

FUNCTION OF MANURE-SCATTERING BEHAVIOR OF  
BURROWING OWLS (*Athene cunicularia*)

by

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## DEDICATION

For my father, Scott R. Smith,  
who taught me that hawks say “crow,”  
and crows say “hawk.”

## TABLE OF CONTENTS

LIST OF FIGURES .....	7	
LIST OF TABLES .....	8	
ABSTRACT .....	9	
INTRODUCTION.....	10	
Mate-Attraction Hypothesis.....	16	
Burrow-Occupied Hypothesis.....	18	
Olfactory-Concealment Hypothesis.....	19	
Prey-Attraction Hypothesis.....	20	
Conservation Implications.....	22	
STUDY AREA.....	23	
METHODS.....	24	
Mate-Attraction Hypothesis.....	24	
Burrow-Occupied Hypothesis.....	25	
Olfactory-Concealment Hypothesis.....	28	
Prey-Attraction Hypothesis.....	30	
RESULTS.....	35	
Mate-Attraction Hypothesis.....	35	
Burrow-Occupied Hypothesis.....	36	
Olfactory-Concealment Hypothesis.....	41	
Prey-Attraction Hypothesis.....	41	
DISCUSSION.....	45	
APPENDIX A	Allometric equations from Rogers et al. (1977) used to estimate dry weight (mg) from body length (mm) for invertebrates collected in pit-fall traps in south-central Washington, 2001 and 2002. ....	53
APPENDIX B	Allometric equations used to estimate body length (mm) from body parts commonly found in pit-fall traps. Equations are based on whole insects collected in pit-fall traps in south-central Washington in 2001 and 2002.....	54

## TABLE OF CONTENTS – Continued

APPENDIX C	Sample sizes associated with allometric equations used to estimate body length (mm) from body parts; <i>n</i> refers to the number of known lengths on which the equation is based. ....	56
APPENDIX D	Average body length (mm) of whole ants and pill-bugs found in pit-fall traps in south-central Washington in 2001 and 2002. These lengths were used for all specimens found in pit-fall traps (including partial specimens); <i>n</i> refers to the number of individuals used to obtain the average length.....	58
APPENDIX E	Sources for insects found in the diet of burrowing owls. These sources were used to determine which insects to use in analysis of the prey-attraction hypothesis. Refer to Literature Cited for full references.....	59
APPENDIX F	Number of individuals and total biomass of all taxonomic Orders and Families of insects collected in pit-fall traps in south-central Washington in 2001 and 2002.....	60
APPENDIX G	Institutional Animal Care and Use Committee.....	62
LITERATURE CITED.....		63

## LIST OF FIGURES

- Figure 1. Occupied burrowing owl nest burrows in south-central Washington with dried mammal manure around the entrance to the nest burrow and in the tunnel leading to the nest.....11
- Figure 2. Historic photos (Bent 1938) showing the presence of dried mammal manure at burrowing owl nest burrows... ..... 12
- Figure 3. Sampling design used in 2001 and 2002 for testing the prey-attraction hypothesis to explain manure-scattering behavior of burrowing owls..... 32
- Figure 4. Relationship between date of initiation of manure-scattering and male arrival, and between initiation of manure scattering and pair formation of burrowing owls in south-central Washington in 2002. Points above the line are nests where initiation of manure-scattering occurred after male arrival (a), or after pair formation (b). The burrow-occupied hypothesis predicts points will be close to the line (a), and the mate attraction hypothesis predicts points will be below the line (b).....37
- Figure 5. Biomass of insects caught in pit-fall traps at paired sites with and without supplemented manure in south-central Washington in 2001 and 2002. Total biomass includes all insects collected when all 6 traps at a sampling site were usable. Average biomass uses the average biomass of insects per trap when some traps at a sampling site were unusable..... 43

## LIST OF TABLES

Table 1.	Predictions of 4 alternative hypotheses for function of the manure-scattering behavior of burrowing owls. Tests were conducted in south-central Washington from February to August 2001-2002.....	17
Table 2.	Mean ( $\pm$ SE) dates in 2002 on which burrowing owls arrived at nest-burrows following spring migration, mean ( $\pm$ SE) dates on which burrowing owls initiated manure-scattering behavior, and the mean ( $\pm$ SE) number of days after arrival that initiation of manure-scattering began.....	36
Table 3.	Average mass ( $\pm$ SE) and volume ( $\pm$ SE) of material scattered at the entrance to burrowing owl nest burrows 7 days following presentations of a potential competitor (taxidermic mount and primary call of a burrowing owl) and a control (taxidermic mount and primary call of a European starling). ....	39



## ABSTRACT

Birds often collect non-food materials to use in nest-building. Yet, some birds collect materials that serve functions other than holding and insulating young. Burrowing owls (*Athene cunicularia*) routinely collect dried mammal manure and scatter this dried manure at the entrance to their nest burrow and in the tunnel leading to the nest. Many alternative hypotheses have been proposed to explain the function of this manure-scattering behavior, yet none of the potential explanations have been rigorously tested. I examined the function of this behavior by testing 4 alternative hypotheses. I found no support for the widely-accepted olfactory-concealment hypothesis, or for the mate-attraction hypothesis. Predictions of the burrow-occupied hypothesis were upheld, but results were not statistically significant. Thus, the burrow-occupied hypothesis deserves more attention. My data support predictions of the prey-attraction hypothesis. Pit-fall traps at sampling sites with manure collected more insect biomass than pit-fall traps at sampling sites without manure. The manure-scattering behavior of burrowing owls appears to function to attract insect-prey for sentinel males, incubating females, or nestlings.

## INTRODUCTION

Birds often collect non-food materials to use in nest-building (e.g., vegetation, sticks, mud, animal hair, feathers; Hansell 2000). These materials generally function to hold and insulate developing young. However, particular nest-building materials of some bird species provide important adaptive functions beyond structure and insulation (Clark 1991, Hansell 1996, Yosef and Afik 1999, Hansell 2000). For example, European starlings (*Sturnus vulgaris*) line their nest with green plants containing chemical compounds that reduce parasite loads (Clark 1991). Over 50 species of birds (e.g., blue-grey gnatcatchers, *Polioptila caerulea*) build nests that contain lichen flakes and white spider cocoons on the outer surface of their nests for visual camouflage. This camouflage functions to reduce the probability of nest depredation (Hansell 1996). Birds also collect and use functional materials that are not directly related to nest-building. For example, male bowerbirds (*Ptilonorhynchus* spp.) decorate their mating sites, or bowers, with brightly-colored objects that attract mates and serve as a signal of male quality (Borgia 1985). Males of Lawes' Parotia (*Parotia lawesii*) collect objects such as snake-skin, scat, chalk, mammal fur, and feathers, and place them at their display-sites. The objects are not used by males in their courtship display and are not related to mating success, but may increase female visitations to the display site (Pruett-Jones and Pruett-Jones 1988).

Burrowing owls also collect materials and place them near their nest-site (Bendire 1892, Scott 1940). Though burrowing owls use different materials, mammal manure (e.g., horse and cow) is commonly collected by owls and has received the most attention in the scientific and common literature (Bendire 1892, Scott 1940, Martin 1973, Green

and Anthony 1989). Throughout their range, burrowing owls use this dried manure to build their nest-cup, and to scatter at the entrance to their nest burrow and inside the 3 m long tunnel leading to their underground nest chamber (Figure 1-2). Collecting manure is potentially energetically-costly, potentially increases the risk of depredation, and few other bird species display this odd behavior. Consequently, why burrowing owls scatter manure around their nest burrow is an interesting question.

The manure-scattering behavior was first described over 100 years ago (Bendire 1892), and many authors have suggested that this behavior reduces nest depredation via olfactory-concealment of nest scents (Martin 1973, Green and Anthony 1989, Merlin 1999, Holmes et al. 2003). However, 4 other alternative hypotheses have been proposed to explain the possible adaptive function of the manure-scattering behavior: 1) temperature or humidity regulation (insulation, *sensu* Martin 1973, Green 1988, also see Tortosa and Villafuerte 1999 for use of moist manure as nest insulation by white storks, *Ciconia ciconia*), 2) flood protection (Butts and Lewis 1982, Greibel 2000), 3) to deter parasites (Green 1988), and 4) reduction of carbon-dioxide levels (R. Brady and J. Beltoff, Boise State University, personal communication). Three other alternative hypotheses that have not been previously suggested are 1) mate attraction, 2) signaling burrow occupancy to conspecifics, and 3) attraction of insect prey.



Figure 1. Occupied burrowing owl nest burrows in south-central Washington with dried mammal manure around the entrance to the nest burrow and in the tunnel leading to the nest.

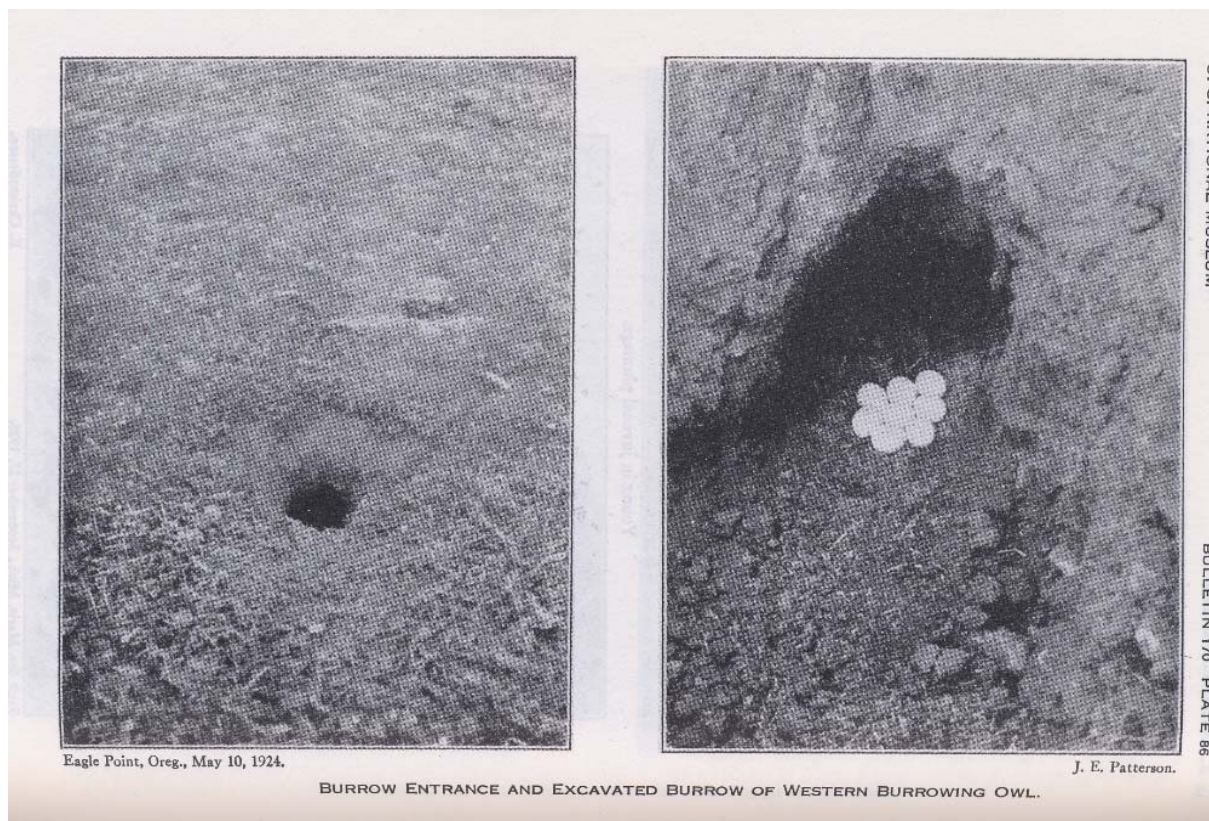


Figure 2. Historic photos (Bent 1938) showing the presence of dried mammal manure at burrowing owl nest burrows.

Prior to testing alternative hypotheses about the function of manure, we should first consider the most parsimonious explanation that the observed pattern of “manure-scattering” is simply a by-product of nest-building. Burrowing owls just may be “messy” and drop excess nest-building material on the mound and in the tunnel. Yet, owls seem to shred manure deliberately onto the burrow mound (M.D. Smith, personal observation), and if removed from the mound (by researchers) owls quickly begin to replace manure (Martin 1973, M.D. Smith, unpublished data). Generally, male burrowing owls retrieve and scatter dried manure (D. Todd and R. Poulin, University of Regina, personal communication). If males deliberately shred manure directly onto the mound, perhaps they leave manure for females to use in nest-building. Female-use could explain why manure is quickly replaced if removed; males may assume that females are still using manure, and thus, they continue to provide manure (see Szentirmai and Szekely 2002, for regulation of nest-material). Yet, seasonal timing does not support this explanation. If males bring and shred manure for female-use, then males should stop bringing manure once the nest is complete. Yet, males continue to bring manure to the nest burrow throughout laying and incubation and even after eggs have hatched (M. D. Smith, unpublished data).

The most commonly-mentioned hypothesis, first proposed by Martin (1973), states that manure scattered around the entrance and in the tunnel functions as predator-protection by camouflaging the scent of burrowing owls from potential predators. Authors of many scientific and general publications assume that this olfactory-concealment hypothesis is the primary explanation for the manure-scattering behavior of

burrowing owls. For example, the use of manure to conceal the scent of young is mentioned on many wildlife agency and educational websites (e.g., Manitoba Conservation - Wildlife and Ecosystem Branch, U.S. National Park Service, Saskatchewan School Division, Center for Biological Diversity), in field guides (Merlin 1999), at zoos (Arizona-Sonora Desert Museum, Tucson, AZ), and has even been perpetuated in a children's book about burrowing owls (Marston 1996). Widespread acceptance of the olfactory-concealment hypothesis is based on a single study in Oregon (Green and Anthony 1989). Green and Anthony (1989) reported higher rates of depredation in areas where owl nests did not have manure at their entrances compared to areas where nest entrances were scattered with manure. Though Green and Anthony's study (1989) was the first (and only) to evaluate the function of the manure-scattering behavior, their study was correlative and they failed to test alternative hypotheses. Consequently, the difference in nest depredation between the two areas could have been due to factors other than the difference in use of manure. For example, the density of predators may have been different between areas where manure was and was not available. Moreover, male burrowing owls are conspicuous because they generally stand at the entrance to the nest-burrow for most of the day throughout the nesting cycle (Coulombe 1971, Thomsen 1971, Martin 1973). It seems unlikely that owls would go to great lengths to hide the scent of their nest while at the same time drawing visual attention to the location of the nest.

Despite these shortcomings, many authors have routinely cited the Green and Anthony (1989) study as proof of the olfactory-concealment hypothesis (Haug et al.

1993, Desmond et al. 1997, Green and Anthony 1997, Griebel 2000, Dechant et al. 2001, Holmes et al. 2003). Experimental studies are needed to more rigorously test the validity of this widely-accepted hypothesis, and predictions associated with the other hypotheses need to be tested simultaneously with the olfactory-concealment hypothesis. Hence, I tested 4 alternative hypotheses (mate-attraction, burrow-occupied, olfactory-concealment, and prey-attraction) to explain the function of manure-scattering behavior in burrowing owls. Below is an explanation of each of the 4 hypotheses and the predictions I used to evaluate the validity of each hypothesis.

#### Mate-Attraction Hypothesis

The manure-scattering behavior of burrowing owls may function to attract females. Structures built by males of various taxa often contain features that reflect individual quality and are used by females to choose among perspective mates (Borgia, 1985, Barber et al. 2001). For example, three-spine sticklebacks (*Gasterosteus aculeatus*) with lower levels of stress (reflective of good health) build higher quality, more organized nests (Barber et al. 2001). Female burrowing owls may choose mates based on the manure (and other materials) brought to the burrow in the same way that female bowerbirds choose mates based on the brightly-colored objects at the male's bower (Borgia 1985). The mate-attraction hypothesis predicts that if the manure-scattering behavior functions to attract mates, then males will initiate manure-scattering prior to pair formation (Table 1).



Table 1. Predictions of 4 alternative hypotheses for function of the manure-scattering behavior of burrowing owls. Tests were conducted in south-central Washington from February to August 2001-2002.

Predictions	Hypothesis			
	Mate Attraction	Burrow Occupied	Olfactory Concealment	Prey Attraction
Stage of nesting cycle when manure is collected	Prior to pair formation	Soon after arrival	Just prior to incubation	All stages <sup>1</sup>
Manure presence will discourage nesting	no	yes	no	no
Increased perception of competition causes increase in manure	yes / no	yes	no	no
Higher fecundity at nests with manure	no	no	no	yes
Lower depredation at real nests with manure	no	no	yes	no
Lower depredation at artificial nests with manure	no	no	yes	no
More insect biomass at nests with manure	no	no	no	yes

<sup>1</sup> During nesting stage when food is most limiting and probably more common after pair formation.

### Burrow-Occupied Hypothesis

The manure-scattering behavior of burrowing owls may function as a signal given by resident males to indicate an occupied burrow. The use of non-food materials to signal occupancy has been suggested in other birds. Green twigs are often found in raptor nests and the presence of this greenery may be a signal to indicate an occupied nest in some raptors (Selas 1988). The presence of green twigs also has been suggested as a territorial advertisement in golden eagles (*Aquila chrysaetos*; Bergo 1987). Because burrowing owls in western North America do not dig their own nest burrows, suitable nest burrows are thought to be a limited resource (Desmond and Savage 1996). Thus, unattended burrows may attract unpaired males searching for vacant burrows. Scattering manure in the nest tunnel and at the entrance to the nest burrow may function as a visual cue to signal occupancy to conspecifics. This visual signal of occupancy may reduce conflicts with conspecifics. Burrowing owls have been observed fighting aggressively with intruders that approached within 10 m of the resident's burrow (Thomsen 1971, Martin 1973). Given that resident males of many species usually win territorial disputes (Davies 1978, Krebs 1982, Alcock & Bailey 1997), non-resident males might obey this signal to reduce costly agonistic interactions. For resident males, the energetic cost of collecting manure may be surpassed by the benefit of reduced aggressive encounters (even though they would typically win those disputes). The burrow-occupied hypothesis predicts that if the manure-scattering behavior of burrowing owls functions as a signal to other males, then 1) owls arriving to the breeding grounds will be reluctant to settle in burrows with manure visible at the entrance, 2) owls with an experimentally-increased

perception of intraspecific competition for burrows will collect more manure (a more amplified signal) compared to owls without the increased perception of competition, and 3) initiation of manure-scattering should occur immediately after male arrival to the breeding grounds (Table 1).

#### Olfactory-Concealment Hypothesis

The manure-scattering behavior of burrowing owls may function to mask the scent of owls from predators and thereby reduce the probability of nest depredation. Other animals appear to use olfactory-concealment to reduce depredation. White-breasted nuthatches (*Sitta carolinensis*) often sweep nest trees with insect remains (Kilham 1968). Squirrels travel up and down tree trunks along established scent-trails in search of food. Kilham (1968) suggested that the insect-sweeping behavior of nuthatches might reduce depredation by squirrels by covering these scent trails. Behaviors that function to conceal nest scents also may have evolved in termitarium-nesting birds in the tropics. Parrots (Psittacidae) and trogons (Trogonidae) often place their nests in cavities in termitaria inhabited by odorous ants (*Dolichoderus* spp). The odor of the ants may mask olfactory cues of nesting birds and reduce the probability of depredation (Brightsmith 2000).

Badgers (*Taxidea taxus*), coyotes (*Canis latran*), and striped skunks (*Mephitis mephitis*) are the most common burrowing owl nest predators (Haug et al. 1993) and rely on olfactory cues to locate prey (Knopf and Balph 1969). Hence, the presence of mammal manure at the entrance to burrowing owl nests may conceal odors associated

with an active nest and reduce the risk of depredation to incubating females, eggs, and nestlings (Green and Anthony 1989). The olfactory-concealment hypothesis predicts that if the manure-scattering behavior functions to reduce the probability of depredation, then 1) active nests supplemented with manure will have a lower probability of nest depredation compared to nests at which manure has been removed, 2) artificial nests supplemented with manure will have a lower probability of depredation compared to artificial nests with no manure, and 3) initiation of manure-scattering will begin just prior to incubation (Table 1).

#### Prey-Attraction Hypothesis

Alternatively, the manure-scattering behavior of burrowing owls may function to attract insect prey for sentinel males, incubating females, or nestlings. The use of non-food materials to attract prey has not been reported previously, however some organisms do use strategies to attract, rather than stalk, prey. Well-known examples include pitcher plants (*Nepenthes rafflesiana*) that emit olfactory and visual cues to attract insects (Moran 1996) and northern shrikes (*Lanius excubitor*) that sing year-round to acoustically lure songbirds (Atkinson 1997). Insects are attracted to and inhabit mammal manure (Rodriguez et al. 2003). Collection of manure to attract insect prey has not been previously described, but birds do take advantage of insect prey found at manure deposits. For example, African jacanas (*Actophilornis africanus*), black crakes (*Amaurornis flavirostris*), and palm-nut vultures (*Gypohierax Angolensis*) forage for insects found in elephant (*Loxodonta africana*) and buffalo (*Syncerus caffer*) dung

(Ruggiero and Eves 1998), and lapwing (*Vanellus vanellus*) chicks in the Netherlands are dependent on arthropods living in soil and cow-dung patties (Bientema et al. 1991). Hence, collecting and scattering manure at a convenient foraging location may be beneficial for insectivorous birds. Insects are a significant prey item of burrowing owls; insects made up 90% of total diet and 13% of biomass in Oregon and Washington (Green et al. 1993), 91% of total diet and 29% of biomass in Idaho (Gleason and Craig 1979), and 90% of total diet and 9% of biomass in Colorado (Marti 1974). Attracting insects to their nest burrow may benefit burrowing owls by increasing food availability or reducing foraging trips by adults. Increasing food availability may increase fecundity or nestling growth rates. Reduced foraging trips might allow additional time for activities such as vigilance and guarding their nest burrow, may reduce temperature fluctuations of developing embryos, and may reduce the probability of depredation (Conway and Martin 2000). Attracting insect prey to the entrance of the nest burrow also may allow nestlings to gain experience in handling prey near the safety of the nest burrow.

Burrows alone may create a microclimate beneficial to insects (Coulumbe 1971). Indeed, insects such as coleopterans are typically associated with rodent burrows (Anduaga and Halfpter 1991). Thus, insects may be attracted to burrowing owl nest burrows even without the presence of scattered manure. Tests of the prey-attraction hypothesis need to distinguish between attraction of insects to manure and attraction of insects due to the burrow itself. The prey-attraction hypothesis predicts that if the manure-scattering behavior of burrowing owls functions to attract insects, then 1) burrows with manure will attract more insect prey compared to burrows without manure,

2) non-burrow sites with manure will also attract more insects than non-burrow sites without manure, 3) fecundity at nests supplemented with manure will be higher than at nests without manure, and 4) manure-scattering will begin at any point of the nesting cycle, but will be most common after pair formation, and during the nesting stage when food is most limiting (Table 1).

### Conservation Implications

Burrowing owls have suffered range contractions or population declines in many portions of their North American range (James and Espie 1997, Dechant et al. 1999). They are currently listed as an endangered species in Canada, Minnesota, and Iowa, and are a *species of national conservation concern* in the United States (U.S. Fish and Wildlife Service 2002). Historically, burrowing owls may have used manure from large mammals such as mastodons (*Mastodon americanus*), mammoths (*Mammuthus primigenius*), bison (*Bison bison*), elk (*Cervus elaphus*), and pronghorn (*Antilocapra americana*). The numbers and range of large mammals roaming grasslands, shrub-steppes, and deserts in North America have decreased (Garretson 1983, MacDonald 1984). If the use of manure serves an important function for burrowing owls, the decrease in available manure may be contributing to current population declines of burrowing owls. Indeed, several authors and management agencies have begun suggesting that mammal manure be supplemented in areas with nesting burrowing owls as a way to help restore local populations (Green and Anthony 1997, Dechant 2001,

Colorado Division of Wildlife 2003). A better understanding of the function (if any) of manure-scattering behavior is needed before we begin advocating spreading dried mammal manure across the landscape to aid burrowing owls. Specifically, understanding why this behavior has evolved will help in directing agency and volunteer resources to the most efficacious conservation strategy. For example, if manure-scattering deters predators, then we might only want to supplement manure in areas with high rates of nest depredation. But, if manure-scattering serves as a signal of occupancy, then supplementing manure in areas with high density of nesting owls might be the highest priority. Finally, understanding the function of this behavior is also important so that we can determine the type of manure and the seasonal timing of any supplementation efforts.

## STUDY AREA

Field research was conducted from February to September 2000-2002, in south-central Washington, USA. The study site covered approximately 518 km<sup>2</sup> in Franklin and Benton counties, Washington. Land use in this area included urban, suburban, industrial, agricultural, and horse and cattle grazing. Burrowing owl nests were located in areas with all types of land use, except dense urban areas. Burrowing owl nests used for this study were predominantly located in moderately-disturbed industrial areas. A number of nests also were located in undisturbed shrub-steppe.

## METHODS

### Mate-Attraction Hypothesis

I tested 1 prediction of the mate-attraction hypothesis. If manure is used by burrowing owls to attract females, then males should initiate manure-scattering behavior prior to pair formation.

### *Nesting-Event Timelines*

During the 2002 field season I monitored 475 burrows, 111 of which were used by burrowing owls ( $\geq 1$  owl seen on  $\geq 4$  visits). From 20 February to 30 September, I visited each burrow every 2-4 days and recorded the presence of manure on the burrow mound, the number of adults and juveniles visible, and any signs of depredation. I also used an infra-red fiberscope (Peeper Video Probe, Sandpiper Technologies, Manteca, CA, USA) once every 7-10 days to look inside the burrow for incubating females, eggs, nestlings, and manure at each burrow. I estimated the dates of male arrival, pair formation, and initiation of manure-scattering behavior by constructing a timeline of these events for each occupied burrow. I assumed that the date of a significant event (e.g., male arrival, pair formation) occurred half way between the date the event was first observed and the date of the prior nest visit.

### *Prediction<sub>1</sub> - Seasonal Timing*

I used nesting-event timelines of each nest to estimate the number of days before or after pair formation that males began collecting material. Owls sometimes brought



material other than manure to the nest burrow, and separating manure from this material often was difficult. Moreover, the average date that owls first collected other material was similar to the average date that owls first collected manure. Hence, I used the date that owls began bringing any material to their nest for my analysis. After log-transforming my data (to correct unequal variance), I used a one-sample, one-tailed *t*-test to test the prediction that males began bringing manure prior to pair formation. I used a one-tailed test because the mate-attraction hypothesis predicts that manure-scattering would begin before pair formation.

#### Burrow-Occupied Hypothesis

I tested 3 predictions of the burrow-occupied hypothesis. If manure functions as a signal to deter conspecific males, then: 1) owls would be reluctant to settle into unoccupied burrows at which manure had been added, 2) owls at nests where I increased the perception of competition would increase their use of manure, and 3) initiation of manure-scattering behavior would occur soon after male arrival to a burrow.

##### *Prediction<sub>1</sub> - Manure Supplementation*

In February 2002, before males returned from migration (11 March  $\pm$  2 d), I randomly selected 19 burrows from a sample of 38 burrows that were used as nests in both 2000 and 2001. At each of these 19 traditional nest burrows, I placed 4 liters of shredded horse manure on the burrow mound and in the first 0.5 m of the burrow tunnel. The other 19 burrows served as controls and I removed any manure remaining from

previous years at these burrows. I visited all 38 of these experimental burrows twice weekly from 31 February to 31 August and documented whether or not each burrow was used as a nest. I used a contingency table analysis to compare the percentage of burrows that became nests between the manure-supplemented and control burrows.

### *Prediction<sub>2</sub> - Presentations*

In April 2002, I artificially increased the perception of competition at 20 nest burrows (burrows where 2 adults were seen on >2 nest visits) by presenting a taxidermic mount and by broadcasting the primary call of a male burrowing owl. I presented 12 other nest burrows with a taxidermic mount and primary call of a non-competitive European starling (*Sturnus vulgaris*) to serve as a control group. For all presentations, I placed the taxidermic mount and broadcast-speaker 10 m away from the nest burrow at a random azimuth. I conducted 3, 10-min presentations (1 from 06:00-11:00, 1 from 13:00-17:00, and 1 from 20:00-24:00) at each burrow within a 4-d period from 12 April to 22 April (96 total presentations). The call-broadcast for both the experimental and control trials consisted of 30 sec of calls followed by 30 sec of silence, repeated for either 10 min or until an owl attacked the taxidermic mount. Prior to the first presentation, I removed all material on the burrow mound and within 0.5 m of the tunnel at each nest. At each of the 32 nests, I collected all material present on the mound and within 0.5 m of the tunnel 7 d after the third presentation. Resident males sometimes collected material other than manure. Separating manure from grass and other materials was difficult, so I measured the mass and volume of all material collected (see discussion). Because the amount of material present at a burrow may be dependent on the stage of the nesting

cycle (Moller 1987, M.D. Smith, personal observation), I also recorded the stage of each nest receiving presentations. I sifted all collected material through a 2-mm sieve to remove any sand or small pebbles accidentally collected. I used a digital scale (accurate to 1 g) to measure mass (dry-weight) of material collected at each of the 32 burrows, and measured volume of material by water displacement. I examined the efficacy of my burrowing owl taxidermic mount in creating the perception of competition by recording the response of resident males to the taxidermic mount. I compared the likelihood that owls would attack the mount between the 2 taxidermic mount types by using a logistic regression analysis. I included nest stage, time of day, and the number (1-3) in my series of presentations as factors in my analysis because each of these variables may affect the response of resident males. I log-transformed the mass and volume of material collected (to correct unequal variance) at each burrow prior to analysis. I then used a one-tailed *t*-test to compare both the mass and volume of material between control and experimental burrows. I used a one-tailed test because the burrow-occupied hypothesis predicts that resident males receiving the burrowing owl mount would collect more manure than the control group. Because stage of the nesting cycle may affect the amount of manure present, I also tested this prediction by using Analysis of Variance including both the nesting stage and treatment group as factors.

### *Prediction<sub>3</sub> - Seasonal Timing*

I used log-transformed dates of male arrival and of initiation of manure-scattering (to correct unequal variance) from the nesting-event timelines to examine how soon after arrival males began manure-scattering. I also compared the relationship between date of

pair formation and date of initiation of manure-scattering between single and paired males by using a 2-tailed *t*-test. I used a two-tailed test because this hypothesis makes no clear prediction about how single and paired males will differ in date of initiation of manure-scattering behavior.

### Olfactory-Concealment Hypothesis

I tested 3 predictions of the olfactory-concealment hypothesis. If manure conceals nest odors to lower the probability of depredation, then: 1) active burrowing owl nests supplemented with manure would suffer less depredation than nests with no manure, 2) artificial nests containing manure or scat for olfactory-camouflage would suffer less depredation than artificial nests without olfactory-camouflage, and 3) initiation of manure-scattering behavior would occur just prior to incubation.

#### *Prediction<sub>1</sub> - Add / Removal Experiment*

In 2001, I added manure at 12 active burrowing owl nest burrows (manure-supplemented), and removed manure at an additional 12 active nest burrows (manure-removed). These 24 active nests were chosen randomly from 61 active nests not used in any other manipulations (because burrowing owls are a species of conservation concern, I did not manipulate the other 33 nests on my study site). Manure-supplemented and manure-removed burrows were paired based on proximity to one another to control for variables such as land use or density of predators. I randomly assigned which of the 2 nests in each pair would have manure added. From 15 April to 25 July 2001, I visited

each nest every 2-4 d and recorded the number of adults and juveniles observed, and any signs of depredation. At manure-removed burrows I discarded all manure found on the burrow mound and within the first 0.5 m of the tunnel. I also removed any other material found, such as grass clippings. At manure-supplemented burrows, I removed all manure (and any other materials) already present and then added horse manure on the burrow mound and in the entrance of the tunnel leading to the nest. On each of the first 2 visits I added 4 liters of shredded horse manure and on each subsequent visit I added 2 liters of manure. I used a contingency table analysis to compare the proportion of nests depredated between treatments.

#### *Prediction<sub>2</sub> - Egg Experiment*

I located 48 burrows within my study area that were not occupied by burrowing owls. Between 5 May and 22 May 2001, I placed 3 un-cleaned chicken eggs in each of the 48 burrows at a depth where they were not visible from the surface (approximately 1 m). The 48 burrows were separated into groups of 4 based on proximity to one another to control for variables such as land use or predator density. I then randomly assigned 1 of 4 possible treatments to each experimental burrow (hence, each treatment had 12 replicates). Treatments differed by the presence or absence of owl sign and by what material was placed in the tunnel and around the burrow entrance. The 4 treatments were: 1) horse manure and owl sign, 2) coyote scat and owl sign, 3) owl sign, and 4) no manure, scat, or owl sign. Burrows in treatment 1 received 4 liters of horse manure and burrows in treatment 2 received 100 g of coyote scat. Coyote scat was included because the presence of scat may also potentially deter predators and was found frequently at owl

nests (M. D. Smith, unpublished data). To simulate an active nest, I placed owl sign (15 burrowing owl pellets and 10 burrowing owl feathers) at burrows in treatments 1-3. I then checked each burrow for depredation after 3 weeks by using an infra-red fiberscope (Peeper Video Probe, Sandpiper Technologies, Manteca, CA, USA). I compared the proportion of artificial nests depredated between the 4 treatments by using a contingency table analysis.

#### Prey-Attraction Hypothesis

I tested 4 predictions of the prey-attraction hypothesis. If manure attracts insect prey for burrowing owls, then: 1) pit-fall traps at burrows supplemented with manure would contain more insect biomass than pit-fall traps at burrows with no manure, 2) pit-fall traps at non-burrow sites supplemented with manure would contain more insects compared to pit-fall traps at non-burrow sites not supplemented with manure, 3) nests supplemented with manure would have higher fecundity than nests without manure, and 4) initiation of manure-scattering behavior would occur at any point of the nesting cycle, but would be most common after pair formation, and during the nesting stage when food is most limiting.

#### *Insect Sampling*

In June of 2001 and 2002, I collected insects in pit-fall traps at experimental (with manure) and control (without manure) sites. Each pit-fall trap consisted of a 473-ml (16-oz) Dixie cup (Georgia Pacific Corp, Atlanta, GA, USA) inserted into the ground with

the rim of the cup flush with the surface of the ground. I used a clear funnel stapled inside the cup and approximately 60 ml of soapy water in the bottom of the cup to prevent the escape of captured insects. I placed 3 pit-fall traps in a triangular pattern at each sampling site (Figure 3). For this experiment, sampling sites were assigned to 1 of 4 treatments (Figure 3): 1) manure, no burrow; 2) no manure, no burrow; 3) manure, burrow; and 4) no manure, burrow. I included treatments 1 and 2 to examine the effects of the burrow alone on insect abundance (independent of manure). At manure sites (treatments 1 and 3), I placed 2 liters of shredded horse manure around and between pit-fall traps (Figure 3).

One potential problem with sampling prey-availability near active nests is that burrowing owls eat insects that would have otherwise fallen into traps. Placing pit-fall traps in areas lacking active nests is not a good solution because owls may not be present due to low prey availability in the area. To deal with these potential problems, I chose the general area in which to set pit-fall traps by choosing areas that appeared to be suitable for burrowing owls, and were within 1.5 km of nesting owls, but were not closer than 200 m to an occupied nest. I used a paired design to examine the effects of manure on insect abundance. For sampling sites that were not at a burrow (treatments 1& 2), I chose the general site by walking 50 m into an area in a random direction (using only those azimuths that led into the selected area). At 50 m, I threw a marker flag in a random direction. I placed the first sampling site where the flag landed and assigned this site as either treatment #1 or #2.

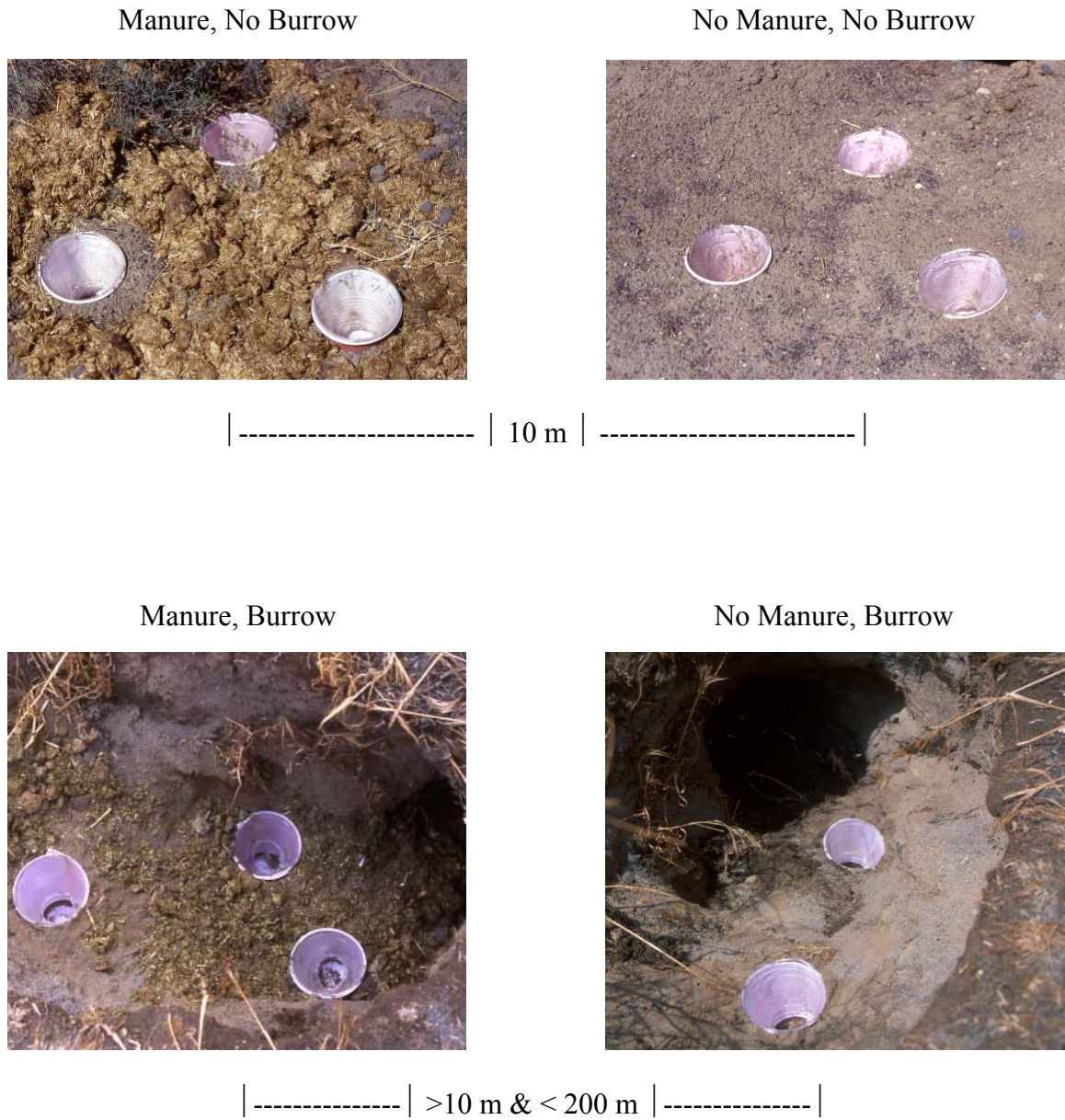


Figure 3. Sampling design used in 2001 and 2002 for testing the prey-attraction hypothesis to explain manure-scattering behavior of burrowing owls.



I then placed the paired sampling site 10 m away in a random direction. Placing sites where the flag landed controlled for inserting pit-fall traps at specific distances from vegetative features such as bunch-grass or sagebrush (i.e., some traps were directly next to sagebrush bushes and others were not). For sampling sites at a burrow, I used different unoccupied burrows than the ones I used for the olfactory-concealment experiment. Overall, I used burrows that were close enough together to be biotically and abiotically similar, but were not closer than 10 m (otherwise, manure might have attracted insects to both sets of traps in the pair). Due to the irregular pattern of burrows in the landscape, pairs were located from 10 m to 300 m apart. In 2001, I set 300 pit-fall traps at 100 sampling sites (25 sampling sites for each of my 4 treatments). In 2002, I set 228 pit-fall traps at 76 sampling sites (25 with manure, no burrow; 25 with no manure, no burrow; 12 with manure, burrow; and 12 with no manure, burrow). In 2001, I collected the insects in pit-fall traps after 14 d. In 2002, I collected insects after only 6 d, because I was concerned that some insects in the 2001 traps had been consumed during the 14-d sampling period.

I placed insects in separate bags for each trap and froze them for 48 hours to kill any living insects. The samples were then taken to the lab where I estimated the biomass (dry-weight) of all insects. For insects that were whole, I measured total body length and then used an allometric equation to obtain an estimate of biomass (see equations in Appendix A). I also used these whole insects to develop allometric equations to predict total body length from various body parts (e.g., thorax, femur). I then used these allometric equations to estimate total body length for those insects in my pit-fall traps that

were not whole (Appendix B-D). I conducted an extensive search of the literature for references to insects found in the diet of burrowing owls in North America and found 25 manuscripts (Appendix E). Insect taxa that were caught in my pit-fall traps, but were not reported in the diet of burrowing owls were excluded from analysis.

#### *Predictions<sub>1&2</sub> - Pit-Fall Traps*

I compared the biomass of captured insects between year and location by using Analysis of Variance. I then pooled data from both years and both locations, and used a one-tailed, paired *t*-test to compare the biomass of captured insects between manure and non-manure sites. My test of the second prediction examined if insects were attracted specifically to manure (as opposed to simply being attracted to a burrow). Thus, I used a one-tailed, paired *t*-test to compare between treatments at only non-burrow sites. For both predictions, I used one-tailed tests because the prey-attraction hypothesis predicts that manure sites will attract more insect biomass than non-manure sites.

#### *Prediction<sub>3</sub> - Fecundity*

For each nest in the *add / remove* test (see methods of P<sub>1</sub> of olfactory-concealment) I counted the maximum number of 21-d old juveniles observed above ground during weekly nest checks. I compared fecundity between the manure-supplemented and manure-removed nests by using a one-tailed, paired *t*-test. I used a one-tailed test because the prey-attraction hypothesis predicts that the manure-supplemented nests should have higher fecundity because of increased food availability.

## RESULTS

### Mate-Attraction Hypothesis

#### *Prediction<sub>1</sub> - Seasonal Timing*

Of the 111 burrows used by owls, 45 were used as primary nest burrows or were located early enough in the season such that I could obtain reliable estimates of dates of pair formation and initiation of manure-scattering. Males at 21 nest burrows collected manure, whereas males at 24 other nests did not collect manure, but used other materials. All males that collected manure also collected other materials. However, there was no difference in the date that manure and other materials were first collected (2-tailed, paired *t*-test,  $t = 0.4$ ,  $df = 18$ ,  $P = 0.694$ ). Thus, mean dates of “manure-scattering” also include nests of males that did not use manure. Mean arrival date for females at the 45 nests was 30 March  $\pm$  2 d (Table 2). Mean date of initiation of manure-scattering behavior at nests was 9 April  $\pm$  3 d (Table 2). Contrary to the prediction for the mate-attraction hypothesis, initiation of manure-scattering behavior began  $9.5 \pm 2$  d after pair formation ( $t = 5.8$ ,  $df = 45$ ,  $P < 0.001$ , Figure 4, Table 2). Manure-scattering behavior began after pair formation at 89% of the 45 nest burrows, and date of pair formation and date of initiation of manure-scattering behavior were highly correlated ( $r^2 = 0.72$ ,  $P < 0.001$ , Figure 4).

Table 2. Mean ( $\pm$ SE) dates in 2002 when burrowing owls arrived at nest-burrows following spring migration, mean ( $\pm$ SE) dates when burrowing owls initiated manure-scattering behavior, and the mean ( $\pm$ SE) number of days after arrival that of manure-scattering behavior began.

	<i>n</i>	Arrival Date		Date Manure-Scattering Began		Days After Arrival That Manure-Scattering Began	
		$\bar{x} \pm \text{SE}$	95% CI	$\bar{x} \pm \text{SE}$	95% CI	$\bar{x} \pm \text{SE}$	95% CI
Single Males <sup>1</sup>	8	21 Mar $\pm$ 9	27 Feb - 11 Apr	19 Apr $\pm$ 7	2 Apr - 5 May	29 $\pm$ 8	11 - 47
Paired Males	45	11 Mar $\pm$ 2	9 Mar - 15 Mar	9 Apr $\pm$ 3	4 Apr - 13 Apr	28 $\pm$ 3	23 - 33
Females <sup>2</sup>	45	30 Mar $\pm$ 2	26 Mar - 3 Apr	9 Apr $\pm$ 3	4 Apr - 13 Apr	9 $\pm$ 2	6 - 13

<sup>1</sup> Excludes a single male detected on 7 Jul that did not initiate manure-scattering

<sup>2</sup> Arrival date of females equals date of pair formation

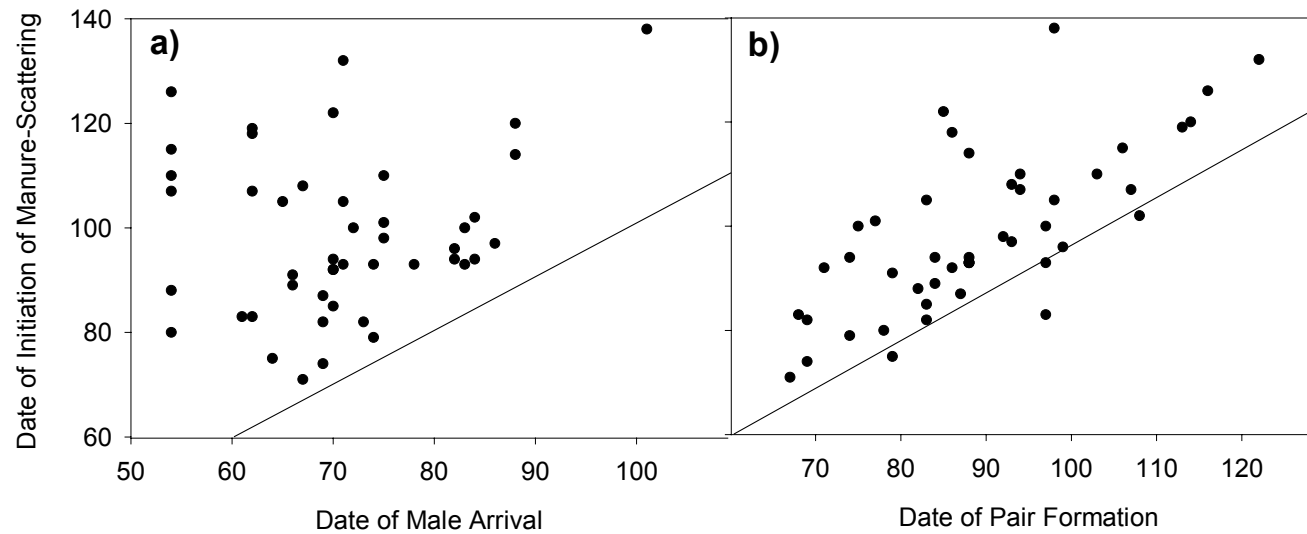


Figure 4. Relationship between date of initiation of manure-scattering and male arrival, and between initiation of manure-scattering and pair formation of burrowing owls in south-central Washington in 2002. Points above the line are nests where initiation of manure-scattering occurred after male arrival (a), or after pair formation (b). The burrow-occupied hypothesis predicts points will be close to the line (a), and the mate-attraction hypothesis predicts points will be below the line (b).

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## Burrow-Occupied Hypothesis

### *Prediction<sub>1</sub> - Material Supplementation*

I failed to detect a difference in the proportion of burrows that became nests between those to which I added manure and those to which I removed all manure (Fisher's exact test  $P = 0.148$ ).

### *Prediction<sub>2</sub> - Presentations*

Burrowing owls that were presented with the taxidermic owl mount were more likely to attack the mount than owls presented with the taxidermic starling mount (Wald's  $\chi^2 = 7.85$ ,  $P = 0.005$ ). The amount of material collected by resident males after 3 presentations of a burrowing owl taxidermic mount was not different compared to 3 presentations of a starling taxidermic mount (Table 3). I failed to detect a difference in the biomass ( $t = 0.8$ ,  $df = 30$ ,  $P = 0.210$ ) or volume ( $t = 0.2$ ,  $df = 30$ ,  $P = 0.433$ ) of material brought to the nest between treatments. After including stage of the nesting cycle as a factor, I also failed to detect a difference in biomass ( $F_{3,28} = 0.8$ ,  $P = 0.514$ ) or volume ( $F_{3,28} = 0.3$ ,  $P = 0.861$ ) of material collected by resident males between treatments.

### *Prediction<sub>3</sub> - Seasonal Timing*

Of the 111 burrows used by owls in 2002, 55 were used as primary nest burrows, used by single males, or were located early enough in the season such that I could obtain reliable estimates of dates of male arrival and initiation of manure-scattering.

Table 3. Average mass ( $\pm$ SE) and volume ( $\pm$ SE) of material scattered at the entrance to burrowing owl nest burrows 7 days following presentations of a potential competitor (taxidermic mount and primary call of a burrowing owl) and a control (taxidermic mount and primary call of a European starling).

Taxidermic mount type	<i>n</i>	Mass (g)		Volume (cm <sup>3</sup> )	
		$\bar{x} \pm \text{SE}$	Range	$\bar{x} \pm \text{SE}$	Range
Burrowing owl	20	136 $\pm$ 34	11 - 707	232 $\pm$ 49	25 - 998
European starling	12	107 $\pm$ 24	4 - 215	210 $\pm$ 46	20 - 470

Forty-six males successfully attracted a mate, and the mean arrival date of these males was 11 March  $\pm$  2 d. Males did not begin collecting material soon after arrival, but waited an average of 28  $\pm$  3 d after male arrival. Date of male arrival and date of initiation of manure-scattering behavior were not correlated ( $r^2 = 0.12$ ,  $P = 0.408$ ).

Males who apparently never obtained a mate (single males) occupied 9 burrows and none of these males collected manure. However, 8 (89%) of these single males brought other materials (e.g., grass and paper) to the burrow. The 1 male who did not collect material arrived at the burrow on 7 July, considerably later than the mean date of arrival for males, 13 March (mean for both single and paired males combined). Mean arrival date for the other 8 single males was 21 March  $\pm$  9 d (Table 2). These 8 single males first collected material on 19 April  $\pm$  7 d (Table 2), an average of 29  $\pm$  8 d after arrival (Table 2).

Paired males initiated manure-scattering behavior on average 10.5  $\pm$  6 d earlier than single males ( $t = -1.7$ ,  $df = 52$ ,  $P = 0.095$ ), but they also arrived earlier (Table 2). Consequently, paired and single males did not differ in the number of days after arrival that initiation of manure-scattering behavior began ( $t = -0.183$ ,  $df = 52$ ,  $P = 0.856$ , Table 2). Only 2 of the 9 single males (22%) ever collected new material after I first detected them. In contrast, 96% of paired males collected new material within 3 weeks after my detection of the initiation of manure-scattering behavior. As a result, nest burrows had substantially more material present than burrows of single males.



## Olfactory-Concealment Hypothesis

### *Prediction<sub>1</sub> - Add / Removal Experiment*

Nest failure was low. Only 1 manure-supplemented nest was depredated and 1 manure-removed nest failed for unknown reasons (possibly depredation). I failed to detect a difference in the proportion of nests that were depredated between manure-supplemented and manure-removed nests (Fisher's exact test  $P = 0.783$ ).

### *Prediction<sub>2</sub> - Egg Experiment*

I failed to detect a difference in probability of nest depredation among the 4 artificial nest treatments (Pearson  $\chi^2 = 2.2$ ,  $df = 3,44$ ,  $P = 0.535$ ). I also found no effect on probability of depredation when I combined the 2 olfactory-concealment treatments (horse manure and coyote scat; Pearson  $\chi^2 = 1.1$ ,  $df = 1,46$ ,  $P = 0.296$ ). Only 4 of the 48 experimental nests were depredated and all 4 were within 25 m of active coyote dens.

## Prey-Attraction Hypothesis

### *Insect Sampling*

In my pit-fall traps, I collected a total of 4,019 insects from 11 Orders and 19 Families that have previously been reported in the diet of burrowing owls (Appendix F). The total biomass (dry weight) was 75,944 mg. Coleopterans and orthopterans accounted for 81% of the biomass and 31% of the total number of insects collected in traps. Ants

(Formicidae) accounted for 55% of the total number of insects, but only 5% of the biomass (Appendix F). I had to discard a number of samples prior to analysis. Some traps were unusable because they were filled with manure or sand, or were pulled out of the ground. When all traps of a particular treatment were unusable, I eliminated that sampling site ( $n = 13$  sampling sites or 78 traps discarded). When 1 or 2 of the 3 traps in a treatment were unusable, I discarded those traps and used an average biomass of insects caught per trap for that sampling site. Analysis of average biomass allowed me to use sites where 1 or 2 traps were eliminated ( $n = 75$  sampling sites used). When all traps were usable I was able to calculate both average biomass per trap and total biomass of insects found in all traps ( $n = 48$  sampling sites used). Hence, I compared insect biomass between manure and non-manure treatments in two ways: using the average of insects caught per trap in each treatment (referred to as “average biomass”), and using the total insects caught in all three traps in each treatment (referred to as “total biomass”).

*Prediction<sub>1</sub> - Pit-Fall Traps (all locations)*

I failed to detect a difference in insect biomass between 2001 and 2002 or between burrow and non-burrow sites regardless of whether I used total biomass (manure:  $F_{2,45} = 0.8$ ,  $P = 0.477$ , non-manure:  $F_{2,45} = 0.8$ ,  $P = 0.454$ ) or average biomass (manure:  $F_{2,72} = 0.5$ ,  $P = 0.615$ , non-manure:  $F_{2,72} = 1.7$ ,  $P = 0.199$ ). Thus, I pooled all data for the analysis of manure versus non-manure sites (prediction 1). Regardless of whether I used total biomass or average biomass, I found that insects were more abundant in manure treatments (Figure 5). Manure traps averaged  $302 \pm 69$  mg more total biomass

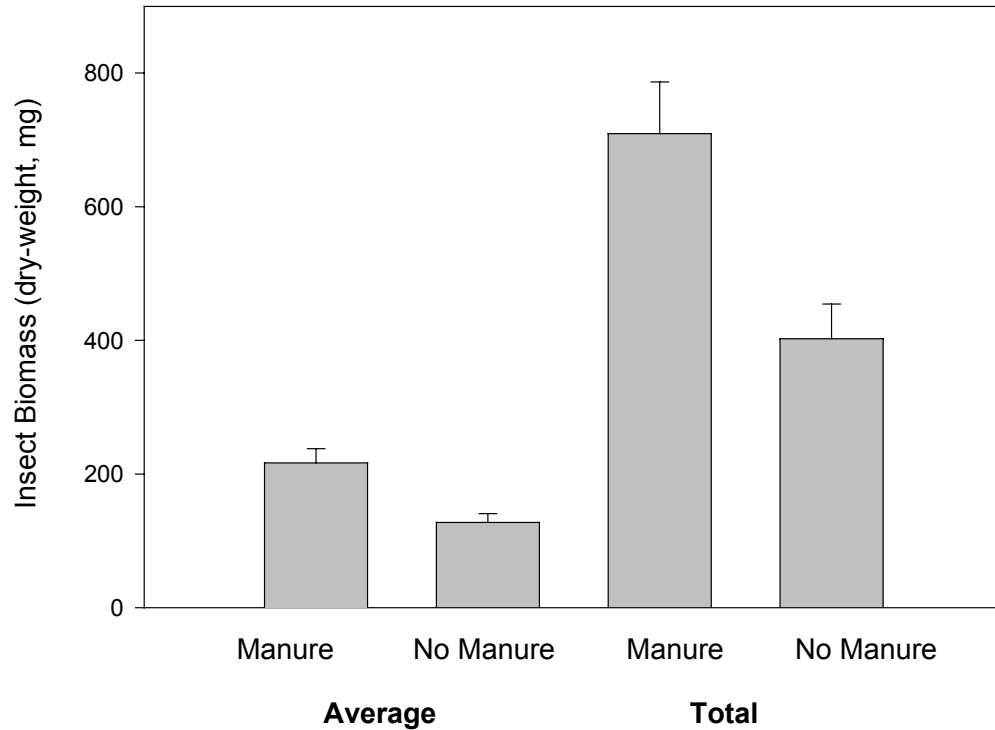


Figure 5. Biomass of insects caught in pit-fall traps at paired sites with and without supplemented manure in south-central Washington in 2001 and 2002. Total biomass includes all insects collected when all 6 traps at a sampling site were usable. Average biomass uses the average biomass of insects per trap when some traps at a sampling site were unusable. Bars represent standard error.

than non-manure traps (95% CI: 163 to 442 mg,  $t = 4.4$ ,  $df = 47$ ,  $P < 0.001$ ). Similarly, manure traps averaged  $88 \pm 21$  mg more biomass per trap than non-manure traps (95% CI: 47 to 129 mg,  $t = 4.3$ ,  $df = 74$ ,  $P < 0.001$ ).

*Prediction<sub>2</sub> - Pit-Fall Traps (no burrow sites)*

Insects were attracted to dried manure, not simply the burrow; there was more insect biomass at manure treatments even when I analyzed only non-burrow sites (total biomass:  $t = 3.0$ ,  $df = 29$ ,  $P = 0.003$ , average biomass:  $t = 2.7$ ,  $df = 29$ ,  $P = 0.006$ ).

*Prediction<sub>3</sub> - Fecundity*

The mean number of juveniles surviving to 21 d of age for the manure-supplemented nests was  $3.2 \pm 0.7$  (95% CI: 1.7 to 4.7). In contrast, the mean number of juveniles surviving to 21 d of age for the manure-removed nests was  $4.1 \pm 0.7$  (95% CI: 2.6 to 5.6). I failed to detect a difference ( $t = -1.5$ ,  $df = 11$ ,  $P = 0.912$ ) in number of young surviving to 21 d of age between manure-removed and manure-supplemented nests pairs. Indeed, the trend was opposite of that predicted by the prey-attraction hypothesis: manure-supplemented nests averaged 0.9 fewer 21-d old juveniles (95% CI: -2.3 to 0.5) compared to manure-removed nests.

## DISCUSSION

My results do not support the widely-accepted hypothesis that burrowing owls litter their nest burrows with dried mammal burrow to conceal the scent of nesting owls, and thereby reduce the probability of nest depredation. Instead, my results suggest that burrowing owls might collect and scatter manure to attract insect prey to their nest.

The mate-attraction hypothesis predicts that males would initiate manure-scattering prior to finding a mate, but manure-scattering began after pair-formation for nearly all nests monitored. Single males did collect material, but burrows occupied by single males never had more than a small amount of biomass present. Tests of the burrow-occupied hypothesis were not statistically significant, but trends in the data from 2 of the 3 predictions were in the expected direction. Manure-supplemented burrows were not less likely to become nests than burrows with no manure. However, my sample size for this test was relatively small and there were two potential problems associated with my supplementation experiment. First, I conducted this test 2 months prior to the average date of initiation of manure-scattering behavior. Thus, owls may have ignored the presence of manure this early in the season. Also, due to time constraints, the first time I was able to visit these nests was 3 weeks after supplementation, and I could visit them only every 3-4 days thereafter. Hence, owls may have been initially deterred by the manure, but simply waited a few days before realizing that no other conspecific male was present (my sampling frequency would not have detected this trend). Future tests of this hypothesis should use larger sample sizes and remote video cameras to detect rate of

visitation and behavior of males at manure-supplemented nests. I increased the perception of intra-sexual competition at a subset of nests; the burrowing owl taxidermic mount elicited a stronger territorial response from resident owls compared to the starling taxidermic mount. Results from this test are mixed. Although I failed to detect a difference in the amount of material collected by experimental males compared to control males, my sample size for these presentations was relatively small ( $n = 32$ ), and the trend was in the predicted direction (experimental males collected 28% more biomass and 11% more volume of material than did control males). However, when controlling for nesting stage, which affects the amount of material present, the difference between experimental and control males was even less. The burrow-occupied hypothesis predicts that resident males should collect manure immediately after returning to the breeding grounds. Instead, owls waited an average of 28 d before bringing material to their burrow. Hence, my results do not rule out this hypothesis and the collection of materials to indicate occupancy deserves further study.

My data do not support 2 of the 3 predictions of the popular olfactory-concealment hypothesis. Although owls typically did not begin manure-scattering behavior until after pair formation (the timing expected if manure functions to conceal the scent of offspring), tests did not support the other 2 predictions for this hypothesis. Probability of depredation at active nests did not differ between nests supplemented with manure and nests with manure removed. However, I was only able to remove manure from the area surrounding the burrow and in the first 0.5 m of the tunnel. Hence, the manure remaining in the lower tunnel may have been enough to still conceal owl scent at

these active nests. In my artificial nest experiment (which solves the problem of unremoved manure because there was no manure in the control burrows), I failed to detect an effect of manure on the probability of nest depredation. The proportion of my artificial nests that were depredated (8%) was similar to the proportion of real nests that were depredated (4.5%) during the same breeding season (an additional 12% of nests failed for unknown reasons and some failures may be attributable to depredation). Because probability of depredation is naturally low, the presumed energetic cost of manure-scattering likely would not be balanced by a benefit of reduced depredation. Furthermore, the olfactory-concealment hypothesis has 2 other problems that are difficult to explain. First, manure scattered on the burrow mound makes the location of a nest obvious, and predators could potentially learn to associate the presence of manure with the presence of owls. Second, at least one adult burrowing owl is often present at the entrance to the nest-burrow for a large portion of each day during the nesting cycle (Coulombe 1971, Thomsen 1971, Martin 1973). If owls were going to great lengths to conceal the scent of their active nest, then one would not expect them to behave in ways that render their nest location obvious to predators. Hence, empirical tests and the behavior of nesting burrowing owls both dispute olfactory-concealment as the function for the manure-scattering behavior in burrowing owls.

My data supported 3 of the 4 predictions of the prey-attraction hypothesis. I found that sampling-sites with manure had 76% more total insect biomass (69% more average biomass) than sampling-sites without manure. My experimental design took into account the possibility that insects might be attracted to the microclimate created by a

burrow, rather than the manure itself. The presence of dried manure (independent of a burrow) attracts more insects than sites without manure. Indeed, sites with a burrow did not attract more insects than sites without a burrow. Even the timing of manure-scattering behavior supports the prey-attraction hypothesis: most burrowing owls started collecting and scattering manure after pair formation but prior to incubation. Such timing makes sense if manure functions to attract insect prey for incubating females and young nestlings.

I used only pit-fall traps to sample insects near burrowing owl nests. Pit-fall traps mainly sample insects that travel by walking along the ground (i.e., Coleoptera and Orthoptera). Hence, my sampling may have missed other taxa of insects that are eaten by burrowing owls. However, previous analyses of burrowing owl diet found that insects from these two Orders constituted 97% of insect prey (Gleason and Craig 1979). For this reason I believe that my pit-fall traps likely captured an accurate representation of burrowing owl insect prey in the areas sampled. I did not check the pit-fall traps every day, so some of the insectivorous beetles I caught may have been attracted to other insects already caught in pit-fall traps. If pit-fall traps attracted insectivorous beetles (Carabidae and Silphidae), then these families should constitute a greater proportion of Coleoptera in my pit-fall traps than is found naturally in the diet of burrowing owls. Carabidae and Silphidae constituted 37% of Coleoptera in burrowing owl pellets in Idaho (Gleason and Craig 1979) and 30% of Coleoptera in burrowing owl pellets in Colorado (Plumpton and Lutz 1993). These two families comprised 32% of Coleoptera collected



in my pit-fall traps. Hence, my results do not appear to be biased due to attraction of insectivorous beetles.

Because insects have a high caloric content (22.4 KJ /g for insects, 21.6 KJ /g for mammals; Golley 1961), increasing the number of insects available to nestlings and females during the nesting cycle would be a beneficial investment of energy and time. The diet of burrowing owls typically changes from primarily rodents to primarily insects as the nesting cycle progresses (Green and Anthony 1989). Whether this change reflects a seasonal change in availability, or a change in preference is unclear. Regardless, I expect owls that attract additional food to obtain some benefit over those that do not. However, I did not find an increase in the number of juveniles at 21 d of age at nests where I continually added manure (in fact, the non-significant trend was in the opposite direction) compared to nests where I continually removed manure. This result is somewhat puzzling because birds with asynchronous hatching (such as burrowing owls) are typically able to take advantage of increases in food by successfully raising the last laid eggs (Temme and Charnov 1987). But my *add/remove* design may not have created a difference in food availability due to manure remaining in the lower tunnel. Or, perhaps manure does not increase fecundity, but has other benefits such as increasing nestling growth rates (I did not measure nestling growth rates). One might ask why owls would collect manure to attract insects, instead of just collecting insects. Scattering manure and attracting insects, rather than simply foraging for insects, may provide fledglings with experience handling insect prey near the safety of the burrow. Attracting insects also may be beneficial from a temporal perspective. For example, collecting and

scattering manure before egg-laying to attract insects may reduce the number of conspicuous foraging trips by the adults once chicks need to be fed. Additionally, males appear to guard the entrance to their nest burrows and give warning calls to nestlings and incubating females when potential predators appear. Hence, scattering manure around the burrow entrance at the outset of the breeding season may allow males to attract prey for nestlings while still providing vigilance for predators. Future studies need to quantify the types of fitness benefits that burrowing owls obtain by scattering manure around their nest-burrows, and should evaluate the effect of manure supplementation on nestling growth rates, prey-handling ability of fledglings, number and length of foraging trips, and male attentiveness.

While burrowing owls often scatter manure, they also will use other materials in similar ways (e.g., coyote scat, grass, moss, pieces of wood, shredded carpet, paper, plastic, cotton, golf course divots, dried vegetables, tin foil; Thomsen 1971, M. D. Smith, unpublished data). In the same way that birds generally use materials from the local environment in nest construction (Hansell 2000), burrowing owls may simply use the most convenient and available material to scatter around their nests. Hence, any hypothesis to explain the manure-scattering behavior, should also be able to explain the use of these other materials. The mate-attraction, burrow-occupied, and prey-attraction hypotheses can potentially explain the use of other materials, but the most commonly-accepted hypothesis (olfactory-concealment) cannot explain the use of all materials. Like manure, other materials may also attract insect prey. Coyote scat and decomposing vegetable-matter may provide food or moisture for insects. Pieces of wood found at nests

often appear similar to coyote scat and may have been mistaken for scat. Grass, paper, and fabric pieces inside a burrow may retain moisture and increase relative-humidity, and thereby attract insects. Future studies should test all materials used by burrowing owls for their efficacy in attracting insects.

The scattering of manure around the entrance to the nest-burrow and in the tunnel leading to the nest has similarities to the nest-building behavior of other birds. For example, the timing of the start and end of manure-scattering is similar to the use of feathers as nest-lining in barn swallows (*Hirundo rustica*; Moller 1987) and of dung collection as nest-lining in white storks (Tortosa and Villafuerte 1999). I suggest the manure-scattering behavior of burrowing owls is an exaggerated form of nest-building. Behaviors associated with nest-building are thought to have a genetic basis (Dawkins 1982, Hansell 1984, Hansell 2000) and thus can be influenced by natural selection. As such, selection should favor novel nest-building behaviors that increase reproductive success. If burrowing owls that used manure to build their nest cups had greater reproductive success than those that did not, the use of more manure (and ultimately the exaggerated pattern of nest-building with manure) may have evolved. In a few known cases, innovations in the materials used for nest-building have resulted in the evolution of novel functions of the nest (Hansell 1984). I believe that the manure-scattering behavior of burrowing owls may be related to nest-building, and that by incorporating dried mammal manure into their nests burrowing owls apparently attract insect prey for incubating females and nestlings. If further work supports the prey-attraction hypothesis,

then burrowing owls would be the first known example of a birds collecting and using non-food materials for prey attraction.

Conservation implications for this study relate to both current practices and potential strategies. Managers, authors, and environmental groups have openly advocated supplementing manure in areas with nesting burrowing owls (Green and Anthony 1997, Dechant 2001, Colorado Division of Wildlife 2003) to promote recovery efforts. But large-scale manure supplementation can have potential costs. For example, manure is a major source of exotic-plant seeds (Hammit and Cole 1987). Thus, moving horse and cow manure may increase the spread of exotic plants. Manure may aid reproductive success of burrowing owls, but we need to better understand the benefits of this management action before advocating such practices.

In order to more effectively manage local populations, managers should consider that manure-scattering appears to attract insects. Supplementing manure in areas where foraging areas for burrowing owls have been anthropogenically reduced might be a good management strategy. For example, artificial burrows often are installed for mitigation purposes when natural nests are taken due to construction. The success of such artificial burrows is often low (C. J. Conway and M. D. Smith, unpublished data). One possible reason for the moderate success of these burrows may be that available foraging areas are also altered during construction. Thus, supplementing manure may increase food available to owls nesting in these artificial burrows, and thereby increase the effectiveness of installing artificial burrows.

APPENDIX A. Allometric equations from Rogers et al. (1977) used to estimate dry weight (mg) from body length (mm) for invertebrates collected in pit-fall traps in south-central Washington, 2001 and 2002.

Order	Equation used	Equation
<b>Araneae &amp; Solpugida</b>	General <sup>1</sup>	$\ln(W) = -3.106 (\pm 0.189) + 2.929 (\pm 0.294) \cdot \ln(\text{length})$
<b>Coleoptera</b>	General	$\ln(W) = -3.460 (\pm 0.105) + 2.790 (\pm 0.050) \cdot \ln(\text{length})$
	Tenebrionidae	$\ln(W) = -3.050 (\pm 0.204) + 2.681 (\pm 0.080) \cdot \ln(\text{length})$
	Curculionidae	$\ln(W) = -3.915 (\pm 0.245) + 3.050 (\pm 0.164) \cdot \ln(\text{length})$
<b>Diptera</b>	General	$\ln(W) = -3.293 (\pm 0.115) + 2.366 (\pm 0.078) \cdot \ln(\text{length})$
<b>Lepidoptera</b>	General	$\ln(W) = -4.037 (\pm 0.133) + 2.903 (\pm 0.080) \cdot \ln(\text{length})$
<b>Hemiptera</b>	General	$\ln(W) = -2.998 (\pm 0.113) + 2.270 (\pm 0.081) \cdot \ln(\text{length})$
<b>Hymenoptera</b>	General	$\ln(W) = -3.871 (\pm 0.108) + 2.407 (\pm 0.060) \cdot \ln(\text{length})$
	Formicidae	$\ln(W) = -4.029 (\pm 0.171) + 2.572 (\pm 0.097) \cdot \ln(\text{length})$
<b>Orthoptera</b>	General	$\ln(W) = -3.020 (\pm 0.284) + 2.515 (\pm 0.105) \cdot \ln(\text{length})$
<b>Other Orders<sup>2</sup></b>	General insect	$W = 0.0305 \cdot \text{Length}^{2.62}$

<sup>1</sup> General equation applies to specified order

<sup>2</sup> General insect equation applicable to all orders from Rogers et al. 1976

APPENDIX B. Allometric equations used to estimate body length (mm) from body parts commonly found in pit-fall traps. Equations are based on whole insects collected in pit-fall traps in south-central Washington in 2001 and 2002.

<b>Order</b>	<b>Family</b>	<b>Morphotype</b>	<b>Equations</b>
<b>Araneae &amp; Solpugida</b>	Unknown		$L = \text{Head} (1.904) + 1.693$
<b>Coleoptera</b>	Silphidae	1) Carrion	$L = \text{Abdomen} (0.876) + 7.082$ $L = \text{Thorax} (4.126) - 3.96$ $L = \text{Femur} (1.958) + 7.763$
	Tenebrionidae	1) BgStrpd	$L = \text{Tarsus} (2.684) + 11.797$
		2) Smth	$L = \text{abdomen} (0.983) + 4.802$
		3) Prfortd	$L = \text{abdomen} (1.287) + 0.928$
	Scarabidae	1) June	$L = \text{abdomen} (1.197) + 1.937$
	Carabidae	1) Strpd	$L = \text{abdomen} (1.215) + 2.54$
Unknown	2) SmBR	$L = \text{abdomen} (1.096) + 1.623$	
	1) Hlmt	$L = \text{abdomen} (1.609) - 1.154$	
<b>Lepidoptera</b>	Unknown	1) Milkwd	$L = \text{Wing} (0.369) + 8.043$
<b>Orthoptera</b>	Acrididae	1) Grasshper	$L = \text{Thorax} (4.278) + 4.489$ $L = \text{Femur} (2.368) - 4.415$

## APPENDIX B (cont.).

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<b>Order</b>	<b>Family</b>	<b>Morphotype</b>	<b>Equations</b>
<b>Orthoptera</b>	Gryllacrididae	1) Jerusalem	L = Femur (3.475) – 5.382 L = Head width (4.857) – 7.578
		2) Cave	L = Femur (1.659) – 3.332 L = Tibia (1.283) + 1.473 L = 1 <sup>st</sup> append (9.417) – 30.626
	Gryllidae	1) Cricket	L = Femur (9.299) – 70.44

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APPENDIX C. Sample sizes associated with allometric equations used to estimate body length (mm) from body parts;  $n$  refers to the number of known lengths on which the equation is based.

Order	Family	Morphotype	Body part	$n$	Number insects <sup>1</sup>	Percent of individuals <sup>2</sup>
<b>Araneae &amp; Solpugida</b>	Unknown		Head	36	74	31
<b>Coleoptera</b>	Silphidae	1) Carrion	Abdomen	12	16	22
			Thorax	12	3	4
			Femur	12	1	1
	Tenebrionidae	1) BgStrpd 2) Smth 3) Prfortd	Tarsus	7	1	2
			Abdomen	15	2	2
			Abdomen	7	4	9
	Scarabidae	1) June	Abdomen	6	1	9
Carabidae	1) Strpd 2) SmBR	Abdomen	12	37	24	
		Abdomen	8	3	6	
Unknown	1) Hlmt	Abdomen	12	8	6	
<b>Lepidoptera</b>	Unknown	1) Milkwd	Wing	6	3	33

<sup>1</sup> refers to the number of insects for which length was estimated by the equation

<sup>2</sup> is the percent of collected individuals for which total length was estimated.



## APPENDIX C (cont.).

<b>Order</b>	<b>Family</b>	<b>Morphotype</b>	<b>Body part</b>	<b><i>n</i></b>	<b>Number insects<sup>1</sup></b>	<b>Percent of individuals<sup>2</sup></b>
<b><u>Orthoptera</u></b>	Acrididae	1) Grashoper	Thorax	29	6	5
			Femur	49	26	37
	Gryllacrididae	1) Jerusalem	Femur	8	13	52
			Head	6	3	12
		2) Cave	Femur	25	108	68
			Tibia	8	1	1
			1st append	4	1	1
			Femur	7	10	37
	Gryllidae	1) Cricket	Femur	7	10	37

APPENDIX D. Average body length (mm) of whole ants and pill-bugs found in pit-fall traps in south-central Washington in 2001 and 2002. These lengths were used for all specimens found in pit-fall traps (including partial specimens); *n* refers to the number of individuals used to obtain the average length.

<b>Order</b>	<b>Family</b>	<b>Morphotype</b>	<b><i>n</i></b>	<b>Average Length</b>
<b>Isopoda</b>	UNK	1) Pill bug	16	6.7
<b>Hymenoptera</b>	Formicidae	1) Fat ant	8	10.7
		2) Red ant	12	5.5
		3) Brown ant	10	3.0

APPENDIX E. Sources for insects found in the diet of burrowing owls. These sources were used to determine which insects to use in analysis of the prey-attraction hypothesis.

Refer to Literature Cited for full references.

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<b>Author</b>	<b>Year</b>
Bent	1938
Bond	1942
Carson	1951
Climpson	1977
Coulombe	1971
Errington and Bennett	1935
Glover	1953
Grant	1965
Gleason and Craig	1979
Green et al.	1993
Hamilton	1941
James and Seabloom	1968
Longhurst	1942
Marti	1974
Maser et al.	1971
Neff	1941
Plumpton and Lutz	1993
Restani et al.	2001
Robertson	1929
Scott	1940
Sperry	1941
Stoner	1932
Thompson and Anderson	1988
Thomsen	1971
York et al.	2002

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APPENDIX F. Number of individuals and total biomass of all taxonomic Orders and Families of insects collected in pit-fall traps in south-central Washington in 2001 and 2002.

<b>Order</b>	<b>Family</b>	<b>Number of individuals</b>	<b>Biomass (mg)</b>	<b>Percent of individuals</b>	<b>Percent of biomass</b>
<b>Araneae &amp; Solpugida</b>	UNK	242	6,979	<b>6</b>	<b>9</b>
<b>Coleoptera</b>	All	868	3,565	<b>22</b>	<b>47</b>
	Buprestidae	1	8	< 1	< 1
	Carabidae	210	4,398	5	6
	Cicindelidae	1	8	< 1	< 1
	Curculionidae	154	634	4	1
	Histeridae	7	10	< 1	< 1
	Scarabidae	50	1,083	1	1
	Silphidae	72	6,457	2	9
	Staphylinidae	29	401	1	1
	Tenebrionidae	202	19,931	5	26
	UNK	142	2,718	4	4
<b>Diptera</b>	Asilidae	19	606	<b>1</b>	<b>1</b>
<b>Hemiptera</b>	All	14	48	< 1	< 1
	Pentatomidae	1	5	< 1	< 1
	UNK	13	43	< 1	< 1
<b>Hymenoptera</b>	All	2,288	4,644	57	6
	Apidae	29	238	1	< 1
	Formicidae	2,202	3,890	55	5
	Vespidae	4	45	< 1	< 1
	UNK	53	470	1	1
<b>Isopoda</b>	UNK	183	821	<b>5</b>	<b>1</b>

## APPENDIX F (cont.).

<b>Order</b>	<b>Family</b>	<b>Number of individuals</b>	<b>Biomass (mg)</b>	<b>Percent of individuals</b>	<b>Percent of biomass</b>
<b>Lepidoptera</b>	UNK	11	694	< 1	1
<b>Odonata</b>	Zygoptera	1	570	< 1	1
<b>Orthoptera</b>	All	391	25,396	10	33
	Acrididae	176	16,543	4	22
	Gryllacrididae	189	6,765	5	9
	Gryllidae	26	2,088	1	3
<b>Scorpiones</b>	Scorpion	2	540	< 1	1
<b>Total</b>		<b>4,019</b>	<b>75,944</b>		

APPENDIX G. Institutional Animal Care and Use Committee

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This study was approved by The University of Arizona Institutional Animal Care and Use Committee protocol # 02-114.

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