), and it is not clear whether those arriving as pairs developed pair bonds on wintering grounds. If so, this may be an important means of connecting otherwise isolated populations. Even in populations that are considered migratory, some individuals may remain behind to overwinter on breeding grounds (Haug et al. 1993). In Oklahoma, 0.5 percent of the breeding pairs remained

as year-round residents (Martin 1973a), and in New Mexico, 3.0 percent remained (Butts 1973). Departure dates for winter migration probably vary among years depending on weather but generally occur in September and October (Haug et al. 1993)

Little is known about migration routes and destinations because of extremely low rates of band recovery (James 1992). Burrowing owls generally migrate in a leapfrog fashion, with Canadian owls migrating farther south than owls in the central United States (James 1992). In general, owls banded in western states and provinces (British Columbia, Washington, Oregon, and California) tend to migrate along the coast, while owls banded on the northern plains (Alberta, Saskatchewan, Manitoba, Idaho, Montana, and North Dakota) tend to migrate through Nebraska, Kansas, and Oklahoma (Haug et al. 1993). Owls banded in Wyoming and neighboring states have been recovered in southern states, including Texas and Oklahoma (Haug et al. 1993), and owls in North Dakota and South Dakota are thought to winter in Texas (Brenkle 1936). Two recent band recoveries suggest that Idaho burrowing owls may overwinter in or pass through southern California during migration (King and Belthoff 2001). Mexico also appears to be an important overwintering location for burrowing owls. A study of museum specimens from Mexico showed that 63 percent of 279 burrowing owls were collected during the non-breeding season, which may have been a result of an increased winter population from North American migrants (Enriquez-Rocha 1997). Regions in Mexico for which there were specimens only during the winter months (which may indicate areas of overwintering importance rather than breeding populations) include the Pacific states and some central states. Although these data suggest that Mexico is host to migratory overwintering birds, the specimens were principally collected in the early 1900's and may not represent current migration destinations for North American populations.

### *Dispersal*

Dispersal studies of burrowing owls have used mark-recapture techniques and radiotelemetry to show that dispersal patterns vary by sex, age, migratory history, and region. Natal dispersal can be defined as dispersal between natal area and breeding site or as permanent dispersal by young away from the nest burrow prior to migration. King and Belthoff (2001) used radiotelemetry to assess natal dispersal, which they defined as a permanent movement of at least 30 m from the nest burrow. Prior to permanent dispersal from the

nest, young made initial movements to satellite burrows that ranged from 38 to 280 m from the nest burrow. Juveniles permanently dispersed from the nest burrow around the end of July, or approximately four weeks after fledging. In a migratory Canadian population, average maximum dispersal distance detected prior to migration was 5.5 km (Clayton and Schmutz 1999). Mean natal dispersal distances were much lower in a Florida population [males: 414 m ( $N = 28$ ), females: 1116 m ( $N = 31$ ); Millsap and Bear 1997], suggesting that these distances may be greater in migratory than in resident populations.

Juvenile fidelity to natal sites as breeding locations in subsequent years was assessed in a Colorado population in which only 5 percent of juveniles returned one or more years after hatch (Lutz and Plumpton 1999). Thirteen of the returning birds (72 percent) were males, and five (28 percent) were female. In the same Colorado population, females always returned to their natal site after a minimum one-year absence while males generally returned the year immediately after hatch (Lutz and Plumpton 1999).

Adult burrowing owls are generally considered to be philopatric (Martin 1973a, Gleason 1978, Rich 1986, Haug et al. 1993, Rosenberg and Haley *in press*). However, this is based primarily on band-return studies, which may falsely equate dispersal outside the study area with mortality. Males and females banded as adults in a Colorado population returned to breeding locations within one or more years at similar ( $P = 0.045$ ) rates (19 percent and 14 percent, respectively; Lutz and Plumpton 1999). Of 273 individuals banded as adults in Florida, 68 percent used the same breeding site in the subsequent year (Millsap and Bear 1997), indicating that breeding site fidelity may be more prevalent in resident populations. There is little published on the degree of site fidelity in other resident populations such as those in southern California, but the pattern of lower dispersal in resident species relative to migratory species is common (Paradis et al. 1998) and may apply to the resident and migratory components within partial migrant species.

Female-biased dispersal was observed in a resident Florida populations, with females dispersing significantly ( $P = 0.005$ ) greater distances than males (230 m and 96 m, respectively) to new territories between years (Millsap and Bear 1997). However, Lutz and Plumpton (1999) observed equally philopatric males and females in a Colorado population and did not observe sex-biased dispersal.

One study has provided evidence for a lack of nomadism in burrowing owls (Poulin et al. 2001). In 1997, there was a large meadow vole outbreak on the Regina Plain of Saskatchewan, and burrowing owl numbers were assessed before, during, and after the outbreak. Although the number of burrowing owls did increase in the year following the outbreak (probably due to increased nestling and fledgling survivorship), there was no evidence that the owls responded to increased prey availability by searching for nesting sites with greater prey availability. This was in contrast to short-eared owl populations, which greatly increased in local abundance due to immigration of individuals, apparently in response to the vole outbreak.

### *Population linkages*

Relatively high connectivity among most populations may be inferred from burrowing owl behavior. Individuals are obviously highly mobile, but population isolation may still be maintained through philopatric behavior that limits dispersal among populations. As mentioned above, burrowing owls are considered to be at least somewhat philopatric to natal sites and faithful to breeding sites, but three lines of evidence point to ample opportunities for population connectivity. First, a researcher in California documented two long-distance dispersal events in a radiotelemetry study in which two adult, breeding burrowing owls in a large California grassland dispersed over 53 km between successive nesting sites following nest failure (Rosenberg personal communication 2003). While it is not clear how frequently these long-distance dispersal events occur in other populations, it is likely that traditional mark-recapture and even many telemetry studies are not of sufficient spatial scale to detect these movements. The second line of evidence for population connectivity comes from observations of burrowing owls arriving already paired on breeding grounds (Martin 1973a). While this phenomenon begs further study to determine if individuals are indeed meeting mates on wintering grounds and to measure the frequency of such behavior, the opportunity exists for connection of otherwise isolated and spatially disparate populations. And finally, genetic data showing panmixia across the western subspecies' range further supports at least some population connectivity (Korfanta 2001). Although populations from California and Wyoming (let alone populations just within Region 2) were not genetically distinguishable in this study, this does not imply direct dispersal among these distant populations. Rather, dispersal probably occurs in a stepwise pattern, with more geographically proximate

populations exchanging individuals. Gene flow among distant populations may then occur indirectly, with intermediate populations conveying genetic information to more distant populations.

While it appears that populations do not currently show genetic effects of isolation, there is certainly a threshold beyond which habitat fragmentation will begin to limit connectivity, a threshold that may already have been met in some landscapes. Clayton and Schmutz (1997) compared two Canadian burrowing owl populations with differing levels of habitat fragmentation. The Regina Plain, Saskatchewan population, which was found on remnant prairie fragments in a matrix of land that was over 90 percent cultivated, was compared with an Alberta population existing in habitat with less than 20 percent cultivation. Juvenile owls from Alberta dispersed significantly earlier, further, and more frequently from the nest than juveniles in the Saskatchewan populations. The authors attributed the lower dispersal of Saskatchewan owls to the highly-fragmented habitat, which discouraged juvenile movements. This was supported by reference to a similar study of crested tits (*Parus cristatus*), which also showed delayed post-fledging dispersal in highly-fragmented landscapes (Lens and Dhondt 1994). However, to more effectively isolate the effects of habitat fragmentation on dispersal, the study would need to be replicated over several years and locations to minimize confounding variables such as differences in prey availability, predation, etc.

## Habitat

### *Nesting macrohabitat*

With a nesting distribution covering much of western North America, the burrowing owl is somewhat of a habitat generalist. Here we identify the main components of burrowing owl macrohabitat and provide further discussion of the variation in patterns of owl use for each habitat component. Main components of burrowing owl macrohabitat within Region 2 are as follows:

- ❖ Open, dry, treeless areas, typically occupied by burrowing mammals that provide nest burrows
- ❖ Rangelands grazed by burrowing mammals and domestic livestock, which maintain short vegetation

Burrowing owl habitat typically consists of open, dry, treeless areas on plains, prairies, and deserts. These areas are also occupied by burrowing mammals and other animals that provide nest burrows (**Figure 10a**; Grinnell and Miller 1944, Haug et al. 1993). Because burrowing owls spend most of their time on or in the ground and are extremely susceptible to predation, short vegetation structure is also a requirement (Butts 1973, Zarn 1974, Green 1983, Plumpton 1992), as it presumably allows for better detection of predators and visibility of prey (Green 1983, Green and Anthony 1989). Given this requirement for short vegetation, burrowing owls are commonly found in association with cattle, prairie dogs, and other grazers that clip vegetation (Konrad and Gilmer 1984).

Although burrowing owls are primarily a grassland species within the Rocky Mountain Region, they can be found in highly-disturbed, human-altered landscapes such as golf courses, airports, campuses, residential areas, agricultural ditches, and in cities (**Figure 10b**; Coulombe 1971, Wesemann and Rowe 1987, Haug et al. 1993, Trulio 1997a). Use of such landscapes may be explained by 1) fidelity to historic nesting locations that were subsequently altered (Wiens 1985); 2) use of sub-optimal habitat due to limited preferred habitat; or 3) preferred use of the altered landscapes. Within Region 2, burrowing owl use of human-altered landscapes would most likely be observed in the Front Range of Colorado (Orth and Kennedy 2001).

Through their selection of certain vegetation and soil characteristics, burrowing owls often use the same habitat preferred for ranching and farming. Their use of agricultural lands for nesting and foraging is well documented throughout much of their range. Burrowing owls will nest on intensively grazed lands (Korfanta et al. 2001, Restani et al. 2001), which is consistent with their nesting and foraging requirement of short vegetation structure. However, Restani et al. (2001) found that burrowing owls neither preferred nor avoided grazed nesting habitat ( $\chi^2$ , 0.00,  $df = 1$ ,  $P = 0.069$ ) in Montana, and Howie (1980) asserted that cattle grazing was a direct source of burrow loss in Canada. While not within USFS Region 2, it is notable that burrowing owl densities can be disproportionately high following conversion of native habitats for agricultural use. In Baja California, Mexico, 43 percent of all burrowing owl records occurred on agricultural lands (not divided into ranching vs. cultivated lands), especially along dirt embankments (Palacios et al. 2000). In the highly agricultural Imperial Valley of California, breeding



**Figure 10.** Burrowing owl habitat is quite variable and ranges from (A) relatively undisturbed mixed-grass prairie and rangelands to (B) residential developments. In both areas shown here, burrowing owls nested in prairie dog burrows. Common to all habitats used by burrowing owls are relatively short vegetation and natural or man-made burrows that serve as nesting and escape cover.

densities of burrowing owls were an estimated 8.3 pairs/km<sup>2</sup>, dramatically higher than the low nest densities in the surrounding deserts (DeSante et al. *in press*, Rosenberg and Haley *in press*). Rich (1986) found that 30 of 80 burrowing owl nests in southern Idaho contained intensively cultivated farmland in at least part of a 693-m radius, as well as in 41 of 53 nest sites in southwestern Idaho on the Birds of Prey Natural Area.

It is important to note that while it is not directly addressed in the literature, it is possible that high road densities within agricultural areas may increase survey area and positively bias burrowing owl detection probabilities. And while it is clear that burrowing owls use agricultural landscapes, there is no consensus on how agriculture affects their persistence. Ranching (livestock grazing) and farming (cultivation) probably

have different implications for burrowing owl habitat suitability in many areas. Livestock grazing may serve to decrease vegetation height and to increase available habitat for nesting burrowing owls (Wedgwood 1976). Gleason and Johnson (1985) found no significant difference ( $F = 1.52, P > 0.05$ ) in brood size between 14 burrowing owl pairs nesting in irrigated alfalfa crops versus 13 pairs nesting in rangeland. Leptich (1994) compared raptor numbers on cultivated lands versus rangelands in Idaho and found that burrowing owls were the only raptor to show a preference for cultivated landscapes during the summer months (June and July). However, during the spring (March 16 through May 31), the relative abundance of burrowing owls was higher on rangeland, which may suggest a preference of rangeland for nesting and cultivated lands for foraging. Haug (1985) also examined the effects of cultivation on burrowing owls in Canada and found that home range increased significantly as a positive function of percent-cultivated land, suggesting that foraging distances may increase with greater cultivation. Haug and Oliphant (1990) also found that intensively cultivated fields were avoided by burrowing owls, as were intensively grazed regions of rangeland. Schmutz (1997) found more burrowing owl nests adjacent to cultivated fields relative to control sites, but the difference was not significant ( $P = 0.328$ ). Rosenberg and Haley (*in press*) speculate that high owl densities within an intensively-cultivated, heavily-irrigated area in California are due to increased prey abundances and tolerance of burrows by local farmers. Belthoff and King (2002) speculated that burrowing owls in southwestern Idaho may benefit from a close proximity to irrigated agriculture, where prey can be more abundant than in the surrounding, more arid landscape. In conclusion, patterns of burrowing owl habitat use within agricultural landscapes are not well understood.

#### *Nesting microhabitat*

Primary factors influencing burrowing owl nest-site selection may vary somewhat within Region 2, and the following summary should not replace local studies of burrowing owl habitat use. However, the following list and subsequent discussion provide a thorough enumeration of the habitat components that consistently emerge with significance in burrowing owl habitat studies throughout Region 2:

- ❖ High densities of available burrows for nesting.
- ❖ Active, or very-recently abandoned, prairie dog colonies.

- ❖ Close proximity to other nesting burrowing owls.
- ❖ Close proximity to occupied prairie dog burrows.
- ❖ Short vegetation around nest burrow, low shrub density, and high forb density.
- ❖ Presence of dried manure for lining of nest burrow.

For western burrowing owls, which do not usually excavate their own nest burrows, the presence of recently-excavated burrows is the primary habitat requirement for nesting. Burrowing owls tend to rely on whatever burrowing animals are most abundant in an area (Haug et al. 1993), including badgers (*Taxidea taxus*; who also widen existing burrows), yellow-bellied marmots (*Marmota flaviventris*), skunks (*Mephitis* spp., *Spilogale putorius*), kangaroo rats (*Dipodomys* spp.), and desert tortoises (*Gopherus agassizii*). Many species of ground squirrels provide burrows, including round-tailed ground squirrel (*Citellus tereticaudus*; Coulombe 1971), Townsend's ground squirrel (*Spermophilus townsendii*; Gleason and Johnson 1985), and Richardson's ground squirrel (*S. richardsoni*; Konrad and Gilmer 1984). In some areas, they also use rock cavities (Rich 1986), holes in arroyo banks (Botelho and Arrowood 1995), and artificial cavities such as drainage pipes (G. Holroyd public communication), so there appears to be significant flexibility in nest-site selection. Within Region 2 and elsewhere, black-tailed (*Cynomys ludovicianus*), white-tailed (*C. leucurus*), and Gunnison's (*C. gunnisoni*) prairie dogs are an important source of burrows (Clark et al. 1982, Sidle et al. 2001).

Many studies show that burrowing owls preferentially use active or very-recently abandoned colonies of black-tailed prairie dogs. For instance, in Oklahoma, Butts and Lewis (1982) found that 66 percent of adult owls were found on active prairie dog colonies, even though this habitat type constituted only 0.16 percent of the study area. Further, in three prairie dog colonies lost to cultivation, no owls nested there in the following three years, and in prairie dog colonies that had been poisoned, no owls nested after three years (Butts and Lewis 1982). The authors further noted that prairie dog burrows quickly became filled in with soil and grass and that nearly all of the vacant burrows lost their identity within three years. In Nebraska, Desmond et al. (2000) found that nesting pairs of burrowing owls declined 63 percent from 1990 (91 nests) to 1996 (34 nests), and this decline was correlated with

declines in burrow densities within surveyed colonies. Desmond et al. (2000) also found depressed fledging rates (1.9 juveniles per nest) among burrowing owls nesting in colonies where the number of active burrows was decreasing. On the Rocky Mountain Arsenal in Colorado, Plumpton and Lutz (1993) found that among all prairie dog colonies surveyed, nesting burrowing owls were found only within active prairie dog colonies. They also found that over a 14-year period (1988 to 2001), burrowing owl nesting densities tracked fluctuations in active prairie dog colony area within the Rocky Mountain Arsenal (Antolin et al. 2002).

Burrowing owls may nest as solitary pairs like most other raptors, but they also nest in loose colonies or aggregations (Haug et al. 1993). Two lines of evidence suggest that colonial nesting is not simply a function of clumped burrow distribution resulting from coloniality of the primary excavator (e.g., prairie dogs or ground squirrels). First, burrowing owls that use burrows excavated by badgers, a species that does not exhibit the level of coloniality seen in prairie dogs, still tend to nest in loose aggregations, although some researchers have attributed this to insufficient burrow availability rather than to a preference for clumped nesting (Gleason 1978, Haug 1985, Green and Anthony 1989). Second, burrowing owls tend to nest in a clumped distribution even when excess burrows are present over a broader area. Desmond et al. (1995) showed that in small prairie dog colonies (<35 ha), burrowing owls nested in a random distribution, while in large prairie dog colonies (>35 ha) owl nests were clumped. The authors argued that in large colonies, the owls were able to exhibit their preferred nesting strategy, which also indicated that a lack of burrows was not driving colonial nesting. What then is the value of nesting in colonies when drawbacks include the potential for greater intraspecific competition, disease transmission, conspicuousness to predators, and infanticide (Welty and Baptista 1988)? Authors point to improved predator detection as an important benefit of coloniality, especially given that burrowing owls are particularly susceptible to predation on the ground (Green and Anthony 1989, Desmond et al. 2000). In a study of nesting density on Nebraska prairie dog colonies, Desmond et al. (1995) found some evidence of greater fledging success with increasing burrowing owl nesting density, although supporting data were not presented.

Among colonial nesting burrowing owls, nesting density varies greatly. This is important because breeding density of raptors often correlates with habitat quality (Newton 1979, 1998, Gehlbach 1994). Average nest densities of burrowing owls in western Nebraska

have been reported as 0.9 to 2.5 owls/ha on the cluster scale (Desmond and Savidge 1999). The highest nesting density reported was in small (<35 ha) prairie dog colonies in Nebraska where nesting densities ranged from 0.1 to 30.0 owls/ha (Desmond and Savidge 1996). In large (>35 ha) prairie dog colonies, burrowing owl densities were 0.03 to 0.4 owls/ha (Desmond and Savidge 1996). These density estimates were lower than those reported for Oklahoma burrowing owls (0.7 owls/ha; Butts 1973). Maximum breeding densities outside of Region 2 include 9 pairs/km<sup>2</sup> in California (Coulombe 1971, Trulio 1997a), and 17 pairs/km<sup>2</sup> in North Dakota (Grant 1965) and Saskatchewan (Wedgwood 1976). Nesting density in a Florida population disrupted by a housing development was 6.9 pairs/km<sup>2</sup> (Millsap and Bear 2000). In Colorado, Plumpton and Lutz (1991) found that burrowing owls nested preferentially (*t*-test, *df* = 18, *P* = 0.009) in areas with greater burrow density relative to control sites in the first year of a two year study; however, there was no difference between control and occupied sites in the following year. In both years of the study, burrowing owl-occupied colonies were no different from unoccupied colonies in overall size ( $\chi^2$  = 1.9, *df* = 1, *P* = 0.16; Plumpton and Lutz 1993). In the first year, burrows used were closer to roads than were controls, but not in the following year (Plumpton and Lutz 1993). Desmond et al. (2000) showed lower predation by badgers on owl nests in prairie dog colonies with higher burrow density. Studies have also shown that burrowing owls may select burrows near the edge of prairie dog colonies where unoccupied prairie dog burrows are abundant (Desmond et al. 1995, Toombs 1997, Orth and Kennedy 2001).

Nesting near active prairie dog burrows also appears to be an important requirement for burrowing owls. Restani et al. (2001) observed a significant difference between burrows with and without nesting burrowing owls; burrowing owl burrows were significantly closer to active prairie dog burrows than to inactive ones (14.6 m ± 7.1 and 21.8 m ± 6.4, respectively; *P* = 0.08). Desmond et al. (2000) found that successful nests (fledging = 1 juveniles) had an average of 96 active prairie dog burrows within 75 m of the nest, while unsuccessful nests had an average of 26. Likewise, Hughes (1993) showed that burrowing owl nesting density was higher in prairie dog colonies where greater than 90 percent of the prairie dog burrows were active (2.85 individuals/ha, as opposed to 0.57 individuals/ha in colonies of 70 to 80 percent activity). Burrowing owls may benefit from nesting near prairie dogs due to the dilution effect, meaning that predators have more prey options when prairie dogs are present (Desmond and Savidge 1999). Also, burrowing owls

may benefit from the alarm calls issued by prairie dogs in response to predators (Desmond and Savidge 1999). Burrowing owls may select nest sites near active prairie dog burrows because in the absence of prairie dogs, vegetation around burrows may become too tall to be suitable for nesting (Butts and Lewis 1982, Plumpton and Lutz 1993).

In addition to the primary nest burrow, juvenile burrowing owls also typically use several satellite burrows in the vicinity of the nest prior to fledging (Haug et al. 1993, Desmond and Savidge 1999, Ronan 2002). Potential advantages of this behavior include defense against predation of the entire clutch (Desmond 1991), relief from crowding or ectoparasite load in the primary nest burrow, and more equitable distribution of food among chicks of slightly differing size (Butts and Lewis 1982). In an Idaho population, juveniles used an average of three satellite burrows within their natal areas for roosting before permanently dispersing (King and Belthoff 2001) while juveniles in Nebraska used an average ( $\pm$  SE) of  $10 \pm 0.98$  burrows in the vicinity of the primary nest burrow (Desmond and Savidge 1999). In this same population, most chicks preferred ( $P < 0.05$ ) active prairie dog burrows to inactive burrows.

When considering burrowing owl preferences for vegetation characteristics in the immediate vicinity of the burrow, it is difficult to tease apart the preferences of the owls from those of the mammal that created the burrow (Schmutz 1997). The one consistent vegetation requirement for burrowing owl nests is that vegetation be short. Plumpton and Lutz (1993) found that Colorado owls were significantly ( $P < 0.05$ ) more likely to nest in burrows that had lower grass height and more bare ground than did control sites. Likewise, MacCracken et al. (1985) found that burrowing owl-occupied burrows in South Dakota had greater forb cover but lower vegetation height than unoccupied burrows. The authors concluded that burrowing owls were nesting in vacant prairie dog burrows that were in an early stage of plant succession where vegetation height was lower than on the surrounding prairie. They also speculated that greater forb cover might help provide concealment for emerging owlets. However, in subsequent years when vegetation height increases and abandoned burrows collapse, burrowing owls may nest in different burrows within the same or different (more active) prairie dog colonies (Conway and Lantz 2003).

Soil composition may be an important consideration, as many studies have reported that burrowing owls often modify the burrow prior to nesting. Thomsen (1971) reported that both male

and female adults kick backward with their feet and move soil with their beak, and Best (1969) reported that the adults walked through burrows with their wings outstretched to dislodge dirt from the burrow walls. MacCracken et al. (1985) found that burrowing owl nest burrows had greater sand content than did unused burrows, and although the relationship was not statistically significant ( $P < 0.14$ ), the authors believed that it was biologically significant. They speculated that the sandier soils would be easier for burrowing owls to modify, a hypothesis that was supported by the fact that nest burrows in a California study (Coulombe 1971) had greater diameters than non-nest burrows, suggesting modification. Use of burrows with sandier soils may also be important for water drainage, to avoid flooding during rainstorms (MacCracken et al. 1985). Coulombe (1971) observed that most nests in the Imperial Valley of California were located between firm, eroded sandstone and a softer layer of silt underneath. Butts and Lewis (1982) did not find a preference of Oklahoma burrowing owls for soil type, but rather, found them nesting in a range of soil types including clay, sand, and gravelly soils. Wellicome and Haug (1995) found that burrowing owls in Saskatchewan nested in lacustrine soils, which are sandy or silty loam soils with few rocks. Like vegetation features, soil characteristics of nest burrows may be a function of the preferences of the primary burrower as well as the nesting burrowing owls.

One of the most unusual burrowing owl behaviors is that adult males will often line the entrance of the nest burrow and the nesting cavity itself (Butts and Lewis 1982) with shredded dried cow or horse manure (**Figure 11**). In the absence of dung, burrows may also be lined with grass, feathers, and other materials (Haug et al. 1993). Nest burrows in urban areas are often adorned with shells, shredded paper, cigarette butts, and other debris (Haug et al. 1993). Owls near a municipal golf course used grass divots on the outside of their nest burrows (Thomsen 1971). Several explanations have been posited for this behavior, including masking the scent of the nest from predators (Martin 1973a), a hypothesis that was supported by significantly ( $\chi^2 = 14.1$ ,  $P < 0.001$ ) lower predation by badgers of dung-lined burrows relative to unlined burrows in north-central Oregon (Green and Anthony 1989). Others have postulated (without statistical support) that the dried manure aids in moisture absorbency (Martin 1973a), or in insulation (Zarn 1974). Levey et al. (2002) showed experimentally that increased manure led to increased density of dung beetles (*Deltachilum gibbosum*), an important food resource in the Florida habitat where the study was conducted. The presence of shredded manure on the outside of burrows is very helpful in identifying burrowing owl burrows,



**Figure 11.** Typical burrowing owl nest burrow in Thunder Basin National Grasslands, Wyoming. The material at the entrance of the burrow is shredded cow and horse manure, and coyote feces. Also note prey remains (lark bunting feathers, mammal bones) and cast pellets.

although not all nest burrows have this lining. Satellite burrows, typically used by adult males and fledgling juveniles, generally lack any manure lining.

Nest burrows are generally oriented without regard to compass direction (Todd and James 1989, Plumpton and Lutz 1993), but they do tend to be on areas of low slope (<10 percent; Rich 1986). The dimensions of the nest burrow vary slightly by region, but in general they are similar to those measured in Oklahoma by Butts and Lewis (1982). Burrow entrances were 14 to 15 cm wide by 11 to 13 cm high, and the tunnel was 150 cm long. The nest chamber was ~ 70 cm belowground and was on average 25 cm wide by 10 to 15 cm tall. Generally, the tunnel is wider at its entrance (Zarn 1974) with a mound of dirt on the outside that is often used for perching (Haug et al. 1993). Any alternative entrances to the nest cavity are usually plugged with dirt and debris (Butts and Lewis 1982). Coulombe (1971) found that the temperature of the nest chamber was not significantly different from that at the entrance of the burrow, but humidity was near saturation 30 cm from the entrance. Underground burrows may be relatively insulated from ambient temperature fluctuations.

Because burrowing owls are often observed using perches for roosting, hunting, or watching the nest

burrow, the presence of perches may be an important nesting habitat criterion (Clayton 1997). A principal component analysis of nesting habitat associations in Durango, Mexico, showed that the number of perches in the vicinity of the nest burrow was an important factor (Rodríguez-Estrella and Ortega-Rubio 1993). In contrast, burrowing owls at the Rocky Mountain Arsenal in Colorado nested in burrows that were significantly further from perches ( $x = 11$  m) than were control burrows ( $x = 6.8$  m) (Plumpton and Lutz 1993). The authors speculated that because the vegetation was less than 8 cm, elevated perches were not necessary for detection of predators or for hunting. Perch avoidance by burrowing owls has also been documented in Oregon, where elevated perches were not typically used when vegetation was  $\leq 5$  cm (Green and Anthony 1989).

#### *Foraging habitat*

The primary requirement for suitable burrowing owl foraging habitat appears to be low vegetation cover that allows visibility and access to prey. In a radiotelemetry study of six burrowing owls in central Saskatchewan, Haug and Oliphant (1990) found that the owls used grass-forb habitat for foraging. Rights-of-way and uncultivated areas were used disproportionately more often in relation to their availability. Crop areas

were avoided, even though prey density [deer mice (*Peromyscus maniculatus*) and voles (*Microtus* spp.)] was higher there. Avoidance of crop areas may have been due to the diminished prey visibility in the taller vegetation, which may be more important than absolute prey density (Haug and Oliphant 1990). Haug and Oliphant (1990) also observed that burrowing owls avoided grazed pastures, probably because there was insufficient vegetative cover for rodents. An important caveat to this study is that it did not take into account the distance of the nest to different habitat types and that all nests were located in grass-forb cover. Butts (1973) found that burrowing owls in Oklahoma foraged mostly in wheat fields, where rodent populations were high. Likewise, Gleason (1978) found that burrowing owls foraged for montane voles (*M. montanus*) in agricultural areas during the breeding season, and Rich (1986) found more vole parts in pellets of burrowing owls with more farmland near the nest burrow. Rosenberg and Haley (*in press*) also found that burrowing owls frequently used cultivated areas for foraging in the Imperial Valley of southern California and speculated that the very high burrowing owl density in this area may be attributable to the prevalence of agricultural development. In another radiotelemetry study of four burrowing owls in Saskatchewan, two owls significantly avoided crops and preferred pasture, while one owl showed significant avoidance of fallow fields (Sissons et al. 2001). Foraging habitat preference was for those areas with the lowest small mammal populations (i.e., pasture), but also lower vegetation height. The authors concluded that the higher prey densities in crops were essentially inaccessible due to vegetation density and height >0.5 m and that prey abundance alone does not drive selection of foraging habitat (Sissons et al. 2001). Sample sizes in this study were low, and it may not be safe to extrapolate the results to the entire population of the study, let alone to populations elsewhere.

Although open areas with short vegetation are critical for nesting, there is some evidence that burrowing owls prefer a vegetation mosaic with nesting habitat interspersed within taller vegetation for hunting (Clayton and Schmutz 1999). Unlike the previously described studies, Clayton and Schmutz (1999) observed burrowing owls in Saskatchewan hunting from perches and gleaning insects in tall vegetation. Tall vegetation may provide the cover necessary to host large populations of rodents, which are then susceptible to predation as they traverse open areas in the mosaic (Clayton and Schmutz 1999). Very low vegetation and sites with exposed soils are important oviposition sites for grasshoppers, another important prey item that

may be supported in a vegetation mosaic (Clayton and Schmutz 1999). In conclusion, the degree of preference for or avoidance of vegetation as a function of its height may reflect a complex set of cost-benefit tradeoffs with increased prey density for capture by the owls playing off against increased risk of predation on owls.

#### *Seasonal habitat use*

Although burrowing owl breeding habitat has been extensively studied, much less is known about their habitat requirements during migration and on wintering grounds. In general, burrowing owls need burrows year-round for resting, escape cover, and protection from the elements, but they may be more flexible in burrow selection during the non-breeding months. Observations of burrowing owls that remain on breeding grounds year-round suggest that they use similar habitat in the winter months, although unlike nest burrows, burrows used in the winter are not necessarily enlarged at the terminus (Butts and Lewis 1982). Although northern burrowing owl populations are thought to winter in Mexico, little is known about their wintering habitats there (Enriquez-Rocha 1997).

#### *Home range*

Estimates of burrowing owl home range are highly variable within and among studies and are probably a function of landscape characteristics, prey availability, and other dynamic factors (Rosenberg and Haley *in press*). In general, burrowing owls remain near the nest burrow during daylight and forage farther from the nest at sunrise and sunset (Klute et al. 2003). Haug and Oliphant (1990) estimated that owls occupying a mosaic of cereal crops and rangeland in Canada had home ranges of 14 to 480 ha ( $\bar{x}$  = 240 ha) and that diurnal activities generally occurred within 250 m of the nest. Burrowing owls in the Central Valley of California had average home ranges of 189 ha (J. Gervais unpublished data), and in the Imperial Valley of California home range estimates varied from  $45.3 \pm 18.2$  ha (fixed kernel estimator) to  $184.5 \pm 65.1$  (adaptive kernel estimator) (Rosenberg and Haley *in press*). Also in the Imperial Valley, over 80 percent of foraging locations were within 600 m of the burrowing owl nest (Rosenberg and Haley *in press*). In Wyoming, Thompson and Anderson (1988) observed that foraging areas encompassed 3.5 ha, and males made foraging movements further from the nest while females tended to forage within 70 m of the nest. Haug (1985) observed that burrowing owl home ranges increased with increasing degree of cultivation in the surrounding landscape.

### *Changes in burrowing owl habitat*

Burrowing owl habitat requirements appear to be relatively flexible once their two critical requirements — short vegetation and burrow availability — are met. Nonetheless, available habitat has decreased as grassland ecosystems have been extensively modified and lost to human land use regimes (Bent 1938, Rowe et al. 1986). In Saskatchewan, loss of native prairies has been particularly alarming, with 21 percent loss of habitat over a 7-year period (Hjertaas and Lyon 1987). Loss of habitat to urban development has been blamed for burrowing owl declines throughout the species' range (DeSante and Ruhlen 1995, Trulio 1995, Trulio 1997b). A more pervasive problem, however, may be the loss of populations of prairie dogs and other burrowing mammals that provide nest sites and escape cover for burrowing owls (Butts 1973). Under the perception that prairie dogs compete for range resources with livestock and are generally a pest species, eradication programs and other anthropogenic landscape changes are estimated to have reduced prairie dog populations to 2 percent of their previous size (Coppock et al. 1983, Miller et al. 1994).

Sylvatic plague (*Yersinia pestis*) has further reduced prairie dog populations in some areas, with the consequence being fewer burrows and a more fragmented distribution. When a plague epizootic occurred on prairie dog colonies of the Ft. Belknap Indian Reservation in Montana, prairie dog density was reduced by 30 percent during the first year (Restani et al. 2002). Restani et al. (2002) found that productivity decreased if fewer than 10 burrows occurred within a 30 m radius of the burrowing owl nest. Recurrent plague epizootics observed from 1988 to 2001 on the Rocky Mountain Arsenal in Colorado resulted in dramatic fluctuations of prairie dog colony area (Antolin et al. 2002), and the numbers of nesting burrowing owls tracked the fluctuations in prairie dog colony area during these epizootics. Finally, in an extensive survey of burrowing owls within 14 national grasslands, Sidle et al. (2001) found that while burrowing owls were found on 307 of 444 (69 percent) of active prairie dog colonies, only 15 of 138 (11 percent) colonies that had experienced plague epizootics contained burrowing owls.

### *Food habits*

#### *Techniques and caveats*

Most studies of burrowing owl diet have focused on quantitative pellet analyses. However, pellets may be a biased indicator of prey intake for the following

reasons: 1) pellets with fur remain intact longer, 2) pellets with chitin may disintegrate quickly, and 3) soft-bodied organisms may not show up in the pellets at all (Grant 1965, Coulombe 1971, Marti 1974). Although burrowing owls have been observed catching amphibians, they rarely show up in pellet remains (Grant 1965). A comparison of prey remains versus castings from Colorado owls showed that spadefoot toads (*Scaphiopus* spp.), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), moths, and black-tailed prairie dogs were more likely to be detected as prey remains than in castings (Plumpton and Lutz 1993). Conversely, beetles and deer mice occurred more frequently in castings (Plumpton and Lutz 1993).

#### *Seasonal shifts*

As a generalization, insects comprise the majority of prey items by number, but rodents comprise the majority of biomass in pellets during the summer months (Green and Anthony 1989, Haug et al. 1993). During winter and spring, burrowing owls shift away from insects and rely more heavily on rodents and other vertebrates. In a study of 5,559 pellets from Idaho burrowing owls, Green and Anthony (1989) found that arthropods made up 92 percent of prey items, with vertebrates accounting for 8 percent; however, in terms of biomass, vertebrates (primarily rodents) made up 78 percent of the diet. Similarly in Wyoming, Thompson and Anderson (1988) found that 88 percent of the prey remains were invertebrates, but vertebrates accounted for 95 percent of the prey items by biomass. Rodents constitute a greater proportion of burrowing owl diet in California (29 percent) and Chile (20 percent), which is likely a reflection of prey availability rather than selection (Jaksic and Marti 1981). Green et al. (1993) found that vertebrates were more important in the diets of Washington owls (17 percent) relative to Oregon owls (8 percent), which they attributed to greater grasshopper availability at the Oregon site. A recent study analyzed the winter diet of burrowing owls in central Mexico and found burrowing owl diet during this time to be quite similar to that in the summer months (Valdez Gomez et al. 2002). Roughly 20 percent of the prey items were mammals while 78 percent were invertebrates (especially crickets and grasshoppers). Rodents comprised the majority (77.95 percent) of the mammal component of the diet, followed by shrews (11.50 percent) and bats (0.88 percent).

#### *Selection in relation to availability*

The specific prey species taken tend to correlate positively with what is abundant and accessible. In

Wyoming, Thompson and Anderson (1988) found a great number of grasshoppers (Acrididae), ground beetles (Carabidae), darkling beetles (Tenebrionidae), and ants (Formicidae) in burrowing owl pellets. Among mammals found in the pellets, the most prevalent were Richardson's ground squirrel, thirteen-lined ground squirrel, deer mouse (*Peromyscus maniculatus*), and prairie vole (*Microtus ochrogaster*). To a lesser extent, birds were present in the pellets as well, including horned lark (*Eremophila alpestris*), lark bunting (*Calamospiza melanocorys*), and lark sparrow (*Chondestes grammacus*). Thompson and Anderson also found evidence of tiger salamander (*Ambystoma tigrinum*) and crayfish (*Cambarus* spp.).

Prey items taken in a Colorado population were similar to those in Wyoming (Plumpton and Lutz 1993). In a use versus availability study of insects in a burrowing owl colony, Plumpton and Lutz (1993) found greater than expected use of carrion beetles (Silphidae) and less than expected use of short-horned grasshoppers, ground beetles, and camel crickets. They also found evidence of large species in prey remains, including prairie rattlesnakes (*Crotalus viridis*) and prairie dogs, which may have been scavenged. The propensity for burrowing owls to scavenge requires further investigation, as there is a risk that the owls will ingest lead shot present in dead prairie dogs (Johnson personal communication 2003).

#### *Diversity and flexibility of the diet*

The diversity of organisms found in burrowing owl pellets and the fact that their diet corresponds with prey availability support the notion that burrowing owls are fairly opportunistic (Green et al. 1993). For instance, burrowing owls living near a marsh in California preyed mostly on black terns (*Chlidonias niger*) and tri-colored blackbirds (*Agelaius tricolor*) (Neff 1941). Green et al. (1993) found ichneumon wasps, blow fly pupae, and juvenile muskrats in pellets. In addition, they observed a diet shift in an Oregon population in 1980 from vertebrates to grasshoppers, followed by a shift in 1981 to beetles. Diet shifts within a population provide further support for opportunism. John and Romanow (1993) commented on the dietary flexibility of an extralimital burrowing owl in Ontario that fed on earthworms and carabid beetles. The burrowing owl diet is clearly very diverse, with variation among regions, seasons, and years, suggesting that within certain bounds, burrowing owls exhibit plasticity in their diet and the ability to respond to new opportunities for food acquisition.

#### *Foraging tactics*

Prey items are caught through a variety of methods including ground foraging, foraging from an elevated perch, gleaning insects from tall vegetation, and hovering (Thompson and Anderson 1988, Schmutz et al. 1991). Ground hunting, where the owl chases prey on foot through low vegetation and captures with talons, was the most common strategy used by burrowing owls in Wyoming (Thompson and Anderson 1988). Hunting from a perch was more common among males than females. Hovering is used less frequently but appears to be more important when hunting over taller vegetation and when hunting for rodents (Thomsen 1971, Thompson and Anderson 1988). Prey items present in many pellet analysis studies (e.g., nocturnal Jerusalem crickets) suggest that burrowing owl foraging often occurs at night (Gleason and Craig 1979).

Coulombe (1971) observed burrowing owls drinking free water in the wild. However, his population was based in the Imperial Valley of southern California, which has very high temperatures. Captive owls were observed drinking more free water as ambient temperatures increased (Coulombe 1971).

#### *Food availability as a factor in population dynamics*

The availability of mammalian prey may be a limiting factor for burrowing owl productivity. Wellicome (1997) found that the number of young fledged per nest was greater for those nests given dead lab mice in excess of dietary requirements during the nesting period. Poulin et al. (2001) showed a delayed functional numerical response of burrowing owls to a meadow vole outbreak in Saskatchewan (i.e., population size was higher in the year after the vole outbreak). In this case, clutch size was not higher during the year of the vole outbreak, but nestling survival and fledging success were both significantly higher than observed in other years. Post-fledging survival was also higher, and the percent of fledglings that returned to their natal grounds to breed in the following year was twice as high as in other years (Poulin et al. 2001). A delayed functional numerical response to high prey density was also shown in a Chilean population (Jaksic et al. 1997). In general, raptors with a broad diet tend to show smaller population fluctuations than do raptors that rely on, for example, a small number of rodent species whose populations are cyclical (Galushin 1974). As such, burrowing owls do not appear to directly select nesting

areas based on prey availability and are not nomadic in response to greater prey availability elsewhere (Poulin et al. 2001).

#### *Variation in prey abundance*

Burrowing owl prey abundance is a function of many factors: cyclical cycles in rodent abundance and the level of rodent predation by competitors; health of vegetation that supports insects and rodent prey populations, which in turn is often a function of precipitation; cycles in insect populations (e.g., grasshopper outbreaks); habitat and forage availability for insect and rodent populations. As discussed, burrowing owls are fairly flexible in the types of prey items they exploit (within a certain size range unless the prey item is scavenged), and so burrowing owl populations are probably less tied to prey populations than other raptor species.

#### Breeding biology

Although most pair formation appears to occur during March and April (Best 1969, Butts 1973), there is conflicting evidence as to how often those pair formations occur on wintering versus breeding grounds. Martin (1973a) observed that migratory burrowing owls returning to their New Mexico breeding grounds arrived either singly or paired, although T. Wellicome (personal communication) suggested that pair formation among Canadian owls does not occur until after arrival on breeding grounds. If pair formation does occur in wintering populations comprising owls from disparate breeding populations, this could be an important source of gene flow among otherwise isolated populations (Korfanta 2001).

Arrival of burrowing owls on the breeding grounds varies latitudinally, with more northern populations arriving later than southern populations. Males and females arrive on breeding grounds at roughly the same time (T. Wellicome personal communication) and begin courtship and territorial behavior immediately (Martin 1973a, Haug et al. 1993). Males typically perform courtship displays just outside the potential nest burrow, which the male may already have prepared with shredded manure. Males sing the primary song, a two-note *coo cooooo* (Martin 1973b) beginning in the evening and continuing through the night. While singing the primary song, the male typically bends forward so that he is nearly horizontal, while displaying patches of white feathers on his throat and brow (Martin 1973a). Grant (1965) observed males in Minnesota performing a courtship flight display in

which they ascended rapidly to about 30 m, hovered for 5 to 10 seconds, and then descended to 15 m; this process was repeated several times. Thomsen (1971) also observed flight displays in which males flew in circles of approximately 40 m in diameter. During courtship, the male may bring food to the female, and the pair may engage in preening (Haug et al. 1993). Courtship behaviors are conspicuous and afford an ideal opportunity for population surveys, especially because males respond vocally to call playbacks of the primary song during this time (Haug and Didiuk 1993). Males and females may also respond by bobbing, which makes them easier to detect (Haug and Didiuk 1993).

Burrowing owls are generally considered to be monogamous (Haug et al. 1993) although new mates often appear when one of the pair dies or when the pair divorces (Thomsen 1971, Martin 1973a). Haug (1985) also observed cases of polygyny in a Saskatchewan population. There is some evidence that mate fidelity is higher in resident populations than in migratory ones (Millsap and Bear 1990). In a study using minisatellite DNA markers, Johnson (1997a) determined that between 5 and 10 percent of juveniles ( $N = 45$ ) in a Davis, California population resulted from extra-pair fertilizations. However, Korfanta (2001) found no evidence of extra-pair fertilizations within 10 family groups drawn from several populations. The potential for movement of juveniles among burrows further complicates the problem of identifying extra-pair fertilizations detected in any but very recent hatchlings.

Egg laying dates vary with latitude and among years. In New Mexico burrowing owls lay eggs around the third week of March (Martin 1973a), and in Oklahoma egg laying occurs in late March or early April (Butts 1973). Green (1983) found egg laying in Oregon occurred from 1 April through 1 May, and in Canada egg laying began during the third and fourth weeks of May (Haug 1985). In Wyoming egg laying begins in mid-April, and the egg laying pattern is primarily one egg per day in the following pattern: one egg, one egg, skip a day, one egg, one egg, skip a day, until all eggs are laid (Conway and Lantz 2003, Conway personal communication 2004). Egg laying in an eastern Oregon population occurred at a rate of  $>1$  per day (Henny and Blus 1981), and in an Idaho population, eggs were laid at 36-hour intervals (Olenick 1990). Burrowing owls typically lay very large clutches relative to other North American raptors, possibly to offset the effects of high predation (Coulombe 1971). Average clutch size in Wyoming is seven eggs (range 1 to 12) (Conway and Lantz 2003). Clutch size in Oregon was between eight and eleven eggs for four nests (Henny and Blus 1981),

which is in agreement with an average clutch size of nine from 26 artificial nest burrows in Canada. Average clutch size in California was reported to be seven ( $N = 28$  nests) (Landry 1979). In a study of 439 burrowing owl clutches from museums and egg collections, average clutch size was 6.48 eggs (range 1 to 11) (Murray 1976). Clutch size appears to decrease the later the female arrives on breeding grounds (T. Wellicome personal communication).

Based on differences in the sizes of young at first emergence, Thomsen (1971) and Butts (1973) assumed that incubation of the clutch began with the laying of the first egg; however, in a study of artificial nest burrows, Henny and Blus (1981) found cold, full clutches of eggs, indicating that incubation does not begin until all eggs are laid. In Wyoming, incubation is assumed to begin at the mid-point of the laying period, approximately at the 4<sup>th</sup> egg, and lasts for 26 days (Conway personal communication 2004). Incubation is by the female only (Haug et al. 1993). Young are altricial, and hatchlings weigh a mean of 8.9 g (range 6 to 12 g; Haug et al. 1993).

During the brooding period, the male does most of the hunting and provides prey items to the female. The female tears up larger prey items into pieces for the chicks (Haug et al. 1993). If the female dies, then the male may continue to hunt and bring food to the burrow but he will not feed the begging young (Haug et al. 1993). The female begins hunting when chicks are approximately two weeks old. Young permanently leave the primary nest burrow around 44 days from hatch (Landry 1979) although juveniles will continue to hunt with and associate with parents until migration (Haug 1985).

The number of young fledged per nest is also variable but is almost always well below clutch size and suggests that mortality between hatch and fledging is an important factor. While the average clutch size of burrowing owl nests in Wyoming is seven eggs (range 1 to 12), the average number of young fledged per nest is three (range 0 to 7) (Conway and Lantz 2002, Conway and Lantz 2003). From 1990 to 1996, the fledge rate in Nebraska was  $1.9 \pm 0.1$  (Desmond et al. 2001). From 1990 to 1994, the fledge rate in Colorado was  $3.6 \pm 0.2$  (0 to 9) (Lutz and Plumpton 1999). Elsewhere latitudinally, the number of young fledged per nest attempt ranged from 1.6 to 4.9 in New Mexico (Martin 1973a), and the number of young fledged per successful nest attempt ranged from 2.9 to 4.9 in Canada (Haug et al. 1993). Wellicome et al. (1997) found that food

supplementation during nesting significantly increased the number of fledglings per nest attempt.

Double-brooding has been observed in a Florida population (Millsap and Bear 1990), but it is not likely to occur in the rest of the species' range, where climatic conditions are more limiting and where populations have limited breeding time due to migration. Evidence from some resident (non-migratory) populations shows that burrowing owls will re-nest if the first nest is lost to predation or if the nest is destroyed (Thomsen 1971, Butts 1973). Re-nesting has also been shown in a migratory Saskatchewan population (Wedgwood 1976).

As discussed in the "Dispersal" section of this assessment, burrowing owls are generally considered to be philopatric. However, there is mounting evidence to support the prevalence of dispersal among populations. Several studies show that individuals return to the same nest burrow in subsequent years for nesting or at least that the same burrow is re-used in subsequent years by other burrowing owls (Wedgwood 1976, Gleason 1978, Butts and Lewis 1982). Two studies report pairings between mother and son, likely because both return to the previous year's nest burrow (Millsap and Bear 1997, Lutz and Plumpton 1999). Although return of some juveniles to their natal areas clearly does occur, dispersal of first year adults to new breeding sites appears to be prevalent. Lutz and Plumpton (1999) found only 5 percent of juveniles returning to their natal populations in Colorado, and females never returned in the year immediately following hatch.

## Demography

### *Genetic characteristics*

Relatively few studies have examined the genetic structure of burrowing owl populations. Johnson (1992, 1993 a-c, 1997a, c) used DNA fingerprinting to examine the genetic structure of a declining population in Davis, CA that went extinct shortly after the study. Desmond (1997) and Desmond et al. (2001) used mitochondrial DNA (mtDNA) to examine the genetic structure of burrowing owls throughout the range of the western subspecies *Athene cunicularia hypugaea*. Korfanta (2001) and Korfanta and McDonald (unpublished) used seven polymorphic microsatellite DNA loci (Korfanta et al. 2002) to examine the genetic structure of the North American populations, including populations of the subspecies *A. cunicularia floridana* found in peninsular Florida. A one-page introduction to the use

of microsatellites as an ecological tool is available at <http://www.uwyo.edu/dbmcd/lab/msatintro.html> (see references therein).

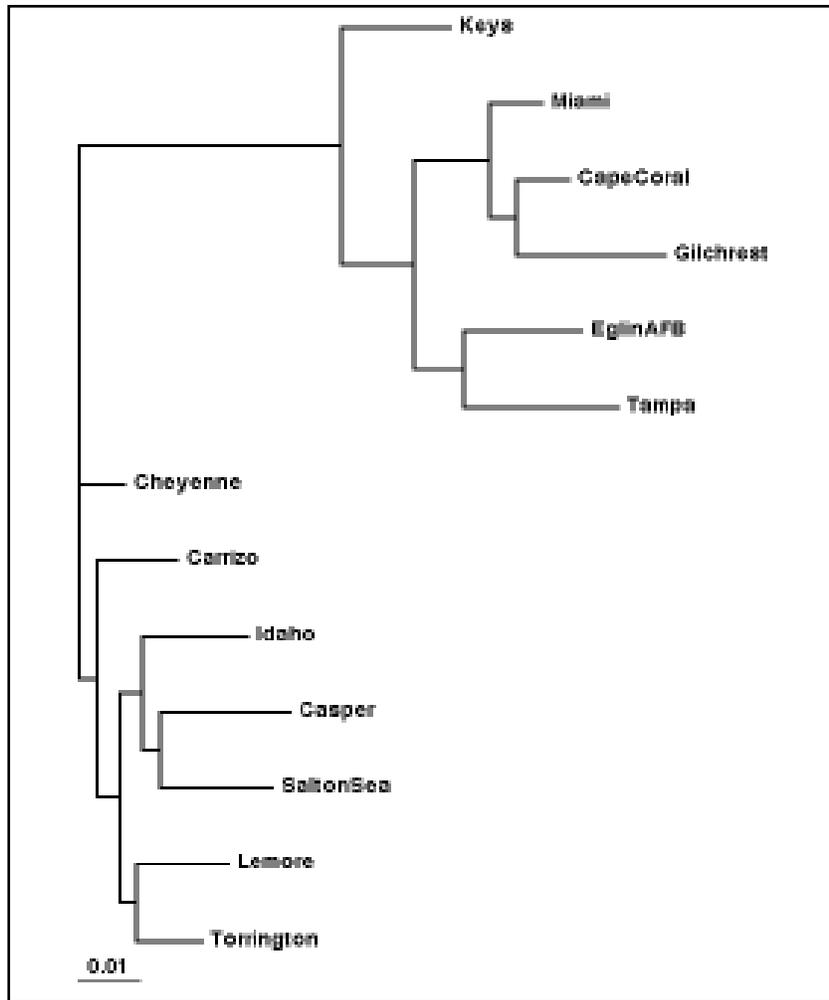
Johnson's results suggested the possibility of inbreeding, but because of the rapidly declining status the population studied, it is unlikely to have been representative of the genetic structure over much of the species' core range. Desmond (1997) and Desmond et al. (2001) found little structure in mtDNA, an unsurprising result within the range of a single subspecies. The results of Korfanta (2001) and Korfanta and McDonald (unpublished) provide some interesting demographic insights not previously available through other means. The western subspecies is genetically homogeneous — phylogenetic trees of populations from Wyoming, Idaho, and California showed no geographic resolution. A useful approach to depicting population structure within populations of a single species or among closely related species when using microsatellite DNA is to construct a phylogenetic tree. A suitable method is to use a neighbor-joining (NJ) algorithm based on either the Cavalli-Sforza chord distance or Nei's (1983) distance, both of which derive from allele frequencies (e.g., McDonald et al. 1999). Applied to burrowing owls, this approach produces trees with no discernible pattern or structure (**Figure 12**). For example, populations from California cluster with populations from Wyoming rather than with nearby populations in California. Essentially, this means that gene flow among burrowing owls is, or has been until recently, so high that the populations are panmictic (genetically homogeneous). In contrast, the microsatellites do indicate considerable divergence between the eastern and western subspecies, as shown by the long branch lengths separating the populations from the two subspecies (**Figure 12**). The populations of the Florida and western subspecies form distinct clusters (clades) on separate branches of the phylogenetic tree. As required for separation of species under the phylogenetic species concept (Zink and McKittrick 1995), the two clades are reciprocally monophyletic. Reciprocal monophyly means that each Florida population is more closely related to each of the other Florida populations than it is to any of the western populations and vice versa.

Like burrowing owls, scrub-jays are widely distributed in western North America, with a disjunct form in peninsular Florida. Recently, the American Ornithologists' Union (1995) declared the Florida scrub-jay (*Aphelocoma coerulescens*) a distinct species from the western scrub-jay (*A. californica*). McDonald et al. (1999) corroborated that split in a study that compared western scrub-jays to Florida scrub-jays using 10

microsatellite loci. The divergence levels between the eastern and western subspecies of burrowing owls are considerably lower than those found by McDonald et al. for Florida and western scrub jays. The internode distance between the west and Florida on a Cavalli-Sforza NJ tree for burrowing owl was 0.042, compared to 0.281 for the analogous scrub-jay comparison. It is therefore debatable whether the Florida subspecies of burrowing owl merits consideration as a distinct species, but it certainly merits consideration as an evolutionarily significant unit (Moritz 1994). Because of its more restricted range, any such separate consideration would have more implications for the Florida populations than for the western form in Region 2 that is the subject of the present report. The major import of the microsatellite data for the demographics of western burrowing owls is to underscore that they are more demographically connected than has generally been suspected heretofore. This connectedness likely results from higher than suspected levels and distances of natal dispersal (movement from place of birth to breeding site) or breeding dispersal (movement of adults within or among seasons from one breeding site to another), as documented for nonmigratory California populations (Rosenberg personal communication 2003).

#### *Life history characteristics – Life cycle graph and model development*

**Life history characteristics – Quality of data and caveats concerning available demographic data.** The life history described by Johnson (1997b) and Lutz and Plumpton (1997) provided the basis for a life cycle graph (**Figure 13**) and a matrix population analysis with an annual post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2001) for burrowing owl. The two-stage model reflects the paucity of age-specific data. Estimated survival rates varied considerably, both across years at a particular location and across locations. For example, Johnson (1997b) estimated annual first-year survival rates ranging from a low of 0.23 to a high of 0.93, and annual adult survival rates ranging from 0.42 to 0.93. Similarly, Lutz and Plumpton (1997) estimated first-year survival at 0.12, and annual “adult” survival rates ranging from 0.18 to 0.71. We used the “missing element” method of McDonald and Caswell (1993) to solve for  $P_{22}$  given  $\lambda = 1.004$ , where  $\lambda$  is the population growth rate. Over the long term  $\lambda$  must be near 1.0, or the species will go extinct or grow unreasonably large. Below, we discuss several variants that do not make the  $\lambda = 1$  assumption. Although the required “adult” survival rate (0.643) is near the high end of the estimates by Lutz and Plumpton (1997), the high

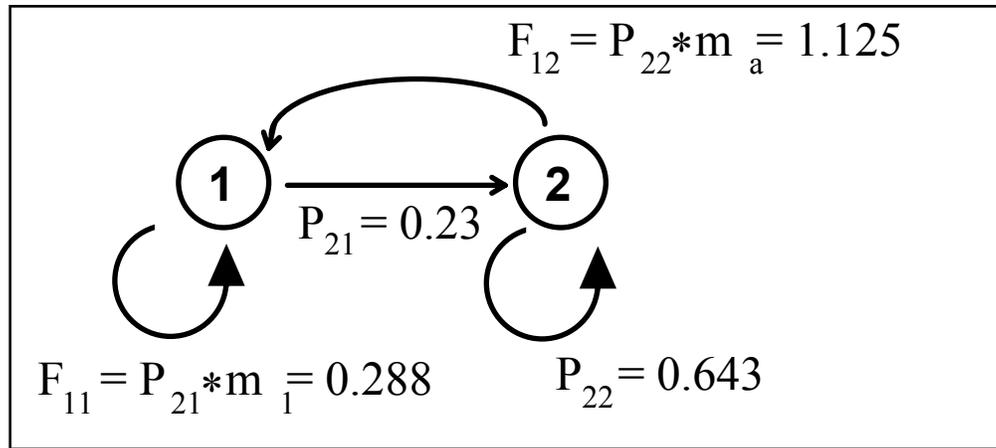


**Figure 12.** Phylogenetic tree depicting the genetic relationships among burrowing owl populations in North America. Two features of the tree are immediately apparent: 1) populations in Florida (*Athene cunicularia floridana*) are clearly distinct from those in Western North America (*A. cunicularia hypugaea*), and 2) no geographic pattern exists to distinguish among western populations. For example, populations from California are as likely to cluster with populations from Wyoming as they are with other populations from California. The tree shown here was constructed from a matrix of Cavalli-Sforza chord distances among populations using a neighbor-joining algorithm (Cavalli-Sforza and Edwards 1967). The lack of geographic pattern in the phylogenetic trees was robust to the use of other methodologies (e.g. Nei's distances or UPGMA tree-building algorithms).

breeding dispersal distances documented in California suggest that mark-recapture studies over restricted areas may often grossly underestimate survival rates (Rosenberg personal communication 2003). Breeding dispersal is the movement of adult birds between nesting attempts, either within or between years. Researchers found that the reputedly more sedentary, non-migratory California populations occasionally engaged in breeding dispersal in the event of nest failure, and those dispersal distances could be as great as 53 km. Such breeding dispersal makes it unlikely that survival rates calculated from returns to feasibly-sized study areas will truly estimate survival of adult

breeders. Natal dispersal may be even greater and involve a higher proportion of the population. Further, a variety of studies cited by Haug et al. (1993) suggest that survival rates may often reach or exceed the high end of Lutz and Plumpton's estimates.

A two-stage model may appear overly simplified for capturing the population dynamics of a reasonably long-lived bird like the burrowing owl. Would a life cycle graph with more nodes (stages or age-classes) provide additional insights? Because we have no basis for varying the vital rates (survival and fertility) as a function of age, the answer is currently "no". An



**Figure 13.** Two-stage life cycle graph for burrowing owl, based on demographic data from Johnson (1997) and Lutz and Plumpton (1997). First stage represents fledgling females (at time of post-breeding census, which occurs at annual intervals), and these individuals are followed through a full one-year cycle to the age of first reproduction as yearlings. The second stage represents “adult” females. It is important to note the distinction between these discrete stages covering a one-year interval (first-year birds, second-year birds, etc.) and the continuous age used for some other kinds of demographic analyses. Because of the self-loop on the “adult” stage, individuals in that stage comprise a mixture of individuals of various ages, distinguishing this model from the strictly age-classified analysis of the more familiar Leslie matrix (Caswell 2001). We assume that first-year breeders produce slightly fewer female fledglings ( $m_1 = 1.25$ ) than do “adult” females ( $m_a = 1.75$ ). See text for outcomes of variant models with different “adult” survival rates ( $P_{22}$ ) or age-classified setup.

expanded multi-age model (used to calculate the loop elasticities of **Table 2** and the stable age distribution of **Table 3**) yielded the same conclusions for other demographic parameters. This is largely because the expansion simply consists of repeating the “adult” survival and fertility rates in an age-classified manner. Parameters such as  $\lambda$  and summed elasticities and sensitivities will be unaffected by any such same-term expansion. Thus, the simplified two-node analysis presented here as the major base model has the advantage of greater simplicity and conciseness without sacrificing important information.

The model has two kinds of input terms:  $P_i$  describing survival rates, and  $m_i$  describing number of female offspring per female (**Table 4**). Fertility terms,  $F_i$ , represent the product of an  $m_i$  term and a  $P_i$  term that tracks the mother’s survival from the time of the

post-breeding census till the time she actually breeds almost a year later (given a census interval of one year). **Figure 14a** shows the symbolic terms in the projection matrix corresponding to the life cycle graph. **Figure 14b** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female fledglings per female. The model of Lutz and Plumpton (1997) erroneously used offspring per pair as the basis for the matrix projection and therefore overestimated  $\lambda$  (published value of  $\lambda = 0.79$  vs. the corrected  $\lambda = 0.58$ , based on their input parameters). Because many bird species have lower reproductive success at first breeding (Woolfenden and Fitzpatrick 1984), we further assumed that first-time breeders would have a lower fledging rate (1.25 vs. 1.75). Although a  $\lambda$  of 1 suggests a stationary population, the value was an assumption for deriving the “adult” survival rate, and it should not be

**Table 2.** Parameter values for the component terms ( $P_i$  and  $m_i$ ) that make up the vital rates in the projection matrix for burrowing owl.

Parameter	Numeric value	Interpretation
$m_1$	1.25	Number of female fledglings produced by a first-year female
$m_2$	1.75	Number of female fledglings produced by an “adult” female
$P_{21}$	0.23	First-year survival rate
$P_a$	0.643	Annual survival rate of “adults”

**Table 3.** Loop elasticity analysis of the life cycle of burrowing owl for an age-expanded eight-stage matrix. Each loop represents the pathway from Node 1 (fledglings) to the given Node and then back to Node 1. The three most important loops are highlighted with boldface font.

Loop (source node)	Description	Loop value	Rank
1	Fledglings (through first year)	0.096	6
2	Second-year females	<b>0.172</b>	1
3	Third-year females	<b>0.165</b>	2
4	Fourth-year females	<b>0.141</b>	3
5	Fifth-year females	0.113	5
6	Sixth-year females	0.087	7
7	Seventh-year females	0.065	8
≥8	“Older adult” females	0.132	4

**Table 4.** Stable stage distribution (right eigenvector), at the census, just after the breeding season. Any population with unchanging vital rates will eventually converge to a stable age distribution regardless of whether the population is declining, increasing or stationary. In order to provide more detail, we expanded the model to include 7 age-classes and a final “older adult” stage. The change has no effect on the calculated  $\lambda$ , nor on other parameters such as the summed sensitivities or reproductive values.

Age-class	Description	Proportion
1	Fledglings (through first year)	0.61
2	Second-year females	0.14
3	Third-year females	0.09
4	Fourth-year females	0.06
5	Fifth-year females	0.04
6	Sixth-year females	0.02
7	Seventh-year females	0.02
≥8	“Older adult” females	0.03

**A)**

Stage	1	2
1	$P_{21}m_1$	$P_{22}m_2$
2	$P_{21}$	$P_{22}$

**B)**

Stage	1	2
1	0.288	1.125
2	0.23	0.643

**Figure 14.** Symbolic and numerical representations of the projection matrix corresponding to the life cycle graph of **Figure 13**. A) Symbolic values for vital rates constituting the projection matrix, **A** (with cells  $a_{ij}$ ) corresponding to the burrowing owl life cycle graph of **Figure 13**. Meanings of the component terms and their numeric values are given in **Table 2**. B) Numeric values for the vital rates in the projection matrix, **A** (with cells  $a_{ij}$ ).

interpreted as an indication of the general well being of the population. Other parts of the analysis provide a better guide for assessment. Combining the relatively high first-year survival of Johnson (1997b;  $P_{21} = 0.23$ ), the upper-end “adult” survival rate of 0.71 found by Lutz and Plumpton (1997), and the same fertilities used in the main base model, we found a  $\lambda$  of 1.07. This suggests that, under optimal conditions, burrowing owls are capable of fairly rapid increase (7 percent per year).

**Sensitivity analysis.** A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on  $\lambda$  of an **absolute** change in the vital rates ( $a_{ij}$ , the arcs in the life cycle graph [Figure 13] and the cells in the matrix, **A** [Figure 14]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-207). First, sensitivities show “how important” a given vital rate is to  $\lambda$  or fitness. For example, one can use sensitivities to assess the relative importance of survival ( $P_i$ ) and reproductive ( $F_i$ ) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to a paucity of data, but it could also result from the use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing  $\lambda$  of endangered species or the “weak links” in the life cycle of a pest. Figure 15 shows the “possible sensitivities only” matrix for this analysis.

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of first-year females is very likely to cause similar changes in the survival rates of “adult”

Stage	1	2
1	<b>0.34</b>	0.21
2	<b>1.04</b>	<b>0.66</b>

**Figure 15.** Sensitivity matrix, **S**, for matrix-based analysis of the burrowing owl. The sensitivities assess the effects of absolute changes in the vital rates. The three transitions to which  $\lambda$  (the population growth rate) is most sensitive are highlighted with bold face font: first-year survival (Cell  $s_{21} = 1.04$ ), “adult” survival ( $s_{22} = 0.66$ ), and first-year reproduction ( $s_{11} = 0.34$ ).

reproductive females (those in Stage 2). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the summed sensitivity of  $\lambda$  to changes in the survival is of overriding importance. Burrowing owls show large sensitivity (76 percent of total) to changes in survival, with first-year survival alone accounting for 46 percent of the total. The summed “reproductive” survival sensitivity was 24 percent of the total. The major conclusion from the sensitivity analysis is that first-year survival is overwhelmingly important to population viability.

**Elasticity analysis.** **Elasticities** are useful in addressing situations in which changes in the vital rates are proportional rather than additive. Elasticities are the sensitivities of  $\lambda$  to **proportional** changes in the vital rates ( $a_{ij}$ ) and have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the  $a_{ij}$  cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction ( $F_i$ ) and survival ( $P_i$ ) for a given species.

Elasticities for the burrowing owl are shown in Figure 16.  $\lambda$  is most elastic to changes in “adult” survival ( $P_{22}$ , the self-loop on the second node in Figure 13) followed by equal values for first-year survival ( $P_{21}$ ) and “adult” reproduction ( $F_{21}$ ). The sensitivities and elasticities for the burrowing owl do not correspond in rank magnitude. The second and third most elastic transitions were equal in magnitude (24 percent) and included adult fertility, while adult survival was the most elastic transition (42 percent). The summed reproductive elasticities accounted for 34 percent of the total (compared to 24 percent for the summed reproductive sensitivities). Thus, adult survival, and to a lesser extent first-year survival

Stage	1	2
1	0.10	<b>0.24</b>
2	<b>0.24</b>	<b>0.42</b>

**Figure 16.** Elasticity matrix,  $E$ , for matrix-based analysis of the burrowing owl. The elasticities assess the effects of proportional changes in the vital rates.  $\lambda$  is most elastic to changes in “adult” survival ( $e_{22} = 0.42$ ), followed by first-year survival ( $e_{21} = 0.24$ ) and reproduction by “adults” ( $e_{12} = 0.24$ ). Note the considerably greater relative importance of survival transitions in the elasticity analysis relative to the sensitivity analysis.

and “adult” reproduction, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis. Because of the high variability in published estimates of demographic parameters, we conducted an elasticity analysis using the low-end survival rates of Lutz and Plumptre (1997;  $P_{21} = 0.12$  vs.  $P_{21} = 0.23$  and  $P_{22} = 0.37$  vs.  $P_{22} = 0.64$ ). Although the resulting elasticities (**Figure 17**) are quantitatively slightly different, the relative rankings and qualitative conclusions are not affected.

**Loop elasticity analysis.** van Groenendael et al. (1994, as refined by Wardle 1998) developed a method of decomposing a life history into distinct loops based on elasticities. For this analysis we developed an age-expanded matrix with eight stages — Nodes 2 through 8 had the “adult” fertilities of Node 2 in **Figure 13**, and annual survival was constant at 0.643, with a survival self-loop on Node 8 that was also 0.643. The only advantage of this age-expanded model over the simpler two-node model of **Figure 13** is the decomposition it allows by age. The model has eight distinct reproductive loops, one from each node. The values for the eight loops are given in **Table 3**. The major conclusion is that the most important loops are those for breeders aged two through five, followed by the aggregate loop of “older adult” breeders and then by first-year reproduction.

**Lower level elasticity analysis.** Lower level elasticity analysis (Caswell 2001, p. 232) allows one to decompose the elasticities to assess the contributions of the component terms. The elasticity results provided above are for the entire arcs/transitions in the life cycle graph. In this case, the fertility transitions,  $F_i = P_i * m_i$ ,

Stage	1	2
1	0.13	<b>0.23</b>
2	<b>0.23</b>	<b>0.41</b>

**Figure 17.** Elasticity matrix,  $E$  for a model based on the declining demographics of Lutz and Plumptre (1997), with  $\lambda = 0.58$ . Although the elasticity of  $\lambda$  to first-year reproduction is slightly higher, the ranking of elasticities is identical and the qualitative conclusions stemming from the main analysis of **Figure 16** are essentially unchanged.

are the products of two kinds of terms —  $m_i$ , describing fledglings per female, and  $P_i$ , describing the survival rate of the female parents. We can decompose the elasticities into the contribution of each of these two kinds of terms. For the model of **Figure 13**, the summed lower level elasticities survival terms ( $P_i$ ) accounted for 87.3 percent of the total lower level elasticity vs. 12.7 percent of the total accounted for by fertility terms ( $m_i$ ). This result emphasizes even more strongly the earlier conclusion of the paramount importance of survival. Because of their contributions to the fertility arcs and their stand-alone importance in the survival transitions ( $P_i$ ), the survival rates are of overwhelming importance. Indeed the “adult” survival rate ( $P_{22}$ ) accounts for fully 61 percent of the total lower level elasticity.

**Other demographic parameters.** The **stable stage distribution (SSD; Table 4)** describes the proportion of each age-class or stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For burrowing owls at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 61 percent of the population, while “adults” represent 39 percent of the population. Fewer than 3 percent of the population are females older than eight years of age. Any senescent increase in mortality would decrease the proportion of older females. **Reproductive values (Table 5)** can be thought of as describing the “value” of a stage as a seed for population growth relative to that

**Table 5.** Reproductive values (left eigenvector). Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage or age-class. By definition, the reproductive value of the first stage is always 1.0 for any life history.

Stage	Description	Reproductive value
1	Fledgling females	1
2	“Adult” females	3.12

of the first (newborn or, in this case, fledgling) stage. The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The reproductive value of the first stage is always 1.0. An “adult” female individual in Stage 2 is “worth” 3.1 fledglings (Caswell 2001). The cohort generation time for burrowing owls was 3.01 years (SD = 2.2 years). For stage-classified models such as this one, a question of considerable interest is the mean age of individuals in a multi-age stage. For the main base model of **Figure 13**, the mean age of “adults” at the time of the annual census, just after the breeding season, was 2.8 years (SD = 2.3 years). This suggests that populations are a mix of yearling and older individuals, with few individuals surviving to ages greater than four or five (although these rare older individuals can make important contributions to population growth).

**Stochastic model.** We conducted a stochastic matrix analysis for burrowing owls. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table 6**). Under Variant 1 we subjected both reproductive arcs ( $F_{11}$  and  $F_{22}$ ) to stochastic fluctuations. Under Variant 2 we varied the survival of all age classes,  $P_{ij}$ , but with lower stochasticity. Under Variant 3 we varied only “adult” survival ( $P_{22}$ ), with high stochasticity. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the SSD under the deterministic model. Beginning at the SSD helps avoid reaching conclusions based on the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random beta distribution from which the stochastic vital rates were selected (Morris and Doak 2002, p. 275). The default value was a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry [vital rate],  $a_{ij}$  under the deterministic analysis). Variant 4 affected the same transition as Variant 3 ( $P_{22}$ ) but was subjected to half the variation (SD was 1/8 of the mean). Variant 2 likewise had low stochasticity (SD was 1/4 of the mean). We

calculated the stochastic growth rate,  $\log \lambda_s$ , according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid the influence of transient dynamics.

The stochastic model (**Table 6**) produced two major results. First, varying “adult” survival had a greater effect on  $\lambda$  than did varying all the fertility transitions. For example, 100 of 100 runs led to extinctions with variable “adult” survival under Variant 3 from the starting size of 10,000. In contrast, varying the fertilities of both stages under Variant 1 led to only 25 extinctions. Variant 2 (varying both survival rates) had very detrimental effects, even under low stochasticity — 96 of 100 runs led to extinctions. Reducing the stochasticity and affecting only adult survival (Variant 4) led to an outcome (22 extinctions) similar to that of Variant 1. This difference in the effects of stochastic variation is largely predictable from the elasticities.  $\lambda$  was more elastic ( $e_{11} = 0.43$ ) to changes in “adult” survival,  $P_{22}$ , than it was to changes in the fertilities (summed fertility elasticities = 0.34). Second, the magnitude of stochastic fluctuation largely determines the negative impact on population dynamics. This negative effect occurs despite the fact that the average (expected) vital rates remain the same as under the deterministic model. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. Note that Variant 4 is reasonably similar to the outcome of Variant 1 — that is, even small magnitude fluctuations acting only on “adult” survival (SD = 1/8) will have detrimental effects similar to those produced by much larger fluctuations (SD = 1/4) acting on reproduction at all ages. These results indicate that populations of burrowing owls are most vulnerable to stochastic fluctuations in “adult” survival. Nevertheless, stochastic fluctuations in any of the vital rates would have noticeably negative effects on population dynamics. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have

**Table 6.** Summary of four variants of stochastic projections for burrowing owl.

	Variant 1	Variant 2	Variant 3	Variant 4
<u>Input factors:</u>				
Affected cells	$F_{11} + F_{22}$	$P_{21} + P_{22}$	$P_{22}$	$P_{22}$
S.D. of random normal distribution	1/4	1/8	1/4	1/8
<u>Output values:</u>				
Deterministic $\lambda$	1.004	1.004	1.004	1.004
# Extinctions/100 trials	25	96	100	22
Mean extinction time	1,363	799	480	1,369
# Declines/# survived pop	61/75	4/4	—	59/78
Mean ending population size	424,925	2169	—	142,489
Standard deviation	$3 \times 10^6$	3,395	—	610,809
Median ending population size	970	724	—	1,317
Log $\lambda_s$	-0.002	-0.0097	-0.02	-0.0019
$\lambda_s$	0.998	0.99	0.98	0.998
% reduction in $\lambda$	0.61	1.37	2.39	0.6

responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously relatively invariant vital rates (such as “adult” survival), with consequent detrimental effects on population dynamics. For the owls, because stochasticity on any of the vital rates will have negative impacts, the opportunities for adjustment of risk load may be limited compared to the opportunities in species with different life histories. The highly variable vital rates documented by Johnson (1997b and Lutz and Plumpton (1997) may predispose burrowing owls to a high risk of local extinction balanced by a reasonably high likelihood of profiting from opportunities provided by favorable habitat changes.

**Potential refinements of the models and data needs.** Clearly, the better the data on survival rates, the more accurate the resulting analysis will be. Additional data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence. Detailed

mark-recapture analyses using sophisticated software such as *SURGE* (Lebreton et al. 1993) will provide only a partial solution to the problem of better understanding of the vital rates. In a species with high rates of natal and breeding dispersal, such as the burrowing owl, the mark-recapture analyses will provide only *apparent* survival. Many surviving individuals will be missed because they leave the study areas. More complete understanding will require cooperation by field biologists over large areas and the use of telemetry and other tools that can establish the proportions of dispersers and the range of distances covered by dispersers as a function of age, sex, and breeding status.

Major conclusions of the matrix model analyses:

- ❖ Survival rates, especially those of “adult” females, are critical to burrowing owl population dynamics; the stochastic as well as elasticity analyses both point to the critical importance of this demographic rate.
- ❖ Population growth rates can vary widely in both space and time. Local extinctions may be a regular occurrence, but opportunities for colonization or recolonization of vacant habitats are critical to landscape level persistence.
- ❖ The critical data for improved understanding of population dynamics will be survival rates that incorporate the probabilities of natal and breeding dispersal.

## Metapopulation dynamics

The high levels of gene flow indicated by the microsatellite DNA analyses discussed earlier, and the high breeding and natal dispersal suggested by studies such as those in California (Rosenberg personal communication 2003) suggest that metapopulation dynamics are unlikely to be a feature of burrowing owl populations. Although local extinctions such as those documented by Johnson (1997b) in Davis, California may occur, they likely occur in marginal habitats at the edges of the species' range. Fluctuations in the core of the range are likely strongly linked to variations in the availability of burrows, particularly those created by prairie dogs. In Colorado, for example, 80 percent of surveyed burrowing owls were associated with prairie dog colonies (VerCauteren et al. 2001). Clearly, improved understanding of the large-scale variation and trends in prairie dog habitat use and population trends are critical to an improved understanding of population trends in burrowing owls. In the many areas where burrowing owls do not co-occur with prairie dogs, an improved understanding of long term habitat use, relationships of population persistence to land use practices, and response to urbanization will provide further insight into the dynamics of this unusually flexible species that nevertheless has certain specialized requirements that make it challenging to explain the full range of population variation across the widely varying habitats in which this species currently exists.

## Community ecology

### *Predators*

Predation is an extremely important limiting factor in birds in general (Martin 1992), and in burrowing owls specifically. Avian predators of burrowing owls (Haug et al. 1993) include Swainson's hawk (*Buteo swainsoni*), ferruginous hawk (*Buteo regalis*), red-tailed hawk (*Buteo jamaicensis*), merlin (*Falco columbarius*), Cooper's hawk (*Accipiter cooperii*), northern harrier (*Circus cyaneus*), great horned owl (*Bubo virginianus*), and American crow (*Corvus brachyrhynchos*) (Haug et al. 1993). Common mammalian predators of burrowing owls include badger, fox (*Vulpes* spp.), striped skunk (*Mephitis mephitis*), weasel (*Mustela* spp.), raccoon (*Procyon lotor*), and opossum (*Didelphis virginiana*) (Hauge et al. 1993, Wellicome et al. 1997). Among these, badgers are probably the most important predator, accounting for predation rates ranging from 90 percent in Oregon (Green 1983) to 7.7 percent in Nebraska (Desmond 1991). Predation by domestic cats

accounted for 30 percent of known deaths in a Florida burrowing owl population (Millsap and Bear 1988) and dogs have been observed feeding on eggs and young (Haug 1985).

Burrowing owls are particularly susceptible to predation because they are small and they nest, hunt, and roost on the ground. For instance, predation by northern harriers, great horned owls, red-tailed hawks, and coyotes accounted for the high mortality rate of reintroduced burrowing owls in British Columbia (Leupin and Low 2001). Nest success was significantly higher in burrows with predator exclusion devices than in natural burrows in a Canadian population (Wellicome et al. 1997). On Santa Barbara Island, off the coast of southern California, a population of barn owls (*Tyto alba*) completely decimated a wintering population of burrowing owls following a decline in the barn owl's primary prey, the deer mouse (Drost and McCluskey 1992). Snakes may also be an important predator. There is speculation that burrowing owls in fragmented landscapes may be more susceptible to predation (Warnock and James 1997), although this relationship has not been critically evaluated.

### *Competitors*

Because of the unique habitat requirements and life history of burrowing owls, there do not appear to be direct interspecific competitors for nesting habitat. Burrowing owls are usually able to evict burrowing mammals from active burrows to retain a nest burrow, so burrowing mammals are not likely direct competitors for burrows. We were unable to find any published studies related to interspecific competition for prey resources. Other raptor species that share the burrowing owl prey base may offer some competition, but because burrowing owls prey on relatively small species, competition is probably not very important.

### *Parasites and disease*

Lice (*Colpocephalum pectinatum*), human fleas (*Pulex irritans*), and sticktight fleas (*Echidnophaga gallinacea*) were found on owls in California (Thomsen 1971). In a survey of nest burrow parasites, Phillips and Dindal (1977) found 39 species of arthropods including 15 species of fleas, although many of these could have been associated with the primary mammalian burrower. Gapeworm (*Cyathostoma americana*) was a cause of mortality among captive owls (Hunter and McKeever 1988), and Newcastle disease was the source of mortality in a Florida owl (Millsap and Bear 1988).

### *Symbiotic and mutualistic interactions*

Burrowing owls may have a mutualistic interaction with prairie dogs through improved detection and protection against potential predators. Burrowing owls may respond to the alarm calls of prairie dogs in response to predators, but it is less clear if burrowing owls confer any benefit to prairie dogs.

### *Envirogram*

An envirogram (Andrewartha and Birch 1984) for the burrowing owl is shown in **Figure 18**. The envirogram outlines processes that affect burrowing owls, dividing them into four centra (resources, reproduction, malentities, and predators). Resources are the items in the environment used by the owls mainly for food or shelter, reproduction refers to aspects of the environment critical for reproduction, malentities are aspects of the environment, including competitors, that negatively impact the owls, and predators are those organisms that use the owls as a food resource. The horizontal scale identifies pathways, with the most distant effects being to the left.

## CONSERVATION

### *Threats*

Primary threats to burrowing owls and their habitat within Region 2 include:

- ❖ **Habitat loss**, due to declines in prairie dog colonies and to land conversion for urban and agricultural uses
- ❖ Loss to **predation** in fragmented and/or urban landscapes where edge-loving and domestic predator densities are high
- ❖ Indirect effects of **sylvatic plague** on burrowing owls that use prairie dog colonies
- ❖ **Insecticides and rodenticides** that can directly kill or reduce the growth and reproductive rates of owls in agricultural areas
- ❖ **Incidental shooting** of burrowing owls as a byproduct of recreational shooting of prairie dogs

- ❖ Lack of information on quality of **wintering habitat** and the demographic consequences of burrowing owls using wintering habitats

### Habitat

#### *Habitat loss*

For many species, including the burrowing owl, habitat loss and degradation is the single most important threat to persistence. Much of the decline in the range and abundance of burrowing owls is linked to the decline of burrowing rodents, primarily prairie dogs in Region 2. Prairie dogs are estimated to have suffered a 98 percent decline in the previous century (Coppock et al. 1983, Miller et al. 1994). That decline has occurred indirectly because of land conversion to uses incompatible with continued persistence of prairie dogs (e.g., urban development, monocultures of agricultural crops) and directly as a result large-scale poisoning and sylvatic plague. Any discussion of threats to burrowing owls must clearly be linked to threats to the persistence of prairie dogs.

Many studies show that burrowing owls preferentially use active- or very recently-abandoned colonies of black-tailed prairie dogs. For instance, in Oklahoma 66 percent of adult owls were found on active prairie dog colonies, even though this habitat type comprised only 0.16 percent of the study area (Butts and Lewis 1982). Furthermore, in three prairie dog colonies lost to cultivation, no owls nested there in the following three years, and in prairie dog colonies that had been poisoned, no owls nested after three years (Butts and Lewis 1982). The authors further noted that prairie dog burrows quickly became filled in with soil and grass and that nearly all of the vacant burrows lost their identity within three years. In Nebraska, Desmond et al. (2000) found that nesting pairs of burrowing owls declined 63 percent from 1990 (91 nests) to 1996 (34 nests), and this decline was correlated with declines in burrow densities within surveyed colonies. Desmond et al. (2000) also found depressed fledging rates (1.9 juveniles per nest) among burrowing owls nesting in colonies where the number of active burrows was decreasing. On the Rocky Mountain Arsenal in Colorado, Plumpton and Lutz (1993) found that among all prairie dog colonies surveyed, nesting burrowing owls were found only within active prairie dog colonies. They also found that over a 14-year period (1988 to 2001), burrowing owl nesting densities tracked fluctuations in active prairie dog colony area within the arsenal (Antolin et al. 2002).

<b>WEB</b>				<b>CENTRUM</b>
4	3	2	1	

**MALENTITIES**

	water soil		agricultural practices	Pesticides
water	human development	roads	automobiles	Human-caused mortality
		management policies for prairie dogs	incidental shooting	
	water	monocultures	agricultural conversion	Habitat loss
	water	human spread	urbanization	
	management policies	poisoning of prairie dogs	prairie dog declines	
water soil	prey base burrows	prime habitat	intraspecific	Competition

		burrow usurpation	interspecific	
water	vegetative cover	prey base		

**PREDATORS**

	water	vegetative cover	habitat suitability	Badgers
			alternative prey base	
	water	vegetative cover	ambush cover	Foxes, coyotes
		water	escape cover	Raptors (purely aerial)
		vegetative cover	perches alternative prey	Raptors (perching)
	patterns	human settlement	human habitations	Cats and dogs

**Burrowing owl**

**RESOURCES**

water	herbaceous plants	vegetative cover	vegetation	Food: arthropods
			soil weather	
water	herbaceous plants	vegetation	arthropods	Food: small mammals
		water	vegetation weather	
	water	vegetation	cover	
water	water herbaceous plants water	vegetation vegetation vegetation	seeds arthropods cover	Food: birds
	vegetation	burrowing mammals	burrows	Thermal cover
vegetation	prey base soil			

**REPRODUCTION**

water	herbaceous plants	vegetative cover	burrowing mammals	Burrows
water		water	herbaceous plants	Prey base (lagged response)

**Figure 18.** Envirogram for the burrowing owl.

### *Habitat fragmentation*

The rapid loss of grasslands to cultivation and other anthropogenic factors is responsible for making the Great Plains of North America one of the most heavily-fragmented landscapes in the world (Rowe 1984). Fragmentation converts large, continuous blocks of natural wildlife habitat into smaller, more isolated patches (Noss and Csuti 1994). The effect of fragmentation on burrowing owls has been examined in Saskatchewan (Warnock and James 1997) and Colorado (Orth and Kennedy 2001). The Saskatchewan study compared habitat characteristics among high-burrowing owl density (core), and low-burrowing owl density (peripheral) sites (Warnock and James 1997). Results showed peripheral sites had greater habitat continuity within a 20-km radius (were less fragmented) than did core sites. Core sites had less continuity of habitat and were smaller than random patches, suggesting that burrowing owl response to habitat fragmentation is not a simple function. The authors concluded that burrowing owls were selecting the best remaining habitat in terms of soil type and proximity to other owls, rather than the largest sites.

The Colorado study compared landscape features of irrigated cropland, non-irrigated cropland, and shortgrass prairie around owl-occupied and owl-unoccupied prairie dog colonies to measure the degree of habitat fragmentation tolerated by nesting burrowing owls. Despite predictions of greater shortgrass continuity surrounding owl-occupied colonies, burrowing owls selected more fragmented landscapes than expected. At the 2500-m scale they found that the probability of detecting an owl increased as the number and size of shortgrass patches increased and as the distance between patches decreased. They speculated that owls prefer large yet fragmented patches of shortgrass, as the increased amount of edge is associated with increased abundances of arthropod and mammalian prey.

While burrowing owls were present within highly-fragmented landscapes in both studies, caution should be taken in the interpretation. Presence does not fully explore the potential negative effects of fragmentation on normal activity patterns for the species. Warnock and James (1997) speculated that burrowing owls nesting in highly-fragmented patches may increase 1) distance to foraging habitat, 2) density of owls on patches with concomitant increases in intraspecific competition, and 3) predation due to edge effects. However, none of these risks was quantified in this study. Increased fragmentation may increase road densities, and in

certain areas, automobiles constitute a significant source of mortality for burrowing owls. Their vulnerability is exacerbated by a positive attraction to various aspects of the roadside environment including the propensity to use fence lines as perches. Clayton and Schmutz (1997) found higher post-fledgling mortality from vehicle collisions in an agricultural landscape (>90 percent of land area under cultivation) relative to an unfragmented rangeland (<20 percent cultivation). Todd and James (2001) found a similar vulnerability of burrowing owls (7 percent of post-fledging mortality, relative to 60 percent by avian predators), and Haug et al. (1993) and James and Espie (1997) also mention collisions with vehicles as a significant source of mortality. Fragmentation may also result in the introduction of novel predators and changes in the distribution and abundance of the prey base.

### Grazing

Burrowing owls prefer grasslands moderately to heavily grazed by herbivores (Butts 1973, Wedgwood 1976, MacCracken et al. 1985). Optimal breeding habitat for burrowing owls within Colorado, Montana, Nebraska, Wyoming, and South Dakota has been identified as grazed land (Kantrud and Kologiski 1982). When the grazing herbivores include prairie dogs and ground squirrels, a positive effect of increased burrow availability can occur (Butts 1973). Domestic livestock grazing may have mixed effects. On the one hand, ranching will likely result in the maintenance of the short vegetation profile that is clearly essential to the occurrence of burrowing owls (MacCracken et al. 1985, Faanes and Lingle 1995). In Nebraska, preferred burrowing owl nest sites occurred in mowed and heavily grazed grasslands (Faanes and Lingle 1995). On the other hand, livestock grazing is often accompanied by an intentional reduction or elimination of prairie dog populations. Furthermore, cattle may occasionally constitute a direct threat to burrowing owls by trampling and collapsing nest burrows (Howie 1980). Thus, the impact of grazing must be considered in conjunction with the presence of prairie dog burrows within Region 2 (Klute et al. 2003).

### Mowing

Mowing is both an agricultural practice (haying) and a management strategy to control growth of grasses and woody shrub species (Klute et al. 2003). In north-central Colorado, mowing is used to manage vegetation height within abandoned prairie dog colonies, specifically to attract burrowing owls (Plumpton 1992).

Dechant et al. (1999) suggest that mowing during the breeding season does not negatively affect nesting burrowing owls.

#### Predation and disease

##### *Predation*

Many studies speculate that burrowing owls may be more vulnerable to predation in fragmented habitats with high edge ratios, where some predators (coyote, fox, badger) are known to forage more efficiently (Warnock and James 1997, Clayton and Schmutz 1999, Orth and Kennedy 2001). Although burrowing owls sometimes appear to thrive in fairly heavily populated suburban and other human-altered areas (Trulio 1997a, Millsap and Bear 2000), owls associated with human habitation (particularly domestic cats and dogs) may also suffer higher mortality rates (Haug 1985, Millsap and Bear 1988, Haug et al. 1993).

##### *Disease*

While there are no known diseases that directly threaten burrowing owl persistence, they may be indirectly impacted by the effect of the sylvatic plague on burrowing mammals, such as black-tailed prairie dogs. Plague is the only source of mortality known to cause significant (>95 percent) die-offs in black-tailed prairie dogs (Barnes 1993, Cully and Williams 2001). Plague epizootics have been documented in black-tailed prairie dog colonies in all states within USFS Region 2, except for South Dakota. Plague has altered natural patterns of colony extinction and re-colonization, and has changed the population dynamics of black-tailed prairie dogs (Antolin et al. 2002). There are few data describing the ecology of the sylvatic plague; its pattern of movement across the landscape and mode of transmission are not well-understood (Cully and Williams 2001, Antolin et al. 2002). However, the influence of plague may cascade to other taxa associated with black-tailed prairie dogs, e.g. the burrowing owl. If burrowing owls select black-tailed prairie dog colonies for nesting, changes in the distribution of those colonies as a result of a plague epizootic may affect the distribution of nesting burrowing owls across the landscape.

A 14-year burrowing owl demography study on the Rocky Mountain Arsenal in Colorado studied the number of nesting burrowing owls as it related to prairie dog population size and colony area (Lutz and Plumpton, as cited in Antolin et al. 2002). The Rocky Mountain Arsenal was affected by multiple plague epizootics during the 14 years of the study. Numbers of

nesting burrowing owls tracked fluctuations in black-tailed prairie dog population size. The association of plague epizootics and burrowing owl nesting density and distribution has not been examined elsewhere, and may be a driving force in patterns observed in other areas within USFS Region 2.

#### Anthropogenic factors

##### *Pesticides*

Several studies have indicated that pesticides constitute a threat to at least certain populations of burrowing owls, both by direct poisoning or by secondary ingestion of pesticide-laden prey items (James and Fox 1987, LeClerc 1990, Baril 1993, World Wildlife Fund 1993, Blus 1996, James and Espie 1997, Mineau et al. 1997, Sheffield 1997b, Gervais et al. 2000, Klute et al. 2003). Rodenticide treatments (fumigation, strychnine-coated grain distribution) used to control burrowing mammals have been shown to have deleterious effects on burrowing owls in the form of: direct mortality, decreased adult body mass, and decreased breeding success (Klute et al. 2003). Insecticide (carbaryl and carbofuran) has been shown to reduce brood production by as much as 83 percent when directly applied to burrowing owl nest burrows (James and Fox 1987). The geographic extent of this threat is unknown, and whether the pesticides accumulate largely on the wintering grounds or the breeding grounds, or some combination of the two, is also largely unknown. However, application of strychnine-coated grains for rodent control, and applications of carbaryl- and carbofuran-based insecticides for corn and alfalfa crops are still legal within the United States and may be used within the agricultural areas of Region 2.

##### *Incidental shooting*

Although not documented for Region 2, shooting as a byproduct of recreational prairie dog shooting is a potential source of anthropogenic mortality in certain areas (James and Espie 1997). For instance, in one Oklahoma population, shooting accounted for 66 percent of total adult mortality (Butts 1973), and in a Canadian study, three populations were entirely decimated by shooting (Wedgwood 1976). Recreational shooting in prairie dog colonies also has a potentially more widespread though subtle and indirect effect on burrowing owl survival and productivity. Woodard (2002) found that nest success rates and number of young fledged by owls in prairie dog colonies subject to recreational shooting were significantly lower than in colonies where shooting of prairie dogs did not occur.

The number of young fledged under shooting was approximately 1.2 ( $N = 39$  nests) vs. approximately 1.8 in prairie dog colonies not subject to shooting ( $N = 58$  nests).

### *Lead ingestion*

Another possible effect of prairie dog shooting on burrowing owls is the ingestion of lead fragments from scavenged prairie dog carcasses. While ingestion of lead fragments is well-documented for other birds of prey (Pattee and Hennes 1983, Henny et al. 1984, Beyer et al. 1988, Pattee et al. 1990, Wayland and Bollinger 1999), examples of scavenging and subsequent lead ingestion by burrowing owls are rare (Stephens et al. 2003). A Wyoming study in 2003 examined if and how much raptors were exposed to harmful doses of lead from scavenging shot prairie dogs in the Thunder Basin National Grasslands (Stephens et al. 2003). Scavenging observations were made within shot prairie dog colonies, metal contents within prairie dog carcasses were analyzed, and blood/feather samples were bioassayed for lead concentrations for several species of raptors. Pin feathers were collected from 43 burrowing owls (20 from shot colonies [7 juvenile/13 adult] and 23 from unshot colonies [11 adult/12 juvenile]). Burrowing owls were not detected scavenging prairie dogs within recreationally-shot colonies, and lead concentration within feathers was below sub-clinical levels. Thus lead ingestion is not known to be a threat to burrowing owls at this time.

### *Wintering grounds*

All the threats cited above may be particularly important on the wintering grounds. For example, regulations concerning pesticide use differ among nations. Even where regulations are similar, enforcement may be lax in some of the important wintering areas. Economic pressures are likely to lead to rapid land conversion in other wintering areas, resulting in major habitat loss that could adversely affect over-winter survival of burrowing owls that migrate to breed within Region 2.

## ***Conservation Status of the Burrowing Owl in Region 2***

Although the data are far from complete, it appears that the western burrowing owl is declining over much of its range, particularly at the eastern and northern peripheries (Haug et al. 1993). To the extent possible, management should be coordinated at the broadest possible geographic scale. A clear understanding of the

large scale trends and an increased understanding of the factors that create considerable variability will allow managers to most fully use trend data for burrowing owls in making management decisions at large as well as small spatial scales. Also, the fate of burrowing owls at the regional scale is largely tied to that of prairie dogs, with ground squirrels as a secondary associate.

### *Temporal and spatial variability in habitats*

Over most of their range in Region 2 burrowing owls are migratory. The breeding habitats are too inhospitable for year-round residence. Probably the major source of habitat variability in Region 2 at this point is the fluctuation in prairie dog colonies due to habitat conversion, sylvatic plague, and poisoning. Other kinds of habitats, such as human residential neighborhoods, provide a different kind of temporal and spatial variability. In human-altered landscapes, disturbance and development may produce fluctuating or temporary benefits. At the beginning of human residential development, previously unsuitable habitats may become suitable (e.g., because of clearing of tall vegetation). As human residential development and urbanization proceeds, these temporary habitats may again become unsuitable; for example, ornamental shrubbery and other vegetation may eliminate the required openness and low stature of the vegetation structure. Managers will need to take into account these sources of variability and clearly distinguish between management practices directed toward those habitats largely driven by the association with prairie dogs and those habitats in which burrowing owls occur in the absence of prairie dogs or tightly clumped ground squirrels.

### *Life history vulnerability*

It is likely that the most productive and persistent burrowing owl populations occur in habitats with considerable stability, where fairly high site fidelity provides benefits at every stage of the life cycle. Although both natal and breeding dispersal can occur over fairly large distances (10 to 50 km), such dispersal is likely risky and may result in reductions in both fertility and survival that may make such dispersing individuals and their relocation sites more like sinks than sources for population growth and persistence. The matrix population analysis provided earlier suggests that "adult" survival is key to population persistence. Managers must make every effort to consider this most vulnerable stage of the life history when making decisions that could have subtle but important ramifications. It is tempting to focus nearly exclusively

on reproduction; clutch size and even fledging success are relatively easy to measure compared to estimating survival rates accurately. Nevertheless, small changes in survival rates may be more important to population dynamics than large fluctuations in reproductive output (**Table 6**).

#### Relative vulnerability to stochastic environments

McDonald has done the bulk of the matrix-based analysis for approximately 12 of the species assessments contracted out in the same program as the present report. Given the range of life histories addressed (e.g., plains killifish, *Fundulus zebrinus*, two bats, several frogs and turtles, water vole, *Microtus richardsoni*), burrowing owls are not, at first glance as vulnerable to environmental stochasticity as some of the others. Nevertheless, some of the short-lived species (e.g., plains killifish, water vole) may be well adapted to repeated local extinctions followed by recolonization. High vulnerability to stochastic fluctuation is balanced by high potential for rapid growth under favorable conditions. Burrowing owls lack any such obvious potential for rapid population growth, although high clutch sizes and recent expansions in Florida suggest some ability to respond to favorable change. Relative to some of the longer-lived turtles and bats, burrowing owls are relatively well buffered against inexorable decline in the face of strong stochasticity. Nevertheless, management decisions that can buffer against additional stochastic or steadily negative pressure on “adult” survival rates should be a major consideration in any conservation planning for burrowing owls in Region 2.

#### Declining habitat or management pressure on habitat

Much of the habitat of the burrowing owl in Region 2 is on lands not controlled by the USFS. On National Forest System lands occupied by burrowing owls, management decisions may require careful charting between conflicting perils. On the one hand, livestock grazing may produce the short vegetation profile that is a critical habitat requirement. In the absence of prairie dogs, grazing may be one of the few feasible options for maintaining such habitats. On the other hand, over much of their range, the decline of prairie dogs is likely linked to management practices associated with livestock grazing, including active eradication programs. In other areas, cultivation, especially in the form of large-scale monocultures, may entail habitat conversion that is inimical not only to prairie dogs but also to any of the burrowing mammals that are alternative providers of

the other critical habitat feature, the burrow. Although human residential development and urbanization are not occurring on USFS lands, any habitat loss outside the National Forest System both increases the relative importance of USFS-controlled habitat and the various kinds of pressures on those lands (i.e., increased recreational use, increased pressure for extractive uses). Practices such as extensive oil and gas development provide a new and unstudied potential for change whose effects are difficult to predict. If, for example, development were accompanied by concerted efforts to boost populations of prairie dogs, it is conceivable that the net effects could be positive.

#### Populations at risk and risk as a consequence of land management practices

Although the western subspecies of burrowing owl found in Region 2 is clearly declining at the eastern and northern limits of its range, the northern area lies outside Region 2. Furthermore, much of the core of the range of the subspecies falls within Region 2, and it is as yet unclear whether declines in Region 2 are sufficiently large to deem burrowing owls to be at risk in the core of the range. Without a doubt, however, declines throughout the range are almost entirely the result of land management practices. The indirect impacts of livestock grazing through their various effects on prairie dogs are clearly related to land management practices, as opposed to changes due to an “external” factor such as global warming.

#### Conclusions concerning conservation status

The Rocky Mountain Region lies roughly at the center of the western burrowing owl’s range, and conservation of the species in this region appears integral to overall species conservation. There is some evidence from surveys of state wildlife agencies, BBS data, and other sources that burrowing owl populations have declined in Region 2, although not to the extent that declines are occurring elsewhere in its range. These population declines are closely linked to declines in prairie dogs (Desmond et al. 2000) and other primary burrowers. However, without extensive and consistent systematic surveys for the species in Region 2, true burrowing owl population trends are still largely unknown.

Given the relatively large burrowing owl populations and the existence of large tracts of rangeland in Region 2, there is an opportunity to manage for sustainable burrowing owl populations in advance of severe declines. The “emergency room” approach used

in the northern parts of their range in Canada provides a cautionary tale on the lack of success that can be expected from such an approach to burrowing owl conservation. In summary, the conservation status of the burrowing owl in Region 2 is considerably brighter than in areas further toward the periphery of the range, such as Canada. Nevertheless, continuing declines in prairie dog populations due to plague, habitat loss, and eradication programs, and increased pressure on grasslands from various sources of land conversion, all combine to force the conclusion that managers can by no means be complacent about the long term persistence of burrowing owls at their current levels of abundance and their current widespread distribution.

### ***Management of the Burrowing Owl in Region 2***

#### Desired landscape condition and changes in the environment

Large-scale land use management decisions that have influenced grazing regimes, burrow availability, and overall availability of open spaces for wildlife are largely to blame for declines in western burrowing owl populations. However, thoughtful land management may slow habitat losses through practices that support the two primary burrowing owl habitat requirements: burrow availability and vegetation structure (i.e., short vegetation for nesting and foraging).

Huge historical changes in landscape-level disturbance regimes have probably had important consequences for burrowing owl habitat. Historically, control of prairie dogs, and to a lesser extent extirpation of buffalo from the Great Plains, have reduced the amount of area with suitable vegetation structure for burrowing owl nesting. Extensive introduction of cattle and other livestock on the western landscape has probably mitigated some of these impacts and introduced an important, if somewhat different, form of disturbance and means of maintaining a mosaic of vegetation patterns conducive to burrowing owl habitat requirements. While agricultural practices such as grazing have increased habitat availability in some areas where vegetation structure was not previously appropriate for burrowing owls, this additional habitat has clearly not been sufficient to offset habitat loss elsewhere. With development in the west occurring at such a rapid pace in unincorporated and rural areas (Taylor and Lieske 2002), a corresponding loss of ranchlands and the cattle that graze them may further exacerbate the loss of burrowing owl habitat.

While livestock grazing may help to maintain the vegetation component, it may also conflict with another component of burrowing owl habitat: the presence and maintenance of burrows. Indeed, extensive burrow availability is critical to the persistence of burrowing owls. In areas of active livestock grazing, large-scale control and eradication efforts for prairie dogs and other burrowing mammals have historically reduced the availability of habitats with suitable burrow density and vegetation height. Persecution of prairie dogs (and ground squirrels) through poisoning and shooting has been encouraged, if not mandated, on private lands, and encouraged and supported on public lands. Poisoning of black-tailed prairie dogs on national grasslands has recently been reduced, and USDA Forest Service management plans have begun to prescribe a variety of prairie dog management options in addition to rodenticide application, and in some places provided for expansion of black-tailed prairie dog colonies on national grasslands (USDA Forest Service 2001, under re-review). While there appears to be a gradual shift in policies toward prairie dogs on public lands, a general cultural shift toward greater tolerance of prairie dogs on private and other lands has been slow in coming, particularly in rural areas.

Intentional historical and ongoing reductions in prairie dog populations must be considered in conjunction with natural impacts to their populations. Epizootics of sylvatic plague can quickly decimate entire colonies, which may be slow to repopulate when isolated from other colonies through habitat conversion or simply via distance among fragmented populations. Well-connected and large prairie dog colonies should be maintained in historical prairie dog and burrowing owl habitats where open spaces exist.

Habitat conversion to urban landscapes is a worsening problem in Region 2. While habitat conversion is not likely to directly impact USFS lands on which burrowing owls reside, it tends to increase the importance of grasslands as they increasingly exist in a matrix of unsuitable habitat. Loss of habitat to urbanization is occurring in a patchy and fairly predictable pattern, with the largest losses occurring in the Colorado Front Range and other rapidly growing areas. While grazing regimes and management of burrowing mammals may be altered in a way that benefits burrowing owls, urbanization creates a more or less permanent habitat loss and tends to isolate existing populations.

## Conservation elements

Management strategies are required that support burrowing owl nesting and foraging habitat, burrowing owl prey species, and the burrowing mammals that provide nest burrows. Primary considerations in developing such management strategies may include the following:

- ❖ **Manage for well-connected, large, active colonies of prairie dogs.**
- ❖ **Reverse the longstanding sentiment towards widespread prairie dog eradication** in the form of poisoning and shooting, and support research into the **control of sylvatic plague** within prairie dog populations.
- ❖ **Manage to maintain historical burrowing owl nest sites.**
- ❖ Practice grazing regimes that **promote vegetation community diversity** and co-exist with primary burrower communities (especially prairie dogs).
- ❖ **Collaborate with private landowners** and public land managers.

In Region 2, management for well-connected and large colonies of prairie dogs should be the first management priority. Reduction of poisoning activities is a first step to this end. Further progress toward complete cessation of poisoning would almost certainly be beneficial to burrowing owls. Management should now assess the indirect and direct consequences of recreational prairie dog shooting on burrowing owls occupying national grasslands. There is sufficient evidence that burrowing owls use prairie dog colonies where recreational shooting occurs, but losses to incidental shooting may be an important mortality factor. The indirect effects of prairie dog shooting on burrowing owl habitat are even more poorly understood. Although it is probably rare that shooting completely decimates a prairie dog colony, there may be subtle but important implications for availability of burrows to burrowing owls. A program of visitor education on national grasslands could minimize these conflicts, particularly among recreational prairie dog shooters. In areas where prairie dog populations have been substantially reduced or eliminated, restoration of populations may be an option.

There is strong evidence that historical nesting places are important to burrowing owls. Identification of historical nesting places on national grasslands is an important first step toward improved management of the species. An extensive survey for burrowing owls on national grasslands in 1998 (Sidle et al. 2001) provided much needed baseline information on their distribution and should be a starting point for regular surveys to detect population trends on grasslands. Management of these historical nesting sites should focus on availability of burrows, protection from hunting, and availability of a vegetation mosaic that supports a diversity and abundance of prey items. In areas where burrowing owls do not exist, a program of grazing and prescribed burns could create a vegetation profile that is more suitable for primary burrowers and burrowing owls.

Manipulation of grazing regimes could be an important tool in improving burrowing owl habitat, although experimental manipulations for this purpose are not well-documented. A program that maintains short vegetation in burrowing owl nesting areas, while maintaining a more diverse vegetation structure in foraging areas, could be tested.

While public lands are an important component of the western burrowing owl range, private lands are very important as well (VerCauteren et al. 2001). Effective conservation of the species requires that management efforts be a collaborative effort among state and federal agencies and private landowners. For instance, special attention to and management of prairie dog colonies with burrowing owls should be a joint venture between public land managers and adjacent private landowners. Operation Burrowing Owl in Canada is an excellent model for garnering private landowner support for burrowing owl conservation. Coordination with private landowners near national grasslands could help reduce pesticide applications, particularly in the vicinity of nest burrows.

## Tools and practices

### *Inventory and monitoring*

Effective conservation of the burrowing owl within North America, and specifically within Region 2, will require the development of a burrowing owl monitoring program. In order to make meaningful comparisons of demographic parameters among burrowing owl populations within Region 2 and elsewhere, standardized monitoring methods are

required. Such a monitoring program should include the following:

- ❖ **Standardized population surveys** that allow for high rates of burrowing owl detection in the face of limited funding and personnel.
- ❖ **Standardized methods for estimating demographic parameters**, such as adult annual survival, juvenile recruitment, and productivity.
- ❖ **Development of a habitat monitoring program**, including macro- and microhabitat models.

### *Species and population monitoring*

Aside from the BBS and CBC data, there is currently no nationally-recognized monitoring program for burrowing owls in the U.S. Although the BBS survey methodology has generated a long-term data set with consistent search effort, it is probably not appropriate for accurately gauging burrowing owl population trends because of small sample size. The data for all of the states in Region 2 are considered to be of very low credibility because of an insufficient number of survey routes that encounter burrowing owls. The consequence is that the BBS data for these states are not sufficient to detect a 5 percent change in the population (Sauer et al. 2001).

In Canada, burrowing owl population monitoring occurs through Manitoba's Threatened Grassland Birds Project (Dundas and Jensen 1995), and in Saskatchewan and Alberta surveys are conducted through Operation Burrowing Owl (Dundas and Jensen 1995). A radiotelemetry project, called the Burrowing Owl Migration Tracking Project, was also recently initiated to attempt to link breeding populations in Canada with their wintering grounds.

Statewide and population-specific burrowing owl surveys are generally absent or inadequate in most U.S. states (Holroyd et al. 2001). In addition to baseline distribution and abundance data, sufficient funds are required to conduct regular and systematic surveys for burrowing owls. With recent population declines, there is an increasing impetus to gather these baseline data so that population trends may be better understood. In Colorado, the Rocky Mountain Bird Observatory has conducted extensive roadside surveys (VerCauteren et al. 2001). In Wyoming, historic burrowing owl distribution has been mapped from Wyoming Game and Fish Department data (Korfanta et al. 2001), and

extensive surveys have been conducted on national grasslands in the Great Plains (Sidle et al. 2001).

Current burrowing owl monitoring techniques range from a complete census (DeSante et al. 1997) to roadside surveys (VerCauteren et al. 2001), and a single, standardized survey method has not been identified (Holroyd et al. 2001). Roadside surveys have been used extensively for burrowing owls (Coulombe 1971, Ross 1974, Wedgwood 1976, VerCauteren et al. 2001, Conway and Simon 2003) as well as other diurnal raptors (Craighead and Craighead 1956, Woffinden and Murphy 1977, Fuller and Mosher 1987). Haug and Didiuk (1993) developed a survey method that helps to maximize the numbers of burrowing owls detected on roadside surveys through the use of recorded call playbacks of the male's primary call (*coo coooo*). In a study to assess the success of this protocol, males typically responded with a territorial posture and by giving the primary call. Males also flew to the female, gave the "white-and-tall" posture, or copulated with the female (Haug and Didiuk 1993). Females exhibited few responses but occasionally bobbed or issued the "chuck-and-chatter" call (Haug and Didiuk 1993). The use of recorded calls significantly increased the detection of burrowing owls relative to observations without the calls. The authors suggested the use of the calls during surveys beginning the first week after burrowing owl arrival on the breeding grounds. There is some evidence that the owls become habituated to the playbacks, but there was still considerable success of detection into the second week of June.

Conway and Simon (2003) recently developed a standardized roadside point-count survey method tested in Wyoming, Washington, and Arizona. This method is currently used in long-term demographic studies within those states. When tested against two other survey methods (line-transects and driving surveys), roadside point-count surveys had higher detection probability (64 percent) than the other two survey methods; line transects were largely ineffective, and driving surveys had a detection probability of 37 percent (Conway and Simon 2003). When the standardized point-count surveys are used with broadcasts of the male territorial call (similar to Haug and Didiuk's (1993) call-broadcast), they are highly effective in detecting owls. Conway and Simon (2003) advocate the use of this standardized method for three reasons: 1) greater statistical power to detect region-wide trends in burrowing owl populations, 2) the use of call-broadcast increases detection probability, and 3) when performed as three replicates, these surveys reduce variation in the probability of detecting burrowing owls. In order to adequately measure

trends in burrowing owl populations, survey results must be comparable across the species' range, and a standardized protocol is required. Conway and Simon's (2003) roadside survey protocol for burrowing owls is provided in **Figure 19**.

#### *Necessary elements of a population monitoring program*

A standardized monitoring protocol is essential for reliable information on burrowing owl population trends. A monitoring protocol for burrowing owls should prevent subjective, ad-hoc sampling decision, but some effort should be made to accommodate the unique behavioral attributes of the species. First, in addition to systematic sampling, some component of a survey protocol should focus on historical nesting sites since there is a great deal of potentially suitable burrowing owl habitat that is not occupied. Relatively high site fidelity means that historical nesting sites are very important and should be surveyed regularly (Korfanta et al. 2001). Most states have some burrowing owl distribution data housed in their Natural Heritage Programs or state wildlife agencies to provide a starting point for more detailed surveys of historical and other sites.

Random surveys of potentially suitable habitat that do not take into account the presence of burrows may not produce useful sample sizes. For instance, in a survey of 85 locations in Wyoming identified strictly by vegetation analyses showing appropriate burrowing owl habitat, only one site had a burrowing owl (Korfanta et al. 2001). In parts of the species' range where they predominantly use prairie dog burrows for nesting, standardized surveys of prairie dog colonies may be a much more efficient means of finding burrowing owls (Sidle et al. 2001). Applications of the standardized point-count survey method (**Figure 19**) to sample only within prairie dog colonies would require only minor modifications to an existing roadside protocol, such that results from the two methods would still be directly comparable. On a cautionary note, however, burrowing owls will nest outside of prairie dog colonies, and in areas with little to no prior information on burrowing owl distribution it would be prudent to begin with a more systematic, roadside method as suggested by Conway and Simon (2003).

Detectability of burrowing owls varies during the year, and surveys should be conducted at consistent times among years (**Figure 19**; Conway and Simon 2003). Diurnal behavior of burrowing owls allows for surveying during daylight hours, although surveys at dawn and dusk are probably preferable due to greater

burrowing owl activity during these times. Because response to call playbacks is such an effective means of locating burrowing owls, survey efforts should be concentrated during the breeding season, when playbacks are most likely to elicit a response (Haug and Didiuk 1993, Conway and Simon 2003). Since burrowing owls tend to be clumped on the landscape, an adaptive sampling technique is advisable, such that when one burrowing owl is found, adjacent areas of land are intensively surveyed. This type of adaptive sampling is appropriate in a rare species that exhibits a clustered distribution (Thompson and Seber 1996). The assumption of this technique is that if one animal is found, it is likely that others are nearby, and using a clustered sampling design will enhance sample size, reducing the variance associated with a population estimate. This will also allow better tracking of density changes in burrowing owl colonies.

Current survey methods are best used during the breeding season when owls are visible and are more firmly tied to a specific area. Survey methodology for the non-breeding seasons has yet to be adopted. Further, current methods are best suited for monitoring historical nesting locations and areas with high burrow density. Burrowing owls nesting singly or in the burrows of non-colonial mammals have a lower probability of detection. Some survey methods may also be biased by proximity to colonies and other biases that enter into a non-random methodology (Korfanta et al. 2001).

#### *Habitat monitoring*

GAP analysis provides a starting point for narrowing down potential burrowing owl habitat. However, GAP analyses rely heavily on vegetation parameters, and while vegetation type is an important criterion for habitat suitability, it does little to narrow habitat down to a realistic representation of where burrowing owls are actually found (e.g., see **Figure 5**). A combination of vegetation, elevation, and primary burrower layers may provide a better estimate of potential burrowing owl habitat.

There is a recognized need for improved understanding of burrowing owl habitat associations and mapping (Holroyd et al. 2001). Uhmman et al. (2001) developed a habitat suitability model for burrowing owls in eastern Canada. The model contained four habitat variables: burrow availability, forage vegetation height, nest vegetation height, and inter-nest distance. A suitability index was calculated for burrowing owl nest burrows and unoccupied burrows. Results indicated that habitat suitability

Roadside point-count survey routes should be selected within some structured sampling frame to ensure that observers do not preferentially place survey routes in areas with high breeding densities. For example, we recommend establishing one point-count survey route within each township/range that falls within the known breeding range of burrowing owls in each state. Each survey route will follow a secondary road, beginning within the center four sections of each township/range (sections 15, 16, 21, and 22). Location of each route will be selected in advance of the survey based on perceived suitable habitat for burrowing owls. The location of these point-count survey routes should in no way be influenced by previous knowledge of burrowing owl observations, historic records, or known nest sites. If no suitable habitat is available within the center four sections, a route can be located in the surrounding 12 sections. We also recommend supplemental survey routes (in addition to the systematic survey routes outlined above) based on areas of known burrowing owl breeding locations. These routes should be treated separately from the systematic survey routes because they will be located in areas of known burrowing owl activity (current or historical).

We recommend that each survey route be  $\geq 7.2$  km (4.5 mi) in length and include 10 survey points separated by  $\geq 0.8$  km (0.5 mi). This interval will help to ensure that observers do not re-count individual owls at adjacent points but still provide adequate detection probability. The exact location of each survey point should be chosen to provide an optimal viewing radius of the surrounding area. Adjacent survey points may be located  $>0.8$  km (0.5 mi) apart if no suitable habitat is available or if visibility of the surrounding habitat is not optimal at the 0.8 km interval. The permanent location of each survey point should be marked or recorded using a GPS receiver so that the exact survey location can be re-surveyed in future years.

Because detection probability associated with a single point-count survey is only 64 percent, we recommend three replicate surveys of each route so that overall detection probability will be 95 percent. Surveys should be conducted after birds have returned from migration but prior to the date when young disperse (e.g., 15 Apr–7 Aug in Wyoming; 1 Apr–21 Jul in Washington). One replicate survey should be conducted during each of three 30-day survey windows with each survey window separated by 10 days (e.g., 20 Apr–19 May; 30 May–28 Jun; 9 Jul–7 Aug in Wyoming). This approach will ensure survey effort during each of the three nesting stages (pre-incubation, incubation/hatching, and nestling) that differ in vocal and visual detection probability. Standardized burrowing owl surveys should include an initial 3-min passive segment followed by a 3-min call-broadcast segment. For the 3-min call-broadcast segment, we recommend a series of 30 sec call-broadcasts (coo-coo call and alarm call-broadcast at 90 dB measured 1 m in front of the speaker) interspersed with 30 sec of silence.

Surveys should be restricted to the early morning (e.g., 0.5 hr before sunrise until 0900 hr) and evening hours (e.g., 1700 hr until 0.5 hr after sunset) because vocalization probability and above-ground activity are often higher during these times compared to mid-day (Grant 1965, Climpson 1977, Johnsgard 1988). However, more studies are needed to evaluate daily variation in detection probability during all stages of the nesting cycle. Surveys should not be conducted during rain or when wind speed is  $>20$  km/hr. At each point, observers should record: (1) the number of adult owls, (2) the number of juvenile owls, and (3) the number of presumed nest sites. Implementing this survey protocol over a large geographic area is feasible. For example, we estimate that approximately five seasonal surveyors could conduct all of the surveys needed for the state of Washington (approx. 450 routes) following this recommended survey protocol.

**Figure 19.** Roadside survey protocol for burrowing owls. Source: Conway, C.J. and J.C. Simon. 2003. Comparison of detection probability associated with burrowing owl survey methods. *Journal of Wildlife Management* 67:501-511.

was most negatively affected by tall vegetation at the nest burrow. The authors found a strong correlation between historical nest site success and value of the suitability index. Index values ranged from 0.58 to 0.79 in unsuccessful historical nest sites, while successful nest sites had index values ranging from 0.7 to 1.0. This study provides promising evidence that habitat suitability elsewhere may be quantitatively assessed.

Recognition and conservation of historic burrowing owl nesting burrows is an important management tool. Understanding the timing of reproductive activities for different burrowing owl populations is important for management activities that require relocation of nests or nesting pairs to new sites, especially in advance of development projects. Relocation of owls during the courtship period was attempted in California where five pairs were moved 31 km to a new site after the initial nesting site was to be developed (Delevoryas 1997). Two of the pairs bred successfully, but of the other three pairs, the females persistently returned to the initial nesting site. Other relocation efforts have been largely unsuccessful because of extreme site tenacity for the original capture or breeding site (Feeney 1997). Many avian species exhibit very strong fidelity to breeding sites where they have enjoyed reproductive success, and relocation of burrowing owls to new sites during the breeding season may not be feasible.

#### *Population or habitat management approaches*

Management guidelines are presented in “Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies.” Holroyd et al. (2001) identified a need to standardize management and disturbance mitigation guidelines. For instance, guidelines for mitigating impacts by petroleum industries on burrowing owls and other prairie species (Scobie and Faminow 2000) may be used as a template for future mitigation guidelines (Holroyd et al. 2001). Operation Burrowing Owl is one of the few projects that have instituted a new management regime (in this case voluntary preservation of burrowing owl nesting sites by private landowners) followed by a quantitative assessment of the effects of that regime (Skeel et al. 2001). In spite of this ambitious effort, burrowing owl populations in eastern Canadian prairies have continued their precipitous declines. However, the study’s results were important in highlighting the importance of population impacts on wintering grounds.

### ***Information Needs***

Although Region 2 comprises much of the core of the distribution of the western subspecies of burrowing owl, the owl has been more intensively studied elsewhere, particularly in Canada and California. The distribution of burrowing owls in Region 2 is reasonably well known. Nevertheless, as noted by Holroyd et al. (2001), many important information and research needs remain. The most pressing needs for further information useful to the management of burrowing owls in Region 2 include:

- ❖ Improved data on **population trends** in Wyoming, Colorado, Nebraska, Kansas, and South Dakota
- ❖ Improved **demographic data**, particularly detailed studies of adult survival rates, and rates and distances of natal and breeding dispersal
- ❖ Increased understanding of **habitat use** in areas not occupied by prairie dogs
- ❖ Increased understanding of various **land use impacts** such as livestock grazing, oil and gas development, and fire regimes on population dynamics
- ❖ Increased understanding of the **indirect effects of sylvatic plague** on burrowing owl ecology, drawing comparisons between populations in plague-affected and plague-free areas within Region 2
- ❖ Elucidation of the wintering range and **linkage of the winter and breeding ranges**
- ❖ Examination of **threats faced by owls on the wintering grounds** in Mexico

#### Population trends

Although the distribution of burrowing owls in Region 2 is reasonably well understood, few studies have carefully assessed population trends in a consistent and statistically robust manner. Attempts such as those of Korfanta et al. (2001) relied on BBS data sets, which contain methodological problems that make it difficult to draw firm conclusions. What will be needed

are consistent, well-designed monitoring programs, preferably ones that use comparable protocols when conducted by different agencies or organizations. Steps in this direction have begun to occur (DeSante et al. 1997, Duxbury and Holroyd 1998) and should be fostered. Only with reliable long term monitoring will it be possible to state with confidence whether populations of burrowing owls in the core of their range in Region 2 are stable, increasing, or declining.

#### Improved demographic data

Few demographic data are available for burrowing owls anywhere, and even fewer for populations in Region 2. Those data that are available (e.g., Lutz and Plumpton 1997) suggest that considerable variability in demographic rates occurs over space and time. Clearly, increased understanding of the population dynamics and conservation needs of burrowing owls will require more detailed studies of adult survival rates and rates and distances of natal and breeding dispersal. Collection of demographic data should be guided by consideration of those vital rates that are highlighted by the sensitivity and elasticity analyses outlined in the earlier section on demography and matrix population models. Any fuller understanding of the population dynamics of burrowing owls in Region 2 will require regionally-based, precise estimates of those transitions to which  $\lambda$  (the population growth rate) is particularly sensitive or elastic. Particularly important are better estimates of the survival of “adult” breeding females. Studies at small spatial scales will be unable to separate disappearance from a local study site into those individuals that truly died and those individuals that simply engaged in breeding dispersal within or among seasons. Increased understanding of the range of temporal and spatial variation in the vital rates is also of paramount importance. Current knowledge does not permit us to suggest which environmental factors are most important to this spatial and temporal variability.

Comparative approaches could be particularly useful. Do mortality rates differ significantly between burrowing owl sites adjacent to roads as compared to areas away from roads? If differences do exist, how does the mortality difference affect the outcomes of matrix population models (values for  $\lambda$ , sensitivity, and elasticity)? In a study of threatened Florida scrub-jays, *Aphelocoma coerulescens*, Mumme et al. (2000) found that mortality in areas adjacent to roads was significantly higher than in areas away from roads. Similarly, how much do feral or domestic cats and dogs affect the mortality of fledging and “adult” burrowing owls?

Land uses such as livestock grazing, oil and gas development, and fire regimes have unknown but potentially important impacts on demographic parameters and population dynamics. Careful studies comparing the population dynamics of areas under different land use regimes would provide both basic background knowledge of burrowing owl population dynamics as well as the basis for informed management decisions regarding the impacts of those land uses on the persistence of burrowing owls.

#### Habitat use not linked to prairie dogs

Clearly a strong link exists between the distribution of burrows made available by prairie dogs and the fate of burrowing owl populations. Just as clearly, burrowing owls appear to be able to persist in areas outside the range of prairie dogs. In some areas, burrowing owls appear to exhibit population increases in the face of fairly intensive agriculture or even suburban development. Increased understanding of the factors that permit population persistence or even increase in the face of some agricultural practices or human development, but not in the face of other sorts of land conversion, would be extremely helpful in managing burrowing owls at landscape level scales.

#### Indirect effects of sylvatic plague

A major uncertainty for the status of burrowing owls in Region 2 is the indirect effects of sylvatic plague. Clearly, plague has drastic effects on prairie dog occurrence and abundance (Restani 2002). Understanding the dynamics of prairie-dog interactions with burrowing owls would be greatly enhanced by comparing plague-free areas with ongoing studies in areas impacted by plague. A major reservoir for plague-free populations of black-tailed prairie dogs is the Conata Basin of South Dakota, including portions of Badlands National Park (Albertson personal communication 2004) and the Buffalo Gap National Grassland (Sargent personal communication 2004). Studies of burrowing owls in this area would be invaluable.

#### Linking breeding and wintering ranges

The fate of burrowing owls in Region 2 may depend on decisions and processes occurring outside the region on the wintering grounds. Factors such as habitat loss or pesticide use on the wintering grounds may be the major determinants of burrowing owl viability. Little is currently known about the link between breeding and winter ranges. Given the lack

of genetic substructure found by Korfanta (2001), the most fruitful approach would apparently be the use of stable isotopes (Rubenstein et al. 2002). Some migratory species have very restricted winter ranges or high local fidelity to traditional sites. For example, Haig et al. (2002) recently found that willets (*Catoptrophorus semipalmatus*) breeding in Utah winter in a small area of San Francisco Bay, whereas willets further east in Nebraska winter in an equally restricted range on the Gulf Coast of Texas.

#### Threats on the winter range

For some species such as Swainson's hawk, precipitous declines have been attributed to particular agricultural practices on the wintering grounds rather than on the breeding grounds (Woodbridge et al. 1995, Goldstein et al. 1999). Either pesticide use or habitat loss via agricultural conversion or urbanization could threaten burrowing owl populations on the wintering grounds in Mexico. Little or nothing is known of the extent of such threats.

## DEFINITIONS

**Altricial** — newly hatched young that cannot open their eyes, leave the nest, or thermoregulate, and they are completely dependent on parental care).

**Breeding dispersal** — movement from site of one breeding attempt to site of subsequent breeding attempt(s).

**Cavalli-Sforza chord distance** — a method for converting gene frequency data from populations into a matrix of distances among those populations (Cavalli-Sforza and Edwards 1967). The distance matrix can then be used to construct a phylogenetic tree using a method such as *neighbor-joining*.

**Census interval** — time between successive censuses used for formulating the time step in a demographic population model. The interval will often be one year (annual census) either just before or just after the breeding season).

**Clade** — monophyletic group of taxa that includes a common ancestor and all of its descendants.

**Crepuscular** — active at dawn or dusk.

**Internode** — the distance between successive branching points in a phylogenetic tree.

**Life cycle graph** — a diagrammatic representation of a matrix population model. Although it provides a useful way to visualize the life cycle, it also serves as the basis for formal graph theory analyses that parallel or augment the more familiar matrix-based methods for demographic analysis.

**Microsatellite DNA** — simple sequence tandem repeats of nuclear DNA found in the genomes of most organisms. Microsatellites consist of tandemly repeated sequences of nucleotides (e.g. AC<sub>19</sub>, meaning 19 repeats of a dinucleotide AC motif). Because of their unique slippage mutation process, microsatellites tend to be highly variable and are well suited for use as markers to examine genetic population structure. The fact that they are codominant (meaning heterozygotes can be distinguished from homozygotes) allelic markers also increases their utility in population genetic analyses. See <http://www.uwyo.edu/dbmcd/lab/msatintro.html> (and references therein)

**Minisatellite DNA** — tandem repeat nuclear DNA consisting of long motifs (several hundred base pairs vs. the two to five of microsatellites). Because screening is of the repeat unit, which may occur at multiple locations in the genome, minisatellites are not locus-specific and therefore result in multiple bands. Their high variability makes them well-suited for problems of identity, parentage and relatedness but less so for problems of population structure. The long motif creates another drawback — the DNA cannot be amplified by the polymerase chain reaction (PCR) and the technique therefore requires large amounts of DNA relative to that required for microsatellite analyses.

**Mitochondrial DNA (mtDNA)** — circular non-nuclear DNA often analyzed by DNA sequencing as a basis for studies of phylogeny and systematics. Because mtDNA is clonally inherited through the female cytoplasm, it has certain genealogical features that make it especially useful for phylogenetic studies. For detailed population studies the molecule is less useful because it forms essentially a single locus, and because it is usually difficult to sequence enough individuals to have representative samples of populations.

**Natal dispersal** — movement from place of birth to site of first or subsequent breeding attempts.

**Neighbor-joining tree** — a method for converting a matrix of pairwise differences (e.g. *Cavalli-Sforza chord distances*) among taxonomic units (e.g. populations, species) into a phylogenetic tree depicting branching patterns of relatedness among the taxa.

**Node** — circle depicting a stage or age-class in a *life cycle graph*. The arrows (arcs) connecting the nodes represent transitions such as survival or fertility.

**Panmixia** — lack of genetic substructure. Populations are said to be panmictic when gene flow is sufficiently high that it prevents any differentiation among subpopulations.

**Philopatry** — returning to the natal site for breeding.

**Vital rates** — demographic transitions, represented by the arcs in a *life cycle graph*. The vital rates often denote survival or fertility transitions, but could also represent transitions such as growth or change in breeding or social status.

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