

EFFECTS OF OLD NEST MATERIAL  
ON OCCUPANCY AND REUSE OF ARTIFICIAL BURROWS,  
AND BREEDING DISPERSAL BY BURROWING OWLS (*ATHENE CUNICULARIA*)  
IN SOUTHWESTERN IDAHO

By  
Corey S. Riding

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Corey S. Riding

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The following individuals read and discussed the thesis submitted by student Corey S. Riding, and they also evaluated his presentation and response to questions during the final oral examination. They found that the student passed the final oral examination, and that the thesis was satisfactory for a master's degree and ready for any final modifications that they explicitly required.

James R. Belthoff, Ph.D. Chair, Supervisory Committee

Alfred M. Dufty, Jr., Ph.D. Member, Supervisory Committee

Ian Robertson, Ph.D. Member, Supervisory Committee

The final reading approval of the thesis was granted by James R. Belthoff, Ph.D., Chair of the Supervisory Committee. The thesis was approved for the Graduate College by John R. Pelton, Ph.D., Dean of the Graduate College.

## DEDICATION

I dedicate this to my family:

To my parents, who have provided enthusiastic psychological and financial support for a very long time.

To my sister, who wants me to be better so that she can be, also.

To my son and daughter, who have brought enormous joy (and challenges) into my life.

And to my wife, who loves me even when I'm a vector for ectoparasites.

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## ABSTRACT

This thesis comprises two chapters describing my investigations of the breeding ecology of burrowing owls (*Athene cunicularia*) in southwestern Idaho. The first chapter details two experimental studies where I examined the effects of old nest material, primarily mammal dung, on the occupancy and reuse of artificial burrows by burrowing owls in 2004 and 2005. For burrows that owls had not used previously for nesting, adding material from actual nests did not induce occupancy. Thus, old nest material does not appear to function as a cue for burrow suitability. Removing old material from burrows that owls had used for nesting in the previous year caused a decrease in reuse rates, but it had no effect on the level of ectoparasitism or reproductive performance (e.g., number of young fledged or body condition of owlets). While the presence of old material does not seem to increase the owls' fitness, it may help owls locate specific burrows (for which they have public information) when returning from migration.

The second chapter consists of an observational study, where I used data collected during a long-term study of burrowing owls (1994-2007) to address questions about breeding dispersal, or the movement between breeding sites. I examined the percent frequency of owls dispersing and the distance they dispersed, and I compared those to published results from other burrowing owl populations. Additionally, I assessed the effects of sex, productivity, age, mate quality, site quality (as measured by four indices), and level of ectoparasitism on breeding dispersal likelihood and distance. The percentage

of owls dispersing (78%; 67 of 86) was greater than previously reported for any owl species. The mean distance owls moved ( $834.6 \text{ m} \pm 98$ ) was slightly greater than reported distances for most other burrowing owl populations. With the exception of mate quality and two site quality metrics (burrow productivity and proportional occupation), all factors had support for an important relationship with dispersal likelihood. Owls were more likely to disperse if they failed to fledge young, were female, were young, nested farther from agriculture, had closer nesting neighbors, and had lower levels of ectoparasitism. Ectoparasitism and distance to nearest neighbor had inverse rather than the expected direct relationships. Age and one index of site quality were the only predictors with strong relationships to dispersal distance; young owls and owls nesting farther from other owls dispersed longer distances. Sex was somewhat important to distance dispersed, with females moving farther. The factors that most influence breeding dispersal behavior in burrowing owls appear to vary among populations.

## TABLE OF CONTENTS

DEDICATION .....	iv
ACKNOWLEDGMENTS .....	v
ABSTRACT .....	vii
LIST OF TABLES .....	xii
LIST OF FIGURES .....	xv
CHAPTER ONE: EFFECTS OF OLD NEST MATERIAL ON OCCUPANCY AND REUSE OF ARTIFICIAL BURROWS BY BURROWING OWLS .....	1
Abstract .....	1
Introduction .....	1
Occupancy Experiment .....	2
Reuse Experiment .....	5
Methods .....	9
Study Site .....	9
Study Species .....	10
Occupancy Experiment .....	11
Reuse Experiment .....	13
Data Collection and Definitions .....	15
Statistical Analyses .....	19
Results .....	20
Occupancy Experiment .....	20
Reuse Experiment .....	21



Discussion .....	22
Occupancy Experiment .....	22
Reuse Experiment .....	24
Difference Between Experiments .....	29
Management Implications .....	30
Literature Cited .....	30
<b>CHAPTER TWO: BREEDING DISPERSAL BY BURROWING OWLS IN SOUTHWESTERN IDAHO .....</b>	<b>54</b>
Abstract .....	54
Introduction .....	55
Objectives .....	61
Methods .....	62
Study Site .....	62
Study Species .....	63
Data Collection and Definitions .....	65
Statistical Analyses .....	69
Results .....	71
Dispersal Patterns .....	71
Within-year Dispersal .....	71
Mate Fidelity .....	72
Dispersal Likelihood .....	72
Dispersal Distance Modeling .....	73
Discussion .....	74
Productivity Comparisons .....	74
Dispersal Frequency .....	75
Dispersal Distance .....	78

Mate Fidelity .....	79
Dispersal Likelihood .....	80
Dispersal Distance Modeling .....	84
Conclusions .....	85
Literature Cited .....	86
APPENDIX A .....	125
Artificial Burrow Systems (ABSs) Included in an Occupancy Experiment for Burrowing Owls in Southwestern Idaho 2004-2005.	
APPENDIX B .....	132
Artificial Burrow Systems (ABSs) Included in a Reuse Experiment for Burrowing Owls in Southwestern Idaho 2004-2005.	
APPENDIX C .....	136
Body Condition Indices (BCIs) for Burrowing Owl Nestlings in Southwestern Idaho 2004-2005. BCIs Were Generated by Regressing Body Mass (g) on Tarsus Length (mm) with Age (days) as a Covariate and Nest ID as a Repeated Subject. A Positive BCI Represents Good Body Condition and a Negative Value Indicates Poor Body Condition.	

## LIST OF TABLES

Table 1.1	Prediction matrix for burrowing owl reuse of experimentally manipulated artificial burrow systems in southwestern Idaho 2004-2005 .....	42
Table 1.2	Estimated mean length of incubation (in days) for burrowing owls breeding in southwestern Idaho 1999–2005 .....	43
Table 1.3	Number of artificial burrows reused by productivity status at that burrow in the previous breeding season for burrowing owls in southwestern Idaho 2004-2005. Associated <i>P</i> value is for one-sided Fisher’s exact test .....	44
Table 1.4	Number of artificial burrows (ABSs) occupied by treatment, separated by ABS age, for burrowing owls in southwestern Idaho 2004-2005. Associated <i>P</i> values are for one-sided Fisher’s exact tests .....	45
Table 1.5	Number of artificial burrows reused by treatment for burrowing owls in southwestern Idaho 2004-2005. Test statistic is Pearson $\chi^2$ .....	46
Table 1.6	Number of artificial burrows reused by treatment, separated by productivity status in the previous year, for burrowing owls in southwestern Idaho 2004-2005. Test statistic is Pearson $\chi^2$ .....	47
Table 1.7	Flea loads by treatment for burrowing owls nesting in artificial burrows in southwestern Idaho 2004-2005. Test statistic is Pearson $\chi^2$ with Yates’ correction for continuity .....	48
Table 1.8	Results of GEE modeling burrowing owl nestling body condition index ( $n = 75$ ) as a function of treatment at reused artificial burrows ( $n = 14$ ) in southwestern Idaho 2004-2005 .....	49
Table 2.1	Prediction matrix for factors affecting breeding dispersal of burrowing owls in southwestern Idaho .....	99
Table 2.2	Analysis of variance (ANOVA) for calculation of repeatability ( $r$ ) of breeding dispersal distance by burrowing owls in southwestern Idaho, 1994-2007 .....	100

Table 2.3	Number of burrowing owls banded in southwestern Idaho, 1994–2007.....	101
Table 2.4	Number of burrowing owls that were identified as breeders in southwestern Idaho in years after being banded. Owls with known breeding locations in the prior year are described as dispersed (breeding in different ABS or natural burrow) or philopatric (breeding in same ABS or natural burrow). Some banded owls returned in more than one year, and all observations from such individuals are included. Banding activities commenced in 1994 and occurred every year through 2007 .....	102
Table 2.5	Number of events of philopatry or dispersal for burrowing owls with known breeding locations in multiple years in southwestern Idaho, 1994–2007 .....	103
Table 2.6	Frequencies of dispersal patterns for burrowing owls that had multiple between-year events of dispersal or philopatry .....	104
Table 2.7	GEE results for modeling the number of young fledged by burrowing owls as a function of dispersal status (yes or no), year (t or t+1) and the interaction status $\times$ year with individual as a repeated subject. (a) Estimates for all parameters and effects in the model. (b) Difference in number of young fledged for selected means comparisons .....	105
Table 2.8	Within-year breeding dispersal distances for burrowing owls in southwestern Idaho .....	106
Table 2.9	Parameter estimates and odds ratios from GEE with logit link function for predictor variables that were modeled individually for breeding dispersal likelihood in burrowing owls in southwestern Idaho .....	107
Table 2.10	QIC values for select candidate models of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year $t$ in southwestern Idaho .....	108
Table 2.11	Parameter estimates and odds ratios from GEE with logit link function for the global model of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year $t$ in southwestern Idaho, 1994–2007 .....	109
Table 2.12	Parameter estimates and odds ratios from GEE with logit link function for the best evidence model ( $\Delta QIC = 0$ ) of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year $t$ in southwestern Idaho, 1994–2007 .....	110

Table 2.13	GEE parameter estimates and 95% confidence intervals for predictor variables that were modeled individually for breeding dispersal distance in burrowing owls in southwestern Idaho, 1994-2007.....	111
Table 2.14	QIC values for candidate models of breeding dispersal distance for burrowing owls (n = 72) in southwestern Idaho .....	112
Table 2.15	GEE parameter estimates and 95% confidence intervals for the inclusive confidence model of breeding dispersal distance for burrowing owls (n = 72) in southwestern Idaho, 1994-2007.....	113
Table 2.16	GEE parameter estimates and 95% confidence intervals for the best evidence model ( $\Delta QIC = 0$ ) of breeding dispersal distance for burrowing owls (n = 72) that successfully bred in year <sub>t</sub> in southwestern Idaho, 1994-2007 .....	114
Table 2.17	Percent frequencies and mean distances of breeding dispersal for several owl species.....	115

## LIST OF FIGURES

Figure 1.1	Nest material around entrances to artificial burrows in southwestern Idaho. (a) Material spread by burrowing owls at a current nest about four weeks into breeding season. Note the shredded cow dung (darker color than surrounding soil) scattered in a fan-shaped pattern around the entrance. (b) Material spread by owls at a nest from the previous breeding season, about four weeks before owls return from migration. As often happens, owl activity at the end of the previous breeding season caused most of the material to become spread in an arc about 15 – 25 cm from the entrance. (c) Material spread by researcher to mimic previous owl use. Photos (a) and (b) depict large amounts of material, while (c) depicts a moderate amount of material .....	50
Figure 1.2	Mean ( $\pm$ SE) number of eggs per clutch by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Numbers within columns are sample sizes.....	51
Figure 1.3	Mean ( $\pm$ SE) estimated Julian date of first egg by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Julian date 91 is April 2 <sup>nd</sup> in 2004 and April 1 <sup>st</sup> in 2005. Numbers within columns are sample sizes .....	52
Figure 1.4	Mean ( $\pm$ SE) number of young fledged by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Gray columns include all pairs; white columns include only pairs that fledged young. Numbers within columns are sample sizes .....	53
Figure 2.1	Mean ( $\pm$ SE) number of young fledged by philopatric (solid circles) and dispersing owls (hollow squares) in years t and t+1. Letters indicate means with overlapping 95% confidence intervals.....	116
Figure 2.2	Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that dispersed based on breeding success in year <sub>t</sub> .....	117
Figure 2.3	Proportion (white columns) and number (black columns) of male and female burrowing owls nesting in southwestern Idaho that underwent breeding dispersal .....	118

Figure 2.4	Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that underwent breeding dispersal as a function of distance to irrigated agriculture ....	119
Figure 2.5	Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that underwent breeding dispersal as a function of ectoparasite level.....	120
Figure 2.6	Mean ( $\pm$ SE) breeding dispersal distance by age for burrowing owls ( $n = 86$ ) nesting in southwestern Idaho. Numbers to right of means are sample sizes for each age. No 5-year old owls dispersed, and the two 6-year old dispersers moved the same distance. Simple linear regression line is shown .....	121
Figure 2.7	Breeding dispersal distance by distance to nearest neighbor for burrowing owls ( $n = 80$ ) nesting in southwestern Idaho. Simple linear regression line is shown.....	122
Figure 2.8	Mean ( $\pm$ SE) breeding dispersal distance by sex for burrowing owls nesting in southwestern Idaho .....	123
Figure 2.9	Breeding dispersal present frequency by approximate latitude for six populations of burrowing owls. Simple linear regression line is shown. Hollow boxes are residential populations and solid circles are migratory populations. General locations of populations (in increasing latitude) are: Florida (Millsap and Bear 1997), California (Catlin et al. 2005), Colorado (Lutz and Plumpton 1999), Idaho (this study), Washington (Conway et al. 2006), and Manitoba (De Smet 1997).....	124

## CHAPTER ONE: EFFECTS OF OLD NEST MATERIAL ON ARTIFICIAL BURROW OCCUPANCY AND REUSE BY BURROWING OWLS

### **Abstract**

I tested the effects of the presence of old nest material, primarily mammal dung, on the occupancy of unused burrows and the reuse of former nest burrows by burrowing owls (*Athene cunicularia*) nesting in artificial burrows in southwestern Idaho during 2004-2005. Adding old material from actual nests did not induce owls to occupy previously unused or newly installed artificial burrows. Thus, old nest material does not appear to function as a cue for burrow suitability. However, removing old material from burrows that owls had used for nesting in the previous year caused a decrease in reuse rates but had no effect on ectoparasite load or measures of reproductive performance. Also, owls reused burrows where young had been fledged in the previous year more often than burrows where breeding attempts had failed. While the presence of old material does not seem to increase the owls' fitness, it may help owls locate specific burrows when returning from migration.

### **Introduction**

Birds are widely recognized for their ability to build nests, sometimes including a highly diverse array of materials in the construction (Hansell 2000). The presence of a



nest, or certain materials within a nest, may affect nest site selection by individuals in subsequent breeding seasons, so that they may be induced to reuse or avoid previous nests. Available literature is mixed about the effects of old nest material on nest reuse and breeding parameters (Thompson and Neill 1991, Davis et al. 1994, Olsson and Allander 1995, Gowaty and Plissner 1997, Stanback and Dervan 2001, Stanback and Rockwell 2003, Mazgajski 2003, 2007, García-Navas et al. 2008, Fast et al. 2010). Western burrowing owls (*Athene cunicularia hypugaea*) line their nest burrows with a variety of items, but are best known for using mammal dung (Haug et al. 1993, Levey et al. 2004, Smith and Conway 2007). The owls do not clean a burrow before or after nesting in it (Haug et al. 1993), so nest material may persist between breeding seasons, especially inside the sheltered burrow. The presence of this material from a previous breeding season in a burrow may affect the decision of an owl to settle in that burrow or to move elsewhere. I conducted two experiments to examine possible effects of old nest material on occupancy of unused burrows and on reuse of former nest burrows.

### Occupancy Experiment

Animal populations are limited by various factors (Newton 1998, Karels et al. 2000, Thirgood et al. 2000, Forsman and Monkkonen 2003, Sergio et al. 2004), including the availability of breeding sites, particularly for species that require unique or specialized sites (Newton 1998). The repeated use of specialized breeding sites may indicate that they are in short supply or more suitable relative to similar sites. A lack of suitable breeding sites may reduce the number of breeders or breeding attempts (Lohmus 2003) or lead to decreased reproductive success in suboptimal sites (Birks et al. 2005). For some

species, the addition of suitable artificial breeding sites can mitigate effects of breeding site limitation (Newton 1998).

Tree cavities, which can be artificially replicated with nest boxes, are specialized breeding sites that have been the focus of much research (Aitken et al. 2002, Fokidis and Risch 2005, Kahler and Anderson 2006, Remm et al. 2006). Secondary cavity nesters, or animals that rely on cavities for nesting but cannot create them, may suffer breeding limitations when cavities are scarce or unsuitable. For example, Poysa and Poysa (2002) found that nest site availability was an important factor limiting a population of cavity-nesting common goldeneyes (*Bucephala clangula*). Another nest box experiment showed that two cavity-nesting birds (*Aphrastura spinicauda* and *Troglodytes aedon*) were nest-site limited during the breeding season (Tomasevic and Estades 2006). However, cavity availability may not limit breeding across all habitats or species (Carlson et al. 1998, Wiebe et al. 2006).

An underground burrow is another specialized breeding site. With the exception of substrate, burrows share many characteristics with tree cavities, including an enclosed microclimate, protection from harsh weather, protection from some predators, and potential for artificial replication by researchers. However, the more extensive substrate allows burrows to be larger and more complex (i.e., multiple chambers, tunnels, and entrances) than tree cavities. Thus, burrows excavated by fossorial animals may be highly variable, and many of them may be unsuitable for secondary burrow users. Where burrows are abundant but few are suitable, secondary burrow users may rely on suitability indicators rather than thorough inspection when prospecting for a burrow. If

prospecting is energetically costly and an animal uses cues to reduce that cost, the energy they save may be redirected toward other activities, such as reproductive performance.

Western burrowing owls are secondary burrow nesters whose abundance and distribution are affected by burrow availability (Coulombe 1971, Green and Anthony 1989, Desmond et al. 1995, 2000, Orth and Kennedy 2001). In fact, Coulombe (1971, p. 174) suggested that “local occurrences of these birds appear to be governed more by the suitability of burrow sites than by any other single factor.” Gleason (1978, p. 44) corroborated this for burrowing owls in eastern Idaho, stating that the “principal limiting factor to the population appeared to be nest site availability.” Other studies have found that burrows used for nesting by burrowing owls differ from unused available burrows in certain physical features, such as burrow diameter (MacCracken et al. 1985), tunnel angle (Belthoff and King 2002), tunnel length (Lantz 2005), and entrance and soil mound height (Poulin et al. 2005), which indicates that some characteristics may indeed make a particular burrow more suitable for use by owls. That owls use some types of artificial burrows more than others (Smith and Belthoff 2001a, Greger and Hall 2009) also suggests that suitability may be important.

Animals may use the presence of conspecifics as a source of information, such as habitat quality (Schuck-Paim and Alonso 2001, Danchin et al. 2004, Ahlering and Faaborg 2006). Current presence may not be required, as some animals leave indications of their previous presence. Stamps et al. (2005) found that female *Drosophila melanogaster* were not only attracted to other females at food, but to feeding locations where other females had been in the previous hour (probably because of olfactory cues). Luschan’s salamanders (*Mertensiella luschani*) in coastal Turkey use conspecific scent

tracks to identify safe shelters (Gautier et al. 2006). In these examples animals used olfactory cues to recognize the previous presence of conspecifics, but animals with high visual acuity may rely on visual cues. In a study of penduline tits (*Remiz pendulinus*), Gergely et al. (2009) found that old nests appear to act as a cue for breeding site suitability. Similarly, secondary burrow users may rely on remnants of conspecific use to identify a suitable burrow. When occupying a burrow for nesting, burrowing owls leave visual cues of their presence, including droppings, regurgitated pellets, prey remains, and nest material. The material used to line the burrow for nesting (mostly cattle dung) and some prey remains usually become scattered in a fan-shaped pattern around the burrow entrance (see Figure 1.1a), and material can remain from one breeding season to the next (see Figure 1.1b). This provides a potential cue to conspecifics that owls previously nested in the burrow, and that the burrow may therefore be suitable for nesting.

My first objective was to determine if burrowing owls rely on old nest material as a cue for burrow suitability and settlement. Specifically, I predicted that burrowing owl occupancy rates would be higher at burrows with material experimentally added to mimic previous owl use than at burrows with no such evidence of use.

### Reuse Experiment

Nests constructed from durable materials or in protective structures may endure from one breeding season to the next and afford animals the opportunity to reuse the nest. The decision to reuse a nest likely involves a cost-benefit trade off analysis. Potential benefits may be greater for individuals returning to a site rather than those simply reusing one previously occupied by another. Familiarity with a site's resources (e.g., food, shelter,

breeding sites) should make it more valuable than an unknown site to returning individuals (Pärt 1994, 1995, Forstmeier 2002, Brown et al. 2008). Site fidelity also may confer site dominance, where individuals that have previous experience with a territory are more successful in subsequently acquiring and defending it (Lanyon and Thompson 1986, Shutler and Weatherhead 1992, Bruinzeel and van de Pol 2004).

Animals reusing an unfamiliar site may still experience benefits. Individuals that reuse or refurbish an existing nest rather than building one from scratch may enhance reproduction by saving time and energy (Gauthier and Thomas 1993, Cavitt et al. 1999, Horn et al. 2007, Wiebe et al. 2007, Ellison 2008). Birds foregoing nest construction for reuse may begin egg-laying earlier, which may positively influence reproductive success (Gauthier 1989, Nilsson 2000, Naef-Daenzer et al. 2001, Thyen and Exo 2005, Burton and Mueller 2006). Also, Mealey (1997) found that Florida burrowing owls (*A. c. floridana*) nesting in previously used burrows had better breeding success (63%) than did those using newly excavated burrows (19%), although he did not specify which factors influenced this difference.

At times these benefits may be offset by costs related to reuse of a nest site. Although nest sites may survive between breeding seasons, they may lose structural integrity. Such decay could lead to complete breeding failure if a nest is reused (Bancroft et al. 2005). However, this is an unlikely problem where artificial sites are employed because of researcher maintenance and repair. Of greater concern is that a predator may learn where a nest is located and return there, especially if the predator has successfully plundered the nest previously (Nilsson et al. 1991, Sonerud 1993, Miller 2002, Styrsky 2005); but

predator effects may be most important when nest reuse is within the same season (Weidinger and Kočvara 2010).

Furthermore, when nest sites are not cleaned, old nest material may contain ectoparasites, which remain in the nest to infest subsequent occupants (Barclay 1988, Möller 1989, Möller and Erritzøe 1996, Tomás et al. 2007, Mazgajski 2007).

Ectoparasites can negatively influence reproductive output by retarding nestling development (Brown and Brown 1986, Möller 1990, Hurtrez-Bousses et al. 1997, Möller 1997, Nilsson 2003, Carleton 2008), increasing nestling mortality (see references in Chapman and George 1991), increasing avoidance of traditional nests (Loye and Carroll 1998), and/or increasing nest abandonment (Emlen 1986). Additionally, ectoparasites can reduce adult body condition, which may decrease reproductive effort (Möller 1997, Fitze et al. 2004). And, when ectoparasites reduce host fitness, hosts are likely to recognize the risk posed by ectoparasitism (O'Brien and Dawson 2005).

However, ectoparasites are only important to nest reuse if they remain in the nest between uses (Rendell and Verbeek 1996a). Ectoparasites that rely on host-to-host transmission rather than nest-to-host transmission will over-winter independently of old nests and not affect reuse (Rendell and Verbeek 1996a). Burrowing owls regularly line their nest burrow, but they do not clean a burrow before reusing it (Haug et al. 1993). Nest material consists primarily of cattle dung that owls shred but may include such items as dung from other mammals, prey remains, feathers, grass, bones, bailing twine, and other human litter (Haug et al. 1993, Brady 2004, Smith and Conway 2007). This remnant material may provide housing for ectoparasites between burrowing owl breeding seasons.

Smith and Belthoff (2001b) found four species of ectoparasites (three fleas, Siphonaptera; one louse, Phthiraptera) infesting burrowing owls in southwestern Idaho. Two of the flea species (*Aetheca wagneri* and *Meringis hubbardi*) had never been collected from burrowing owls in Idaho and probably represented accidental or phoretic associations with the owls (Smith and Belthoff 2001b). The most common flea (*Pulex irritans*) was previously known to infest burrowing owls (Baird and Saunders 1992). The single louse species (*Strigiphilus speotyti*) is specific to burrowing owls (Clayton 1990) and has been implicated in contributing to reproductive failure (Smith 1999). However, lice usually rely on physical contact between hosts for transmission, and neither larvae nor adults survive for extended periods apart from a host (Bush et al. 2001). Thus, *S. speotyti* would not over-winter in old nest material to affect burrow reuse.

Unlike lice, fleas are highly mobile and do not require host-to-host transmission (Bush et al. 2001). In fact, the fleas infesting burrowing owls in southwestern Idaho appear to be linked more with the burrow than with individual owls. For instance, in the early stages of nesting, the adult owls, especially females, spend more time inside the burrow and have low to moderate flea loads; but in the later stages of nesting, the adults (which spend more time outside the burrow) seldom harbor fleas, while the nestlings (which are usually in or very near the nest burrow) tend to have moderate flea loads and rarely lack fleas (J. Belthoff unpubl. data).

Adult fleas usually lay eggs within the host's nest or bedding; these eggs are non-adhesive, so any eggs laid on the host usually fall off into the nest (Roberts and Janovy 2005). The larvae typically pupate after several weeks, but they can delay emergence for many months if conditions are unfavorable (Roberts and Janovy 2005). Although adult

*P. irritans* can live for prolonged periods (125 days at 7°C to 10°C) without a blood meal (Roberts and Janovy 2005), it is during the pupal stage that fleas are most likely to overwinter in burrowing owl nest material. When a potential host returns to occupy the nest for the next breeding season, indications of its presence (vibrations, increased temperature, and increased CO<sub>2</sub>) can induce the fleas to emerge (Daly et al. 1998).

My second objective was to determine if burrowing owls benefit from reusing burrows with old nest material while avoiding burrows infested with ectoparasites. I predicted that owls reusing burrows with old nest material will 1) begin laying eggs sooner and 2) increase productivity relative to owls nesting in burrows with material removed during field experiments. Also, I predicted that 3) owls will reuse burrows with old nest material at higher rates than burrows with material removed. Regarding the avoidance of ectoparasites, I predicted that 4) owls will reuse burrows with ectoparasites (but not material) removed at the highest rate, and 5) owls reusing ectoparasite-removed burrows will have the highest productivity. All of the predictions for this experiment are outlined in Table 1.1.

## **Methods**

### Study Site

I conducted field experiments in and near the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho during 2004-05. The NCA was established in 1993 by Congress (Public Law 103-64) for the conservation, protection, and enhancement of raptor populations and habitats (Sharpe and Van Horne 1998), and it now covers over 2400 km<sup>2</sup> (about 1960 km<sup>2</sup> of public land) in Ada, Elmore,



and Owyhee Counties. The area was originally shrub-steppe habitat dominated by big sagebrush (*Artemisia tridentata*), but fire and human disturbance have converted large portions to grassland dominated by exotic annual grasses and forbs like *Bromus tectorum* and *Sisymbrium altissimum* (Hironaka et al. 1983, U.S.D.I. 1996). The area also contains agricultural fields, dairy farms, many roads and rights-of-way, BLM-managed rangelands, and structures such as homes and silos (King 1996).

The Snake River is the major geologic feature, and it flows through a steep, narrow canyon in the southern and western portions of the NCA. The topography of the surrounding river plain is flat to rolling with rocky outcrops and scattered buttes. Average daily temperatures are lowest in January (-2.1°C), highest in July (23.1°C), and increase from 5.5°C to 23.1°C during the breeding season, March to July (N.O.A.A. 2002). Temperature extremes range from -29°C in winter to 45°C in summer (N.O.A.A. 1985). Precipitation averages 31.7 cm annually, with 12.1 cm falling during the breeding season (N.O.A.A. 2002).

### Study Species

Western burrowing owls occur throughout open, well-drained grasslands, steppes, deserts, prairies, and agricultural lands of western North America (Haug et al. 1993). They breed from southern Canada to central Mexico and from Pacific coast states to Manitoba and Texas. Northern populations tend to be migratory, while those in the southern U.S. and Mexico may be year-round residents (Haug et al. 1993). In southwestern Idaho, burrowing owls are typically present from March to September or October, but small numbers of individuals remain on the breeding grounds throughout the

winter (this occurs in other areas, see Martin 1973, Butts 1976, Conway et al. 2006). The migration routes and wintering areas for owls from this population are poorly known, although a small number of band returns indicates that at least some of the owls winter in southern California (King 1996, King and Belthoff 2001).

Western burrowing owls are obligate burrow nesters, and they primarily nest in abandoned mammal burrows (Haug et al. 1993). Natural burrows are available throughout the study site for nesting and shelter, and badgers (*Taxidea taxus*) are the primary excavators of most burrows suitable for burrowing owl nests (King 1996, Belthoff and King 1997). However, not all badger burrows are suitable for nesting by burrowing owls because of insufficient depth or overly steep tunnels (Belthoff and King 2002). Burrowing owls will readily use and reuse artificial burrow systems (ABSs), which are more conducive to research because they provide easy access to the nest chamber (Smith and Belthoff 2001a, Belthoff and Smith 2003). Where ABSs are present within my study site, burrowing owls rarely use natural burrows for nesting (pers. obs.).

### Occupancy Experiment

I investigated the possible role of nest material as a cue of burrow suitability and settling behavior by comparing burrowing owl occupancy of experimentally modified ABSs. At ABSs that had not been occupied by burrowing owls in the previous three years ( $n = 194$ ), I added material from actual owl nests or removed any nest-like material. At new ABSs ( $n = 34$ ; see Appendix A), I added nest material or nothing. I installed and altered ABS before owls returned from the wintering grounds for the 2004 and 2005 breeding seasons. I deployed new ABSs in a cluster of two artificial burrows

with the tunnel entrances placed 2 to 3 m apart, except for one ABS with a lone artificial burrow. Older ABSs may have had entrances separated by as much as 9 m (Smith and Belthoff 2001a). Clustered burrows are important because burrowing owls often use satellite burrows to roost, cache prey, and hide from predators (Haug et al. 1993, King and Belthoff 2001). Also, a higher density of surrounding burrows may increase nest use (Plumpton and Lutz 1993, Poulin et al. 2005) and reproductive success (Desmond and Savidge 1999).

Each new artificial burrow consisted of a 15.7 L (25 cm diameter × 32 cm height) or 20.6 L (27 cm diameter × 36 cm height) plastic bucket and a 2 m section of 10 cm diameter flexible, perforated plastic pipe inserted 1 cm above the bucket floor. I drilled four to six 1 cm holes for drainage in the bucket floor and covered it with 2 cm of loose soil. I buried the buckets so that their lids were covered by  $\geq 15$  cm soil. Tunnels sloped downward 20 – 30° from the entrance, made a 90° turn, and inserted into the chamber on a level plane. I oriented tunnel entrances generally between east and south to avoid prevailing winds. I used excavated soil to form a small mound at each entrance and placed a wooden perch between the entrances. In the rare case where an ABS consisted of a single burrow, I erected the perch within a few meters of the entrance. I placed new ABSs within 200 m of burrows where owls nested or roosted the previous year. Older ABSs were generally similar to these new ABSs, but varied in chamber size, tunnel size, and number of burrows (for descriptions, see Smith and Belthoff 2001a). Artificial burrows were first installed on a large scale in the NCA in 1997 (small numbers were deployed in 1995 and 1996), and they numbered over 240 in 2005.

I randomly assigned new and old ABSs separately to one of two treatments: adorned ( $n = 115$ ) or unadorned ( $n = 113$ ). I randomized treatment each year, so that ABSs in the occupancy experiment in 2004 and 2005 may have had one treatment twice or both treatments once. I visited the unadorned ABSs and removed any nest-like material (e.g., dung, grass, or prey remains), if present, so that they lacked signs of owl use. When I removed chamber contents, I added soil to the chamber floor. For the adorned ABSs, I visually mimicked prior owl nesting by adding material obtained from actual owl nests to the entrance and chamber of all burrows (see Figure 1.1c). I pretreated added material with microwave heating to kill possible ectoparasites (see reuse experiment for details). Microwave treatment did not alter consistency or other known aspects of material but presumably killed any ectoparasites present in the material (see Richner et al. 1993, Rendell and Verbeek 1996b).

Following adornment or cleaning, I monitored ABSs throughout the breeding season for owl activity, nesting, and productivity. I considered an ABS to be occupied if a pair of burrowing owls settled and laid at least one egg in any of the burrows.

### Reuse Experiment

To examine the potential effects of old nest material on burrowing owl reuse of artificial burrows, I manipulated the contents of ABSs used by owls for nesting in the preceding year ( $n = 75$ ; see Appendix B). Before owls returned from wintering grounds for the 2004 and 2005 breeding seasons, I removed all contents (e.g., prey remains and nest material) from ABSs in which owls nested in 2003 and 2004. This included material from the chamber, tunnel, and entrance of each burrow in the ABS. I then manipulated

the material based on assignment of the cleaned ABSs into one of three treatment groups: control ( $n = 21$ ), microwave ( $n = 20$ ), or removal ( $n = 34$ ). I allocated more units to the removal group to obtain sufficient nest material for use in the occupancy experiment. I assigned treatments to the ABS rather than the individual burrow that contained the nest. As most ABSs had multiple burrows, it would have introduced ambiguity if owls reused an ABS but nested in a different burrow than the year before. Therefore, I obstructed non-nest burrows with rocks in the chamber or lower portion of the tunnel. The tunnels were still available for use as satellites, but the chambers were not available for nesting. This forced owls to nest in the same burrow occupied in the previous year when reusing an ABS.

After cleaning the control group burrows, I restored all material to its approximate pre-treatment location. This served as a control for signs of my visitation and disturbance. For the removal group, I placed 2 cm of loose soil on the chamber floor and retained all material, which I stored and microwave heated (as below) for subsequent use in the occupancy experiment. For the microwave group, I microwave heated all material before returning it to the ABS from which it was removed. I placed about 1.5 L of material in 2.25 L closed containers (Ziploc® 9½ cup Snap ‘n Seal) to prevent moisture loss, and microwave heated the containers singly on full power for five minutes to kill ectoparasites (Richner et al. 1993, Rendell and Verbeek 1996b). When possible I did this on-site with a microwave powered by an inverter attached to battery of a truck. Otherwise, I transported the material to a laboratory on the Boise State University campus (Boise, Idaho, USA), microwave heated it, and returned it to the original ABS in one to eight days.

After modifying burrow contents, I monitored ABSs throughout the breeding season for owl activity. I defined reuse as owls settling and laying at least one egg in the focal burrow. Although some adult females bred at the same burrow in consecutive years, it was hard to identify if the same pair reused a burrow because most adult male owls were unbanded in my population because they were more difficult to capture than females. However, I considered a burrow as reused even if one or both of the nesting pair was known to be different from the prior year.

### Data Collection and Definitions

I monitored 216 ABSs (158 experimental) in 2004 and 240 ABSs (145 experimental) in 2005 for nesting by burrowing owls (see Appendices A and B for lists of experimental ABSs). I visited every ABS, experimental or not, at least twice during the breeding season to check for signs of owl activity. I focused detection efforts on visual sweeps of surrounding areas and inspection of ABSs for owls or signs of activity, such as dung, cached prey, droppings, pellets, or footprints. Usually, I sighted owls while moving through an area on foot or in an automobile. After detecting owls or signs of activity at an ABS, I returned to confirm nesting by excavating burrow chambers and checking for eggs.

Because identification of individual adults was important to concurrent studies, I attempted to trap all unmarked adults to fit them with a unique combination of one USGS aluminum band (size 4) and three colored plastic leg bands. Previously marked owls were identified by capture or by sighting the leg bands with binoculars or a spotting scope. I fitted owlets ( $\geq 15$  days post-hatch) with a distinctive combination of leg bands.

I usually employed a one-way basket trap (described in Smith 1999) to capture adults, but I often captured owlets by hand in the nest chamber. From each owl I collected ~200  $\mu$ l of blood by venipuncture of the brachial vein for use in other studies.

After confirming nesting at an ABS, I returned to determine clutch size, hatch date, and number of young fledged, and to take measurements of the owlets. I dug to the chamber lid and examined nest contents at each visit, so that some were excavated up to five times over the course of the breeding season (discovery, clutch size check, hatching check, banding, and fledging check). At most nests I measured young twice, first when I banded them (~16 days post-hatch) and then again when I checked for number fledged (~26 days post-hatch). Young are capable of sustained flight by approximately five weeks of age (Landry 1979, King 1996), so I considered any young alive at around four weeks to have “fledged” (Steenhof and Newton 2007). I classified a pair as successful if at least one young fledged.

I used measurements taken at the fledge check to produce a body condition index (BCI) for each nestling. BCIs for avian species are often based on the residuals of body mass regressed on body size (Green 2001, Schulte-Hostedde et al. 2005, Moore et al. 2007), where body size may be a single measurement (flipper length in penguins: Cockrem et al. 2006; tarsus length in peafowl: Pike and Petrie 2005) or the first principal component of a principal component analysis of several external measurements, such as tarsus length, culmen length, and wing chord (Chastel et al. 1995, O’Dwyer et al. 2006, Williams et al. 2007). Less commonly, a ratio of body mass to a combination of measurements is used instead of residuals (bill length + tarsus length: Kitaysky et al. 1999, Poisbleau et al. 2005). Although I measured mass, tarsus length, wing chord, tail

length, and exposed culmen length at banding both years and at fledge check in 2005, I only measured mass and tarsus length at fledge check in 2004. As I was most interested in the “quality” of young near the time of fledging, I created a BCI using body mass regressed on tarsus length (the only body size metric available for both years at fledge check). Freeman and Jackson (1990) suggested that the best univariate descriptor of body size, at least among passerine species, is tarsus length. Combining sexes for this type of analysis may generate possible bias from intersexual differences (Williams et al. 2007). However, I pooled the sexes for analyses for two reasons. First, burrowing owls in southwestern Idaho exhibit only minor sexual size variation as nestlings (male tarsus 4.1% larger: Taylor 2005). Second, I did not know the sex for most nestlings because burrowing owl nestlings cannot be reliably sexed in the field by plumage or structural measurements. Although some of the nestlings from 2004 were sexed by DNA analyses (Taylor 2005), other nestlings from 2004 and all nestlings from 2005 only had a known sex if they were identified as breeders within the study area in 2006 or 2007.

For most of the owls nesting in ABSs included in the reuse experiment, I estimated clutch initiation date because I could not determine exact dates through these monitoring efforts. Using data from the 1999-2005 breeding seasons, I calculated that burrowing owls in this population lay an egg every 1.33 days, and they have a mean incubation of 23 days (Table 1.2). These numbers are similar to, but lower than, those reported for burrowing owls in other locations (Haug et al. 1993, Wellicome 2000). I defined incubation as the period from clutch completion to median hatch date for all eggs that hatched, even though females may begin incubating before the final egg is laid (Wellicome 2005). I used the median date for all eggs successfully hatched as the hatch



date because some broods hatched asynchronously. For all nests, experimental or not, where I knew hatch timing with confidence in 2004 and 2005, the mean span between first and last hatched eggs in a clutch was 1.31 days ( $n = 26$ , range: 0 – 4). In many cases I checked the nest before the clutch was complete, so I was able to approximate a first-egg date by subtracting 1.33 days for every egg. For nests that I did not check until after clutch completion, I subtracted length of egg-laying (1.33 days per egg) and mean length of incubation (23 days) from the median hatch date to estimate date of clutch initiation. I used Julian dating when performing analyses involving clutch initiation dates.

I indexed flea levels based on the number of fleas seen on the owl and on my hands during handling of an owl (for similar methods counting haematophagous mites, see Möller 1993, Rendell and Verbeek 1996a). The levels I used were None (no fleas seen), Low (one to four fleas), Medium (five to nine fleas), or High (ten or more fleas). I used an index rather than an absolute count because the fleas moved and the possibility of recounting a flea as it emerged and disappeared in an owl's feathers was high. To examine the relationship between experimental treatments and subsequent ectoparasite loads of nestlings, I recorded the median flea level of all young in the nest at ~16 days post-hatch. However, nesting failure (primarily caused by flooding) occurred prior to or soon after hatching for nine pairs in 2005, and I was unable to observe flea levels on young. For these nests and two others where flea levels of nestlings were not recorded, I substituted the flea level of the adult female early in the breeding attempt (egg-laying, incubating, or hatching). At nests where flea levels of adult females and young were both known during 1999-2005, there was a weak, but significant, positive correlation between them ( $r_s = 0.21$ ,  $P = 0.0176$ ;  $n = 126$ ).

### Statistical Analyses

I used SAS 9.1 (SAS Institute Inc., Cary, NC) for statistical analyses. During a single breeding season, experimental ABSs were never occupied by more than one burrowing owl pair, so I used the ABS as the experimental unit for all statistical tests except BCI analyses. I used one-sided Fisher's exact test for all  $2 \times 2$  contingency tables. For larger contingency tables, I used Pearson's  $\chi^2$ , to which I applied Yates' correction for continuity if any cell had an expected value less than five (Zar 1999). Means are reported with  $\pm$  SE.

For the occupancy experiment, I performed a contingency analysis to determine if occupancy was independent of adornment status. I subdivided the contingency test for effect of adornment status between newly installed ABSs and old, unused ABSs to examine possible treatment effect differences between burrows that were truly novel or potentially already known.

For the reuse experiment, I used a contingency analysis to determine if reuse was uniform across the three treatment groups. Reproductive success often influences individual site fidelity in birds (see Chapter 2), so I used another contingency analysis to assess if reuse in general was independent of owl productivity status (failed or successful) at a particular ABS in the previous breeding season. Because owls were more likely to reuse burrows where young were fledged (Table 1.3), I subdivided the first contingency analysis between sites with a successful pair and sites where owls failed to fledge young in the previous year. I did not include three ABSs in the subdivided analysis because owl productivity status at those locations for the previous year was unknown.

I used one-way ANOVAs to test the effects of treatment on clutch initiation date and number of young fledged. I excluded five ABSs from the initiation date analysis: four because I could not accurately estimate the day the first egg was laid, and one because it was suspected as a reneest after a failed nesting attempt at a different location. I only included ABSs where owls successfully fledged young in the ANOVA of number fledged. Because of non-normality, I used a Kruskal-Wallis test to examine the effect of treatment on clutch size. I did not include two ABSs in the clutch size analysis because the owls abandoned the nest before completing the clutch. I used a contingency analysis to examine the relationship between treatment and flea load in subsequent nests.

I generated BCIs for nestlings at all nests in 2004 and 2005 by regressing body mass on tarsus length with age in days as a covariate and with nest as a repeated factor because siblings are not independent. Positive residuals indicated good body condition, and negative residuals implied poor body condition (see Appendix C). I then used Generalized Estimating Equations (GEE; PROC GENMOD in SAS) with normal distribution and identity link function to model nestling BCI as a function of ABS treatment with nest as a repeated factor.

## **Results**

### Occupancy Experiment

Burrowing owls occupied slightly more adorned (17 of 115) than unadorned ABSs (12 of 113), but the trend was not statistically significant (one-sided Fisher's exact test,  $P = 0.244$ ; Table 1.4). Similarly, there was no difference in burrowing owl occupation by

adornment status for newly installed ABSs (one-sided Fisher's exact test,  $P = 0.784$ ; Table 1.4) or old, unused ABSs (one-sided Fisher's exact test,  $P = 0.196$ ; Table 1.4).

I did not make *a priori* predictions for breeding parameters (e.g., clutch size and number fledged), but I did record them. Burrowing owls nesting in unadorned ABSs laid  $8.6 \pm 0.58$  eggs ( $n = 11$ ; range: 7 – 10) and successful breeders fledged  $4.9 \pm 0.90$  young ( $n = 8$ ; range: 2 – 10). I did not include one nest in the calculation of mean clutch size because it was abandoned during egg-laying, and the clutch was presumably incomplete. Burrowing owls nesting in adorned burrows had a mean clutch size of  $8.9 \pm 0.34$  ( $n = 16$ ; range: 6 – 11) and a mean number of young fledged per successful pair of  $4.7 \pm 0.70$  ( $n = 15$ ; range: 1 – 9). I was unable to confirm the clutch size and outcome of one nest in one adorned burrow. Interestingly, more nesting pairs were successful in adorned nests (94%) than in unadorned nests (75%), even though owls added their own material to both.

### Reuse Experiment

Burrowing owls reused 24 of the 75 experimental ABSs, but reuse was not uniform across treatment groups (Pearson  $\chi^2 = 5.91$ ,  $df = 2$ ,  $P = 0.052$ ; Table 1.5). Owls reused the removal group least often (17.6%), and they reused the control (42.9%) and microwave (45.0%) groups almost equally, but this varied by year. They most frequently reused the control ABSs (50.0%) in 2004 and the microwave ABSs (63.6%) in 2005.

Burrowing owls reused ABSs where pairs had been previously successful at higher rates than ABSs where owls had failed to fledge young (one-sided Fisher's exact test,  $P = 0.016$ ; Table 1.3). There was no difference in reuse rates among treatment groups for

ABSs where owls failed to fledge young the prior year (Pearson  $\chi^2$  with Yates' correction = 0.016,  $df = 2$ ,  $P > 0.990$ ; Table 1.6). However, among ABSs where young fledged, owls tended to reuse burrows in the removal group least often (Pearson  $\chi^2 = 5.14$ ,  $df = 2$ ,  $P = 0.077$ ; Table 1.6).

Treatment group had no effect on clutch size (Kruskal-Wallis  $U = 3.19$ ,  $df = 2$ ,  $P = 0.203$ ; Figure 1.2), clutch initiation date ( $F_{2,16} = 0.66$ ,  $P = 0.533$ ; Figure 1.3), or number of young fledged per successful pair ( $F_{2,10} = 0.40$ ,  $P = 0.681$ ; Figure 1.4). Furthermore, treatment group was also unrelated to flea load (Pearson  $\chi^2$  with Yates' correction = 3.15,  $df = 6$ ,  $P = 0.790$ ; Table 1.7) and body condition of young (Table 1.8).

## Discussion

### Occupancy Experiment

The results did not support my prediction that burrowing owls would occupy adorned burrows at higher rates than unadorned burrows. This indicates that burrowing owls probably did not rely on the presence of old nest material as a cue for burrow suitability and subsequent occupancy. There are at least four possible explanations for this result, although some are more plausible than others. First, burrow prospecting is a relatively easy endeavor and cues that direct owls to suitable burrows may be unnecessary. I am unaware of any studies that have explored the time-budgets or energetics of burrow prospecting in burrowing owls, but if prospecting for and selecting an acceptable burrow require minimal investment, then a trait related to recognition of old nest material as a suitability cue may never evolve.

The second possible alternative is that burrowing owls may use suitability cues other than old nest material. For something to function as a visual cue, it must be obvious from casual observation. The only obvious inherent cue is the small mound of soil left near the entrance of badger-excavated burrows. However, this mound can be found at nearly all burrows, regardless of suitability, and would not function as a suitability cue. Aside from old nest material, there are no obvious indicators of previous owl use that could function as a visual cue. Also, the remnant material is more likely to function as a visual rather than olfactory cue because owls are generally considered microsmatic, and odors associated with the material may not persist from the end of one breeding season to the beginning of the next (generally August to March).

Third, the time of day that owls search for nesting burrows is unknown but is assumed to be near dusk or at night (Haug et al. 1993). Although obvious during the day, old nest material may be less valuable as a visual cue at night. However, if owls are detecting the location of a burrow at night through visual means, they are likely able to see the old nest material, as well. Or, if the owls are detecting the burrow through other means (e.g., auditory perception of wind passing over burrow entrances), then they may recognize the presence of old nest material (through vision or touch) when approaching the burrow. Thus, the material could still act as a potential cue for the owls, even if they prospect for nesting locations at night.

Fourth, suitability of the burrow may be less important than other factors, such as habitat quality or distance to nearest neighbor. For instance, a suitable burrow in poor habitat may be less desirable than a marginal burrow in good habitat. Also, western burrowing owls sometimes modify or improve existing burrows (Thomsen 1971, Gleason

1978). Thus, if more important conditions for location are met, burrowing owls may be willing to expend effort to make a burrow more suitable. If suitability is a less important factor, especially if owls are capable of and willing to modify burrows, then owls are less likely to use burrow suitability cues.

Based on the results of the occupancy experiment, burrowing owls do not use old nest material as a cue for burrow suitability and settlement. Of the four alternative explanations presented here, I find the first (burrow prospecting may not require cues) and fourth (other factors may outweigh burrow suitability) to be most plausible. These, however, are not mutually exclusive and both may be operating.

#### Reuse Experiment

Neither of the predictions concerning the removal of ectoparasites was supported by the results. The fact that reuse for microwave ABSs was approximately equal to control ABSs, but higher than removal ABSs, indicates that there is no appreciable difference between the control and microwave groups. This may be because no burrowing owl ectoparasites over-winter in old nest material, which would make ABSs in the microwave group qualitatively equal to ABSs in the control group. I tested this indirectly by comparing flea loads at reused nests, and I found that there was no difference among the treatment groups, which is consistent with the idea that treatments did not affect flea load because fleas may not over-winter in old nest material. The interpretation of this result may be confounded by small sample sizes and an inability to measure flea loads at similar nesting stages. However, an anecdotal experience suggests the interpretation was correct and fleas do not rely on old burrowing owl nests for over-wintering (see below).

Old nest material that was transported to the laboratory for microwave heating was usually stored untreated for two to three days. However, it sometimes remained for as long as three weeks before being used in the occupancy experiment. I regularly left the storage containers uncovered in a room with moderate human presence, but I never noted fleas in the material or surrounding work areas. During winter of 2005, I collected material from a burrow in which an owl was roosting. Although the owl was covered in fleas (which I assume were obtained from mammalian prey), I noted no fleas in the collected material. About one week later (long enough for any larvae to have pupated) the room with the stored material was infested with fleas. Even though material from dozens of burrows was cumulatively stored for months with increased temperature, CO<sub>2</sub>, and vibrational stimuli, this was the only time I observed fleas possibly emerging from pupae in collected material. As this material was collected from a current roost site rather than an old nest site, it suggests that fleas do not over-winter in old nest material of burrowing owl nests when owls are absent.

However, whether fleas over-winter in old nest material may be irrelevant if they have no detrimental effects on burrowing owl fitness. I found that level of ectoparasitism was not correlated with number of young fledged, and burrowing owls dispersed away from nests with low flea levels at higher rates than they did from nests with higher flea levels (see Chapter 2). Research on burrowing owls in southwestern Idaho subsequent to this study suggests that fleas like *P. irritans* may not negatively affect nestling body condition (Welty 2010; see also Gallizzi et al. 2008). In fact, if fleas are acquired solely from prey, then ectoparasite load may be an indication of prey availability, in which case



burrowing owls may prefer to nest in areas where they will likely have high levels of ectoparasites.

The results only supported one of my predictions concerning the removal of nest material. Owls tended to reuse control ABSs at higher rates than removal burrows. Contrary to the results here, Smith and Conway (2007) found that the proportion of burrows reused by owls for nesting was not significantly different at burrows with dung added (58%;  $n = 19$ ) from burrows with dung removed (78%;  $n = 19$ ). They state that all of their experimental burrows were used for nesting in the previous two breeding seasons, but they do not indicate if young successfully fledged. As noted, burrowing owls in southwestern Idaho were much more likely to reuse burrows where young successfully fledged the previous year (Table 1.3), which was corroborated by burrowing owls breeding in Manitoba (De Smet 1997). De Smet (1997) recorded owls reusing successful nests more often (23%; 28 of 122) than failed nests (7%; 4 of 57), and this may be typical in other parts of their range. Thus, the difference in results between Smith and Conway (2007) and this study could be related to previous productivity rather than experimental treatment.

The other predictions were not supported: egg-laying date, clutch size, nestling BCI, and number of young fledged did not differ significantly between owls reusing control and removal ABSs. Although owls reused uncleaned burrows more often, they did not seem to increase their reproductive fitness over owls reusing cleaned burrows. The apparent lack of difference in productivity may be a result of small sample sizes. Owls only reused 24 burrows, with treatment group sample sizes of nine, nine, and six for the control, microwave, and removal groups, respectively. The total sample size was further

reduced for some of the statistical tests, and the total sample size for number of young fledged from successful pairs included only 13 pairs. Such small sample sizes may not accurately detect any trends, let alone significant differences. The comparison of nestling BCIs was perhaps more robust, as the analysis included 75 nestlings from 14 experimental nests.

I assumed that energy saved via reduced investment in nest preparation would be redirected to productivity, but that did not show in number of eggs laid, number of young fledged, or body condition of fledglings. Surplus energy still may have been budgeted to caring for young but may not have manifested in any of the variables I measured here. Alternatively, any saved energy may have been used for increased defense of mates or territories, fat deposition, preening, or other self-maintenance. However, owls reusing burrows containing old material still brought in additional dung (pers. obs.), suggesting they may have used as much energy in nest preparation as owls nesting in cleaned burrows. Also, owls nesting in control burrows did not begin laying eggs sooner than those nesting in cleaned burrows. This indicates that the presence of old nest material may not reduce the time required to prepare a nest. Thus, even with old nest material present, burrowing owls may not save any time or energy.

So, if owls do not enhance their productivity by reusing uncleaned burrows, why reuse them more than cleaned burrows? There are at least two possible reasons why burrowing owls exhibit higher reuse rates of burrows with old nest material. First, old nest material may provide immediate benefits to owls returning from migration by enhancing burrow microclimate or attracting prey. Brady (2004) found that chamber dung volume was significantly related to temperature range and % CO<sub>2</sub> in nest chambers

during incubation, so that increasing amounts of dung stabilized temperatures and decreased CO<sub>2</sub> concentration. Temperatures in southwestern Idaho in March (when burrowing owls return to breed) can be cold, especially at night, which may be physiologically costly for owls accustomed to warmer temperatures on wintering grounds. Owls may seek out mechanisms, such as dung, to aid in external control of temperature while acclimatizing. Also, some arthropods eaten by burrowing owls are more abundant where dung is present (Levey et al. 2004, Smith and Conway 2007). When returning from migration, owls may preferentially settle at burrows already containing dung because prey are more abundant immediately around the burrow.

Second, I suggest that burrowing owls rely on public information (Doligez et al. 2002, Valone and Templeton 2002, Sergio and Penteriani 2005). In other words, they make decisions about nesting location using not only their own reproductive experiences, but the success or failure of others, as well. In colonially nesting birds, individuals may visit other colonies near the end of the breeding season to assess mean colony productivity, which they then use to decide where to breed in the future (Valone and Templeton 2002). While burrowing owls are sometimes described as semi-colonial or nesting in “loose colonies” (Haug et al. 1993), the use of public information is not restricted to colonial birds (Valone and Templeton 2002). Burrowing owls may base public information on productivity at specific burrows or burrow clusters. As noted earlier, among the ABSs in the reuse experiment, owls reused 20 of 49 (41%) burrows where young had fledged, versus 3 of 23 (13%) burrows where no young had fledged, regardless of treatment group. Owls may favor nesting in burrows from which young were successfully fledged in the previous year.

Old nest material may still be important when the owls return from migration and are searching for a particular burrow based on public information from the previous breeding season. The owls may expect the burrow to show signs of previous use (i.e., old material), and might fail to recognize a burrow if the material has been removed. This is unlikely for owls returning to the same site, but because of mortality and dispersal it is uncommon for an individual to nest in the same burrow in consecutive years in this population of burrowing owls (see Chapter 2). So, without necessarily providing fitness benefits to owls (although philopatric individuals could accrue some benefits through familiarity), the material may simply act as a cue that the owl has found the burrow for which it was looking.

#### Difference Between Experiments

If old nest material does act as a cue for reusing a burrow, why does it not act as a cue for occupying a previously unused burrow adorned with nest material? In other words, how do the two experiments here differ? From the perspective of an individual moving into the area for the first time (i.e., does not possess public information), there may be no difference between the experiments. The adorned ABSs from the occupancy experiment and control/microwave ABSs from the reuse experiment would be the same, as would the unadorned ABSs and removal ABSs. I suggest that this is somewhat uncommon in southwestern Idaho. Although it is not clear which member of the pair selects a burrow (Haug et al. 1993), I suspect that (at least in my study area) males return from migration prior to females, settle into a burrow, and begin advertising for mates. Males are less likely to exhibit breeding dispersal and, when they do, tend to disperse shorter distances

than females (see Chapter 2). So, males are highly likely to return to sites for which they possess public information. This may be why old nest material did not work as a cue for burrow suitability at unused burrows, but it possibly functioned as a cue to indicate a particular burrow for reuse.

### Management Implications

Western burrowing owls have experienced restrictions at the edges of their distribution and are considered endangered in Canada, threatened in Mexico, and a species of conservation concern in nine states in the U.S. (Klute et al. 2003). Sciurid mammal declines by eradication programs and epizootics of sylvatic plague have severely reduced the number of primary excavators in large portions of the Great Plains (Klute et al. 2003, Poulin et al. 2005). The use of artificial burrows is one possible method to mitigate the loss of primary excavators. For wildlife managers that are using or considering the use of artificial burrows for burrowing owls, I suggest the following. Addition of nest material to new artificial burrows to induce occupancy may not be effective, as burrowing owls did not occupy adorned burrows at higher rates than unadorned burrows. Annual maintenance of burrows should not include removal of nest material; burrowing owls reused burrows at a reduced rate after removal of nest material. Lastly, ectoparasites may not over-winter in nest burrows, so microwave heating of old nest material to kill ectoparasites is not necessary as a management tool.

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Table 1.1. Prediction matrix for burrowing owl reuse of experimentally manipulated artificial burrow systems in southwestern Idaho 2004-2005.

Metric for which prediction was made	Treatments		
	Removal <sup>1</sup>	Control <sup>2</sup>	Microwave <sup>3</sup>
Reuse rate	Lowest	Higher	Highest
Productivity			
Clutch initiation	Later	Earlier	Earlier
Clutch size	Lowest	Higher	Highest
Number of young fledged	Lowest	Higher	Highest
Body condition of fledglings	Lowest	Higher	Highest
Ectoparasite load	Lower	Higher	Lower

<sup>1</sup> All material and ectoparasites removed from nest burrow.

<sup>2</sup> No material or ectoparasites removed from nest burrow.

<sup>3</sup> Ectoparasites, but not material, removed from nest burrow.

Table 1.2. Estimated mean length of incubation (in days) for burrowing owls breeding in southwestern Idaho 1999–2005.

Year	<i>n</i>	Mean Incubation	SE	Range
1999	6	20.8	0.601	19 - 22
2000	8	23.1	1.076	18 - 27
2001	7	20.9	0.595	18 - 23
2002	23	24.5	0.683	19 - 29
2003	7	22.7	0.778	20 - 26
2004	12	23.2	0.588	20 - 26
2005	18	22.1	0.347	19 - 25
1999–2005 Total	81	22.9	0.295	18 - 29

Table 1.3. Number of artificial burrows reused by productivity status at that burrow in the previous breeding season for burrowing owls in southwestern Idaho 2004-2005. Associated *P* value is for one-sided Fisher's exact test.

Status	<i>n</i>	Reused (%)	Not reused (%)	<i>P</i>
Successful	49	20 (41)	29 (59)	
Failed	23	3 (13)	20 (87)	
Total	72	23 (32)	49 (68)	0.016

Table 1.4. Number of artificial burrows (ABSs) occupied by treatment, separated by ABS age, for burrowing owls in southwestern Idaho 2004-2005. Associated *P* values are for one-sided Fisher's exact tests.

ABS age	Treatment	<i>n</i>	Occupied (%)	Not occupied (%)	<i>P</i>
Old	Adorned	96	15 (15.6)	81 (84.4)	0.196
	Unadorned	98	10 (10.2)	88 (89.8)	
	Total	194	25 (12.9)	169 (87.1)	
New	Adorned	19	2 (10.5)	17 (89.5)	0.784
	Unadorned	15	2 (13.3)	13 (86.7)	
	Total	34	4 (11.8)	30 (88.2)	
All	Adorned	115	17 (14.8)	98 (85.2)	0.244
	Unadorned	113	12 (10.6)	101 (89.4)	
	Total	228	29 (12.7)	199 (87.3)	

Table 1.5. Number of artificial burrows reused by treatment for burrowing owls in southwestern Idaho 2004-2005. Test statistic is Pearson  $\chi^2$ .

Treatment	<i>n</i>	Reused (%)	Not reused (%)	$\chi^2$	<i>P</i>
Control	21	9 (42.9)	12 (57.1)		
Microwave	20	9 (45.0)	11 (55.0)		
Removal	34	6 (17.6)	28 (82.4)		
Total	75	24 (32.0)	51 (68.0)	5.910	0.052

Table 1.6. Number of artificial burrows reused by treatment, separated by productivity status in the previous year, for burrowing owls in southwestern Idaho 2004-2005. Test statistic is Pearson  $\chi^2$ .

Status Previous Year	Treatment	<i>n</i>	Reused (%)	Not reused (%)	$\chi^2$	<i>P</i>
Successful	Control	16	9 (56.3)	7 (43.7)	5.139	0.077
	Microwave	14	7 (50.0)	7 (50.0)		
	Removal	19	4 (21.1)	15 (78.9)		
	Total	49	20 (40.8)	29 (59.2)		
Failed	Control	5	0 (0)	5 (100)	0.016 <sup>a</sup>	>0.990
	Microwave	5	1 (20.0)	4 (80.0)		
	Removal	13	2 (15.4)	11 (84.6)		
	Total	23	3 (13.0)	20 (87.0)		

<sup>a</sup> With Yates' correction for continuity.

Table 1.7. Flea loads by treatment for burrowing owls nesting in artificial burrows in southwestern Idaho 2004-2005. Test statistic is Pearson  $\chi^2$  with Yates' correction for continuity.

Treatment	<i>n</i>	Flea Load								$\chi^2$	<i>P</i>
		None (%)		Low (%)		Medium (%)		High (%)			
Control	7	1	(14.3)	4	(57.1)	1	(14.3)	1	(14.3)		
Microwave	8	1	(12.5)	4	(50.0)	2	(25.0)	1	(12.5)		
Removal	5	0	(0.0)	3	(60.0)	2	(40.0)	0	(0.0)		
Total	20	2	(10.0)	11	(55.0)	5	(25.0)	2	(10.0)	3.145	0.790

Table 1.8. Results of GEE modeling burrowing owl nestling body condition index ( $n = 75$ ) as a function of treatment at reused artificial burrows ( $n = 14$ ) in southwestern Idaho 2004-2005.

Parameter	DF	Estimate	SE	95% CI <sup>1</sup>		Z	P
				Lower	Upper		
Intercept	1	-1.882	5.595	-12.848	9.084		
Treatment: Control	0	0.000	0.000	0.000	0.000		
Treatment: Microwave	1	0.956	7.927	-14.580	16.4915	0.12	0.904
Treatment: Removal	1	-2.481	7.324	-16.836	11.874	-0.34	0.735

<sup>1</sup> 95% confidence interval for the parameter estimate.



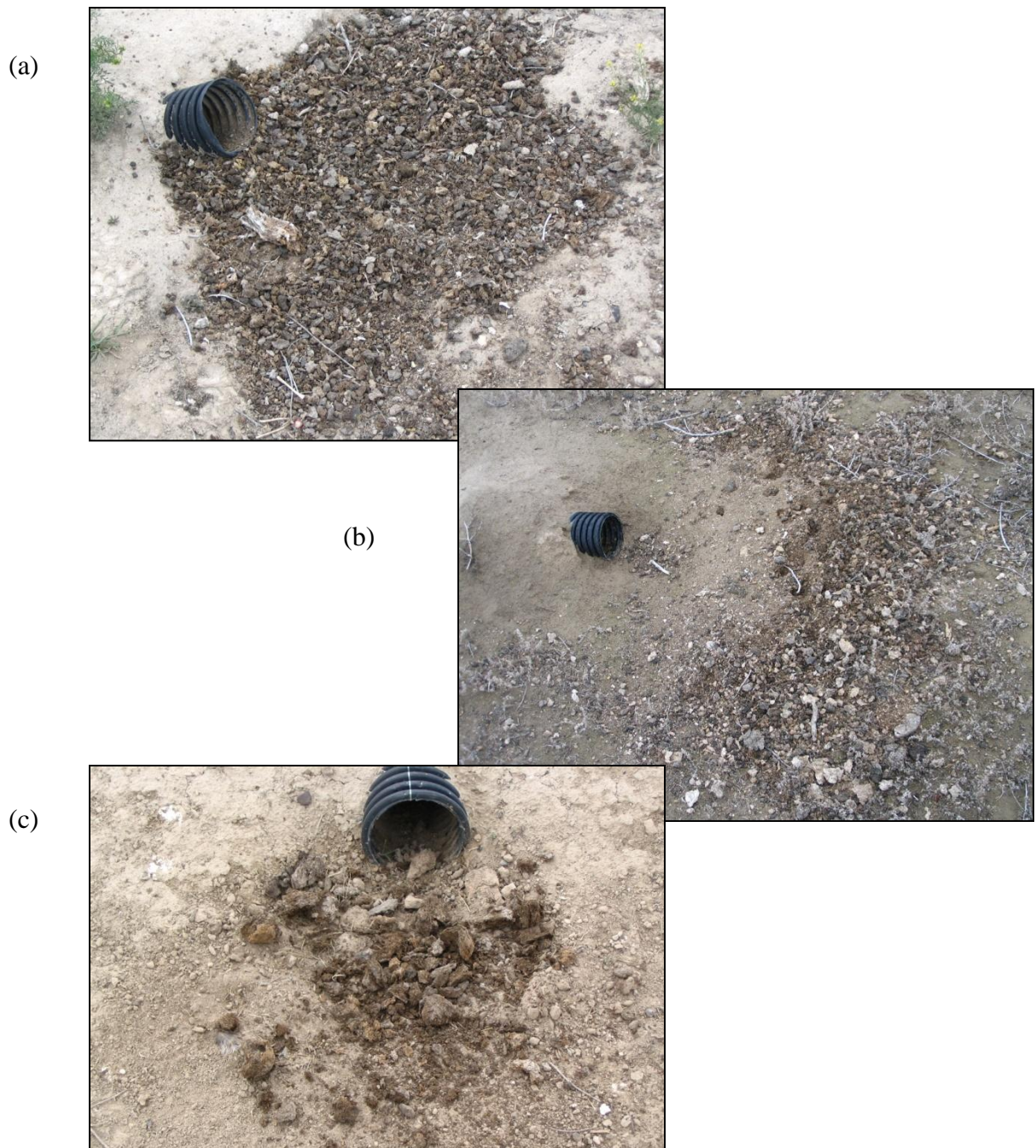


Figure 1.1. Nest material around entrances to artificial burrows in southwestern Idaho. (a) Material spread by burrowing owls at a current nest about four weeks into the breeding season. Note the shredded cow dung (darker color than surrounding soil) scattered in a fan-shaped pattern around the entrance. (b) Material spread by owls at a nest from the previous breeding season, about four weeks before owls return from migration. As often happens, owl activity at the end of the previous breeding season caused most of the material to become spread in an arc about 15 – 25 cm from the entrance. (c) Material spread by researcher to mimic previous owl use. Photos (a) and (b) depict large amounts of material, while (c) depicts a moderate amount of material.

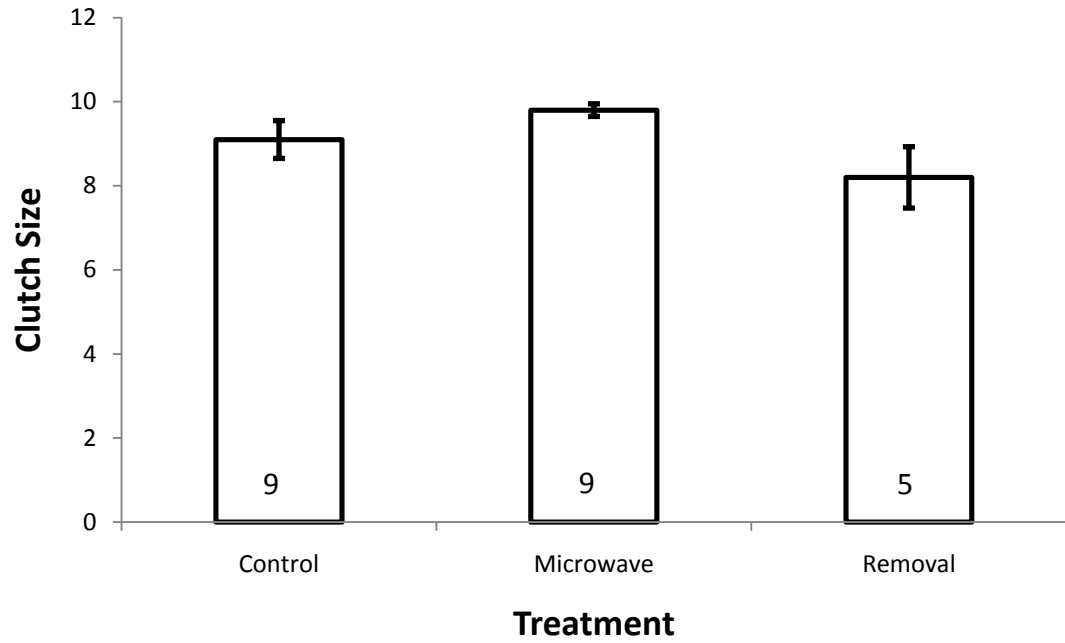


Figure 1.2. Mean ( $\pm$  SE) number of eggs per clutch by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Numbers within columns are sample sizes.

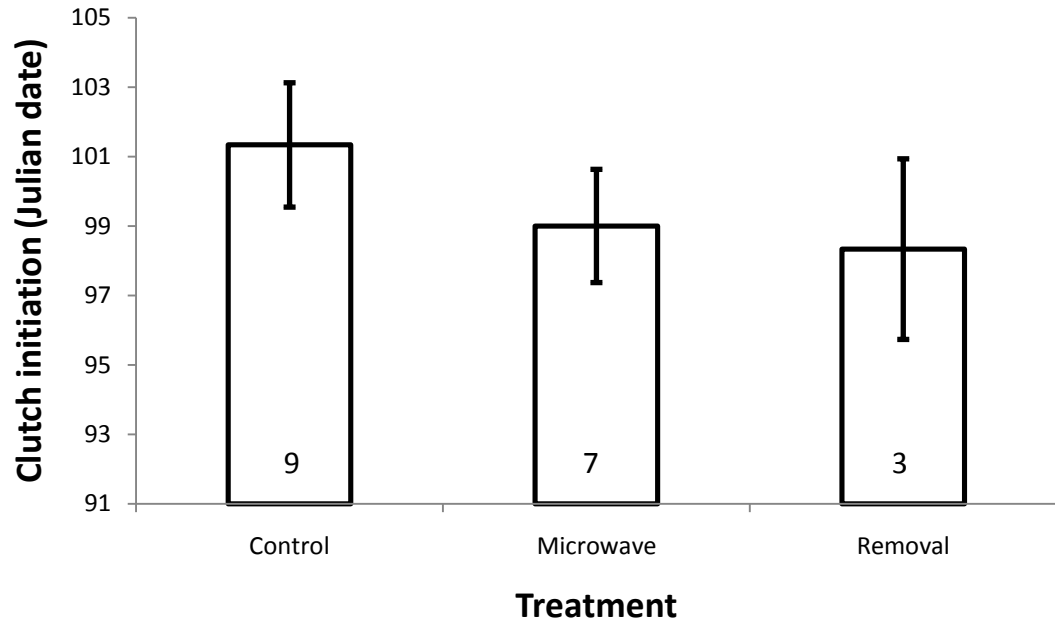


Figure 1.3. Mean ( $\pm$  SE) estimated Julian date of first egg by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Julian date 91 is April 2<sup>nd</sup> in 2004 and April 1<sup>st</sup> in 2005. Numbers within columns are sample sizes.

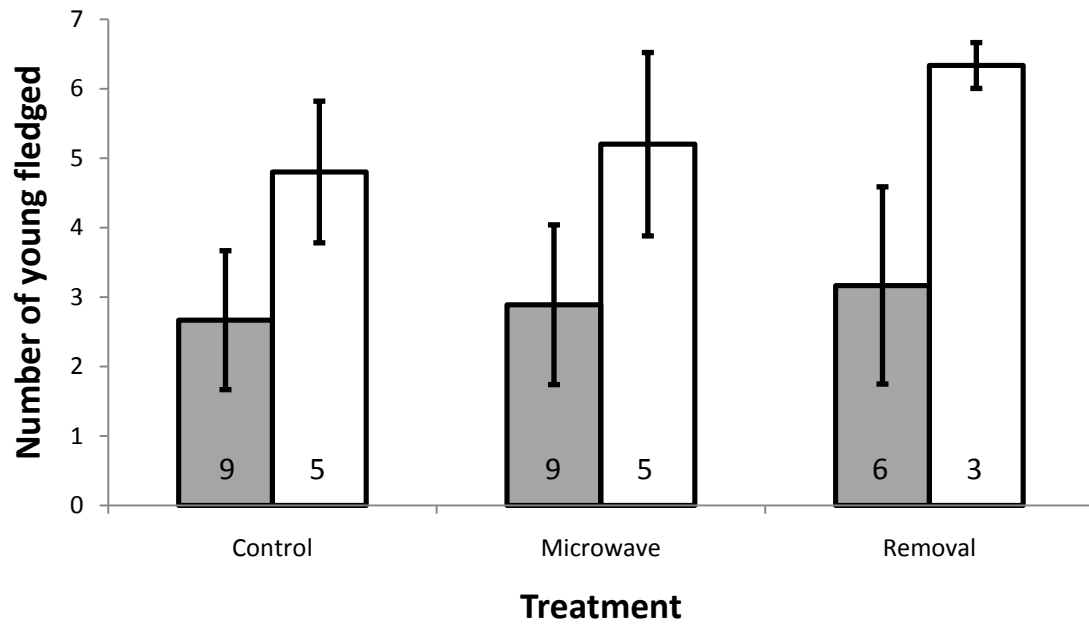


Figure 1.4. Mean ( $\pm$  SE) number of young fledged by treatment group for burrowing owls reusing artificial burrows in southwestern Idaho 2004-2005. Gray columns include all pairs; white columns include only pairs that fledged young. Numbers within columns are sample sizes.

CHAPTER TWO: BREEDING DISPERSAL BY BURROWING OWLS IN  
SOUTHWESTERN IDAHO

**Abstract**

Breeding dispersal, the movement between breeding sites, is important to many aspects of life history, but it is poorly understood for most populations. I used data from a long-term study of burrowing owls (*Athene cunicularia*) nesting in southwestern Idaho to examine breeding dispersal behavior. First, I measured percent frequency and distance of breeding dispersal, and I compared those to published results from other burrowing owl populations. Second, I assessed the effects of sex, productivity, age, mate quality, site quality, and level of ectoparasitism on breeding dispersal likelihood and distance. The percentage of owls dispersing (78%; 67 of 86) was greater than previously reported for any owl species. The mean distance dispersed ( $834.6 \text{ m} \pm 98$ ) was slightly greater than reported distances for most other burrowing owl populations. With the exception of mate quality and two site quality metrics (burrow productivity and proportional occupation), all factors had support for an important relationship with dispersal likelihood. Owls were more likely to disperse if they failed to fledge young, were female, were young, nested farther from agriculture, had closer nesting neighbors, and had lower levels of ectoparasitism. Ectoparasitism and distance to nearest neighbor had inverse rather than the expected direct relationships. Age and one index of site quality were the only predictors with strong relationships to dispersal distance: young owls and

owls nesting farther from other owls dispersed longer distances. Sex was somewhat important to distance dispersed, with females moving farther. The factors that most influence breeding dispersal behavior in burrowing owls appear to vary among populations.

### **Introduction**

The mobility of birds allows them to vacate their natal areas and to relocate between breeding events. These movements are generally called dispersal, and they can affect important aspects of natural history, such as individual fitness (Forero et al. 1999, Steiner and Gaston 2005), genetic structure (Nelson 1993, Ibrahim et al. 1996), population dynamics (Freemark et al. 1995, Drake 2006), geographic distribution (Sutherland et al. 2000, Clobert et al. 2001), and social behavior (Greenwood and Harvey 1982, Sterck 1998). Despite this importance, dispersal is not well understood for many species and situations, partially because of the challenges associated with its study. Often, studies of dispersal are logistically and financially difficult to perform (Nathan 2001). Another complication, especially in migratory and highly mobile species, is separating dispersal from mortality when an individual is not encountered again (Haas 1998, Marshall et al. 2004). Lastly, biases or trends in dispersal may not be constant across time or among populations within a species (Clarke et al. 1997), so that knowledge of dispersal trends within one population may be difficult to apply to a separate population.

Howard (1960) initially characterized dispersal as movement from birth site to first breeding site. Greenwood (1980) called such movement natal dispersal to separate it from breeding dispersal, which he defined as movement between successive breeding

sites. Breeding dispersal offers an individual the opportunity to avoid inbreeding (Johnson and Gaines 1990) or to improve fitness by moving to a better breeding site (Blakesley et al. 2006) or by breeding with a better mate (Daniels and Walters 2000). However, individuals that move are not guaranteed to acquire better territories or mates (see references in Forero et al. 1999), and they could fail to breed entirely (Danchin and Cam 2002). In some cases individuals may experience decreased reproductive success after dispersing (e.g., Dow and Fredga 1983, Vergara et al. 2006), possibly because of emigration from the area for which an individual is locally adapted (i.e., movement into non-favorable habitat). In addition, dispersing may increase exposure to predators (Ims and Andreassen 2000, Yoder et al. 2004) and mortality (Daniels and Walters 2000, Brown et al. 2008; but see Beaudette and Keppie 1992, van Vuren and Armitage 1994). Furthermore, philopatry, or fidelity to a breeding territory, bestows familiarity, which may increase reproductive success (Johnson and Walters 2008). Familiarity with a territory's resources (e.g., food, shelter, breeding sites) should make it more valuable than an unknown site (Pärt 1994, 1995, Forstmeier 2002, Brown et al. 2008). Fidelity also may confer dominance, where individuals that have held a territory previously are more successful in subsequently reacquiring and defending it (Lanyon and Thompson 1986, Shutler and Weatherhead 1992, Bruinzeel and van de Pol 2004). Familiarity with a mate also may increase reproductive success (Schieck and Hannon 1989, Bradley et al. 1990; but see Johnson and Walters 2008), and familiar pairings may be more likely when not dispersing. Given the potentially high costs of dispersal versus philopatry, an individual should be expected to disperse only when it is reasonably certain of experiencing suboptimal fitness if it breeds again at the same location. But deciding whether to

disperse and deciding how far to disperse should be considered separate processes because the selection pressures may differ (Forero et al. 1999, Doerr and Doerr 2005).

Although no single factor may cause breeding dispersal, previous research has identified many correlates, including sex (Greenwood 1980, Clarke et al. 1997), age (Greenwood and Harvey 1982, Kim et al. 2007), reproductive success (Haas 1998, Hoover 2003), habitat or site quality (Newton and Marquiss 1982, Blakesley et al. 2006), mate quality (Wiklund 1996, Green et al. 2004), and ectoparasitism (Brown and Brown 1986, Fitze et al. 2004). Distinguishing the importance of each factor to breeding dispersal is difficult because they often interrelate. For instance, successful reproduction may depend on acquiring a high quality breeding site, a high quality mate, or both (Goodburn 1991, Przybylo et al. 2001, Valcu and Kempenaers 2008). In an example of age and sex interacting, Payne and Payne (1993) found that male indigo buntings (*Passerina cyanea*) were more likely to disperse after their first breeding year than after subsequent years, whereas female buntings did not show significant age-related differences; females, however, were more likely to disperse than males at all ages. While the importance of each factor may change in space and time, causing dispersal patterns to differ within and among populations of the same species (Andreu and Barba 2006), published literature indicates that avian breeding dispersal trends generally correlate predictably with the above factors.

Among birds, females tend to disperse more often and farther than males (Newton and Marquiss 1982, Harvey et al. 1984, Shields 1984, Drilling and Thompson 1988, Gavin and Bollinger 1988, Korpimäki 1988, 1993, Payne and Payne 1993, Pärt 1995, Paton and Edwards 1996, Murphy 1996, Wiklund 1996, Collister and De Smet 1997,



Blondel et al. 2000, Howlett and Stutchbury 2003, Arsenault et al. 2005, Ward and Weatherhead 2005). Some research found a female bias for dispersal likelihood but not distance (Marti 1999, Linkhart and Reynolds 2007, Arlt and Pärt 2008a), or vice versa (Gratto et al. 1985, Millsap and Bear 1997, Andreu and Barba 2006). Greenwood (1980) speculated that sex-biased dispersal evolved as a consequence of mating system type. In a resource defense system, the sex that selects and defends a territory (male in most birds) is less likely to disperse because of benefits accrued via resource familiarity (Pärt 1995, Piper et al. 2008) and increased ability to retain a territory previously held (Lanyon and Thompson 1986, Shutler and Weatherhead 1992). Females, however, could use dispersal as a method for inspecting and choosing among males or their resources. While males may choose from any available territory, females may be limited to territories where males are present (Arlt and Pärt 2008b). Females may have no option aside from dispersal if their previous territory is not occupied by a male because of his death or dispersal. Avian species exhibiting no sex bias (Haig and Oring 1988, Montalvo and Potti 1992, Harris et al. 1996, Nager et al. 1996, Robinson and Oring 1997, Forero et al. 1999, Lutz and Plumpton 1999, Pyle et al. 2001, Sedgwick 2004, Blakesley et al. 2006, Middleton et al. 2006,) or, rarely, male-biased dispersal (Greenwood 1980, Beheler et al. 2003, Drake 2006), typically deviate from the resource defense mating system.

Dispersal likelihood and distance usually decrease with increasing age (Harvey et al. 1984, Pärt 1995, Millsap and Bear 1997, Forero et al. 1999, Daniels and Walters 2000, Winkler et al. 2004, Andreu and Barba 2006, Blakesley et al. 2006, Vergara et al. 2006, Kim et al. 2007), which may be related to competitive ability or familiarity with a location. Andreu and Barba (2006) found that the probability of dispersal in great tits

(*Parus major*) decreased more or less linearly with age, at least through the first six years of life. Kim et al. (2007) noted similar results for blue-footed boobies (*Sula nebouxii*) through the first 10-11 years of life, after which they suspected senescent decay in competitive ability caused increased dispersal. In some cases age appears to have no effect on breeding dispersal (Harris et al. 1996) or affects only one sex (females: Montalvo and Potti 1992, Pyle et al. 2001; males: Payne and Payne 1993, Arlt and Pärt 2008a).

Breeding dispersal usually varies inversely with reproductive success, so that birds experiencing breeding failure are more likely to disperse (Newton and Marquiss 1982, Shields 1984, Gratto et al. 1985, Gavin and Bollinger 1988, Gauthier 1990, Payne and Payne 1993, Nager et al. 1996, Paton and Edwards 1996, Gowaty and Plissner 1997, Marjakangas et al. 1997, Haas 1998, Doligez et al. 1999, Forero et al. 1999, Lutz and Plumpton 1999, Daniels and Walters 2000, Hoover 2003, Howlett and Stutchbury 2003, Porneluzi 2003, Sedgwick 2004, Winkler et al. 2004, Blakesley et al. 2006, Middleton et al. 2006, Naves et al. 2006, Vergara et al. 2006, Linkhart and Reynolds 2007, Pasinelli et al. 2007, Arlt and Pärt 2008a), disperse farther (Wiklund 1996, Robinson and Oring 1997, Drake 2006), or both (Dow and Fredga 1983, Drilling and Thompson 1988, Bollinger and Gavin 1989, Catlin et al. 2005). However, breeding dispersal does not always correlate with reproductive success (Haig and Oring 1988, Korpimäki 1993, Murphy 1996, Collister and De Smet 1997, Millsap and Bear 1997, Shutler and Clark 2003). Reusing a location when the previous breeding attempt produced young, but moving if the attempt failed has been termed the 'Win-Stay, Lose-Switch' (WSLS) strategy (Switzer 1993, Hoover 2003, Piper et al. 2008). The WSLS strategy is expected

to be most profitable if habitat and resources are patchy and temporally autocorrelated, such that an individual would experience the same conditions at a site from one year to the next (Switzer 1993). Thus, birds breeding in habitats that are ephemeral, unpredictable, or homogenous over large areas should disregard the WLS strategy, and they may not rely on reproductive success in decisions about dispersal.

Birds tend to exhibit a negative relationship between site (habitat) quality and dispersal (Newton and Marquiss 1982, Bollinger and Gavin 1989, Montalvo and Potti 1992, Korpimäki 1993, Doligez et al. 1999, Forero et al. 1999, Blondel et al. 2000, Byholm et al. 2003, Stanback and Rockwell 2003, Ward and Weatherhead 2005, Blakesley et al. 2006, Pasinelli et al. 2007, Arlt and Pärt 2008a), despite the variation in definition of site (e.g., previously held territory, patch, study area) and method of measuring quality (e.g., prey availability, patch reproductive success, relative territory occupancy). In fact, studies examining site quality and breeding dispersal rarely fail to find a correlation (but see Sedgwick 2004). Given the association of breeding dispersal to reproductive success, this trend seems predictable because birds breeding in lower quality sites may experience depressed productivity or reproductive failure (Przybylo et al. 2001, Sergio and Newton 2003, Sergio et al. 2009).

Breeding dispersal often shows a direct relationship to ectoparasitism and increases with higher levels of infestation (Brown and Brown 1986, Stanback and Dervan 2001, Stanback and Rockwell 2003, Fitze et al. 2004). Given that ectoparasites can negatively influence avian reproductive efforts (Brown and Brown 1986, Emlen 1986, Möller 1990, Chapman and George 1991, Hurtrez-Boussès et al. 1997, Möller 1997, Loye and Carroll 1998, Nilsson 2003, Fitze et al. 2004), dispersal may be a mechanism to avoid infestation

by ectoparasites, which can remain at a nest site from one breeding event to the next (Barclay 1988, Möller 1989, Mazgajski 2007). If acquisition of ectoparasites is related to reuse of nest sites, ectoparasitism is likely to be less important to species that return to the same territory but build a new nest for each breeding attempt.

Less effort has been applied to exploring the relationship between mate quality and breeding dispersal, but the available evidence supports a negative correlation (Korpimäki 1988, Wiklund 1996, Daniels and Walters 2000, Green et al. 2004). These results were only significant for females, although two studies did not include males in their analyses (Daniels and Walters 2000, Green et al. 2004). Only one study failed to discover a significant association between mate quality and dispersal for either sex (Forero et al. 1999). In many avian species the male selects a territory and then the female selects a male or his territory. Therefore, obtaining a good territory may be more important than obtaining a good mate for males, especially if having a poor territory means not breeding at all. Thus, it may only be females that consider mate quality when making decisions about dispersal.

### Objectives

For this observational study of breeding dispersal, I used data collected from 1994-2007 for western burrowing owls (*Athene cunicularia hypugaea*) nesting in southwestern Idaho. My objectives in studying breeding dispersal in this population of burrowing owls were twofold. First, I wanted to describe the percent frequency and distance of breeding dispersal and compare them to dispersal in other populations of burrowing owls from the literature. My second aim was to assess the relationship of breeding dispersal likelihood

and distance with sex, age, reproductive success, site quality, ectoparasitism, and mate quality (for females only). Based on the tendencies noted in the literature cited above, I made predictions for each of these factors (Table 2.1). I predicted that dispersal likelihood and dispersal distance would be greater for females than males, greater for young owls than old owls, greater for owls that failed to fledge young, greater for those using low quality burrows, and greater for owls experiencing higher ectoparasite loads. I also predicted that females would disperse more often and farther after breeding with low quality males than they would after breeding with high quality males.

As noted, breeding dispersal has high potential costs (e.g., loss of breeding opportunity), so owls should be expected to favor philopatry. As philopatry may enhance reproductive efforts, I predicted that owls not dispersing between breeding attempts would increase productivity over their previous attempt and fledge more young in the next attempt than dispersing owls. However, the costs of dispersal (and the benefits of philopatry) are not always realized, and they may be offset if dispersing increases fitness (e.g., moving to an area with greater food resources). Therefore, I also predicted that dispersing individuals would fledge more young post-dispersal than they fledged pre-dispersal.

## **Methods**

### Study Site

I used data from burrowing owls nesting in and near the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) in southwestern Idaho in 1994-2007. The NCA was established in 1993 by Congress (Public Law 103-64) for the conservation,

protection, and enhancement of raptor populations and habitats (Sharpe and Van Horne 1998), and it now covers over 2400 km<sup>2</sup> (about 1960 km<sup>2</sup> of public land) in Ada, Elmore, and Owyhee Counties. The area was originally shrub-steppe habitat dominated by big sagebrush (*Artemisia tridentata*), but fire and human disturbance have converted large portions to grassland dominated by exotic annual grasses and forbs like *Bromus tectorum* and *Sisymbrium altissimum* (Hironaka et al. 1983, U.S.D.I. 1996). The area also contains agricultural fields, dairy farms, many roads and rights-of-way, BLM-managed rangelands, and structures such as homes and silos (King 1996).

The Snake River is the major geologic feature, and it flows through a steep, narrow canyon in the southern and western portions of the NCA. The topography of the surrounding river plain is flat to rolling with rocky outcrops and scattered buttes. Average daily temperatures are lowest in January (-2.1°C), highest in July (23.1°C), and increase from 5.5°C to 23.1°C during the breeding season, March to July (N.O.A.A. 2002). Temperature extremes range from -29°C in winter to 45°C in summer (N.O.A.A. 1985). Precipitation averages 31.7 cm annually, with 12.1 cm falling during the breeding season (N.O.A.A. 2002).

### Study Species

Western burrowing owls occur throughout open, well-drained grasslands, steppes, deserts, prairies, and agricultural lands of western North America (Haug et al. 1993). They breed from southern Canada to central Mexico and from Pacific coast states to Manitoba and Texas. Northern populations tend to be migratory, while those in the southern U.S. and Mexico may be year-round residents (Haug et al. 1993). In

southwestern Idaho, burrowing owls are typically present from March to September or October, but small numbers of individuals remain on the breeding grounds throughout the winter (this also occurs in other areas; Martin 1973, Butts 1976, Conway et al. 2006). The migration routes and wintering areas for owls from this population are poorly known, although a small number of band returns indicates that at least some of the owls winter in southern California (King 1996, King and Belthoff 2001). Although the longevity record for a burrowing owl in the wild is over eight years (Haug et al. 1993), only five individuals from the study population were known to breed after their fourth calendar year during 1994-2007 (J. Belthoff unpubl. data).

Western burrowing owls are obligate burrow nesters, and they primarily nest in abandoned mammal burrows (Haug et al. 1993). Natural burrows are available throughout this study site for nesting and shelter, and badgers (*Taxidea taxus*) are the primary excavators of most burrows suitable for burrowing owl nests (King 1996, Belthoff and King 1997). There are also many artificial burrow systems (ABSs), which the owls readily and frequently use (Smith and Belthoff 2001a, Belthoff and Smith 2003). The ABSs vary in composition, but usually consist of 2 or 3 buried plastic chambers with tunnels of flexible plastic pipe that open to the surface (see descriptions in Chapter 1; Smith and Belthoff 2001a). ABSs are more conducive to research than natural burrows because they provide easy access to the nest chamber.

With population reductions and range restrictions, especially at the edges of their distribution, burrowing owls are considered endangered in Canada, threatened in Mexico, and a species of conservation concern in nine western U.S. states (Klute et al. 2003). Understanding crucial elements of their natural history, such as breeding dispersal, may

help to accurately estimate population dynamics and gene flow for areas where the owls are declining and understand population dynamics where they are more stable.

### Data Collection and Definitions

Throughout the years of this study (1994-2007), data collection methods differed and the study site increased in size. In 1994-1996, most monitored burrowing owl pairs nested in natural burrows in the northwestern portion of the NCA near Kuna, Ada Co. In 1997-2000, many monitored pairs nested in ABSs in the northwest and south-central (near Grand View, Elmore Co.) portions of the NCA. In 2001-2007, nearly all monitored pairs nested in ABSs, the number of which increased dramatically as they were installed over a broader portion of the NCA. In all years, non-standardized foot and vehicle surveys for burrowing owls nesting in natural and artificial burrows began in mid-March to early April. In earlier years (1994-1996), the small study area was more intensively surveyed to discover nests among natural burrows. From 1997-2007, detection efforts focused primarily on artificial burrows and historical nest sites in natural burrows. These efforts were augmented by serendipitous discovery of pairs nesting in natural burrows near survey areas. Where ABSs were present within the study site, burrowing owls rarely used natural burrows for nesting (pers. obs.), so most nesting attempts were probably detected.

Once located, all nesting pairs were monitored for productivity, and attempts were made to capture adults and young for marking, measurements, and tissue sampling. Capture methods varied (King 1996, Smith 1999, Taylor 2005, Welty 2010), but adults were primarily captured in one-way traps at nest burrows, and juveniles were usually



captured by hand while excavating the ABS. Adult males spend little time inside nest burrows and therefore were captured less frequently than adult females which spend most of their time within the burrow during incubation and brooding. This gave a female bias to the sample, and it hindered my ability to statistically assess mate change (via death or divorce) or mate quality. Captured owls were fitted with a combination of colored, plastic leg bands and a USGS aluminum band (size 4). Previously marked owls were identified by recapturing them or by sighting their leg bands with binoculars or a spotting scope.

I considered an individual to have attempted breeding if it attended a burrow (natural or artificial) where at least one egg was laid. I classified owls using the same ABS (or natural burrow) in consecutive breeding attempts as philopatric. I defined breeding dispersal as an individual nesting in a different ABS (or natural burrow) in its subsequent breeding attempt. I measured dispersal distance as the straight-line distance between burrows of pre- and post-dispersal nesting attempts. Although multiple nesting attempts by an individual in one year occurred, most observations were between-year events where an owl had known breeding locations in year<sub>t</sub> and year<sub>t+1</sub>. Thus, I did not perform statistical analyses of within-year dispersals. With their relatively short lifespans, I assumed that burrowing owls were unlikely to skip breeding, so statistical analyses only included observations where I knew nesting locations in consecutive years. To describe the quantity of dispersing owls, I used the percent frequency

$$100 \times n_i / (n_i + n_j)$$

where  $n_i$  is the frequency of dispersing owls and  $n_j$  is the frequency of philopatric owls. For the sake of brevity, I used the term frequency rather than percent frequency in the main text.

For pairs nesting in natural burrows, I recorded the number of young fledged as the maximum number of young observed at the nest at one time or captured at the burrow. In ABSs, where nestling numbers could be counted with a great degree of certainty, I considered any young alive at about four weeks post-hatching as fledged. I defined productivity as the number of young fledged in a single breeding attempt. I considered a pair to be successful if they fledged at least one young. As there are no accepted methods for distinguishing among adult age classes in burrowing owls, I used minimum possible calendar years for assigning age class. For example, an individual first captured as a breeding adult would be in at least its second calendar year, so I aged it as '2', even though it potentially could be older. I used mate age as a proxy for mate quality (see Daniels and Walters 2000, Brooks and Kemp 2001, Green et al. 2004). When used in statistical analyses, I coded sex as male = 0 and female = 1.

Measures of habitat or burrow quality did not exist for all nest burrows in all years, so I used four indices to estimate the site quality of each burrow. Johnson (2007) endorsed such an approach and stated that it is important to use several metrics when indirectly measuring habitat quality. First, I used proportional occupation, which was the number of years a burrow was occupied divided by the number of years it was available during a seven year span (year<sub>t-3</sub> to year<sub>t+3</sub>). Second, I used burrow productivity, which was the total number of young fledged at a burrow divided by the number of years it was available during year<sub>t-3</sub> to year<sub>t+3</sub>. I used a seven year window for both indices because

sites were generally the same from one year to the next but sometimes exhibited substantial changes over longer periods. Thus, owls nesting at the same burrow in consecutive years would likely experience similar conditions, but owls nesting at the same burrow ten years apart may face very different habitat, prey availability, human activity level, and so forth. So, for example, occupancy or productivity at a burrow in year<sub>t-10</sub> probably does little to explain the quality of that burrow in year<sub>t</sub>. I expect that better sites should be occupied more often (Linkhart and Reynolds 1997, Sergio and Newton 2003) and more young should be produced at better sites, so higher values indicate higher quality for both indices. Third, I used the distance from the nest burrow to the nearest irrigated agriculture. Finally, I used the distance from the nest burrow to the closest neighboring burrowing owl nest. Some evidence suggests that burrowing owls derive benefits from nesting close to irrigated agriculture (Moulton et al. 2005, Conway et al. 2006, Restani et al. 2008) and to other burrowing owls (Welty 2010), indicating that burrows with shorter distances to agriculture and neighbors may be of higher quality.

I used an index of ectoparasites rather than gross numbers because the various methods of counting ectoparasites throughout the study were all indexed (e.g., Smith 1999, Brady 2004, Chapter 1 of this thesis). Although many ectoparasites associate with burrowing owls (Smith and Belthoff 2001b), I only include data for fleas (Order: Siphonaptera), primarily *Pulex irritans* (Family: Pulicidae), because they were the only ectoparasites regularly recorded. The index comprised four levels: 0 = None, 1 = Low, 2 = Medium, and 3 = High. The 2006-2007 data included a fifth level (4 = Very High), which I incorporated into the 'High' level. Ectoparasite data were not recorded 1994-

1996 and were often lacking in other years because a nesting attempt failed before researchers could capture young and record their flea levels. I used the mean (or median for nests in 2005) ectoparasite load of all young at time of banding (~15 days post-hatch) to determine nest ectoparasitism. When those data were unavailable, I used mean (or median for 2005) ectoparasite load of young at time of fledging (~28 days post-hatch). Although the level of ectoparasites may fluctuate slightly during a nesting cycle, flea loads were positively correlated for nests where both were known at banding and fledging (Spearman rank correlation:  $r_s = 0.75$ ,  $P < 0.0001$ ,  $n = 111$ ).

### Statistical Analyses

I used individual owls as the basic unit for analyses, which introduced non-independence because there were multiple observations for some individuals. To determine if observations from the same individual could be considered independent, I analyzed the repeatability of breeding dispersal distance per Lessells and Boag (1987), where philopatric individuals had a dispersal distance of 0 m. Repeatability was moderately high (Table 2.2; see guidelines in Harper 1994), so I analyzed data with Generalized Estimating Equations (GEE; Liang and Zeger 1986, Burnham and Anderson 1998), which can account for repeated measures. I used SAS 9.2 (SAS Institute Inc., Cary, NC) for analyses, and I report means  $\pm$  SE throughout unless noted.

To assess predictions concerning the number of young fledged (productivity), I used GEE with poisson distribution and a log link function (PROC GENMOD in SAS). This model included status (dispersed or philopatric), year ( $t$  or  $t+1$ ), and the interaction term status  $\times$  year, and individual was a repeated factor. I made pairwise comparisons of

relevant means with the LSMEANS statement, and I considered the difference between means important if the 95% confidence interval (CI) for the estimated difference did not contain zero.

I used GEE with binomial distribution and logit link function to examine the influence of predictor variables on breeding dispersal likelihood. The factors that I considered were sex, age, distance to nearest neighbor, distance to agriculture, and ectoparasitism. I modeled mate quality separately because it had a small sample size and because I applied it only to females. Also, I used univariate models for proportional occupation and burrow productivity because of multicollinearity with other factors.

I used GEE with normal distribution and identify link function to assess the relationship of sex, productivity, distance to nearest neighbor, and distance to agriculture with distance moved by dispersing owls. I modeled mate quality and ectoparasitism univariately because they had reduced sample sizes. Three more factors (age, proportional occupation, and burrow productivity) had to be modeled separately because of multicollinearity with predictors in the multivariate modeling.

For GEE analyses that included only one factor (mate quality, proportional occupation, and burrow productivity for likelihood; age, mate quality, ectoparasitism, proportional occupation, and burrow productivity for distance), I considered the predictor variable important if the 95% CI for the parameter estimate did not include zero. When selecting models in multivariate analyses with GEE, I compared quasi-likelihood information criterion (QIC) values among possible models. To determine a subset of important models (confidence set), I looked for gaps in QIC values.

## Results

### Dispersal Patterns

The number of adult and nestling burrowing owls banded during 1994-2007 was 2842 (Table 2.3). Banded owls returned to breed within the study site at least 172 times (Table 2.4), with 106 individuals known to breed in more than one year (Table 2.5). Among the 86 owls with known nesting locations in consecutive years, 22 had multiple cases resulting in 113 total observations of breeding in consecutive years within the study area (Table 2.5). For individuals with multiple cases, within-individual repeatability was moderately high ( $r = 0.648$ ; Table 2.2). Fifteen of 22 (68.2%) individuals with multiple observations were always philopatric or always dispersed (Table 2.6).

Burrowing owls in southwestern Idaho displayed high dispersal frequency (76.1%; 86 of 113), and dispersing owls moved  $882.6 \text{ m} \pm 92$  (range: 55 – 3454 m;  $n = 86$ ). Multiple observations from an individual may not be independent, as indicated by the repeatability analysis. So, I also calculated breeding dispersal frequency (77.9%; 67 of 86) and distance ( $834.6 \text{ m} \pm 98$ ; range: 55 – 3396 m;  $n = 67$ ) using only one randomly selected observation per individual for comparison. The number of young fledged did not differ in any of the three comparisons for which I had predictions (Table 2.7, Figure 2.1).

### Within-year Dispersal

Within-year breeding dispersal (an owl nesting in two separate locations in one breeding season) was recorded eight times (2 males, 6 females) during the study (Table 2.8), and the mean distance was  $118.8 \text{ m} \pm 30.2$  (range: 50 – 312 m). There were probably a small number of other within-year dispersals each year, but they were only

documented in 1998, 2005, and 2007. Within-year philopatry (an owl making multiple nesting attempts in the same burrow in one breeding season) also probably occurred but was not effectively recorded. All recorded within-year dispersals occurred after an unsuccessful nesting attempt. There were no records of a second nest attempt (at the same burrow or elsewhere) by any owls that successfully reared a brood, indicating that owls in this population are single-brooded.

### Mate Fidelity

Of 30 owls (21 males, 9 females) with identified mates in consecutive years, only two individuals (6.7%) exhibited mate fidelity; this occurred when a known pair bred together in 2002 and again in 2003. Given the near lack of variation in mate fidelity (all but one pair bred with different individuals in year<sub>t+1</sub>), I did not include mate fidelity as a predictor variable in models of dispersal likelihood or distance.

### Dispersal Likelihood

All owls that failed to produce young in year<sub>t</sub> dispersed (Figure 2.2), which caused quasi-complete separation of data for productivity status (success or failure in year<sub>t</sub>). Therefore, I could not include productivity status as a predictor variable in any modeling of dispersal likelihood. Consequently, I only included successfully breeding owls in the analyses of dispersal likelihood. For female burrowing owls that bred successfully in year<sub>t</sub>, mate quality was not an important factor for breeding dispersal likelihood (Table 2.9). Likewise, neither burrow productivity nor proportional occupation predicted dispersal likelihood for successful breeders (Table 2.9).

For the owls that successfully fledged young in year<sub>t</sub>, only 4 of 32 multivariate candidate models examining relationships with dispersal likelihood were included in the confidence set (Table 2.10). All four of these models included the factors sex, distance to agriculture, and ectoparasitism. Age and distance to nearest neighbor appeared in two models each. Thus, all possible parameters emerged in multiple confidence set models. The global model (Table 2.11) was included in the confidence set as well, but the 95% CI for estimates of two parameters (age and distance to nearest neighbor) contained zero. Removing those factors gave the model with the lowest QIC (Table 2.12), which I then used to make inferences. This model indicated that owls were more likely to undergo breeding dispersal if they were female, nested farther from agriculture, and had lower levels of ectoparasitism. Conversely, owls were less likely to disperse if they were male, nested closer to agriculture, and had more ectoparasites (Figures 2.2 – 2.5).

### Dispersal Distance Modeling

Among the predictors I assessed for breeding dispersal distance with univariate models, only age had a 95% CI not containing zero (Table 2.13). That model indicated that older owls had shorter breeding dispersal distances (Figure 2.6). Two of 16 possible multivariate models were competitive for dispersal distance (Table 2.14). Distance to nearest neighbor occurred in both models, and sex occurred in one. In the model with both of these factors (Table 2.15), the 95% CI for the parameter estimate of sex included zero, and removing that term gave the model with the lowest QIC (Table 2.16). However, when distance to nearest neighbor was the only parameter in the model, its 95% CI contained zero, so I used the two-parameter model for inferences. Thus,



breeding dispersal distance was shorter for males and owls with nearer neighbors (Figures 2.7 – 2.8).

## **Discussion**

I had two primary objectives in this study of breeding dispersal by burrowing owls in southwestern Idaho. My first objective was to determine breeding dispersal frequency and mean breeding dispersal distance and to compare them to other burrowing owl populations for possible variation in dispersal behavior. My second objective was to ascertain the effects of several possible predictor variables (sex, age, productivity, mate quality, site quality, and ectoparasitism) on the likelihood of dispersal and the distance dispersing owls moved.

### Productivity Comparisons

I predicted that 1) philopatric owls would fledge more young in year<sub>t+1</sub> than year<sub>t</sub>, 2) dispersing owls would fledge more young in year<sub>t+1</sub> than they did in year<sub>t</sub>, and 3) philopatric owls would fledge more young than dispersing owls in year<sub>t+1</sub>. None of those predictions for productivity comparisons were supported. Combined with the high frequency of dispersal, this indicates that philopatry does not confer realized fitness benefits over dispersal in this population of burrowing owls. In fact, it appears that owls may be more likely to improve fitness by dispersing (perhaps to higher quality sites) than by returning to former nest sites.

### Dispersal Frequency

The frequency of breeding dispersal that I found here was much higher than previously reported for burrowing owls in southern locations, but only slightly higher than northern populations (Table 2.17). The combined frequency of both sexes appears to be the highest for any owl species in the literature (Table 2.17), but some of the other reported frequencies may represent minimum values. Based on the supposition that philopatry confers greater fitness benefits than dispersal, I presumed that the frequency of owls dispersing in this population would be similar to that found for burrowing owls in other locations. Furthermore, in mark-recapture studies such as this, individuals dispersing beyond study area boundaries will go undetected, which will reduce estimated dispersal frequency (Barrowclough 1978, Koenig et al. 1996). Thus, the high breeding dispersal frequency that I found here is somewhat surprising.

Several factors may have contributed to the high dispersal frequency. The first possible influence is that my sample was female biased. Females had a higher dispersal frequency than males (87% and 52%, respectively), and the disproportionate number of females would have increased the measured frequency for the population as a whole. However, the frequency of dispersal for females was lower in other studies than in this population, so even with a comparably female-biased sample those studies would still have lower dispersal frequencies.

Differing methodologies may also play a roll. For example, Catlin et al. (2005) appear to focus on the movement away from a territory, so they defined dispersal as movement >100 m from the previous nest burrow. In the current study, I focused on movement away from a nest site, so I defined dispersal as nesting in a different natural

burrow or ABS. Five of 67 dispersing owls in my study moved <100 m from their previous burrow. Applying Catlin et al.'s (2005) definition would decrease dispersal frequency in my study to 72%. This is a relatively small decrease, and the reduced frequency still exceeds other reported breeding dispersal frequencies for owls.

Another possible influence on the high dispersal frequency was a greater than expected fitness cost for philopatry. Burrowing owls are somewhat short-lived (the longevity record for a free-living individual is 8 yr 8 mo; Haug et al. 1993), and in southwestern Idaho only seven individuals were known to breed within the study area in more than three years during the study period (J. Belthoff unpubl. data). Published estimates of adult survivorship show that typical survival is moderate (37-68%; Haug et al. 1993), so it is likely that at least one-third of territory holders will not return for the next breeding season. Because they do not live long, burrowing owls should favor moving to better sites when they become vacant, rather than remaining in a territory. This may be why dispersal likelihood was higher for owls with closer neighbors (Table 2.11). They possibly were able to assess other nest burrows and obtain information on reproductive success of their neighbors. Then they could attempt to acquire any superior territory that was not occupied in the following year. Also, I found that burrowing owls dispersed more frequently from burrows that were farther from agriculture. This is consistent with the notion that owls are dispersing away from burrows of lower quality, perhaps to increase their fitness by breeding at higher quality burrows.

Migratory birds tend to disperse longer distances than residents (Paradis et al. 1998, Belliure et al. 2000; but see Middleton et al. 2006), and they may also disperse with greater frequency. The Florida and California burrowing owl populations (Millsap and

Bear 1997 and Catlin et al. 2005, respectively) were residential and did in fact have relatively low dispersal frequencies. The migratory populations (Haug et al. 1993, De Smet 1997, Lutz and Plumpton 1999, Conway et al. 2006) had generally higher dispersal frequencies (Table 2.17), but the Saskatchewan and Colorado populations did not differ much from the non-migratory populations. Thus, migratory habit seems to explain only some of the variation in burrowing owl breeding dispersal frequency.

Geographic location also may be important. The operational definition of breeding dispersal for the Saskatchewan population (Haug et al. 1993) is unclear, and if that population is removed there is a trend for dispersal rate to increase with latitude (Figure 2.9). One possible underlying cause for this trend may be a genetic predisposition towards dispersing (Hansson et al. 2003, Doligez and Pärt 2008, Doligez et al. 2009). Several studies have reported a resemblance in parent-offspring propensity to disperse (see references in Doligez and Pärt 2008), which may indicate a genetic component. The high repeatability that I found within individuals in this study also fits with this notion. Individuals that disperse are likely to move to, or even expand, the edges of their species' range. If dispersal tendency is heritable, then individuals that have dispersed to the edge of their distribution may pass on that trait. Subsequently, populations farther from the range core may exhibit greater dispersal frequency because of genetic proclivity. Among the five populations of western burrowing owls with published frequencies of breeding dispersal (Saskatchewan population excluded), the three populations with high frequencies are near the northern border of their distribution for their longitude. This may in part account for the low dispersal frequency seen in the migratory Colorado population (Lutz and Plumpton 1999), which is far from the northern extent of the range.

Hence, genetic predisposition is one possible factor that may help explain why dispersal frequency correlates with latitude.

### Dispersal Distance

The method of data collection used for assessing burrowing owl breeding dispersal in southwestern Idaho should have biased distance estimates by shortening them (Barrowclough 1978, Porter and Dooley 1993, Koenig et al. 1996, Thompson and Goodman 1997, Brommer and Fred 2007). However, the mean breeding dispersal distance of burrowing owls in this population was greater than distances for burrowing owls in most other locations (Table 2.17). Migratory birds tend to disperse farther than those in sedentary populations (Paradis et al. 1998, Belliure et al. 2000). The migratory burrowing owl populations did move farther when undergoing breeding dispersal, but owls in southwestern Idaho were closer in mean breeding dispersal distance to non-migratory populations than to the other migratory population (Table 2.17). Other than flammulated owls (*Otus flammeolus*), owl species for which breeding dispersal data are published had much longer mean dispersal distances (Table 2.17). Therefore, the mean distance recorded here was neither unexpected nor exceptional.

Bowman (2003) found that natal dispersal distances covaried with territory size in some birds. If habitat necessitates large territories or low nesting densities, then dispersal distances should be longer, as individuals would have to travel farther to move beyond occupied territories. Therefore, longer breeding dispersal distances by other owl species may simply be a function of these having larger territories than burrowing owls. It is possible that differences in mean dispersal distance among burrowing owl studies

(Millsap and Bear 1997, De Smet 1997, Catlin et al. 2005) indicate breeding densities vary among locations. In support of this, I found that distance to nearest neighbor, which should reflect nesting density, was important to dispersal distance for owls in my study population. Owls dispersed farther when their nearest neighbor was farther away (low density).

### Mate Fidelity

Mate fidelity may also influence breeding dispersal, so that birds that retain a mate are less likely to disperse or disperse shorter distances (Gratto et al. 1985, Schieck and Hannon 1989, Murphy 1996, Wiklund 1996, Pyle et al. 2001, Catlin et al. 2005, Andreu and Barba 2006, Blakesley et al. 2006, Middleton et al. 2006, Kim et al. 2007). This relationship is probably associated with familiar pairings having better reproductive success (Schieck and Hannon 1989, Bradley et al. 1990). It is possible that mate fidelity influences the breeding dispersal behavior of burrowing owls nesting in southwestern Idaho, but I lacked sufficient sample size to statistically assess mate fidelity as a correlate of breeding dispersal. Also, a mated pair may not act independently, which could confound the relationship of breeding dispersal of an individual with other correlates. However, I observed almost no mate fidelity in this population of burrowing owls, so very few of my observations might be affected by this potential lack of independence.

The high dispersal frequency and near lack of mate fidelity suggest that breeding with a familiar mate may not benefit burrowing owls in southwestern Idaho. I cannot say whether separation of pairs (through either mortality or failure to re-mate) led to dispersal, or whether dispersing owls failed to retain their mates. Regardless, I observed

very low site and mate fidelity in burrowing owls in southwestern Idaho. Catlin et al. (2005) reported relatively high site and mate fidelity among burrowing owls in California, and they noted that this positive correlation fit with an hypothesized relationship between the two (Cézilly et al. 2000). My results, although differing greatly from Catlin et al. (2005), also showed a direct correlation between site and mate fidelity.

### Dispersal Likelihood

Mate quality, as measured by age, did not appear to be important for predicting the likelihood of breeding dispersal in female burrowing owls. However, one caveat about this conclusion is that I had some imprecision with aging methods because I lacked a rigorous method to accurately age adults in the field. Therefore, I had to consider every owl first marked as an adult to be in its second calendar year. While many individuals may indeed have been in their second calendar year, it is quite possible that some were not initially marked until they were in their third or fourth calendar year. In addition, the low number of males captured in most years meant that there were relatively few females that bred with males of known age. This combination of imprecise aging and small sample size may have prevented me from finding a relationship between mate quality and dispersal likelihood.

In separate univariate analyses, the parameter estimates of proportional occupation and burrow productivity had 95% CIs that included zero, indicating that these measures of site quality had no influence on the likelihood of breeding dispersal by burrowing owls. This is somewhat surprising because evidence in the literature suggests strong relationships for avian breeding dispersal with occupancy (Newton and Marquiss 1982,

Montalvo and Potti 1992, Arlt and Pärt 2008a) and site productivity (Bollinger and Gavin 1989, Doligez et al. 1999, Forero et al. 1999, Blondel et al. 2000, Blakesley et al. 2006, Pasinelli et al. 2007). Sometimes measures of occupancy may not accurately reflect quality (Johnson 2007), and landscape disturbance, changes in population size, and social constraints can cloud the interpretation of occupancy (Johnson 2007). By incorporating a seven-year time frame (year<sub>t-3</sub> to year<sub>t+3</sub>), I should have suppressed the distortion of landscape and population size changes that contribute to site quality differences over long periods. However, that does not account for social constraints, such as trying to nest closer to other owls to derive possible benefits (see Welty 2010). Burrow productivity may also be subjected to some of the same complications, especially social constraints. Thus, the lack of a relationship between these indices and dispersal likelihood may have two meanings. First, these indices may not accurately measure quality, which I believe is more likely to be true for proportional occupation. Second, other factors are inducing some owls to regularly select suboptimal sites, which undermines the value of these indices. In other words, site quality may not be influencing the likelihood of breeding dispersal by burrowing owls, which may be the case for burrow productivity. This does not mean that site quality has no effect on burrowing owl breeding dispersal because, as discussed below, the other two measures of both appeared in models in the multivariate confidence set.

Reproductive failure in year<sub>t</sub> was important to dispersal likelihood, as all owls that failed to fledge young underwent breeding dispersal. However, many successful breeders also dispersed (see Figure 2.2). Thus, successful breeding did not necessarily lead to philopatry, but breeding failure always led to dispersal. I could not include productivity



status in analyses because of quasi-complete separation, so inferences of analyses are based on observations that only include owls that successfully fledged young in year<sub>t</sub>. In such analyses the factors important for dispersal likelihood were sex, distance to agriculture, and ectoparasitism. The relationships of sex and distance to agriculture with breeding dispersal likelihood matched my predictions. Females were more likely to disperse than males, and owls were more likely to disperse as the distance to agriculture increased. However, owls nesting in burrows with higher levels of ectoparasites were less likely to disperse, which was a trend that was opposite to my prediction.

The inverse association of ectoparasitism with breeding dispersal likelihood may be related to three things. First, fleas may not impart any costs beyond minor irritation to burrowing owls. In an *a posteriori* analysis of observations used in the breeding dispersal analyses, the mean level of ectoparasites for a nest was not strongly correlated to the number of young fledged from that nest ( $r_s = -0.168$ ,  $P = 0.122$ ,  $n = 86$ ). Second, adults may develop strong immune responses to local endoparasites (often transmitted via ectoparasites), and long-distance movements may expose them to strains against which they are not 'vaccinated' (Möller and Erritzöe 2001, Möller et al. 2004). Such selection for immunity may act to minimize dispersal. Third, fleas are most likely acquired from mammalian food sources (see Smith and Belthoff 2001b), so higher levels of fleas may be an indicator of greater vertebrate prey availability (i.e., higher quality area). If owls are able to increase their fitness in areas of higher prey availability despite harboring more fleas, then it is reasonable to assume that they are more likely to return to those locations to breed. If ectoparasite level accurately indexes site quality (based on prey

availability), then owls may be expected to exhibit higher rates of philopatry at burrows with higher flea levels, which they did in my study.

The factors age and distance to nearest neighbor were in some of the confidence models of the multivariate analysis but neither was highly influential. Age related to dispersal likelihood in the predicted direction, as younger owls were more likely to disperse. Contrary to my prediction, however, owls with closer nearest neighbors were more likely to disperse than owls with more distant neighbors. It should be easier for owls with nearer neighbors to obtain public information (i.e., breeding success of neighbors). Moreover, if having a closer neighbor also indicates a shorter mean distance to a larger group of neighbors (greater nesting density), those owls will probably possess information about breeding success for more neighbors. The increased dispersal likelihood with nearer neighbors and the high dispersal rate may be because some owls are making short movements to take over territories that have become vacant. Such a possibility is indirectly supported by a decrease in dispersal distance with closer neighbors.

The results of the breeding dispersal likelihood modeling only agree in part with previous studies of burrowing owls (Millsap and Bear 1997, Lutz and Plumpton 1999, Catlin et al. 2005). Unlike the current study, those studies did not examine the effects of site quality, mate quality, or ectoparasitism on breeding dispersal. Consistent with my results, two of the studies found that breeding failure in year<sub>t</sub> increased the likelihood of dispersal (both sexes: Catlin et al. 2005; females only: Lutz and Plumpton 1999). Millsap and Bear (1997) found no such relationship. Catlin et al. (2005) did not test directly for effects of sex but appeared to assume that they would differ. Both Millsap and Bear

(1997) and Lutz and Plumpton (1999) found no difference in dispersal likelihood between males and females. Only Millsap and Bear (1997) studied the effects of age and, similar to my results, they found that younger owls were more likely to undergo breeding dispersal than older owls. Catlin et al. (2005) were able to investigate the effects of mate fidelity, which I could not, and found that owls not re-mating with the same individual dispersed more often than owls that retained mates.

### Dispersal Distance Modeling

Separate treatment for modeling of likelihood and distance was validated because the confidence factors differed and, perhaps more importantly, some factors had different relationships with dispersal distance than they did with dispersal likelihood. In contrast to being important predictors of breeding dispersal likelihood, distance to agriculture and ectoparasitism were not relevant to dispersal distance. Moreover, age, distance to nearest neighbor, and ectoparasite level all had different relationships with likelihood than with distance.

All of the retained factors associated with dispersal distance in the predicted direction. Younger owls and owls with farther neighbors dispersed greater distances. Also, females tended to display longer breeding dispersal movements than males. That coincides with the observations of Millsap and Bear (1997) in a population of Florida burrowing owls. Surprisingly, number of young fledged did not seem to influence distance dispersed. I expected a result similar to Catlin et al. (2005), who observed that burrowing owls in California whose nests failed dispersed farther than owls that successfully bred.

The association of dispersal distance with proximity to nesting neighbors that I detected in southwestern Idaho burrowing owls may simply show that when owls are nesting farther apart, the larger territories necessitate a longer dispersal to find a vacant territory (Bowman 2003). But another reason may be the acquisition and use of public information. Owls with close neighbors are likely to have public information about breeding success, on which they may base decisions about where to breed in the future. When nearby burrows where owls had been successful are not occupied, then other owls may move to them. When owls nest farther apart they may not have public information on other nesting sites, so they would engage in searching that may lead to a longer dispersal before an appropriate site is found.

### Conclusions

Limitations in study design or data availability prevent most researchers from examining the relationship of breeding dispersal with many factors that may be important. I was able to address some factors that may affect breeding dispersal of burrowing owls in southwestern Idaho by examining a long-term data set from owls nesting in and near the Morley Nelson Birds of Prey National Conservation Area. Breeding dispersal likelihood was influenced by sex, age, productivity, site quality, and ectoparasites. Among these, sex, distance to agriculture (measure of site quality), and ectoparasite level may be the most influential factors, as they appeared in all confidence models. Burrowing owls were less likely to move if they were male, nested close to agriculture, and had more ectoparasites. Breeding dispersal distance was most strongly linked to age and distance to nearest neighbor (another measure of site quality). Older

owls and owls with closer neighbors dispersed shorter distances. Sex may also be important (females disperse farther), but evidence supporting that relationship was weak. The relative importance of each factor differed between the likelihood of dispersal and the distance dispersed, which confirmed the need to analyze them separately and highlights that selection may operate differently on the decision to disperse and the decisions regarding how far an individual should move. The factors influential for each process for burrowing owls in southwestern Idaho did not completely coincide with results from burrowing owls in other locations. It is important to reiterate that dispersal trends are not constant across space and time, even within a species. The other studies on breeding dispersal in burrowing owls all differed in geographic location, local habitat, focus of the study, ability to measure characteristics, migratory tendency of the population, time frame, applied experimental treatments, and sample size. Any of these aspects could have influenced the differences observed between various populations of burrowing owls.

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Table 2.1. Prediction matrix for factors affecting breeding dispersal of burrowing owls in southwestern Idaho.

Factor	Dispersal Likelihood <sup>1</sup>	Dispersal Distance <sup>2</sup>
Sex	Female	Female
Age	Young	Young
Mate Quality <sup>3</sup>	Low	Low
Reproductive Success <sup>4</sup>	Failed	None
Site Quality		
• Proportional Occupation	Low	Low
• Burrow Productivity	Low	Low
• Distance to Nearest Neighbor	Large	Large
• Distance to Agriculture	Large	Large
Ectoparasitism	High	High

<sup>1</sup> Level of factor with greatest expected likelihood of dispersal.

<sup>2</sup> Level of factor with largest expected dispersal distance.

<sup>3</sup> Predictions are for female dispersal only, as males are more likely to rely on site quality than mate quality.

<sup>4</sup> For likelihood the measure used is status (success or failure), and for distance the measure used is productivity (number of young fledged).

Table 2.2. Analysis of variance (ANOVA) for calculation of repeatability ( $r$ ) of breeding dispersal distance by burrowing owls in southwestern Idaho, 1994-2007.

Source of variation	df	Sums of squares	Mean squares	F	$r^1$
Among individuals	21	35168772	1674703.4	5.086	0.648
Within individuals	27	8891270	329306.3		
Total	48	44060042			

<sup>1</sup>see Lessells and Boag (1987) for calculation of  $r$ .

Table 2.3. Number of burrowing owls banded in southwestern Idaho, 1994–2007.

Year	Adults	Owlets	Total
1994	23	38	61
1995	19	31	50
1996	22	73	95
1997	39	237	276
1998	69	199	268
1999	22	282	304
2000	35	94	129
2001	16	180	196
2002	22	112	134
2003	37	149	186
2004	28	191	219
2005	39	177	216
2006	46	299	345
2007	71	292	363
1994–2007 Total	488	2354	2842

Table 2.4. Number of burrowing owls identified as breeders in southwestern Idaho in years after being banded. Owls with known breeding locations in the prior year are described as dispersed (breeding in different ABS or natural burrow) or philopatric (breeding in same ABS or natural burrow). Some banded owls returned in more than one year, and all observations from such individuals are included. Banding activities commenced in 1994 and occurred every year through 2007.

Year	Known breeding location in previous year		Unknown breeding location in previous year	Total <sup>1</sup>
	Dispersed	Philopatric		
1995	0	0	0	0
1996	2	1	0	3
1997	5	1	0	6
1998	10	5	3	18
1999	17	2	5	24
2000	7	4	6	17
2001	11	5	3	19
2002	10	3	5	18
2003	1	0	6	7
2004	6	1	4	11
2005	8	2	10	20
2006	4	0	4	8
2007	5	3	13	21
All years	86	27	59	172

<sup>1</sup> Does not include some returning owls that were banded but not positively identified. There was at least one banded but unidentified breeder in the years 2000–02, 2004, and 2006.

Table 2.5. Number of events of philopatry or dispersal for burrowing owls with known breeding locations in multiple years in southwestern Idaho, 1994–2007.

Number of times an individual had known breeding locations in consecutive years	Number of owls by sex		Events <sup>1</sup>
	Male	Female	
0	8	12	0
1	19	45	64
2	3	14	34
3	1	4	15
TOTAL	31	75	113

<sup>1</sup> An event is an instance of between-year breeding dispersal or philopatry.

Table 2.6. Frequencies of dispersal patterns for burrowing owls that had multiple between-year events of dispersal or philopatry.

Pattern <sup>1</sup>	Male	Female	Total (%) <sup>2</sup>
Always dispersed			
• Dispersal, dispersal	1	10	11 (50.0)
• Dispersal, dispersal, dispersal	0	2	2 (9.1)
Dispersed then became philopatric			
• Dispersal, philopatry	0	3	3 (13.6)
• Dispersal, dispersal, philopatry	0	1	1 (4.5)
Philopatric then dispersed			
• Philopatry, dispersal	1	0	1 (4.5)
• Philopatry, dispersal, dispersal	0	1	1 (4.5)
• Philopatry, philopatry, dispersal	1	0	1 (4.5)
Always philopatric			
• Philopatry, philopatry	1	1	2 (9.1)
Total	4	18	22

<sup>1</sup> The pattern describes the chronological order of events (dispersal or philopatry) for an individual.

<sup>2</sup> Percentage of grand total.

Table 2.7. GEE results for modeling the number of young fledged by burrowing owls as a function of dispersal status (yes or no), year (t or t+1) and the interaction status  $\times$  year with individual as a repeated subject. (a) Estimates for all parameters and effects in the model. (b) Difference in number of young fledged for selected means comparisons.

(a)

Parameter	Effect	Estimate	SE	95% CI <sup>1</sup>	
				Lower	Upper
Intercept		1.5321	0.0696	1.3956	1.6686
Year	t	-0.1552	0.1076	-0.3662	0.0557
Year	t+1	0.0000	0.0000		
Disperse	No	0.0396	0.1264	-0.2082	0.2873
Disperse	Yes	0.0000	0.0000		
Disperse*Year	No, t	0.2426	0.1952	-0.1399	0.6252
Disperse*Year	No, t+1	0.0000	0.0000		
Disperse*Year	Yes, t	0.0000	0.0000		
Disperse*Year	Yes, t+1	0.0000	0.0000		

<sup>1</sup> 95% confidence interval for parameter estimate.

(b)

Comparison	Difference	SE	95% CI <sup>1</sup>	
			Lower	Upper
Year t v. t+1 for philopatric owls	0.4396	0.8324	-1.2096	2.0900
Year t v. t+1 for dispersing owls	-0.6655	0.4636	-1.5845	0.2532
Philopatric v. dispersing owls for year <sub>t+1</sub>	0.1869	0.6411	-1.0838	1.4576

<sup>1</sup> 95% confidence interval for difference of means.



Table 2.8. Within-year breeding dispersal distances for burrowing owls in southwestern Idaho.

Year	Sex	Distance (m)
1998	Female	50
1998	Female	155
2005	Male	312
2005	Female	132
2007	Male <sup>1</sup>	74
2007	Female <sup>1</sup>	74
2007	Female <sup>2</sup>	70
2007	Female <sup>2</sup>	83

<sup>1</sup> This male and female dispersed together.

<sup>2</sup> This female dispersed twice in the same year.

Table 2.9. Parameter estimates and odds ratios from GEE with logit link function for predictor variables that were modeled individually for breeding dispersal likelihood in burrowing owls in southwestern Idaho.

Parameter	n	Estimate	SE	95% CI <sup>1</sup>		Odds Ratio	95% CI <sup>2</sup>	
				Lower	Upper		Lower	Upper
Mate Quality	29	0.0350	0.366	-0.6816	0.7516	1.0356	0.5058	2.1204
Burrow Productivity	100	-0.2652	0.184	-0.6260	0.0957	0.7671	0.5347	1.1004
Proportional Occupation	100	-1.1932	1.103	-3.3546	0.9682	0.3032	0.0349	2.6332

<sup>1</sup> 95% confidence interval for parameter estimate.

<sup>2</sup> 95% confidence interval for odds ratio.

Table 2.10. QIC values for select candidate models of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year  $t$  in southwestern Idaho.

Model	Factors in model <sup>1</sup>	QIC	$\Delta$ QIC <sup>2</sup>
1	Sex, DistAg, Ectos	64.4220	0.0000
2	Sex, DistAg, DistNN, Ectos	64.4501	0.0281
3	Sex, Age, DistAg, Ectos	65.7699	1.3479
4	Sex, Age, DistAg, DistNN, Ectos	65.9801	1.5581
5	Sex, DistAg	68.0297	3.6077
6	DistAg, DistNN, Ectos	68.8158	4.3938
7	Sex, Age, DistAg	69.0301	4.6081
8	Sex, DistAg, DistNN	69.7250	5.3030
9	Sex, DistNN, Ectos	69.9729	5.5509
10	Sex, Ectos	70.2966	5.8746
11	DistAg, Ectos	70.3900	5.9680
12	Sex, Age, DistAg, DistNN	70.7483	6.3263
13	Age, DistAg, DistNN, Ectos	70.8672	6.4452
14	Sex, Age, DistNN, Ectos	71.3741	6.9521
15	Sex, Age, Ectos	71.4594	7.0374
16	Age, DistAg, Ectos	72.1132	7.6912
17	DistAg	72.5386	8.1166
18	DistAg, DistNN	73.5411	9.1191
19	Sex	73.8063	9.3843

<sup>1</sup> Possible factors, which are described in methods, include Sex, Age, DistAg (distance to agriculture), DistNN (distance to nearest neighbor), and Ectos (ectoparasites).

<sup>2</sup> Difference in QIC between this model and model with lowest QIC. The largest gap in QIC values occurred between models 4 and 5, so the confidence set includes models 1-4.

Table 2.11. Parameter estimates and odds ratios from GEE with logit link function for the global model of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year<sub>*t*</sub> in southwestern Idaho, 1994-2007.

Parameter <sup>1</sup>	Estimate	SE	95% CI <sup>2</sup>		Odds Ratio	95% CI <sup>3</sup>	
			Lower	Upper		Lower	Upper
Intercept	3.7025	1.2179	1.3155	6.0895			
Sex	-1.6313	0.6470	-2.8994	-0.3631	0.1957	0.0551	0.6955
Age	0.0606	0.2636	-0.4561	0.5773	1.0624	0.6338	1.7812
DistAg	0.0051	0.0018	0.0016	0.0085	1.0051	1.0016	1.0085
DistNN	-0.0047	0.0030	-0.0105	0.0012	0.9953	0.9896	1.0012
Ectos	-1.0396	0.3884	-1.8010	-0.2783	0.3536	0.1651	0.7571

<sup>1</sup> Parameters in global model include Sex, Age, DistAg (distance to agriculture), DistNN (distance to nearest neighbor), and Ectos (ectoparasites).

<sup>2</sup> 95% confidence interval for parameter estimate.

<sup>3</sup> 95% confidence interval for odds ratio.

Table 2.12. Parameter estimates and odds ratios from GEE with logit link function for the best evidence model ( $\Delta\text{QIC} = 0$ ) of breeding dispersal likelihood for burrowing owls ( $n = 74$ ) that successfully bred in year<sub>t</sub> in southwestern Idaho, 1994-2007.

Parameter <sup>1</sup>	Estimate	SE	95% CI <sup>2</sup>		Odds Ratio	95% CI <sup>3</sup>	
			Lower	Upper		Lower	Upper
Intercept	2.5801	0.8277	0.9579	4.2023			
Sex	-1.8142	0.5893	-2.9693	-0.6592	0.1630	0.0513	0.5173
DistAg	0.0050	0.0018	0.0015	0.0085	1.0050	1.0015	1.0085
Ectos	-0.8181	0.3329	-1.4705	-0.6157	0.4413	0.2298	0.5403

<sup>1</sup> Parameters in model include Sex, DistAg (distance to agriculture), and Ectos (ectoparasites).

<sup>2</sup> 95% confidence interval for parameter estimate.

<sup>3</sup> 95% confidence interval for odds ratio.

Table 2.13. GEE parameter estimates and 95% confidence intervals for predictor variables that were modeled individually for breeding dispersal distance in burrowing owls in southwestern Idaho, 1994-2007.

Parameter	n	Estimate	SE	95% CI	
				Lower	Upper
Age <sup>1</sup>	86	-153.0	62.6	-275.66	-30.41
Mate quality	26	-80.8	77.7	-233.20	71.53
Burrow productivity	86	-88.6	49.9	-186.42	9.24
Proportional occupation	86	-443.1	308.7	-1048.10	161.91
Ectoparasites	64	16.3	67.9	-116.73	149.26

<sup>1</sup> Only univariate predictor whose parameter estimate did not include zero in the 95% CI.

Table 2.14. QIC values for candidate models of breeding dispersal distance for burrowing owls ( $n = 72$ ) in southwestern Idaho.

Model	Factors in model <sup>1</sup>	QIC	$\Delta$ QIC <sup>2</sup>
1	DistNN	72.340	0.000
2	Sex, DistNN	72.492	0.152
3	Sex	73.075	0.735
4	Sex, #Fledged, DistNN	73.223	0.883
5	DistAg, DistNN	73.358	1.018
6	#Fledged, DistNN	73.382	1.042
7	DistAg	73.469	1.129
8	Sex, DistAg, DistNN	73.618	1.278
9	#Fledged	73.639	1.299
10	Sex, DistAg	73.840	1.500
11	Sex, #Fledged	74.008	1.668
12	Sex, #Fledged, DistAg, DistNN	74.247	1.907
13	Sex, #Fledged, DistAg	74.463	2.123
14	#Fledged, DistAg, DistNN	74.482	2.142
15	#Fledged, DistAg	74.680	2.340
16	Null	129.144	56.804

<sup>1</sup> Possible factors, which are described in methods, include Sex, #Fledged (number of young fledged), DistAg (distance to agriculture), and DistNN (distance to nearest neighbor).

<sup>2</sup> Difference in QIC between this model and model with lowest QIC. Except for the obvious gap separating the null model from all other models, the largest gap in QIC values occurred between models 2 and 3. Therefore the confidence set includes models 1 and 2.

Table 2.15. GEE parameter estimates and 95% confidence intervals for the inclusive confidence model of breeding dispersal distance for burrowing owls (n = 72) in southwestern Idaho, 1994-2007.

Parameter <sup>1</sup>	Estimate	SE	95% CI	
			Lower	Upper
Intercept	712.015	34.238	644.910	799.120
Sex	-267.418	190.037	-639.882	105.047
DistNN	0.813	0.361	0.106	1.521

<sup>1</sup> Parameters in model include Sex and DistNN (distance to nearest neighbor).



Table 2.16. GEE parameter estimates and 95% confidence intervals for the best evidence model ( $\Delta\text{QIC} = 0$ ) of breeding dispersal distance for burrowing owls ( $n = 72$ ) that successfully bred in year<sub>*t*</sub> in southwestern Idaho, 1994-2007.

Parameter <sup>1</sup>	Estimate	SE	95% CI	
			Lower	Upper
Intercept	746.4985	33.7812	680.2886	812.7084
DistNN	0.4819	0.3061	-0.1181	1.0818

<sup>1</sup> DistNN is distance to nearest neighbor.

Table 2.17. Percent frequency and mean distance of breeding dispersal for several owl species.

Species	Location	% Frequency			Distance (m)			Source
		Males	Females	Combined	Males	Females	Combined	
<i>Aegolius funereus</i>	Finland	–	–	–	1300 <sup>A</sup>	5500 <sup>A</sup>	3400 <sup>B</sup>	Korpimäki 1993
<i>A. funereus</i>	Finland	–	–	–	~1200 <sup>A</sup>	~5000 <sup>A</sup>	~3100 <sup>B</sup>	Korpimäki 1987
<i>A. funereus</i>	Finland	0 <sup>C</sup>	91 <sup>C</sup>	≤ 36 <sup>C</sup>	–	–	–	Korpimäki 1988
<i>A. funereus</i>	Finland	25 <sup>D</sup>	–	–	0 <sup>AD</sup>	–	–	Hakkarainen et al. 2001
<i>Athene cunicularia</i>	Idaho	52	87	78	558	895	835	This study
<i>A. cunicularia</i>	Colorado	25	37	31 <sup>B</sup>	–	–	–	Lutz and Plumpton 1999
<i>A. cunicularia</i>	Florida	17	26	22 <sup>B</sup>	96 <sup>A</sup>	230 <sup>A</sup>	163 <sup>B</sup>	Millsap and Bear 1997
<i>A. cunicularia</i>	California	32	37	34	431	526	472	Catlin et al. 2005
<i>A. cunicularia</i>	Washington	60	71	64	–	–	–	Conway et al. 2006
<i>A. cunicularia</i>	Manitoba	49	67	55	3000	10900	5700	De Smet 1997
<i>A. cunicularia</i>	Saskatchewan	–	–	26	–	–	–	Haug et al. 1993
<i>Otus elegans</i>	Lanyu Island	–	–	–	1700	1800	1750 <sup>B</sup>	Severinghaus 2002
<i>O. flammeolus</i>	New Mexico	20	46	33	179	289	263	Arsenault et al. 2005
<i>O. flammeolus</i>	Colorado	8	44	26 <sup>B</sup>	–	–	–	Linkhart and Reynolds 2007
<i>Strix occidentalis</i>	California	–	–	7	–	–	7000 <sup>A</sup>	Blakesley et al. 2006
<i>S. occidentalis</i>	northwestern USA	–	–	–	–	–	6100	Forsman et al. 2002
<i>S. occidentalis</i>	California	–	–	9	–	–	–	Seamans and Gutierrez 2007
<i>Tyto alba</i>	Utah	–	–	4 <sup>E</sup>	2200	2300	2300	Marti 1999

<sup>A</sup> Denotes a median distance. Mean distance is probably greater.

<sup>B</sup> Not given by authors. I assumed an equal number of males and females to derive.

<sup>C</sup> Not given by author. “Only two females stayed on the same territory...there are no observations of territory shifts by males within the study area and no recoveries of males outside the study area” (p. 103). Sample size for females appears to be 22 (from Table 5, p. 101); hence, female frequency is 90.9% (20 of 22). Based on Table 8 (p. 102), there were ≥ 33 males, so combined frequency is ≤ 36.4% (20 of ≥ 55).

<sup>D</sup> Values are for a control group. An experimental group exposed to predation risk had a frequency of 80% and a median distance of 1.5 km.

<sup>E</sup> Includes some within-year observations.

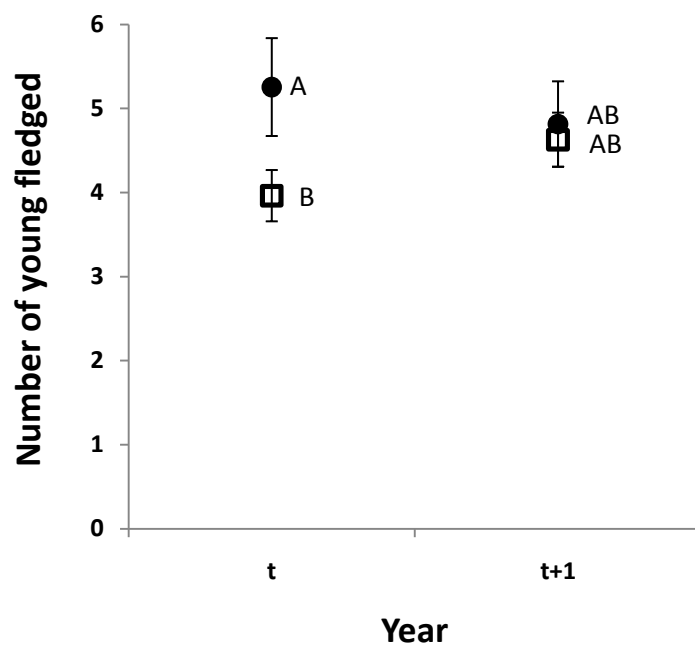


Figure 2.1. Mean ( $\pm$  SE) number of young fledged by philopatric (filled circles) and dispersing owls (hollow squares) in years t and t+1. Letters indicate means with overlapping 95% confidence intervals.

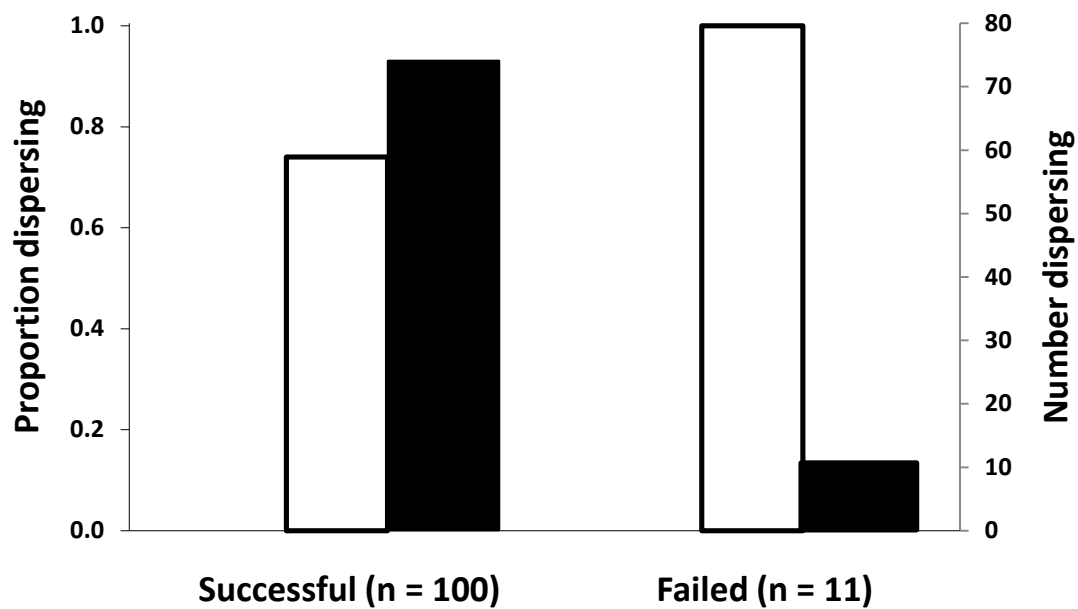


Figure 2.2. Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that dispersed based on breeding success in year<sub>t</sub>.

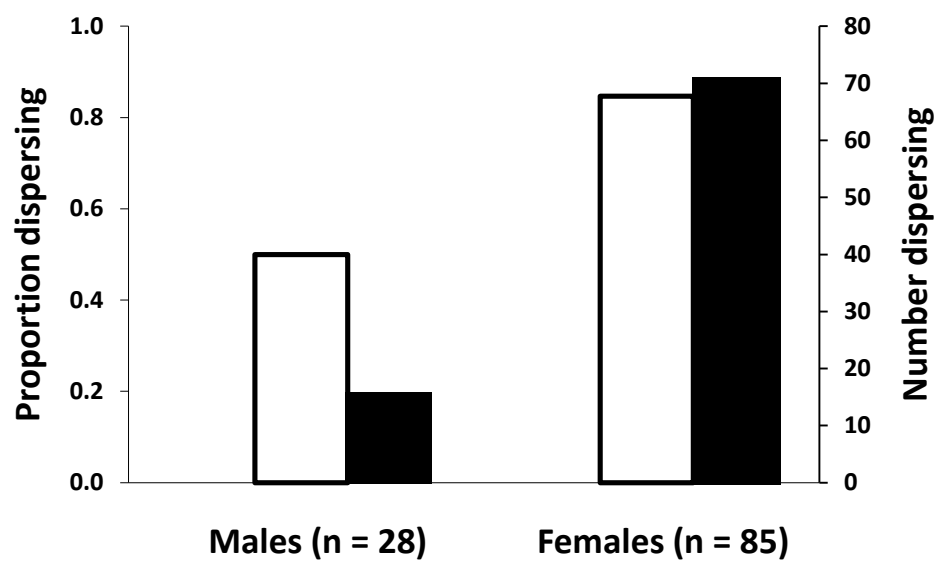


Figure 2.3. Proportion (white columns) and number (black columns) of male and female burrowing owls nesting in southwestern Idaho that underwent breeding dispersal.

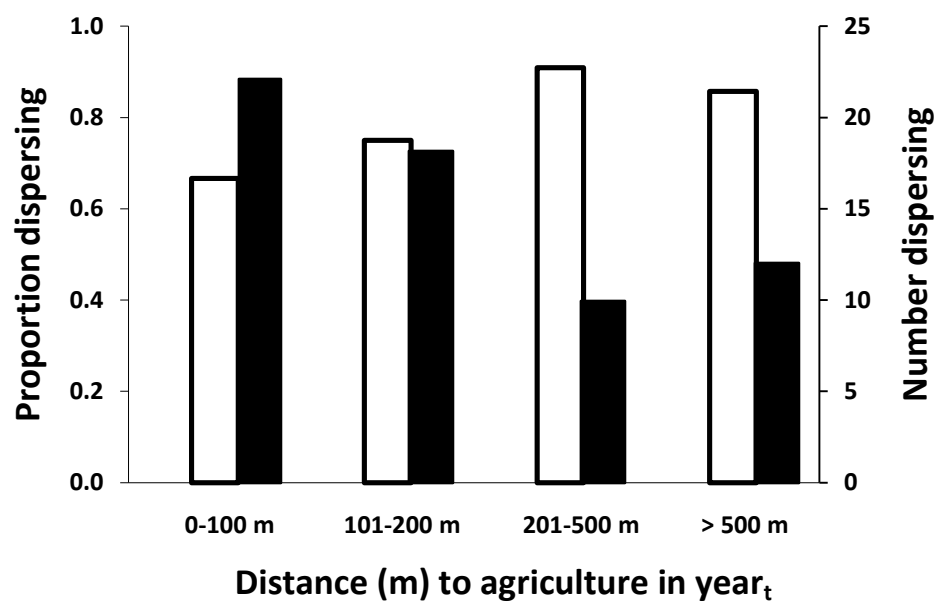


Figure 2.4. Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that underwent breeding dispersal as a function of distance to irrigated agriculture.

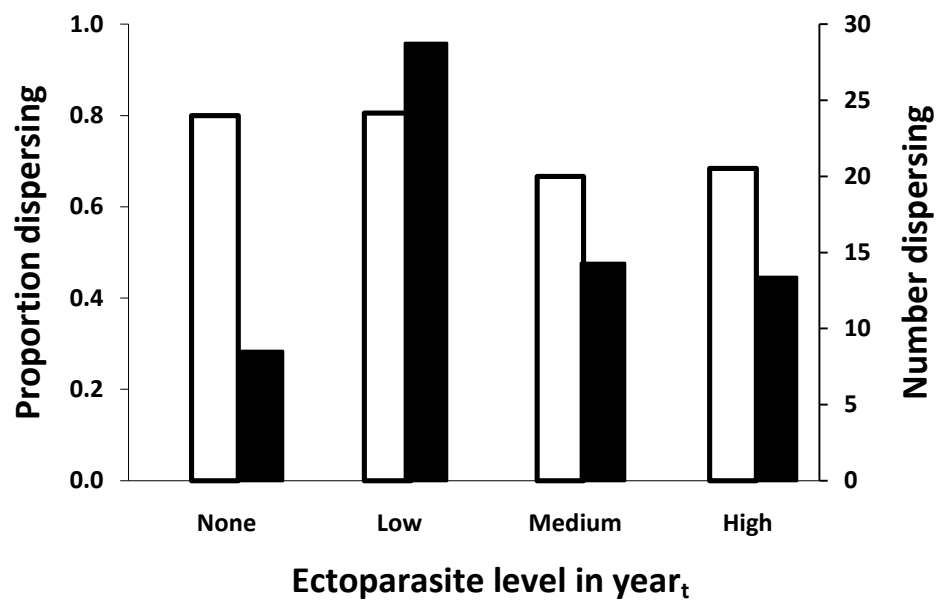


Figure 2.5. Proportion (white columns) and number (black columns) of burrowing owls nesting in southwestern Idaho that underwent breeding dispersal as a function of ectoparasite level.

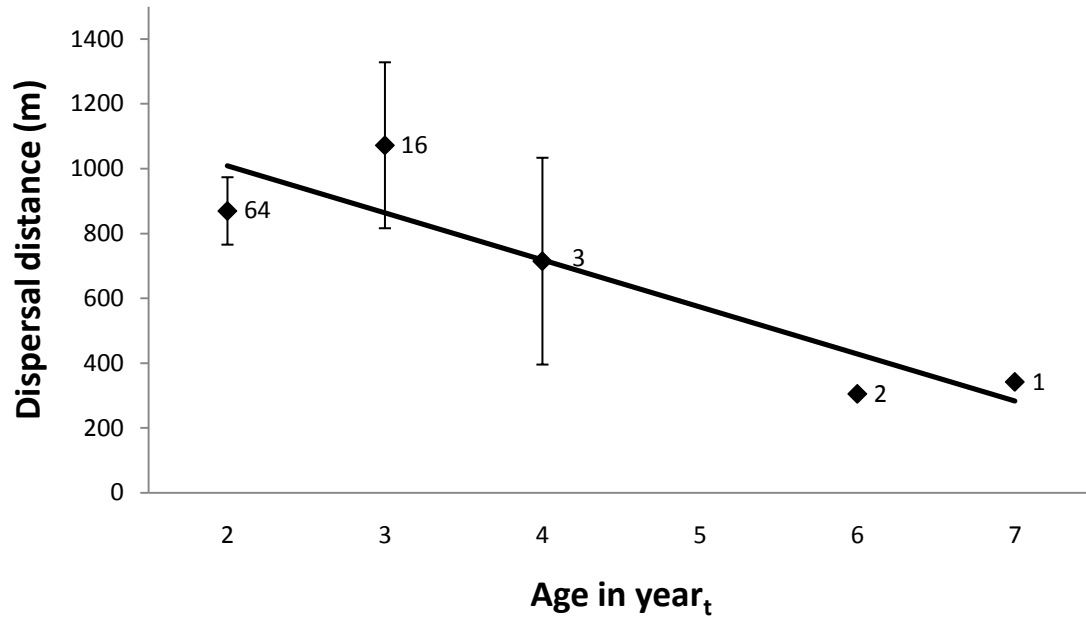


Figure 2.6. Mean ( $\pm$  SE) breeding dispersal distance by age for burrowing owls ( $n = 86$ ) nesting in southwestern Idaho. Numbers to right of means are sample sizes for each age. No 5-year old owls dispersed, and the two 6-year old dispersers moved the same distance. Simple linear regression line is shown.



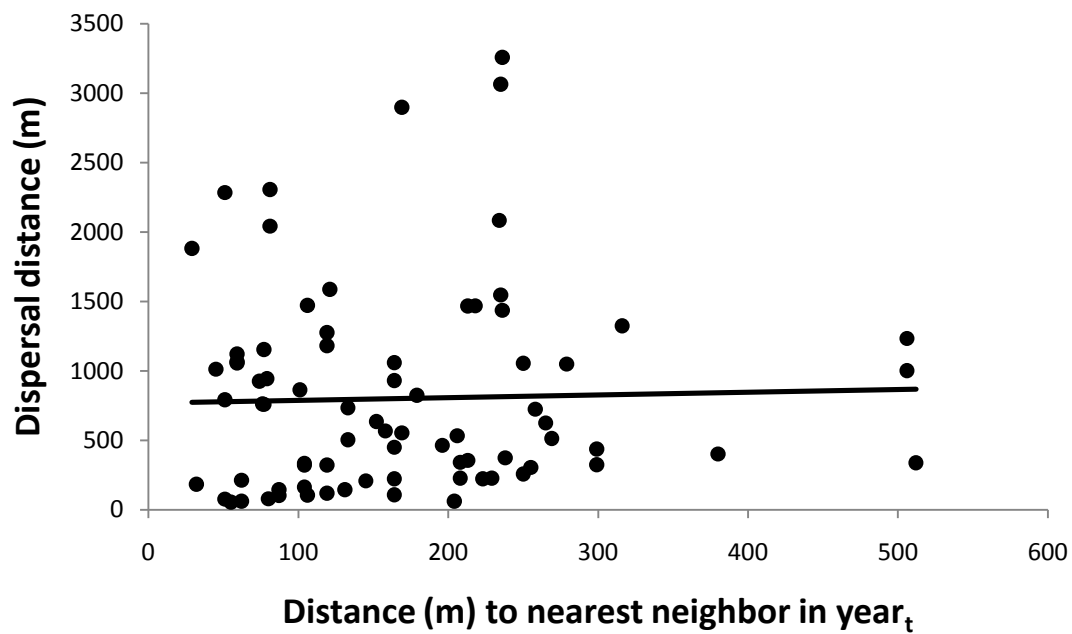


Figure 2.7. Breeding dispersal distance by distance to nearest neighbor for burrowing owls ( $n = 80$ ) nesting in southwestern Idaho. Simple linear regression line is shown.

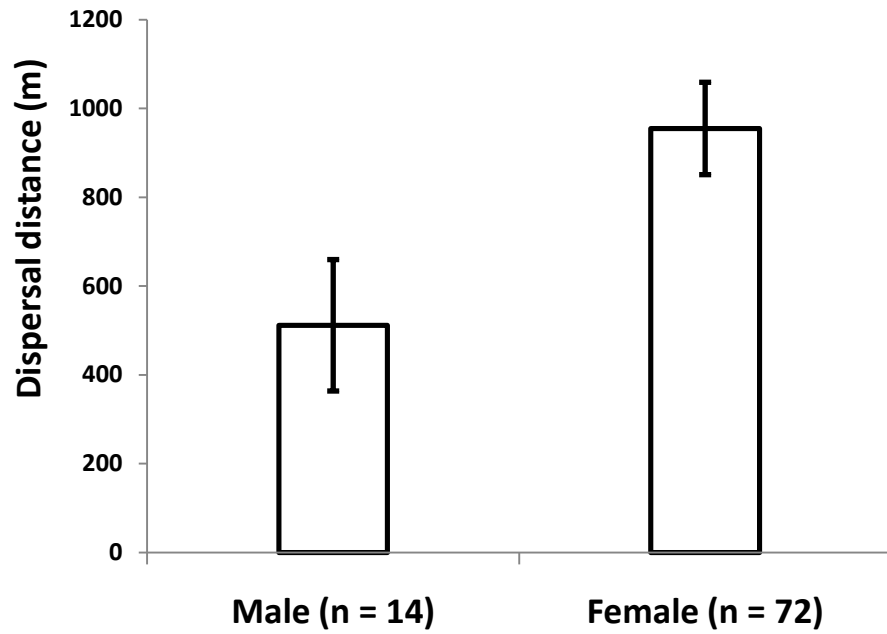


Figure 2.8. Mean ( $\pm$  SE) breeding dispersal distance by sex for burrowing owls nesting in southwestern Idaho.

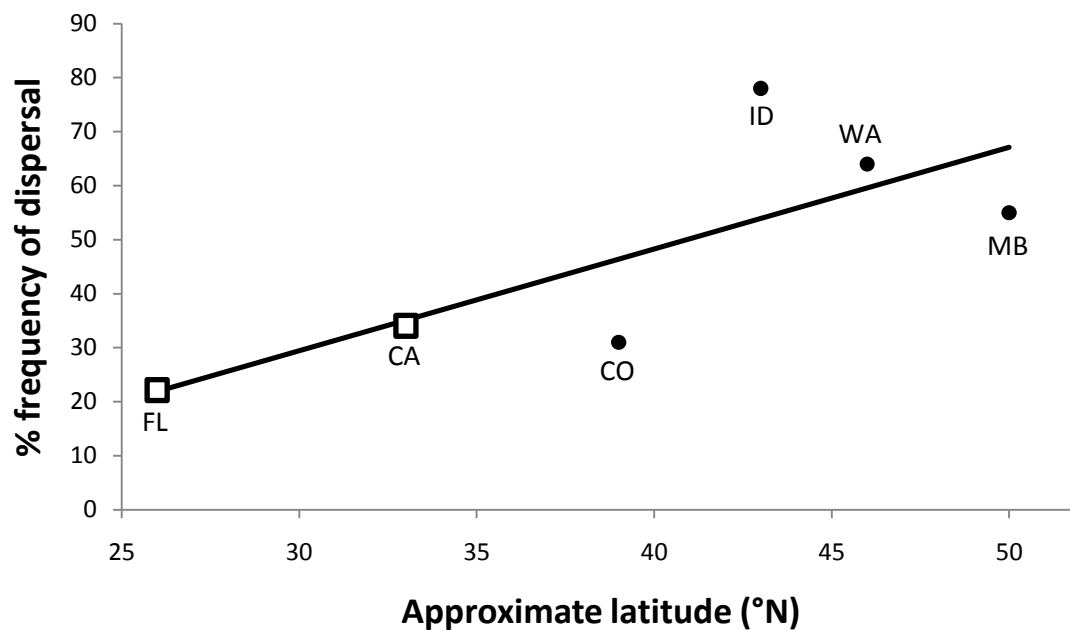


Figure 2.9. Breeding dispersal percent frequency by approximate latitude for six populations of burrowing owls. Simple linear regression line is shown. Hollow boxes are residential populations and solid circles are migratory populations. General locations of populations (in increasing latitude) are: Florida (Millsap and Bear 1997), California (Catlin et al. 2005), Colorado (Lutz and Plumpton 1999), Idaho (this study), Washington (Conway et al. 2006), and Manitoba (De Smet 1997).

APPENDIX A

**Artificial Burrow Systems (ABSs) Included in an Occupancy Experiment for  
Burrowing Owls in Southwestern Idaho 2004-2005.**

ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
398 3	2004	Not used	Unadorned	Not used	-
97 1	2004	Not used	Adorned	Not used	-
Backyard 4	2004	Not used	Adorned	Not used	-
Backyard 5	2004	Not used	Unadorned	Successful	5
Backyard 6	2004	Not used	Adorned	Not used	-
Backyard 8	2004	New in 2004	Adorned	Not used	-
Backyard 9	2004	New in 2004	Adorned	Not used	-
Baja 10	2004	Not used	Adorned	Not used	-
Baja 2	2004	Not used	Unadorned	Not used	-
Baja 6	2004	Not used	Adorned	Not used	-
Baja 8	2004	Not used	Adorned	Not used	-
Baja 9	2004	Not used	Unadorned	Successful	2
Baja Bachelor 1	2004	Not used	Adorned	Not used	-
Baja Pole 39	2004	Not used	Adorned	Not used	-
Baja Pole 40	2004	Not used	Adorned	Not used	-
Baja Pole 42	2004	New in 2004	Unadorned	Not used	-
Baja Pole 46 1	2004	Not used	Adorned	Not used	-
Baja Pole 46 2	2004	Not used	Unadorned	Not used	-
Baja Pole 46 3	2004	Not used	Adorned	Not used	-
Bennett 1	2004	Not used	Unadorned	Not used	-
Bennett 2	2004	Not used	Adorned	Not used	-
Bennett 3	2004	Not used	Unadorned	Not used	-
Bennett 4	2004	Not used	Unadorned	Not used	-
Canyon 1	2004	Not used	Unadorned	Not used	-
Canyon 2	2004	Not used	Adorned	Not used	-
Canyon 3	2004	Not used	Unadorned	Not used	-
Cinder 1	2004	Not used	Unadorned	Not used	-
Cinder 2	2004	Not used	Adorned	Not used	-
Cinder 3	2004	Not used	Unadorned	Not used	-
Cinder 4	2004	Not used	Adorned	Not used	-
Cinder 5	2004	New in 2004	Adorned	Not used	-
Curlew 5	2004	New in 2004	Adorned	Successful	6
Curlew 6	2004	New in 2004	Unadorned	Not used	-
Curlew 7	2004	New in 2004	Adorned	Not used	-
Curlew 8	2004	New in 2004	Unadorned	Not used	-
Delta 1	2004	Not used	Adorned	Not used	-
Delta 2	2004	Not used	Adorned	Not used	-
Delta 3	2004	Not used	Unadorned	Not used	-
Dirtmound 1	2004	Not used	Unadorned	Successful	4
Dirtmound 5	2004	Not used	Unadorned	Not used	-
Dorsey 1	2004	Not used	Unadorned	Not used	-
Dorsey 3	2004	Not used	Adorned	Not used	-

ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
Dorsey 5	2004	New in 2004	Unadorned	Not used	-
Dorsey 6	2004	New in 2004	Adorned	Not used	-
Dorsey East 1	2004	Not used	Unadorned	Not used	-
Dorsey East 4	2004	Not used	Unadorned	Not used	-
Dorsey East 5	2004	New in 2004	Unadorned	Not used	-
Dorsey East 6	2004	New in 2004	Adorned	Not used	-
Dorsey East 7	2004	New in 2004	Adorned	Not used	-
Ferrug 1	2004	Not used	Unadorned	Not used	-
Ferrug 2	2004	Not used	Adorned	Not used	-
Ferrug 3	2004	Not used	Unadorned	Not used	-
Ferrug 4	2004	Not used	Unadorned	Not used	-
Grand View 2	2004	Not used	Unadorned	Successful	5
Grand View 3	2004	Not used	Unadorned	Not used	-
Guard 1	2004	Not used	Adorned	Not used	-
Guard 2	2004	Not used	Unadorned	Not used	-
Guard 3	2004	Not used	Unadorned	Not used	-
Hilltop 1	2004	New in 2004	Adorned	Not used	-
Honeybee 1	2004	Not used	Adorned	Not used	-
Honeybee 2	2004	Not used	Unadorned	Failed	Adult died <sup>2</sup>
Kuna Butte 7	2004	Not used	Adorned	Not used	-
Kuna Butte Ag 1	2004	Not used	Unadorned	Not used	-
Kuna Butte Ag 3	2004	Not used	Adorned	Not used	-
Kuna Cave 2	2004	Not used	Adorned	Not used	-
Kuna Cave 3	2004	Not used	Unadorned	Not used	-
Kuna Cave Ag 2	2004	Not used	Adorned	Not used	-
Kuna Cave Ag 4	2004	New in 2004	Unadorned	Not used	-
Kuna Cave Ag 5	2004	New in 2004	Adorned	Not used	-
Kuna Cave Ag 6	2004	New in 2004	Unadorned	Not used	-
Kuna Cave Satellite 2	2004	Not used	Adorned	Not used	-
Missile 1	2004	Not used	Adorned	Successful	7
Missile 2	2004	Not used	Adorned	Successful	5
Missile 4	2004	Not used	Unadorned	Successful	10
Nicholson 1	2004	New in 2004	Unadorned	Not used	-
Nicholson 2	2004	New in 2004	Adorned	Not used	-
North Cinder 1	2004	Not used	Unadorned	Not used	-
North Cinder 2	2004	Not used	Unadorned	Not used	-
North Cinder 3	2004	Not used	Adorned	Not used	-
North Cinder 4	2004	Not used	Adorned	Not used	-
North Cinder 5	2004	Not used	Unadorned	Not used	-
North Cinder 6	2004	Not used	Unadorned	Not used	-
North Cinder 7	2004	Not used	Unadorned	Not used	-
North Cinder 8	2004	Not used	Adorned	Not used	-
Poen 1	2004	Not used	Unadorned	Not used	-

ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
Powerline 2	2004	Not used	Unadorned	Not used	-
Railroad 1	2004	Not used	Unadorned	Not used	-
Railroad 2	2004	Not used	Adorned	Not used	-
Railroad 3	2004	Not used	Unadorned	Not used	-
Railroad 4	2004	Not used	Adorned	Not used	-
Rock 1	2004	Not used	Adorned	Not used	-
Rock 2	2004	Not used	Adorned	Not used	-
Rock 3	2004	Not used	Unadorned	Not used	-
Rock 4	2004	Not used	Adorned	Not used	-
Sage 1	2004	Not used	Unadorned	Not used	-
South Cinder 1	2004	Not used	Unadorned	Not used	-
South Cinder 2	2004	Not used	Adorned	Not used	-
South Cinder 3	2004	Not used	Unadorned	Not used	-
South Cinder 4	2004	Not used	Unadorned	Not used	-
South Cinder 5	2004	Not used	Unadorned	Not used	-
South Cinder 6	2004	Not used	Adorned	Not used	-
South Cinder 7	2004	Not used	Unadorned	Not used	-
South Cinder 8	2004	Not used	Adorned	Not used	-
Sprinkler 2	2004	Not used	Adorned	Not used	-
Sprinkler 3	2004	Not used	Adorned	Not used	-
Sprinkler 4	2004	Not used	Adorned	Successful	2
State 1	2004	Not used	Adorned	Not used	-
State 2	2004	Not used	Adorned	Not used	-
State 3	2004	Not used	Unadorned	Not used	-
State 4	2004	Not used	Unadorned	Not used	-
Sub East 1	2004	Not used	Unadorned	Not used	-
Sub South 6	2004	Not used	Adorned	Successful	7
Sub West 1	2004	New in 2004	Adorned	Not used	-
Swan Falls 6	2004	Not used	Adorned	Not used	-
Swan Falls Ag 1	2004	Not used	Adorned	Successful	4
Swan Falls Satellite 5	2004	Not used	Unadorned	Not used	-
Tadpole 1	2004	Not used	Unadorned	Not used	-
Tadpole 2	2004	Not used	Adorned	Not used	-
Tadpole NW 1	2004	Not used	Unadorned	Not used	-
Trailer View 3	2004	Not used	Unadorned	Not used	-
Trailer View 4	2004	Not used	Unadorned	Successful	6
West Baja 1	2004	New in 2004	Unadorned	Not used	-
97 1	2005	Not used	Adorned	Successful	9
Backyard 4	2005	Not used	Unadorned	Not used	-
Backyard 6	2005	Not used	Adorned	Successful	7
Backyard 8	2005	Not used	Unadorned	Not used	-
Backyard 9	2005	Not used	Adorned	Successful	2
Badger 1	2005	New in 2005	Unadorned	Not used	-

ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
Badger 2	2005	New in 2005	Adorned	Used <sup>1</sup>	-
Baja 10	2005	Not used	Unadorned	Failed	Flooded
Baja 6	2005	Not used	Adorned	Not used	-
Baja Bachelor 1	2005	Not used	Unadorned	Not used	-
Baja Pole 39	2005	Not used	Adorned	Not used	-
Baja Pole 42	2005	Not used	Adorned	Not used	-
Baja Pole 46 1	2005	Not used	Unadorned	Not used	-
Baja Pole 46 3	2005	Not used	Adorned	Not used	-
Bennett 1	2005	Not used	Unadorned	Not used	-
Bennett 2	2005	Not used	Adorned	Not used	-
Bennett 3	2005	Not used	Unadorned	Not used	-
Bennett 4	2005	Not used	Adorned	Not used	-
Boggs 1	2005	New in 2005	Adorned	Not used	-
Boggs 2	2005	New in 2005	Unadorned	Not used	-
Canyon 1	2005	Not used	Adorned	Not used	-
Canyon 2	2005	Not used	Adorned	Not used	-
Canyon 3	2005	Not used	Unadorned	Not used	-
Cinder 1	2005	Not used	Unadorned	Not used	-
Cinder 2	2005	Not used	Unadorned	Not used	-
Cinder 3	2005	Not used	Adorned	Not used	-
Cinder 4	2005	Not used	Unadorned	Not used	-
Cinder 5	2005	Not used	Adorned	Not used	-
Corner 1	2005	New in 2005	Unadorned	Not used	-
Corner 2	2005	New in 2005	Adorned	Not used	-
Corner 3	2005	New in 2005	Adorned	Not used	-
Coyote Den 1	2005	Not used	Adorned	Failed	Unknown <sup>3</sup>
Curlew 6	2005	Not used	Adorned	Not used	-
Curlew 7	2005	Not used	Adorned	Successful	1
Delta 1	2005	Not used	Adorned	Successful	5
Delta 2	2005	Not used	Unadorned	Not used	-
Delta 3	2005	Not used	Unadorned	Not used	-
Dirtmound 5	2005	Not used	Adorned	Successful	1
Dorsey 1	2005	Not used	Unadorned	Not used	-
Dorsey 3	2005	Not used	Unadorned	Not used	-
Dorsey 5	2005	Not used	Adorned	Not used	-
Dorsey 6	2005	Not used	Adorned	Not used	-
Dorsey East 1	2005	Not used	Adorned	Not used	-
Dorsey East 4	2005	Not used	Unadorned	Not used	-
Dorsey East 5	2005	Not used	Adorned	Not used	-
Dorsey East 6	2005	Not used	Adorned	Successful	3
Dorsey East 7	2005	Not used	Unadorned	Not used	-
East Cinder 1	2005	New in 2005	Adorned	Not used	-
East Cinder 2	2005	New in 2005	Unadorned	Not used	-



ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
Ferrug 1	2005	Not used	Adorned	Not used	-
Ferrug 2	2005	Not used	Unadorned	Not used	-
Ferrug 3	2005	Not used	Unadorned	Not used	-
Ferrug 4	2005	Not used	Unadorned	Not used	-
Grand View 3	2005	Not used	Unadorned	Not used	-
Guard 1	2005	Not used	Adorned	Not used	-
Guard 2	2005	Not used	Unadorned	Not used	-
Guard 3	2005	Not used	Adorned	Not used	-
Hilltop 1	2005	Not used	Unadorned	Not used	-
Kuna Cave Ag 5	2005	Not used	Unadorned	Not used	-
Kuna Cave Ag 6	2005	Not used	Adorned	Not used	-
Mid Simco 1	2005	New in 2005	Adorned	Not used	-
Missile 5	2005	New in 2005	Unadorned	Failed	Unknown <sup>3</sup>
Nicholson 1	2005	Not used	Adorned	Not used	-
Nicholson 2	2005	Not used	Unadorned	Not used	-
North Cinder 1	2005	Not used	Unadorned	Not used	-
North Cinder 2	2005	Not used	Adorned	Not used	-
North Cinder 3	2005	Not used	Adorned	Not used	-
North Cinder 4	2005	Not used	Unadorned	Not used	-
North Cinder 5	2005	Not used	Unadorned	Not used	-
North Cinder 6	2005	Not used	Adorned	Not used	-
North Cinder 7	2005	Not used	Unadorned	Not used	-
North Cinder 8	2005	Not used	Adorned	Not used	-
Railroad 1	2005	Not used	Unadorned	Not used	-
Railroad 2	2005	Not used	Adorned	Not used	-
Railroad 3	2005	Not used	Adorned	Not used	-
Railroad 4	2005	Not used	Unadorned	Not used	-
Range 30 1	2005	Not used	Unadorned	Not used	-
Rock 1	2005	Not used	Adorned	Not used	-
Rock 2	2005	Not used	Adorned	Not used	-
Rock 3	2005	Not used	Unadorned	Not used	-
Rock 4	2005	Not used	Unadorned	Not used	-
Sage 1	2005	Not used	Adorned	Not used	-
Simco 1	2005	Not used	Unadorned	Not used	-
Simco 2	2005	Not used	Unadorned	Not used	-
Simco 3	2005	Not used	Adorned	Not used	-
Simco 4	2005	Not used	Adorned	Not used	-
South Cinder 1	2005	Not used	Unadorned	Not used	-
South Cinder 2	2005	Not used	Adorned	Successful	8
South Cinder 3	2005	Not used	Unadorned	Not used	-
South Cinder 4	2005	Not used	Adorned	Successful	7
South Cinder 6	2005	Not used	Unadorned	Not used	-
South Cinder 7	2005	Not used	Unadorned	Not used	-

ABS name	Year	Status Previous Year	Treatment	Status	Number Fledged, or Reason for Failure
South Cinder 8	2005	Not used	Adorned	Not used	-
Sprinkler 2	2005	Not used	Unadorned	Successful	5
Sprinkler 3	2005	Not used	Unadorned	Failed	Flooded
State 1	2005	Not used	Adorned	Not used	-
State 2	2005	Not used	Adorned	Not used	-
State 3	2005	Not used	Adorned	Not used	-
State 4	2005	Not used	Unadorned	Not used	-
Sub West 1	2005	Not used	Adorned	Not used	-
Swan Falls Satellite 5	2005	Not used	Adorned	Not used	-
Tadpole 1	2005	Not used	Adorned	Not used	-
Tadpole 2	2005	Not used	Adorned	Not used	-
Tadpole NW 1	2005	Not used	Unadorned	Not used	-
Valley 1	2005	New in 2005	Unadorned	Successful	2
Valley 2	2005	New in 2005	Adorned	Not used	-

<sup>1</sup> Used for nesting by owls, but unable to determine outcome.

<sup>2</sup> Adult, probably male, found dead of unknown causes <3m from burrow.

<sup>3</sup> Cause of failure likely disease or starvation.

APPENDIX B

**Artificial Burrow Systems (ABSs) Included in a Reuse Experiment for Burrowing  
Owls in Southwestern Idaho 2004-2005.**

ABS name	Year	Status Previous Year	Treatment	Reused	Clutch Initiation	Clutch Size	Hatch Date	Flea Load	Number Fledged, or Reason for Failure
398 1	2004	Successful	Microwave	No	-	-	-	-	-
398 2	2004	Successful	Control	Yes	4 April <sup>2</sup>	7	5 May	Unknown <sup>5</sup>	5
Backyard 2	2004	Successful	Removal	No	-	-	-	-	-
Backyard 3	2004	Successful	Removal	No	-	-	-	-	-
Backyard 7	2004	Successful	Control	Yes	10 April <sup>3</sup>	10	18 May	Low <sup>6</sup>	7
Baja 4	2004	Failed	Removal	No	-	-	-	-	-
Baja 5	2004	Failed	Control	No	-	-	-	-	-
Baja Pole 19	2004	Successful	Control	Yes	10 April <sup>3</sup>	9	11 May	Medium <sup>6</sup>	7
Baja Pole 20	2004	Failed	Control	No	-	-	-	-	-
Baja Pole 30	2004	Successful	Microwave	Yes	9 April <sup>3</sup>	10	13 May	Unknown <sup>5</sup>	6
Baja Pole 31	2004	Successful	Control	Yes	10 April <sup>3</sup>	10	18 May	Unknown <sup>5</sup>	3
Baja Pole 37	2004	Failed	Removal	No	-	-	-	-	-
Baja Pole 38	2004	Successful	Microwave	No	-	-	-	-	-
Baja Pole 46 4	2004	Failed	Removal	No	-	-	-	-	-
Camp 1	2004	Used <sup>1</sup>	Microwave	Yes	8 April <sup>2</sup>	9	12 May	Low <sup>6</sup>	9
Canyon 4	2004	Successful	Microwave	No	-	-	-	-	-
Curlew 2	2004	Successful	Removal	Yes	12 April <sup>2</sup>	10	17 May	Medium <sup>7</sup>	Unknown <sup>9</sup>
Curlew 4	2004	Failed	Removal	Yes	7 April <sup>3</sup>	9	13 May	Medium <sup>6</sup>	7
Dorsey 2	2004	Failed	Control	No	-	-	-	-	-
Dorsey 4	2004	Failed	Removal	No	-	-	-	-	-
Dorsey East 2	2004	Successful	Removal	No	-	-	-	-	-
Dorsey East 3	2004	Successful	Microwave	No	-	-	-	-	-
Grand View 19	2004	Failed	Removal	No	-	-	-	-	-
Highway 1	2004	Failed	Removal	No	-	-	-	-	-
Kuna Butte 1	2004	Failed	Microwave	No	-	-	-	-	-
Kuna Butte 3 (Andy 1)	2004	Successful	Microwave	No	-	-	-	-	-
Kuna Butte Ag 2	2004	Used <sup>1</sup>	Removal	No	-	-	-	-	-

ABS name	Year	Status Previous Year	Treatment	Reused	Clutch Initiation	Clutch Size	Hatch Date	Flea Load	Number Fledged, or Reason for Failure
Missile 3	2004	Used <sup>1</sup>	Removal	No	-	-	-	-	-
Powerline 3	2004	Successful	Removal	No	-	-	-	-	-
Sub South 2	2004	Failed	Removal	No	-	-	-	-	-
Sub South 4	2004	Failed	Removal	No	-	-	-	-	-
Sub South 7	2004	Successful	Control	Yes	17 April <sup>2</sup>	9	21 May	High <sup>6</sup>	2
Sub Southeast 1	2004	Failed	Microwave	No	-	-	-	-	-
Swan Falls Ag 2	2004	Successful	Control	No	-	-	-	-	-
Trailer View 2	2004	Successful	Removal	No	-	-	-	-	-
Well 1	2004	Successful	Control	No	-	-	-	-	-
398 2	2005	Successful	Removal	No	-	-	-	-	-
Backyard 1	2005	Successful	Microwave	Yes	11 April <sup>3</sup>	10	14 May	Medium <sup>6</sup>	1
Backyard 5	2005	Successful	Removal	No	-	-	-	-	-
Backyard 7	2005	Successful	Control	No	-	-	-	-	-
Baja 1	2005	Successful	Control	Yes	2 April <sup>2</sup>	9	6 May	Low <sup>7</sup>	Flooded
Baja 7	2005	Successful	Removal	No	-	-	-	-	-
Baja 9	2005	Successful	Microwave	No	-	-	-	-	-
Baja Pole 19	2005	Successful	Microwave	No	-	-	-	-	-
Baja Pole 30	2005	Successful	Microwave	Yes	Unknown	10	Did not hatch	Low <sup>7</sup>	Flooded
Baja Pole 31	2005	Successful	Removal	No	-	-	-	-	-
Camp 1	2005	Successful	Control	No	-	-	-	-	-
Curlew 2	2005	Failed	Microwave	Yes	Unknown	10	Did not hatch	Low <sup>7</sup>	Flooded
Curlew 3	2005	Failed	Removal	No	-	-	-	-	-
Curlew 4	2005	Successful	Control	Yes	15 April <sup>3</sup>	7	Did not hatch	Low <sup>7</sup>	Flooded
Curlew 5	2005	Successful	Control	Yes	11 April <sup>3</sup>	10	14 May	None <sup>7</sup>	Flooded
Dirtmound 1	2005	Successful	Control	No	-	-	-	-	-
Dirtmound 3	2005	Failed	Microwave	No	-	-	-	-	-
Honeybee 2	2005	Failed	Removal	No	-	-	-	-	-
Missile 1	2005	Successful	Removal	No	-	-	-	-	-

ABS name	Year	Status Previous Year	Treatment	Reused	Clutch Initiation	Clutch Size	Hatch Date	Flea Load	Number Fledged, or Reason for Failure
Missile 2	2005	Successful	Microwave	Yes	2 April <sup>2</sup>	10	7 May	Low <sup>7</sup>	6
Missile 4	2005	Successful	Removal	Yes	Unknown	6	Did not hatch	Low <sup>7</sup>	Unknown <sup>10</sup>
Mountain View 1	2005	Successful	Microwave	Yes	6 April <sup>3</sup>	9	11 May	High <sup>6</sup>	4
Mountain View 2	2005	Failed	Removal	Yes	4 April <sup>3</sup>	9	6 May	Low <sup>6</sup>	6
Shadscale East 1	2005	Successful	Control	Yes	18 April <sup>3</sup>	11	Did not hatch	Low <sup>7</sup>	Flooded
Shadscale South 2	2005	Failed	Control	No	-	-	-	-	-
Shadscale West 2	2005	Successful	Removal	Yes	Unknown	2	Did not hatch	Unknown <sup>8</sup>	Unknown <sup>10</sup>
Sprinkler 1	2005	Successful	Microwave	Yes	9 April <sup>3</sup>	10	Did not hatch	Medium <sup>7</sup>	Flooded
Sprinkler 4	2005	Successful	Control	No	-	-	-	-	-
Sub East 2	2005	Successful	Control	No	-	-	-	-	-
Sub South 1	2005	Failed	Microwave	No	-	-	-	-	-
Sub South 5	2005	Failed	Removal	No	-	-	-	-	-
Sub South 6	2005	Successful	Removal	Yes	10 May <sup>4</sup>	7	10 June	Low <sup>6</sup>	6
Sub South 7	2005	Successful	Removal	No	-	-	-	-	-
Swan Falls Ag 1	2005	Successful	Removal	No	-	-	-	-	-
Trailer 2	2005	Successful	Removal	No	-	-	-	-	-
Trailer 4	2005	Successful	Microwave	Yes	16 April	10	Did not hatch	None <sup>7</sup>	Flooded
Trailer View 4	2005	Successful	Removal	No	-	-	-	-	-
Well 2	2005	Successful	Removal	No	-	-	-	-	-
Well 3	2005	Failed	Control	No	-	-	-	-	-

<sup>1</sup> Used for nesting by owls, but unable to determine fate.

<sup>2</sup> Estimated from hatch date.

<sup>3</sup> Estimated from egg count before clutch complete.

<sup>4</sup> Likely a renest after early breeding failure.

<sup>5</sup> Not recorded.

<sup>6</sup> Based on median flea load of young.

<sup>7</sup> Based on flea load of adult female.

<sup>8</sup> Failed before banding age and adults not captured.

<sup>9</sup> Cause of failure likely disease or starvation.

<sup>10</sup> Cause of failure possibly researcher disturbance.

## APPENDIX C

**Body Condition Indices (BCIs) for Burrowing Owl Nestlings in Southwestern Idaho 2004-2005. BCIs Were Generated by Regressing Body Mass (g) on Tarsus Length (mm) with Age (days) as a Covariate and Nest ID as a Repeated Subject. A Positive BCI Represents Good Body Condition and a Negative Value Indicates Poor Body Condition.**

Band Number	Age	Nest ID	Treatment	Mass	Tarsus	BCI
1204-24960	24	2004Backyard 7	Control	103	41	-38.17
1204-24961	24	2004Backyard 7	Control	119	37	-9.02
1204-24963	24	2004Backyard 7	Control	93	37	-35.02
1204-24964	24	2004Backyard 7	Control	123	41	-18.17
1204-24965	24	2004Backyard 7	Control	89	36	-35.73
1204-24966	24	2004Backyard 7	Control	101	39	-33.59
1204-24967	24	2004Backyard 7	Control	135	40	-2.88
1204-24873	24	2004Baja Pole 19	Control	140	38	8.69
1204-24874	24	2004Baja Pole 19	Control	164	38	32.69
1204-24875	24	2004Baja Pole 19	Control	139	36	14.27
1204-24876	24	2004Baja Pole 19	Control	146	37	17.98
1204-24877	24	2004Baja Pole 19	Control	133	38	1.69
1204-24878	24	2004Baja Pole 19	Control	142	34	23.85
1204-24879	24	2004Baja Pole 19	Control	134	34	15.85
1204-24957	24	2004Baja Pole 31	Control	127	38	-4.31
1204-24958	24	2004Baja Pole 31	Control	96	32	-15.58
1204-24959	24	2004Baja Pole 31	Control	95	30	-10.00
1204-24865	26	2004398 2	Control	151	40	13.78
1204-24866	26	2004398 2	Control	143	42	-0.80
1204-24868	26	2004398 2	Control	137	39	3.07
1204-24869	26	2004398 2	Control	145	43	-2.08
1204-24870	26	2004398 2	Control	143	43	-4.08
1204-24975	29	2004Sub South 7	Control	147	42	4.20
1204-24976	29	2004Sub South 7	Control	165	44	15.63
804-24288	29	2005West Baja 1	Control	142	42	-0.80
804-24289	29	2005West Baja 1	Control	142	44	-7.37
804-24290	29	2005West Baja 1	Control	143	42	0.20
804-24291	29	2005West Baja 1	Control	146	43	-0.08
804-24292	29	2005West Baja 1	Control	143	45	-9.66
804-24293	29	2005West Baja 1	Control	134	41	-5.51
804-24143	24	2005Mountain View 1	Microwave	96	32	-15.58
804-24144	24	2005Mountain View 1	Microwave	107	30	2.00
804-24146	24	2005Mountain View 1	Microwave	94	32	-17.58
804-24149	24	2005Mountain View 1	Microwave	117	35	-4.44
804-24167	25	2005Backyard 1	Microwave	143	38	12.03
1204-24882	25	2004Baja Pole 30	Microwave	118	38	-12.97
1204-24883	25	2004Baja Pole 30	Microwave	131	42	-13.13
1204-24884	25	2004Baja Pole 30	Microwave	108	37	-19.69
1204-24885	25	2004Baja Pole 30	Microwave	122	38	-8.97
1204-24886	25	2004Baja Pole 30	Microwave	108	37	-19.69
1204-24887	25	2004Baja Pole 30	Microwave	105	36	-19.40
804-24137	26	2005Missile 2	Microwave	160	41	19.49
804-24138	26	2005Missile 2	Microwave	160	43	12.92
804-24139	26	2005Missile 2	Microwave	168	45	14.34
804-24140	26	2005Missile 2	Microwave	148	40	10.78
804-24141	26	2005Missile 2	Microwave	176	44	25.63
804-24142	26	2005Missile 2	Microwave	155	40	17.78
1204-24914	28	2004Camp 1	Microwave	148	43	1.58



Band Number	Age	Nest ID	Treatment	Mass	Tarsus	BCI
1204-24915	28	2004Camp 1	Microwave	135	44	-14.70
1204-24916	28	2004Camp 1	Microwave	140	41	0.16
1204-24917	28	2004Camp 1	Microwave	148	43	1.58
1204-24918	28	2004Camp 1	Microwave	131	42	-12.13
1204-24919	28	2004Camp 1	Microwave	150	43	3.58
1204-24920	28	2004Camp 1	Microwave	127	42	-16.13
1204-24921	28	2004Camp 1	Microwave	106	36	-17.40
1204-24922	28	2004Camp 1	Microwave	141	40	4.45
1204-24891	25	2004Curlew 4	Removal	125	37	-2.69
1204-24892	25	2004Curlew 4	Removal	124	37	-3.69
1204-24893	25	2004Curlew 4	Removal	100	35	-21.11
1204-24894	25	2004Curlew 4	Removal	123	38	-7.97
1204-24895	25	2004Curlew 4	Removal	107	37	-20.69
1204-24896	25	2004Curlew 4	Removal	85	33	-29.53
1204-24897	25	2004Curlew 4	Removal	130	37	2.31
804-24127	25	2005Mountain View 2	Removal	152	43	4.59
804-24128	25	2005Mountain View 2	Removal	143	41	2.16
804-24129	25	2005Mountain View 2	Removal	136	40	-1.55
804-24130	25	2005Mountain View 2	Removal	157	40	19.45
804-24131	25	2005Mountain View 2	Removal	144	38	13.03
804-24132	25	2005Mountain View 2	Removal	152	43	4.59
804-24259	31	2005Sub South 6	Removal	142	45	-10.00
804-24260	31	2005Sub South 6	Removal	135	43	-10.42
804-24261	31	2005Sub South 6	Removal	159	47	0.43
804-24262	31	2005Sub South 6	Removal	136	43	-9.42
804-24263	31	2005Sub South 6	Removal	142	44	-6.71
804-24264	31	2005Sub South 6	Removal	136	44	-12.71
804-24279	23	2005Trailer 1	None	152	43	3.92
804-24280	23	2005Trailer 1	None	137	41	-4.50
804-24281	23	2005Trailer 1	None	142	43	-6.08
804-24282	23	2005Trailer 1	None	143	44	-8.37
804-24283	23	2005Trailer 1	None	139	42	-5.79
804-24118	24	2005Baja Pole 46 2	None	138	34	19.85
804-24119	24	2005Baja Pole 46 2	None	122	33	7.13
804-24121	24	2005Baja Pole 46 2	None	115	33	0.13
804-24273	24	2005Strike Dam 1	None	151	43	3.25
804-24274	24	2005Strike Dam 1	None	145	44	-6.03
804-24275	24	2005Strike Dam 1	None	144	45	-10.32
804-24276	24	2005Strike Dam 1	None	152	44	0.97
804-24277	24	2005Strike Dam 1	None	127	38	-4.31
804-24278	24	2005Strike Dam 1	None	130	40	-7.88
804-24191	25	2005398 3	None	145	39	10.74
804-24193	25	2005398 3	None	150	37	22.31
804-24194	25	2005398 3	None	146	42	1.87
804-24197	25	2005398 3	None	154	40	16.45
804-24224	25	2005Backyard 3	None	138	40	0.45
804-24225	25	2005Backyard 3	None	113	37	-14.69
804-24226	25	2005Backyard 3	None	134	38	3.03
804-24227	25	2005Backyard 3	None	133	39	-1.26

Band Number	Age	Nest ID	Treatment	Mass	Tarsus	BCI
804-24228	25	2005Backyard 3	None	139	40	1.45
804-24229	25	2005Backyard 3	None	117	32	5.76
804-24134	25	2005Baja 5	None	132	34	14.18
804-24135	25	2005Baja 5	None	151	38	20.03
804-24136	25	2005Baja 5	None	140	35	18.89
1204-24902	25	2004Mountain View 1	None	168	44	17.30
1204-24903	25	2004Mountain View 1	None	170	42	25.87
1204-24904	25	2004Mountain View 1	None	159	41	18.16
1204-24905	25	2004Mountain View 1	None	153	38	22.03
804-24133	25	2005Mountain View 4	None	128	33	13.47
804-24201	25	2005Shadscale West 3	None	139	39	4.74
804-24202	25	2005Shadscale West 3	None	121	40	-16.55
804-24203	25	2005Shadscale West 3	None	124	39	-10.26
804-24204	25	2005Shadscale West 3	None	130	39	-4.26
804-24205	25	2005Shadscale West 3	None	150	40	12.45
804-24206	25	2005Shadscale West 3	None	123	40	-14.55
1204-24888	25	2004Sprinkler 1	None	133	41	-7.84
1204-24889	25	2004Sprinkler 1	None	132	42	-12.13
1204-24890	25	2004Sprinkler 1	None	128	41	-12.84
1204-43488	25	2004Trailer 4	None	134	45	-19.99
1204-43489	25	2004Trailer 4	None	125	39	-9.26
1204-43490	25	2004Trailer 4	None	114	40	-23.55
1204-43491	25	2004Trailer 4	None	115	40	-22.55
1204-43492	25	2004Trailer 4	None	134	41	-6.84
804-24168	25	2005Trailer 5	None	142	37	14.31
804-24169	25	2005Trailer 5	None	121	37	-6.69
804-24170	25	2005Trailer 5	None	134	39	-0.26
804-24171	25	2005Trailer 5	None	137	38	6.03
804-24172	25	2005Trailer 5	None	122	37	-5.69
804-24173	25	2005Trailer 5	None	118	34	0.18
804-24174	25	2005Trailer 5	None	129	34	11.18
1204-24994	26	2004Backyard 1	None	132	38	1.36
1204-24995	26	2004Backyard 1	None	135	37	7.65
1204-24997	26	2004Backyard 1	None	93	33	-21.20
1204-24999	26	2004Backyard 1	None	124	36	-0.06
804-10376	26	2004Baja 1	None	145	38	14.36
804-10377	26	2004Baja 1	None	120	36	-4.06
1204-24907	26	2004Baja 7	None	123	36	-1.06
1204-24908	26	2004Baja 7	None	140	38	9.36
1204-24909	26	2004Baja 7	None	151	38	20.36
1204-24910	26	2004Baja 7	None	138	35	17.22
1204-24912	26	2004Baja 7	None	152	42	8.21
1204-24913	26	2004Baja 7	None	143	38	12.36
804-24265	26	2005Baja Pole 38	None	92	37	-35.35
804-24266	26	2005Baja Pole 38	None	108	40	-29.22
804-24267	26	2005Baja Pole 38	None	98	39	-35.93
1204-24860	26	2004Sub East 2	None	145	42	1.21
1204-24861	26	2004Sub East 2	None	150	40	12.78
1204-24862	26	2004Sub East 2	None	130	34	12.51

Band Number	Age	Nest ID	Treatment	Mass	Tarsus	BCI
1204-24864	26	2004Sub East 2	None	130	37	2.65
1204-24906	26	2004Sub East 2	None	138	42	-5.79
1204-24986	26	2004Trailer 2	None	135	41	-5.51
1204-24987	26	2004Trailer 2	None	147	39	13.07
1204-24989	26	2004Trailer 2	None	127	40	-10.21
1204-24990	26	2004Trailer 2	None	126	41	-14.51
1204-24991	26	2004Trailer 2	None	156	43	8.92
1204-24993	26	2004Trailer 2	None	130	40	-7.22
1204-24827	26	2004Well 2	None	141	43	-6.08
1204-24828	26	2004Well 2	None	141	42	-2.79
1204-24829	26	2004Well 2	None	148	44	-2.37
1204-24830	26	2004Well 2	None	145	40	7.78
804-24159	27	2005Powerline 4	None	124	37	-3.02
804-24161	27	2005Powerline 4	None	116	35	-4.44
804-24165	27	2005Powerline 4	None	112	34	-5.16
1204-24900	27	2004Shadscale West 2	None	156	48	-7.19
1204-24901	27	2004Shadscale West 2	None	152	45	-1.33
804-24112	27	2005Trailer View 1	None	153	38	22.69
804-24113	27	2005Trailer View 1	None	155	39	21.40
804-24230	28	2005Baja 3	None	157	40	20.45
804-24231	28	2005Baja 3	None	160	40	23.45
804-24232	28	2005Baja 3	None	157	43	10.58
804-24233	28	2005Baja 3	None	158	40	21.45
804-24234	28	2005Baja 3	None	152	40	15.45
804-24284	30	2005Curlew 8	None	132	42	-10.46
804-24285	30	2005Curlew 8	None	141	41	1.82
804-24286	30	2005Curlew 8	None	125	40	-10.89
804-24287	30	2005Curlew 8	None	137	40	1.11
1204-24853	30	2004Shadscale East 1	None	145	43	-0.75
1204-24855	30	2004Shadscale East 1	None	125	41	-14.18
1204-24898	30	2004Shadscale East 1	None	128	39	-4.60
1204-24899	30	2004Shadscale East 1	None	130	42	-12.46