BEHAVIORAL RESPONSES OF BURROWING OWLS TO EXPERIMENTAL CLUTCH MANIPULATIONS: AN INVESTIGATION OF CONSPECIFIC BROOD PARASITISM AND LAYING DETERMINACY

By

Jamie Lynn Groves

A thesis
submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Raptor Biology
Boise State University

August 2014

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BOISE STATE UNIVERSITY GRADUATE COLLEGE

DEFENSE COMMITTEE AND FINAL READING APPROVALS

of the thesis submitted by

Jamie Lynn Groves

Thesis Title:	Behavioral Responses of Burrowing Owls to Experimental Clutch Manipulations: An Investigation of Conspecific Brood Parasitism and Laying Determinacy.

Date of Final Oral Examination: 13 June 2014

The following individuals read and discussed the thesis submitted by student Jamie Lynn Groves, and they evaluated her presentation and response to questions during the final oral examination. They found that the student passed the final oral examination.

James R. Belthoff, Ph.D.	Chair, Supervisory Committee
Jesse R. Barber, Ph.D.	Member, Supervisory Committee
Ian C. 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

For Tucker Lee

ACKNOWLEDGEMENTS

I would like to express my gratitude to the members of my committee, Dr. Jesse Barber and Dr. Ian Robertson, for their assistance and support in the preparation of this manuscript. I also thank Dr. Al Dufty for his insight during the early days of this project. Special thanks to my major professor Dr. Jim Belthoff for the guidance and encouragement he provided me during the 2.5 years that I have been at Boise State. I owe much appreciation to my field assistants Nadine Brock, Amanda Renken, Kylie Riebe, Nicole Santiago, and Diane White for all of their hard work. I am grateful to Mike Knutsen for his humor and superb hole-digging skills, and Maggie McCowin for her tremendous help and ability to keep me laughing in spite of the heat and abundant fleas and to my fellow graduate students for their advice and much appreciated friendships. I thank Sigma Xi, The Scientific Research Society, and Boise State University's Hemingway Western Studies Center, Student Research Initiative, Raptor Research Center, and Department of Biological Sciences for helping to fund this study. I also thank the National Science Foundation GK-12 Fellowship program at Boise State University and the MK Nature Center for presenting me with opportunities that have enriched my graduate experience. I owe much appreciation to my family (both two and four legged) for all of their love and encouragement, and for keeping me sane throughout this process. I especially thank my best friend Kylene for her love and for 12 years of unwavering friendship. And most of all I thank my husband Jake for his remarkable support and

patience, and for accepting my highly erratic schedule during the first six months of our marriage. I could not have completed this thesis without him.

ABSTRACT

During 2012-2013, I investigated the behavioral responses of western burrowing owls (*Athene cunicularia hypugaea*) in southwestern Idaho to experimental conspecific brood parasitism to determine if they were capable of egg discrimination, and if they would accept or reject a parasitic egg introduced into their nest. I experimentally added one egg derived from source nests to host nests either during the egg-laying period or just after adult females initiated incubation and examined acceptance or rejection of the parasitic egg in relation to control nests where eggs were handled but not exchanged. Burrowing owl responses to parasitic eggs varied with nesting stage. Burrowing owls rejected at 3 of 11 (27%) nests in which an experimental conspecific egg was added during the laying period and accepted the parasitic egg at each of the 11 nests experimentally parasitized during incubation. None of the control nests (n = 17) experienced rejection of eggs or abandonment of the nest after handling of eggs. Early deposited parasitic eggs may pose a greater threat to host fitness because of increased chance of hatching, which may explain why more early deposited parasitic eggs were rejected. Burrowing owls rejected the nest at an additional 3 of 12 (25%) nests in which an experimental egg was reciprocally exchanged. This behavior suggests that hosts were able to perceive that their nest had been parasitized based on the presence of the parasitic egg rather than on any sudden increase in clutch size. Size differences between host and parasitic eggs and the degree of size variability among eggs within host clutches had no effect on rejection. Instead of selectively rejecting the individual parasitic eggs, hosts buried them along with their own eggs. This implies that the hosts could not remove the parasitic egg or they were unable to individually recognize it. I also assessed changes in parental care by evaluating images from motion-activated infrared cameras placed at owl nests. There was no significant difference in burrow attendance of both male and female adult burrowing owls between treatment (male: 15.6 ± 2.14 (SE) min/hr; female: 25.7 ± 1.80) and control (male: 12.9 ± 2.88 min/hr; female: 30.5 ± 3.85) nests; nor was there a significant difference in prey delivery rate (treatment: 0.3 ± 0.15 prey/nestling/hr; control: 0.5 ± 0.34 prey/nestling/hr) or prey biomass delivered (treatment: 5.5 ± 1.82 g/nestling/hr; control: 4.2 ± 1.76 g/nestling/hr). Thus, burrowing owls may either be unable to identify parasitic nestlings or unwilling to decrease parental care if the cost is decreasing their own offspring's survival. Finally, I assessed laying determinacy by comparing completed clutch sizes of nests where I removed (i.e., source nests for parasitic eggs) or added one egg during laying, to completed clutch sizes of un-manipulated control nests. Mean clutch size was significantly larger at nests where I added an egg (10.7 ± 0.67, $n = 9$) than at control nests (8.8 ± 0.18, $n = 17$), while clutch sizes for control and in nests where we removed one egg (8.3 ± 0.44, $n = 9$) did not differ. These findings suggest that female burrowing owls responded to the removal of an egg by laying a replacement, yet they did not curtail laying in response to the addition of an egg to their nest. Thus, female burrowing owls in my study area may be described as removal indeterminate and addition determinate. The results of my study are consistent with the notion that conspecific brood parasitism is part of the behavioral repertoire of burrowing owls, and they also may provide insight into how laying determinacy can facilitate conspecific brood parasitism or mitigate its costs in this species.

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LIST OF ABBREVIATIONS

CBP	Conspecific Brood Parasitism
FSH	Follicle Stimulating Hormone
LH	Luteinizing Hormone
NCA	Morley Nelson Birds of Prey National Conservation Area

GENERAL INTRODUCTION

This thesis consists of two chapters describing my investigation of the nesting behavior of western burrowing owls (*Athene cunicularia hypugaea*) in southwestern Idaho. In 2012 and 2013, I performed a series of clutch manipulations designed to simulate conspecific brood parasitism. These experiments also provided insight into the parental care and laying patterns of burrowing owls. The purpose of my field research was to (1) determine if and how burrowing owls respond to simulated parasitic eggs from conspecifics in their nests, (2) characterize how laying stage, increased clutch size, and egg size affect the response of burrowing owls to a parasitic egg, (3) describe any changes in parental care patterns as a function of unrelated offspring present in the nest, and (4) determine whether burrowing owls are determinate or indeterminate egg-layers. Information contained in this thesis may be particularly useful to those interested in the behavioral and reproductive ecology of burrowing owls, and to those concerned with the management and conservation of this owl species.

Study Species

Western burrowing owls (*Athene cunicularia hypugaea*) occur throughout western North America in arid and semi-arid environments characterized by sparse vegetation and bare ground (Poulin et al. 2011). They breed in open, well-drained grasslands, prairies, and steppes from as far north as British Columbia to as far south as central Mexico (Enriquez-Rocha 1997, Wellicome and Holroyd 2001, Poulin et al. 2011). The eastern limit of their breeding range lies roughly along a line from central Manitoba to northwest Louisiana (Zarn 1974). In the northern portions of their range, western burrowing owls are annual migrants; they often arrive on breeding grounds in March and April and then migrate south to winter during September and October (AOU 1998, Poulin et al. 2011). In southern regions of their distribution, they are generally year-round residents. In Idaho, burrowing owls are typically only present during the breeding season (March - October), although a small number of owls remain during winter. Little information is available describing the migration routes of burrowing owls breeding in Idaho (King and Belthoff 2001, Poulin et al. 2011); however, a small number of band returns indicate that some Idaho owls appear to overwinter in California (Belthoff, unpublished data).

Burrowing owls are small, weigh approximately 150-200 g as adults, and have brown-colored plumage with white streaks and spots. They have a rounded head, which lacks ear tufts, buffy-white margins around yellow eyes, and a white throat patch. Juveniles appear similar to adults but lack streaking on their buffy-colored abdomen. Burrowing owls are the only North American strigiform that do not exhibit reversed sexual size dimorphism (Poulin et al. 2011). Males and females have similar plumage, although fading and feather wear tends to leave males somewhat lighter dorsally during the breeding season (Thomsen 1971, Zarn 1974, Poulin et al. 2011).

Burrowing owls are opportunistic predators that feed primarily on small mammals and arthropods but also on birds, amphibians, and reptiles. They typically forage in croplands, pastures, fallow fields, and grasslands. Areas with vegetation taller than 1 m is less suitable, perhaps because the owls have difficulty capturing prey or detecting approaching predators (Haug and Oliphant 1990, Wellicome 1994). Burrowing owls are primarily crepuscular hunters, although they can forage during all times of the day (Moulton et al. 2005, Poulin and Todd 2006, Littles et al. 2007, Williford et al. 2009, Poulin et al. 2011).

Burrowing owls are socially monogamous, although Barclay and Menzel (2011) reported a rare case of polygyny where one male paired with two females that each raised young. Burrowing owls are capable of breeding at one year of age, but some females may not breed until their second year (Lutz and Plumpton 1999). The owls nest in underground burrows that they do not dig themselves. They frequently use black-tailed prairie dog (*Cynomys ludovicianus*) and ground squirrel (Spermophilus sp.) burrows; although in southwestern Idaho, natural burrows used for roosting and nesting are typically dug by American badgers (*Taxidea taxus*; Gleason and Johnson 1985, Rich 1986). Burrowing owls nest in both high-density and low-density configurations in many portions of their range and are described as semi-colonial in some situations (Desmond and Savidge 1996, Desmond et al. 2000, DeSante et al. 2004, Lantz et al. 2007, Tipton et al. 2008). In Idaho, the distributions of nesting pairs vary: owls have nested with six neighboring pairs within 400 m of a focal nest, whereas in other cases kilometers separate nesting pairs (Welty 2010, Welty et al. 2012). The average clutch size of a female owl breeding in Idaho is 9.9 eggs (Olenick 1990), while throughout their range clutch size can vary from 4-14 eggs (Todd and Skilnick 2003, Poulin et al. 2011). Females perform incubation, which lasts for approximately 23 days (Welty 2010), although other studies have reported longer (28-30 days; Coulombe 1971, Thomsen 1971, Poulin et al. 2011) and shorter (22 days; Conway et al. 2012) incubation periods. The onset of incubation can range from the first to the last egg laid, but females typically initiate incubation after more than half of the clutch has been laid (Conway et al. 2012). The female will brood recently hatched nestlings for one to two weeks and relies upon her mate to provide food (Poulin et al. 2011). Nestlings typically emerge from the burrow at 10-14 days of age, run and forage by four weeks, and are capable of sustained flight by six weeks of age (King and Belthoff 2001, Poulin et al. 2011).

Overview of Chapters One and Two

In Chapter One, I present the findings of an experiment designed to examine how burrowing owls respond to the presence of a parasitic egg in their nest. I simulated conspecific brood parasitism by introducing an experimental egg (removed from a source burrowing owl nest) into the nests of host burrowing owls during either the laying (laying addition) period or during the incubation (incubation addition) period. In these two treatment groups, I was able to evaluate the host response to the experimental addition of an egg such as would occur if a female burrowing owl parasitized the nest of another female. I also performed reciprocal swaps (laying reciprocal) of eggs at nests where I added an experimental egg but also removed one of the host eggs; in laying reciprocal nests, hosts experienced a foreign egg, but their clutch size was not changed. This treatment group allowed me to examine the response of hosts to experimental eggs without the added stimulus of an extra egg, such as perhaps might occur if a parasitic female removed one of the host’s eggs prior to parasitizing the nest, as occurs in some species of birds. I ultimately compared the incidence of nest abandonment at treatment nests to that of controls (no experimental egg introduced) so I could account for any potential effects of human disturbance on nest abandonment. In addition, I used motion-activated infrared cameras positioned in front of owl nests to monitor any post-hatch changes in parental behavior that may have resulted from the presence of an unrelated nestling in the brood. Potentially, burrowing owls may be constrained from rejecting a parasitic egg from their clutch, but they in turn may alter provisioning or nest attendance behavior (i.e., warning calls, guarding and/or defending the nest) to avoid investing effort into non-genetic offspring. To assess this, I quantified and characterized nest attendance, prey delivery rates, and prey biomass at both treatment and control nests.

Some burrowing owls rejected experimental eggs that I introduced to their nests during the laying period, but none rejected experimental eggs added during incubation. In each case of rejection, the owls either abandoned the parasitized clutch and re-nested nearby, or they completely abandoned the nest site. Repeated human disturbance did not cause abandonment at any control nests. Therefore, burrowing owls appeared to respond to the presence of a foreign egg by abandoning the parasitized clutch and starting a new one. They also appeared to respond similarly regardless of whether one of their own eggs was swapped with the parasitic egg or the parasitic egg was simply added. The response of burrowing owls to foreign eggs in their nest appears to be strongly influenced by nesting stage, whereby owls will accept a foreign egg if it appears later in their breeding cycle (incubation).

The degree of difference between the host’s own eggs and the parasitic egg did not affect the host’s response. Both parasitic eggs that were similar and different in size from the host’s own eggs were accepted within host nests. Furthermore, intraclutch variation in size of host eggs did not affect the likelihood of rejection of a parasitic egg. Some parasitic eggs were rejected from host nests that had the largest degree of intraclutch variation, while the majority of parasitic eggs were accepted at host nests that had little intraclutch variation. Thus, burrowing owls did not appear to rely on their familiarity with their own eggs to detect the “odd” parasitic egg. At the end of Chapter One, I discuss the potential implications of this behavior in burrowing owls.

Furthermore, burrowing owls did not appear to adjust their parental care in response to a parasitic nestling amongst their own brood. Nest attendance, prey delivery rates, and the biomass of prey delivered were no different between treatment and control nests. Among the possible explanations for observing no difference in parental care behavior is burrowing owls may not discriminate between their own offspring and those that are parasitic, and thus they continue to invest parental effort at a high rate. Another possibility is that the owls can sense that an imposter lurks amongst their own offspring, but the costs of decreasing parental effort for the entire brood outweighs the benefits of starving the parasitic nestling. Finally, it is possible that I failed to detect any difference because too few of the parasitic nestlings survived long enough to have an influence on parental behavior.

Chapter Two focuses on determining whether there is a determinate or indeterminate egg-laying response of burrowing owls to an increase or decrease in clutch size. I defined clutch size as the total number of eggs present in a female’s nest at the onset of incubation. I took advantage of the manipulations that I performed in Chapter One, and compared the final clutch sizes at nests where I removed (removal nests) or added (addition nests) an egg to the final clutch sizes of the control nests. In doing so, I was able to determine if the females factored the removed or added egg into their final clutch size assessments. That is, did females lay an additional egg to replace the one that I had removed, or did they lay one fewer of their own eggs to account for the one that I added?

Burrowing owls did not appear to respond to the addition of an egg by curtailing their own laying; instead, they continued to lay an entire clutch of eggs uninterrupted. When I compared the completed clutch size of nests where I experimentally added one egg to the completed clutch size of controls, the former had significantly more eggs present. This result suggests that burrowing owls are addition determinate. On the other hand, when I compared the completed clutch sizes of the nests where I experimentally removed one egg to the completed clutch sizes of the control nests, I did not find a significant difference in the final number of eggs that were present in the nest when the female began incubating. Thus, burrowing owls responded to the removal of one of their eggs by apparently laying a replacement egg. This suggests that burrowing owls are removal-indeterminate. I conclude Chapter Two of my thesis with a discussion of the implications of indeterminate and determinate laying patterns in burrowing owls and how these results may clarify our understanding of conspecific brood parasitism and its potential role in burrowing owl nesting behavior.

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CHAPTER ONE: BEHAVIORAL RESPONSES OF BURROWING OWLS TO EXPERIMENTAL CONSPECIFIC BROOD PARASITISM

Abstract

I investigated the behavioral responses of western burrowing owls (*Athene cunicularia hypugaea*) to experimental conspecific brood parasitism in southwestern Idaho during 2012 and 2013. By introducing one conspecific egg into host owl nests, I wanted to determine (1) if nesting burrowing owls were capable of egg discrimination, and (2) if they would accept or reject a simulated parasitic egg that I introduced into their nest. To assess the potential effect of nesting stage on host response, I added one egg into some nests during the laying period and added one egg into other nests during the incubation period. I further tested the ability of burrowing owls to detect a parasitic egg by swapping one of the host's own eggs with the parasitic egg during the laying period. The latter manipulation resulted in a set of nests where the host encountered a parasitic egg, but their original clutch size did not change. In this case, hosts could not rely on sudden increases in clutch size to detect a parasitic egg. In addition to assessing the response of burrowing owls to parasitic eggs, I installed 10 motion-activated infrared nest cameras in both 2012 and 2013 so I could examine any changes in parental care as a result of a parasitic nestling. Overall, I experimentally parasitized 34 burrowing owl nests and created 17 control owl nests. Burrowing owls rejected at 3 of 11 (27%) nests in which an experimental conspecific egg was added during the laying period and accepted the parasitic egg at each of the 11 nests experimentally parasitized during incubation.

Burrowing owls rejected the nest at an additional 3 of 12 (25%) nests in which an experimental egg was reciprocally exchanged. This result was unexpected, because this behavior suggests that hosts were able to perceive that their nest had been parasitized based on the presence of the parasitic egg rather than on any sudden increase in clutch size. Instead of selectively rejecting the parasitic egg, hosts responded by burying the parasitic egg along with any of their own eggs that were present at that time. This is an unusual response to conspecific brood parasitism because it implies that the hosts were either physically incapable of removing the parasitic egg from their nest, or that they were unable to recognize which was the parasitic egg, and therefore responded by rejecting the entire parasitized clutch. If the hosts were able to detect the parasitic egg, the cue they used to identify it remains unclear. The degree of difference in size between host eggs and the parasitic egg and the level of intraclutch variation within the host's own eggs had no effect on whether a parasitic egg was rejected; however, it is possible that the owls used some other morphological or biochemical cue that was imperceptible to human senses. Parasitic eggs that are introduced during laying may pose a greater threat to host fitness because of an increased chance of successfully hatching, which may explain why burrowing owls rejected a greater number of early deposited parasitic eggs. The burrowing owls in my study displayed great intraclutch variation in egg size and shape; thus, it is not surprising that the degree of difference between the host's eggs and the parasitic egg was not a strong predictor of rejection behavior. Furthermore, I was unable to detect any differences in parental behavior between nests that had been parasitized and those that had not. Burrowing owls may be unable to identify an unrelated nestling among their own brood, or they may be unwilling to decrease their effort to expunge the imposter if the price they pay is decreasing the survival of their own young. If clutch desertion and burial are defensive behaviors that burrowing owls used to avoid the costs of raising a single parasitic egg, then these adaptive responses are poorly developed in this species because of the apparent high cost of rejection.

Introduction

Parental care (i.e., nest building, incubation, brooding, food provisioning, and defense) is energetically costly and consequently may reduce future parental reproductive success and survival (Trivers 1972, Andersson 1984). For this reason, it is not surprising that some birds attempt to avoid the costs of parental care under some circumstances (Rohwer and Freeman 1989). Conspecific brood parasitism (CBP) is an alternative reproductive strategy in which females lay eggs in the nests of other females of the same species (Yom-Tov 1980, Andersson 1984, Robertson et al. 1992). By transferring the care of some offspring to the host, the parasite may lessen or avoid the costs of parental care and enhance lifetime reproductive success (Davies and Brooke 1988, Field 1992, Brockmann 1993). On the other hand, the host may experience decreased reproductive success by investing parental effort into genetically unrelated offspring. CBP was once thought to be rare (Payne 1977), but it is now confirmed in over 236 species of birds (Yom-Tov 2001). The frequency of CBP varies widely within and among species (Sayler 1992), yet the factors that favor parasitism remain unclear. Current hypotheses on the adaptive value of CBP are typically classified into three types (Andersson 1984, Eadie et al. 1988, Petrie and Møller 1991, Sorenson 1991, Lyon 1993a), as I describe below.

First, brood parasitism may be a conditional tactic, such that any female may lay parasitically in a certain set of circumstances. For example, a female may lay eggs parasitically when an environmental factor, such as nest site limitation, affects her ability to breed independently. Nest-site availability is particularly important in cavity nesting species, where suitable nest-sites are often limiting (Andersson and Ericksson 1982, Eadie 1989, 1991, Semel and Sherman 2001). In the same way, a female who loses her nest to predation (Feare 1991, Jackson 1993) or some other factor may respond by laying her remaining eggs parasitically. For the parasitic female, this strategy may be less costly than attempting to re-nest or forgo reproduction entirely (Haramis et al. 1983). CBP may also be a conditional strategy arising from intrinsic factors. For example, if a female is in poor body condition or is inexperienced (Sorenson 1991), she may lay some or all of her own eggs parasitically because of her inability to access the resources she would need to nest on her own. Furthermore, floater females (females without nests) may lay parasitically in one season when they lack some vital resource but, given the chance, will lay eggs in their own nest the following season (Forslund and Larsson 1995, Sandell and Diemer 1999). Given these points, brood parasitism may allow females to obtain some reproductive fitness that would not have otherwise been possible, although it likely yields lower payoff than nesting independently. In more general terms, females may nest independently under some conditions but, under other conditions, may switch to brood parasitism as a conditional strategy.

Second, parasitism may be a specialist strategy, such that parasitic females rely entirely on other females to raise their offspring and do not lay eggs in their own nests. Presumably, successful specialist parasitic females would enjoy higher lifetime fitness because of advantages gained from emancipation from parental care. However, these advantages could only be realized if specialist parasitic females were rare in the population. Parasitic females rely entirely on nesting individuals to raise their offspring, therefore, if all females in the population were specialist brood parasites there would be an obvious lack of suitable host nests. Regardless, there are no accounts from any species that some females specialize as conspecific brood parasites (Lyon and Eadie 2008).

Finally, CBP could emerge as a mixed reproductive strategy. In this case, individual females would adopt a dual strategy and lay eggs in their own nests, but also lay eggs parasitically. Under this scenario, females do not lay parasitically because they are constrained from laying eggs in their own nests because of some intrinsic or extrinsic factor. These nesting females elect to lay some eggs parasitically when the opportunity arises, and as a result they may experience increased fitness beyond what would have been possible through nesting alone (Trivers 1972). A number of ecological and behavioral factors, such as nesting density (Brown 1984, Eadie and Fryxell 1992, Sayler 1992, Møller 1998), nesting synchrony (Lyon 1993a, b; McRae and Burke 1996) and large clutch size (Ar and Yom-Tov 1978) may affect the opportunity for females to lay eggs parasitically.

CBP can be costly to hosts in the following ways: parasites may displace or damage the host's own eggs during the act of parasitism (Lombardo et al. 1989); hosts may experience lower hatching or fledging success relative to non-parasitized pairs (Lank et al. 1990, Brown and Brown 1991, Sorenson 1991, Semel and Sherman 2001); the enlarged parasitized clutches could take longer to incubate and may be at a greater risk of predation (Gibbons 1986, Nielsen et al. 2006); or the hosts may even experience lower adult survival (Brown and Brown 1991). However, apart from the parasite damaging host eggs, it is possible that any of these potential costs to hosts could simply reflect that lower quality birds or territories may be more susceptible to parasitism (Eadie 1989, Lank et al. 1990). Furthermore, hosts may accept parasitic young because they gain some fitness benefit. For example, hosts may benefit through enhanced vigilance, or the enlarged brood dilutes the risk of predation for the host's own offspring (Andersson 1984, Eadie and Lumsden 1985, Eadie et al. 1988).

If the costs of CBP are high and hosts suffer lower fitness as a result of caring for unrelated offspring, hosts likely would evolve anti-parasitic behavior. The simplest way to avoid the costs of CBP is to prevent it from occurring. Hosts can aggressively guard their nest and drive off prospecting brood parasites (Emlen and Wrege 1986, Møller 1987, Brown and Brown 1989), selectively reject the parasitic egg, or abandon the parasitized clutch and start a new nest (Petrie and Møller 1991). Host responses to CBP vary, but the type of response may depend on how frequently CBP occurs within a population, and also the time that the parasitic egg is laid relative to the initiation of the host's own clutch. For instance, if a nest is parasitized early in the host's own laying cycle, the host may have less to lose and more to gain by abandoning the parasitized clutch and starting a new nest (McRae 1995). On the other hand, if the nest is parasitized later in that host's laying cycle or late enough in the season that a second nesting attempt would likely result in failure, the host may hedge its bets and accept the parasitic egg rather than desert a nearly completed clutch.

Another option that a host could explore to reduce the costs of brood parasitism is to adjust parental effort if the parasitic eggs are likely to hatch along with the host's own eggs. If the hosts of brood parasites accept a parasitic egg and continue to invest parental effort into that nestling, it is likely doing so at the expense of its own offspring (Lack

1968, Rothstein 1990). Therefore, it follows that birds should attempt to avoid expending parental effort on unrelated offspring. However, the influence that parentage has on parental care surely varies with the ability of the bird to assess its own parentage (Whittingham et al. 1992, Westneat and Sherman 1993). Indeed, many studies have shown a positive relationship between parental effort and parentage (Møller 1988, 1991, Davies et al. 1992).

As a result of the overall lack of conspecific variation in egg appearance among most species of birds, it can be nearly impossible for humans to determine if a bird's nest has been parasitized from visual inspection alone. Researchers can mark each egg as it is laid so as to detect odd laying patterns that may be indicative of brood parasitism (e.g., more than one egg laid in one day). However, this technique can be impractical for birds whose nests are relatively inaccessible, such as cavity nesting species. Moreover, the daily nest checks needed to detect CBP in this manner can be disruptive and cause breeding birds to abandon their nests. Molecular analyses are effective in detecting CBP, but these are problematic if the parasitic egg in question cannot be sampled before the host rejects it (MacWhirter 1989).

A different method of assessing the presence of CBP in a given species is to test for an evolved host defense against it. Any host defense behavior that involves rejecting a foreign egg implies that the host is able to recognize that its nest has been parasitized. Thus, the incidence of CBP in a given species of bird can be tested by experimentally adding conspecific eggs to host nests and then monitoring host behavior for signs of rejection (Peek et al. 1972, Rothstein 1975a, Hoogland and Sherman 1976, Lanier 1982).

To date, CBP has not been confirmed in western burrowing owls (*Athene cunicularia hypugaea*), or any other strigiform (Yom-Tov 1980, MacWhirter 1989, Rohwer and Freeman 1989). However, burrowing owl natural history is consistent with other avian species where CBP is known and further fits each of the ecological and behavioral criteria that Yom-Tov (1980) outlined in his review of CBP literature. Yom-Tov stated that a high rate of CBP is expected when (1) suitable nest sites are limited, as nest sites frequently are in non-excavating cavity nesters, (2) available nests are crowded into a small space, such as in colonial species or those that nest in high density, and (3) when potential host nests are available for extended periods of time resulting from large clutch sizes and prolonged female laying periods. The potential of CBP in burrowing owls is further supported by Johnson's (1992) anecdotal observations in which females of reproductive age entered the nest burrows of other females.

Furthermore, offspring recognition has not been documented in burrowing owls and has rarely been investigated in other species that may experience conspecific brood parasitism (Fenske and Burley 1995). However, if CBP is a component of burrowing owl reproductive behavior and if the cost of accepting parasitic offspring is high, recognition of and discrimination against parasitic offspring may occur. Furthermore, offspring recognition in colonial species may be better developed than solitary species (Cullen 1957). For example, herring gulls (*Larus argentatus*; colonial) show more finely tuned offspring recognition than solitary gull species (i.e., kittiwakes, Rissa sp.), which suggests that recognition may be an important behavior in colonial species (Cullen 1957, Storey et al. 1992, Lefevre et al. 1998).

As their name suggests, burrowing owls nest in underground burrows, but they do not dig them; as a result, suitable nest burrows can be limiting. The fact that burrowing owls nest in artificial burrows so readily (Belthoff and Smith 2003, Todd et al. 2003, Smith et al. 2005, Barclay et al. 2011) suggests that suitable nest sites are indeed limiting. Also, burrowing owls at times nest in high density and have been described as semi-colonial (Figure 1.1; Poulin et al. 2011), which may predispose them to CBP (MacWhirter 1989, Rohwer and Freeman 1989). Finally, for their size, burrowing owls lay relatively large clutches of up to 14 eggs (Todd and Skilnick 2003). For comparison, western screech-owls (*Megascops kennicottii*) are somewhat similar in size to burrowing owls, yet they typically lay just 3-6 eggs (Cannings and Angell 2001). For these reasons, among strigiform owls, burrowing owls are good candidates for study of CBP.

The goal of my research was to determine if burrowing owls are capable of recognizing and responding to CBP. I implemented a series of experiments designed to test the behavioral responses of burrowing owls to experimental parasitic eggs introduced into their nests. I developed three a priori hypotheses to explain some possible cues that burrowing owls may use to detect experimental parasitic eggs. First, the “Timing is Everything” hypothesis makes predictions regarding the response of burrowing owls to parasitic eggs based on nesting stage. Second, the “Three’s a Crowd” hypothesis makes predictions regarding the ability of burrowing owls to detect a parasitic egg even if clutch size remains the same. Thirdly, the “Odd Man Out” hypothesis makes predictions based on the role that size differences play in parasitic egg detection.

Timing Is Everything Hypothesis

Parasitic eggs may have a better chance of hatching if they are deposited while the host female is still laying eggs. If the host fails to recognize that her nest has been parasitized, she would likely incorporate the parasitic egg into her clutch and incubate it along with the rest of her own eggs. Thus, a parasitic egg that is deposited into the host's nest early in the laying cycle is more likely to have negative fitness implications for that host relating to its increased chances of hatching. On the other hand, parasitic eggs may have a slimmer chance of hatching if they are deposited after the host has initiated incubation. Given that the parasitic egg did not receive any incubation prior to being deposited into the host's nest, it may be that the parasitic egg is too far behind in development to hatch synchronously with the host's eggs. In this case, the parasitic egg is unlikely to hatch and impose negative fitness costs onto the hosts. If this is true, and accepting an early laid parasitic egg is more costly, then selection would favor a stronger defense against parasitism that occurs prior to the onset of incubation. As a result, hosts should be more suspicious of parasitism early on in their laying cycle and therefore reject parasitic eggs that are deposited during laying more often than those that are deposited after clutch completion (Figure 1.2A). Another possibility is that hosts may be better able to detect parasitism because parasitic eggs that are laid early on in laying represent a larger percent increase in clutch size and thus may be easier to detect.

Three's a Crowd Hypothesis

Unless a parasite removes one of the host eggs in addition to laying its own, clutch size at the host nest will increase under CPB. Under these conditions, a host that is unable to discriminate between its own eggs and the parasitic egg may still be able to detect a parasitic event because of the sudden increase in clutch size. In this case, the host may not eject the parasitic egg, but they can still mitigate the costs of parasitism by deserting the parasitized clutch. The Three’s a Crowd hypothesis predicts that hosts will perceive that a parasitic event has occurred because they recognize a sudden increase in clutch size (Figure 1.2B). This hypothesis assumes that the hosts are aware of how many eggs they laid previously. For a host to selectively reject a parasitic egg, they must be able to discriminate between their own eggs and the parasitic egg. However, if hosts are unable to discriminate, they may still respond to parasitism because they can detect an extra egg. Therefore, the Three’s a Crowd hypothesis predicts that burrowing owls will tend to reject parasitic eggs at nests where an egg is added because they recognize the extra.

Odd Man Out Hypothesis

Hosts may also be able to recognize that their nest has been parasitized based on variations in size and color between the parasitic egg and their own eggs (Lyon 1992, Davies 2000). If the parasitic egg differs substantially from the host’s own eggs, it may be at increased risk of the host detecting it and then rejected. On the other hand, parasitic eggs that are similar to host eggs may stand a greater chance of going undetected. Under the Odd Man Out hypothesis, hosts are expected to reject the parasitic eggs that are most different from their own eggs and fail to reject parasitic eggs that are most similar (Figure 1.2C).

American coots (*Fulica americana*) reduce the costs of brood parasitism by recognizing the parasitic eggs that are most different from their own eggs and then ejecting the odd egg from the nest (Lyon 2003). This method of egg recognition and rejection is most effective when there is little variation within the host's own clutch, as otherwise hosts run the risk of ejecting one of their own odd-shaped eggs. Given that burrowing owl eggs are white and lack distinguishing color patterns, hosts may rely on discrepancies in egg size and/or shape when they evaluate a potential parasitic egg. Many species that are regularly parasitized (either by other species or by conspecifics) typically have low intraclutch variation in egg characteristics (Soler and Møller 1996, Davies 2000, Soler et al. 2000). When the hosts' own eggs are similar to one another and exhibit little variation in size and shape, the ability of the host to discriminate between its own eggs and a parasitic one is enhanced. Thus, the Odd Man Out hypothesis also predicts that burrowing owls may reject a dissimilar parasitic egg when the variation within their own clutch of eggs is low. Also, if there is high variability within the host's own clutch, then parasitic eggs may be accepted.

Study Area and Methods

Study Area

During the 2012 and 2013 breeding seasons, I studied western burrowing owls within the Morley Nelson Birds of Prey National Conservation Area (NCA) in southwestern Idaho (Figure 1.3). The NCA covers approximately 2,430 km^2 (about 1,962 km^2 of which is public land) in Ada, Elmore, and Owyhee counties. Congress established the NCA in 1993 (Public Law 103-64) to provide for the conservation, protection, and enhancement of raptor populations and habitats (Sharpe and van Horne 1998). The Snake River Canyon is the dominant geologic feature, flowing through 130 km of the southern and western portions of the NCA. The topography of the surrounding river plain above the canyon is flat to rolling, with rocky outcrops and a few isolated buttes. Elevation within my focal study area ranged from 877 - 914 m. Precipitation averages 31.7 cm annually, with 12.1 cm occurring during the breeding season (March through July). During the breeding season, average daily temperatures increase from 5.5^{o} C in March to 23.1^{o} C in July (N.O.A.A. 2002).

While some native shrub-steppe habitat remains, range fires and human disturbances have converted large portions of the NCA to exotic annual grasslands. Once covered by expansive shrub-lands, burned and other highly disturbed areas are now dominated by invasive plants such as cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kalil*), and tumble mustard (*Sisymbrium altissimum*; Hironaka et al. 1983, USDI 1996). The study area also contains BLM-managed rangelands, agricultural fields, several paved and dirt roads, a few homes, and the Orchard Combat Training Center (a military training area used by the Idaho Army National Guard). Agricultural areas grow primarily sugar beets, corn, grain, alfalfa, beans, and potatoes. Cattle and sheep grazing also occur within portions of the NCA, primarily during winter (USDI 1996, Moulton et al. 2005).

There are approximately 350 artificial burrows (deployed in clusters of 2 or 3 artificial burrows per nest-site location; Smith and Belthoff 2001) within the NCA available to burrowing owls for nesting or roosting (Belthoff and Smith 2003, Moulton et al. 2006). Since 1997, burrowing owl nesting pairs have occupied 30-60 of the artificial burrows in the NCA each year (Belthoff and Smith 2003, Belthoff, unpublished data). Distributions of burrowing owls at both natural and artificial nests vary from high density, with up to six neighbors nesting within 400 m of a focal nest, to very low density where many kilometers separate nesting pairs (Welty 2010, Welty et al. 2012). For the purpose of my study, only artificial nest sites were considered for experimentation, although I monitored both natural and artificial burrows during each breeding season. Using artificial burrows allowed me to accurately count, measure, and mark eggs; record the date of egg laying, incubation, and hatching; and capture and mark adult and juvenile burrowing owls.

Locating and Capturing Burrowing Owls

Surveillance for burrowing owl pairs began in mid-March and continued through mid-May in each year. I visited all existing artificial burrow sites at least twice during each breeding season to check for evidence of burrowing owl use. I considered a nest site occupied if I observed an owl repeatedly or signs of use (e.g., whitewash, pellets, dung) at the burrow entrance. I inspected nests every 7-14 days and checked for eggs to confirm the presence of a nesting pair.

To capture adult burrowing owls I employed one of the following methods: one-way basket trap placed at the entrance of the nest burrow (described in Smith 1999), bow-net baited with a mouse (*Mus musculus*), or by hand directly from the chamber of the artificial burrows. I captured juvenile burrowing owls by hand directly from the nesting chamber, although I occasionally captured some juveniles using a one-way basket trap.

Measuring and Marking Owls

Upon capture, I measured the following for each owl: mass (to the nearest g using a 300-g Pesola spring scale), relaxed wing-chord length, tail length, and tarsus length (all to the nearest 1 mm using a metric ruler). In addition, I measured the culmen (to the nearest 0.01 mm using digital calipers) and also measured the length of the emerged primary feathers (from end of shaft to tip of emerging feather) for juveniles. These measurements are standard in my study area and are collected as part of long-term research and monitoring of the local burrowing owl population.

Because males do not incubate, I classified adult owls with brood patches as females (Martin 1973, Poulin et al. 2011). From a distance, I was also able to identify the sex of some pairs of owls based on plumage color differences (males are typically lighter during the breeding season). I was unable to determine the gender of juvenile burrowing owls because they are generally monomorphic in both size and plumage (Poulin et al. 2011). Using venipuncture of a wing vein, I collected 300 µl of blood from adult owls and 100 µl of blood from juvenile owls for use in other studies. Each owl received a U.S. Geological Survey aluminum leg band (size 4). In addition, adult owls received three colored plastic leg bands arranged in a unique combination so they could be easily identified in the field.

Experimental Brood Parasitism

I simulated CBP by introducing a single experimental conspecific egg into burrowing owl nests. I marked both the parasitic egg and the host eggs with waterproof ink and measured the length and width of each egg to the nearest 0.01 mm using digital calipers. Experimental eggs were always marked with the number zero so I could easily identify them after adding them to the host nest. I always added the experimental egg to the center of the host's own clutch and then noted its position as central or periphery during each subsequent visit. For each of the host's own eggs, I calculated egg volume by using the formula: $\text{Volume} = 0.51 \times LB^2$, where L = length of egg in mm and B = breadth of egg in mm (Hoyt 1979). I then took the average volume of the host's eggs and subtracted the volume of the parasitic egg to produce a difference score and examined host acceptance or rejection as a function of this difference.

I collected the experimental eggs from other burrowing owl nests in my study area. I chose experimental eggs from nests that were at a similar developmental stage as those of the host clutch into which they were introduced, which reduced the possibility of parasitic eggs hatching asynchronously relative to the host's clutch. I transported experimental eggs in a padded container and placed them into their host nest 2-4 h after removal from source nests. The straight-line distance separating host and source nests was 7.92 ± 2.87 (SE) km (range: 0.11 – 55.50 km).

I visited host nests every 7-10 days to check for signs of egg acceptance or rejection. I considered experimental eggs rejected if they were missing, damaged, buried, or otherwise disturbed on my first visit following the initial manipulation. Nests were classified as abandoned if I found cold eggs on two consecutive visits. Finally, I considered experimental eggs to be accepted if they remained incubated and in the nest for ≥14 days.

Altogether, my study included 73 burrowing owl nests (n = 35 from the 2012 breeding season, and n = 38 from the 2013 breeding season). In 2012, nine nests served as controls, 16 nests served as treatment nests, and 10 nests served as sources for experimental parasitic eggs. In 2013, eight nests served as controls, 18 served as treatment nests, and 12 nests served as sources for experimental parasitic eggs. I did not perform clutch manipulations at control nests; instead, I visited control nests as frequently, and handled eggs (marking and measuring) in the same way as those in the experimental groups. To simulate the effects of repeatedly moving a particular egg to the center of the clutch, I randomly selected an egg at each control nest, handled that egg on each consecutive visit, and moved it to the center of the clutch, just as in experimental nests.

Egg Additions during Laying and Incubation

In 2012 and 2013, I simulated CBP by adding one egg to each of 22 burrowing owl nests. At 11 nests, I added the egg during the female's normal laying period, and when there were between one and five eggs present in the host owl's nest (Figure 1.4A). At the remaining 11 nests, I added one egg during the incubation period, after the host female had completed her own clutch of eggs (completed clutch sizes ranged from 7 – 13) and was incubating (Figure 1.4B). In each case, the female's clutch size was increased by one egg. I refer to nests where I added an egg during laying as laying-hosts, whereas nests where I added an egg during incubation are referred to as incubation-hosts. I used these manipulations to evaluate the Timing is Everything hypothesis (Figure 1.2A).

Reciprocal Egg Swaps during Laying

To further examine burrowing owl capacity for egg recognition, I performed six reciprocal egg swaps between 12 burrowing owl nests during the normal laying period (Figure 1.4C). In this case, I removed one of the host female's own eggs and then replaced it with an experimental egg I took from another burrowing owl nest. The result of this manipulation was that each female encountered a foreign egg, but her clutch size did not change. This procedure allowed me to determine if the hosts were able to recognize that their nest had been parasitized based on factors other than a sudden increase in clutch size. For example, females may reject their nest more frequently when a parasitic egg much different than her eggs is introduced (Rothstein 1975b).

Monitoring Parental Care

I monitored burrowing owls nesting in artificial burrows using infrared, motion-activated trail cameras (Model Moultrie Game Spy M-80, EBSCO Industries Inc., Birmingham, Alabama, U.S.A.) to minimize human disturbance and capture burrowing owl behavior. These cameras can store up to 15,000 images on a 16-GB SD memory card and will only take a photograph when there is movement within the field of view. All cameras were programmed to take two photographs followed by a time lag of 30 seconds. Each photograph has an information stamp that records the date and the time of the burrowing owls' activities, which allowed me to record exactly when each prey delivery (or other event) occurred. The cameras were mounted on stakes approximately 1 m from the opening of the artificial burrow entrance. I positioned the cameras 0 - 60 cm above the ground, depending upon the characteristics of the nest site and cleared vegetation and other obstructions that were in front of the cameras. In both 2012 and 2013, I placed nest cameras at three control nests and seven treatment nests.

The nest cameras were deployed throughout all stages of nesting (i.e., egg laying, incubation, nestling, and fledging). I left the cameras in place until fledglings began to disperse, which typically occurred in mid-July of each year. Although the nest cameras were present throughout the breeding season, I only analyzed 17 consecutive days of parental care data, which corresponded to the first 17 days after hatching for each nest. Based on my own observations, nestlings older than 2.5 weeks of age started to spend more time away from the focal nest burrow (e.g., in nearby artificial or natural burrows) and were progressively less likely to be directly at the mouth of the nest burrow when begging for food. Given these points, I determined that the nest cameras would not be able to accurately record all prey deliveries after the initial 17 days of observation.

Given that vertebrate prey comprises the majority of the biomass delivered to the nest, and that other studies have shown that vertebrate prey is primarily delivered during the crepuscular periods, I chose to subset my data and only evaluated parental care during the crepuscular periods of the day (i.e., dawn and dusk; Poulin and Todd 2006). I defined dawn and dusk as two hours before sunrise until sunrise and from sunset until two hours after sunset, respectively. This roughly corresponded to astronomical twilight (the period of time when the sky is not completely dark, when the sun is 18 degrees below the horizon). I rounded the beginning and end of each time period to the nearest whole hour. For example, dawn began at 04:00 and ended at 06:00, and dusk began at 21:00 and ended at 23:00. All sunrise, sunset, and twilight times were determined from the U.S. Naval Observatory Astronomical Applications Department website (http://aa.usno.navy.mil/) and were specifically determined for my study area (i.e., southwestern Idaho) in May and June 2012-2013.

Burrow attendance was calculated as the total number of minutes the male or female owl was present within view of the nest camera each hour. Each image featuring a focal owl was counted as 0.5 min of burrow attendance (given that each image was preceded or followed by a 0.5 min delay). I did not include any duplicate images (i.e., consecutive images with an identical time stamp) in the analysis. I calculated male and female burrow attendance separately so I could compare burrow attendance of each adult owl at treatment and control nests. I made no distinction between the specific behaviors of the adults (e.g., preening, sleeping). To measure provisioning behavior, I calculated a prey delivery rate by dividing the total number of prey deliveries per hour by the number of nestlings in the nest at that time. I recorded the type of prey that was delivered and the identity (i.e., male or female) of the owl that delivered each prey item. Typically, I was able to identify vertebrate species to genus and invertebrate species to order (i.e., Coleoptera or Orthoptera).

Data Analysis

I performed all analyses using JMP Pro 10 Statistical Software (SAS Institute, Inc., Cary, NC). Means are given with standard errors. Results were considered significant when alpha < 0.05.

Experimental Brood Parasitism

To examine the effect of an experimental parasitic egg on the behavior of burrowing owls, I compared the response of hosts (accept, reject) where an egg was added/swapped during laying, or added during the incubation period to the response of control owls (un-manipulated clutch but with equal disturbance). To examine the effect of egg difference on a host’s response, I calculated the mean volume of the host’s eggs and then subtracted from this number the volume of the parasitic egg. I excluded control nests from the analysis and only included egg differences in the model as a predictor for nest fate (i.e., accept or reject). I analyzed these data in two different fashions: once with the actual difference values (i.e., including negative values that represent small parasitic eggs) and again using the absolute value of the differences so I could test the effect of an odd parasitic egg regardless of whether it was larger or smaller in size than the mean of the host’s eggs. I also examined the potential effect of intraclutch variability on host response to a parasitic egg. I calculated the standard deviation of the volume of the host's eggs (only including those eggs that were laid prior to the introduction of the parasitic egg), and then used logistic regression to determine if variability of host eggs was related to whether hosts accepted or rejected eggs.

Parental Care

For all photographic analyses, I assumed that the nest cameras captured all burrow attendance and provisioning activity during the observation period. For these analyses, I excluded data from any nests where rejections occurred (i.e., rejection of the parasitic egg or parasitized clutch), excluded nests from which the parasitic egg did not successfully hatch, and only included those nests for which I had at least 3,000 images taken over the 17-day period of interest. To determine the effects of a parasitic nestling on male and female burrow attendance and provisioning behavior, I performed Wilcoxon Signed Rank tests, as the data were not normally distributed. I compared burrow attendance, prey delivery rates, and biomass delivered at parasitized treatment nests and non-parasitized controls. To determine biomass delivered per nestling per hour, I assigned each identified prey item a representative mass (g) value (Appendix 1).

Results

Experimental Brood Parasitism Experiments

Hosts that were experimentally parasitized with a conspecific egg (*n* = 34) responded in one of three ways: (1) hosts accepted the parasitic egg into their clutches and incubated it along with their own eggs; (2) hosts rejected the parasitic egg and responded by burying it, along with any host eggs that were present at the time, and then re-nested within the same burrow or in the adjacent satellite burrow, or (3) hosts abandoned the nest-site entirely without disturbing the eggs (Table 1.1).

Effects of Nesting Stage

At laying addition nests, hosts rejected the parasitic egg at three nests and accepted the parasitic egg at eight nests (Table 1.1). At one of the rejected nests, the host responded by burying all of the eggs from the original parasitized clutch under prey remains and nest debris and then re-nested within the same burrow chamber. At the other two nests, the hosts abandoned the site entirely without disturbing any of the eggs in the parasitized clutch. In each case, the parasitized clutch was abandoned within one week of egg addition. At one of the abandoned nests, a new female initiated a clutch of eggs within the same nesting chamber as the previous female's rejected clutch. The new female's eggs were intermingled with the original, un-damaged clutch. As owls at none of the control nests (n = 17) abandoned or otherwise rejected their clutch in response to repeated disturbance, I considered the two nests abandoned by hosts in the week following the manipulation as rejections. Of the eight parasitic eggs that were accepted by hosts, three successfully hatched, one failed to hatch, and the ultimate fate (i.e., hatched or un-hatched) of four parasitic eggs was uncertain.

Burrowing owls accepted 100% of the experimental parasitic eggs that I added during the incubation period (n = 11; Table 1.1). In each nest, the host female incorporated the experimental egg into her clutch and incubated it along with her own eggs. Four of the parasitic eggs added during incubation successfully hatched, while two parasitic eggs failed to hatch. I found no evidence that the parasitic eggs failed to hatch because the host identified them. It is possible that I added these two eggs to clutches of eggs that were further along in development, and once the host nestlings hatched host adults no longer incubated the remaining foreign eggs. While the hosts accepted them, I was uncertain of the ultimate fate (i.e., hatched or un-hatched) of the parasitic egg at five nests.

Effects of an Extra Egg

The response of burrowing owls to parasitic eggs did not depend on whether one of the host's own eggs was swapped with the parasitic egg (clutch size did not change) or the parasitic egg was added to the host's nest (clutch size increased by one egg). At nests that had an experimental egg swapped with one of the host's eggs, hosts rejected the parasitic egg at three nests while hosts at eight nests accepted the parasitic egg (Table 1.1). In two nests where rejection occurred, the hosts buried the original parasitized clutch under nest debris and cached prey, and then immediately re-nested within the same burrow chamber (Figure 1.5). In one other nest where rejection occurred, the hosts also rejected the parasitized clutch by burying the eggs; however, in this case, the hosts re-nested in the adjacent satellite burrow rather than within the same burrow chamber. Of the nine parasitic eggs that were accepted by the hosts, five hatched successfully, while the ultimate fate (i.e., hatched or un-hatched) of the parasitic egg at four nests was uncertain.

Effects of an Odd Egg

The response of burrowing owls to experimental parasitic eggs did not depend on the degree of difference between the parasitic egg and the average of the host's eggs (Table 1.2; logistic regression: actual differences, $B = 0.004 \pm 0.008$, DF = 1, $\chi^2 = 0.28$, P

= 0.59; abs(differences), $B = 0.0003 \pm 0.017$, DF = 1, $\chi^2 = 0.0004$, $P = 0.98$). The difference between the average volume of the host's eggs and the volume of the parasitic egg was 50.1 ± 26.35 mm^2 (absolute value of the differences) and 0.69 ± 57.30 mm^2 (actual differences). Furthermore, the amount of variation within the host's clutch of eggs was not a significant predictor of nest fate (logistic regression: $B = 0.06 \pm 0.072$, DF = 1, $\chi^2 = 0.79$, $P = 0.37$). Parasitic eggs were not more likely to be rejected in host nests where intraclutch variation was low (Table 1.3).

Parental Care

Overall, nest cameras recorded >150,000 images. Each nest camera was in place for an average of 82 days during the respective breeding season. Of the 20 nests in which I recorded behavioral observations using nest cameras, I excluded three because the host owls rejected the parasitized clutch, two because nests were depredated, three because the parasitic egg was known to have not hatched, and a further three nests were excluded because they failed to record a minimum of 3,000 images during the period of interest (i.e., 17 days post hatch). This left nine nests from which I analyzed parental care data.

Burrow attendance of both male and female adult burrowing owls did not differ between treatment (male: 15.6 ± 2.14 min/hr; female: 25.7 ± 1.80) and control (male: 12.9 ± 2.88 min/hr; female: 30.5 ± 3.85) nests (Wilcoxon ranked sums: Male, $Z = 0.43$, DF = 1, $P = 0.67$; female, $Z = -0.61$, DF = 1, $P = 0.54$). Overall, female owls were present at the nest burrow more often than males at both treatment and control nests (Table 1.4). Females were often present directly at the mouth of the nest burrow (Figure 1.7A), but once the nestlings became more active, females began to spend time on a nearby perch or at the satellite burrow. Males were much less frequently at the nest burrow, and when they were it was often during or shortly after transferring prey to the female (Figure 1.7B). Instead, males were more frequently at a perch or the satellite burrow.

I ultimately observed 560 invertebrate and 1,075 vertebrate prey deliveries. There was no significant difference in prey delivery rate (Wilcoxon ranked sums: $Z = -0.37$, DF = 1, $P = 0.71$) between treatment (0.3 ± 0.15 prey/nestling/hr) and control (0.5 ± 0.34 prey/nestling/hr) nests. Of all vertebrate prey deliveries at treatment nests, males delivered 80% and females delivered 20%, while at control nests males delivered 75% and females delivered 25% of all vertebrate prey (Table 1.5). At both treatment and control nests, males and females delivered approximately the same number of invertebrate prey (Table 1.5). There was no significant difference (Wilcoxon ranked sums: $Z = 0.86$, DF = 1, $P = 0.39$) in total biomass (i.e., both the male and female contribution) between treatment (5.5 ± 1.82 g/nestling/hr) and control (4.2 ± 1.76 g/nestling/hr) nests.

Discussion

Experimental Brood Parasitism

I conducted experimental manipulations of eggs within burrowing owl nests to investigate host responses to simulated brood parasitism. In many cases, host females accepted the experimental eggs into their clutch and continued incubation. In others, hosts rejected. In each case of rejection, burrowing owls either buried the parasitized clutch and either re-nested nearby, or abandoned the nest-site completely. Owls did not selectively reject the parasitic egg. Instead, they responded by rejecting the parasitic egg along with any of the host’s own eggs that were present at the time. Thus, the owls may have been constrained in some way from rejecting only the parasitic egg. One possible explanation is that the owls may have been physically unable to remove the parasitic egg from their nest. In this case, the owls would then be faced with the choice of either accepting the parasitic egg, or rejecting all of the eggs in their nest. Moreover, the majority of the owls displaced and buried the parasitized clutch and proceeded to initiate a new clutch of eggs within the same nesting chamber. Whittingham and Dunn (2001) observed this behavior in tree swallows (*Tachycineta bicolor*). Similar to burrowing owls, tree swallows nest in cavities that they do not create themselves. Species such as burrowing owls and tree swallows are cavity adopters; that is, they depend entirely on other species to excavate cavities and consequently can be nest-site limited (Holroyd 1975). Egg burying may benefit both burrowing owls and tree swallows in that instead of delaying reproduction while searching for another suitable nest, they can reuse a nest-site in an already established territory. This may explain why the owls chose to remain in their original, parasitized nest rather than seek out new and potentially limited opportunities elsewhere.

The Effect of Nesting Stage

I found that the response of female burrowing owls to experimental parasitic eggs depended on when in the nesting cycle parasitic eggs were deposited. The probability of rejection was greater when experimental eggs were added during the host’s laying period. These results support the hypothesis that timing plays a significant role in the response of hosts to CBP, and that parasitic eggs introduced during laying are rejected more often than those introduced during incubation. The difference may be related to the greater cost of accepting early-laid parasitic eggs.

Typically, parasitic eggs have an improved chance of hatching when they are deposited early in the host's laying cycle. If a parasitic egg is laid in a nest after the host has initiated incubation, it is unlikely to develop quickly enough so that it can hatch along with the host's eggs (Lemons and Sedinger 2011). In such a case, the parasitic egg would pose little threat to host fitness and, consequently, may be unlikely to drive the selection of recognition and rejection behavior to late-laid parasitic eggs. It may be difficult for hosts to respond to CBP that occurs outside of the natural time frame. In my study, burrowing owls accepted all of the experimental eggs that I added during incubation but rejected some experimental eggs when they were added during the laying period. Thus, burrowing owls appear to reject parasitic eggs when the potential costs of parasitism are higher. Rejection of early parasitic eggs and acceptance of late parasitic eggs occurs in several other species with CBP (e.g., cedar waxwings, *Bombycilla cedrorum*; yellow warblers, *Setophaga petechia*; Rothstein 1976, Sealy 1995).

Alternative explanations for the observed differences in host response to experimental parasitic eggs are possible. For example, hosts may recognize that their nest has been parasitized during incubation, but they may be constrained from responding. Possibly, once a clutch has reached a certain reproductive value, it would be more costly to the host to desert the clutch than it would be to accept the parasitic egg. Indeed, the potential value of a clutch of eggs may increase throughout the nesting season in terms of continued avoidance of predation. McRae (1995) found this to be true for common moorhens (*Gallinula chloropus*) in that females were less likely to desert their nest if they had five or more eggs present when the parasitic egg was laid. McRae (1995) suggested that once a certain threshold of parental care had been reached, moorhens would accept the parasitic egg. Reproductive success in birds declines with date (Perrins 1970); so hosts may not desert a parasitized clutch if the possibility of success via re-nesting is low.

Interestingly, I was able to confirm that several of the experimental eggs I used in the incubation treatment hatched along with the host's own clutch. This likely occurred because the experimental eggs had already been incubated for some time in their original nest. Under natural conditions, this is unlikely to occur, as it would require that parasites physically move one of their incubated eggs into a host nest. Given that the host female is present in her nest throughout most of incubation, it is unlikely that a parasite would have many opportunities to sneak an egg in. However, Brown and Brown (1989) documented that in cliff Swallows (*Hirundo pyrrhonota*) parasites physically transfer eggs from one nest to another throughout the nesting cycle. In these cases, parasitic eggs may have an equal chance at succeeding, so the potential cost of accepting parasitic eggs remains high even through incubation. If burrowing owls were able to parasitize each other's nests during incubation via egg transfer, one would expect that hosts would respond to late parasitism by rejecting the parasitic egg. However, there is no evidence that egg transfer occurs in burrowing owls, and my study demonstrates burrowing owls accept parasitic eggs when they are introduced during incubation.

The Effect of an Extra Egg

Burrowing owls did not appear to rely on a sudden increase in clutch size to recognize that their nest had been parasitized. Because burrowing owls rejected an equal number of clutches that were parasitized without the added cue of an extra egg, this suggests that it was the presence of the parasitic egg (not an extra egg) that caused hosts to reject. This result is not consistent with the hypothesis that hosts use spatial cues, such as number of eggs present prior to and following parasitism, to recognize that parasitism has occurred. If burrowing owls did use a “counting” method, there should have been a greater proportion of rejections at the nests where parasitic eggs were added, rather than an equal proportion of rejections between parasitic egg swaps and parasitic egg additions. In a similar study in which common cuckoo (*Cuculus canorus*) eggs were introduced to reed warbler (*Acrocephalus scirpaceus*) nests, Davies and Brooke (1988) also failed to detect a difference in reed warbler response between nests where the parasitic egg was swapped with a host egg or the parasitic egg was added to the nest. Other studies have shown similar results (e.g., Polaĉiková et al. 2007). The fact that hosts rejected parasitized clutches even when clutch size did not change implies that the host was able to discriminate between its own eggs and the parasitic one. This result is consistent with the notion that hosts rejected the parasitized clutch, not because they were unable to recognize the parasitic egg, but because they were physically unable to remove it from their nest. Given these points, it is difficult to justify the destruction of an entire clutch of eggs for the potential benefit of rejecting one parasitic egg. If egg rejection behavior is going to evolve in a given species, one would expect it to evolve in such a way as to minimize the costs of rejection (Davies et al. 1996, Røskaft and Moksnes 1998, Welbergen et al. 2000, Lyon 2003, Shizuka and Lyon 2010). If burrowing owls employ clutch desertion and burial as a defense against CBP, then their adaptive response to CBP appears poorly developed. When considering fitness costs to the hosts, wouldn’t it be less costly to accept a single parasitic egg than to reject one’s own clutch?

The Effect of an Odd Egg

I investigated whether host responses depended on the degree of difference in egg volume between the hosts and the parasitic eggs. In other words, might hosts reject more frequently when there are larger mismatches between parasitic and host eggs, in which case detection would be easier for hosts than when parasitic eggs more closely match those of hosts. However, I found no evidence that differences in egg volume predicted burrowing owl responses to experimental nest parasitism. This result is consistent with that found in other species (Peek et al. 1972, Hoogland and Sherman 1976, Burtt 1977, Grzybowski 1979, Lanier 1982). Therefore, the hypothesis that the hosts would be able to detect parasitic eggs because they differed greatly from the host's own eggs was not supported. This result is not entirely unexpected, given that conspecific egg discrimination has only been documented in a handful of species (Buckley and Buckley 1972, Victoria 1972, Bertram 1979). Several other species reject conspecific eggs, but they generally only do so if the parasitic egg has been laid prior to host laying (Mumme et al. 1983, Emlen and Wrege 1986, Møller 1987, Braa et al. 1992, Moksnes 1992). My results showed that burrowing owls have substantial variability in the size and shape of their eggs (Figure 1.8). Thus, it is unlikely that the hosts would have been able to discriminate between their own eggs and a parasitic egg because the size of the parasitic egg could fall within the wide range of sizes of the host's eggs. While some of the parasitic eggs were rejected from host owl nests that had little variability in egg sizes, the majority of parasitic eggs were accepted. In species that are regularly parasitized by conspecifics, the variation within an individual female's clutch is generally low, which helps the host identify and reject an odd parasitic egg (Freeman 1988, Jackson 1992). The burrowing owls in my study had substantial variability in their egg sizes, and if CBP were a strong selective factor in their nesting biology, I would have expected the females to lay more uniformly sized eggs (low intraclutch variation) rather than lay a clutch of variable eggs (high intraclutch variation). A possible explanation for the egg rejections in spite of high intraclutch variation may be that burrowing owls do not rely on tactile cues such as size for egg discrimination, but rather they rely on some other characteristic to identify their own eggs.

Parental Care

I found no evidence that burrowing owls altered parental care as a result of experimental brood parasitism. Nest attendance and prey provisioning did not differ between nests that had been experimentally parasitized and those that had not. These results are consistent with those found in many other studies, which show time and again that a bird will allocate food items and parental care without regard to the genetic relatedness of nestlings (Beecher 1991, Davies et al. 1992, Westneat et al. 1995, Kempenaers and Sheldon 1996, Brown and Brown 1998, Whittingham and Dunn 1998). What is puzzling is that the hosts of brood parasites often invest in the parasitic nestlings at the expense of their own young (Rothstein 1990). At two nests, the hosts fed the parasitic nestling (which I was able to identify because the parasitic egg hatched well before the host's own eggs) at the expense of their own offspring. Because that egg hatched first, the parasitic nestlings were able to gain a head start and outcompete their foster siblings for food. Discrimination against parasitic nestlings has only been documented in a handful of cases (Payne et al. 2001, Grim et al. 2003, Soler 2008), whereas discrimination against foreign eggs is widespread and well-studied for many bird species (Rothstein 1990, Davies 2000, Lahti and Lahti 2002, Lyon 2003). The burrowing owls in my study area appeared to recognize that a foreign egg was present in their nest, but they were not capable of discriminating between their own eggs and nestlings and those that may be parasitic. Discrimination against parasitic nestlings may be absent in most brood parasite hosts because the risk of mistakenly rejecting one of their own offspring is too high (Beecher 1991). Another explanation for the absence of nestling discrimination may be that birds do not discriminate between their own offspring and the offspring of other birds, and instead they only discriminate between young that are in their nest and those that are not, e.g., they use a kin recognition rule that relies on spatial proximity. In addition to hosts provisioning young that hatched from experimental parasitic eggs, throughout my study, I observed multiple instances of burrowing owls caring for presumably unrelated young that originated from abandoned or depredated nests nearby (pers. observ.). Given that these nestlings were in good condition, I concluded that their new foster parents had been caring for them. Although it is possible that these burrowing owl care givers were simply playing the part of the “helpful neighbor,” other studies have shown that the owls may not extend their parental care and protection to nestlings that are outside of their own nest. Poulin and Todd (2006) observed a single pair of burrowing owls preying upon 10 nestlings from nearby conspecifics. These two points could indicate that burrowing owls may recognize the nestlings within their own nest and choose to provision them, but they cannot discriminate between them. Other explanations for these results could be that the burrowing owls in my study area were constrained from reducing parental care at their nest because doing so would potentially decrease survival for their own nestlings as well, and thus decrease their fitness.

Conclusions

My study was designed to simulate CBP in free-living burrowing owls for the purpose of evaluating their behavior in response to parasitic eggs, as well as to assess changes in patterns of parental care given unrelated young in nests. I did not find any natural evidence for CBP in burrowing owls (e.g., more than one egg per day appearing in a nest), nor did I observe any differences in parental care as a result of experimental CBP. However, I was unable to exclude CBP as a possible factor to explain the rejection behavior of burrowing owls in response to parasitic eggs. What I found was that burrowing owls will desert a clutch of eggs, not because of repeated human disturbance, but from the presence of a foreign conspecific egg. Given these points, the methods and results presented in my study are similar to others in which CBP is unequivocal. In addition to the evidence I observed, three additional studies of burrowing owls have reported unusual or unexpected findings that may indeed be attributable to CBP. First, in a single burrowing owl nest, Henny and Blus (1981) reported finding 10 eggs laid in only eight days. Given that burrowing owls lay approximately two eggs every three days, the appearance of 10 eggs in less than two weeks suggests that more than one female was laying eggs in the nest. Second, Conway et al. (2012) reported unusual laying patterns in burrowing owls in Washington and pondered about the potential effect of CBP. Finally, Johnson (1997) documented a series of genetic discrepancies in a small population of burrowing owls in which she found 20% of putative parent-offspring relationships to disagree with parentage reported using DNA analyses. She also observed female burrowing owls of reproductive age entering the nesting burrows of other females during multiple stages of the breeding season (Johnson 1992). Thus, there is mounting evidence that CBP may be a part of the behavioral repertoire of burrowing owls. What is now needed is a comprehensive evaluation of burrowing owl family data for the purpose of lending molecular support to the behavioral evidence.

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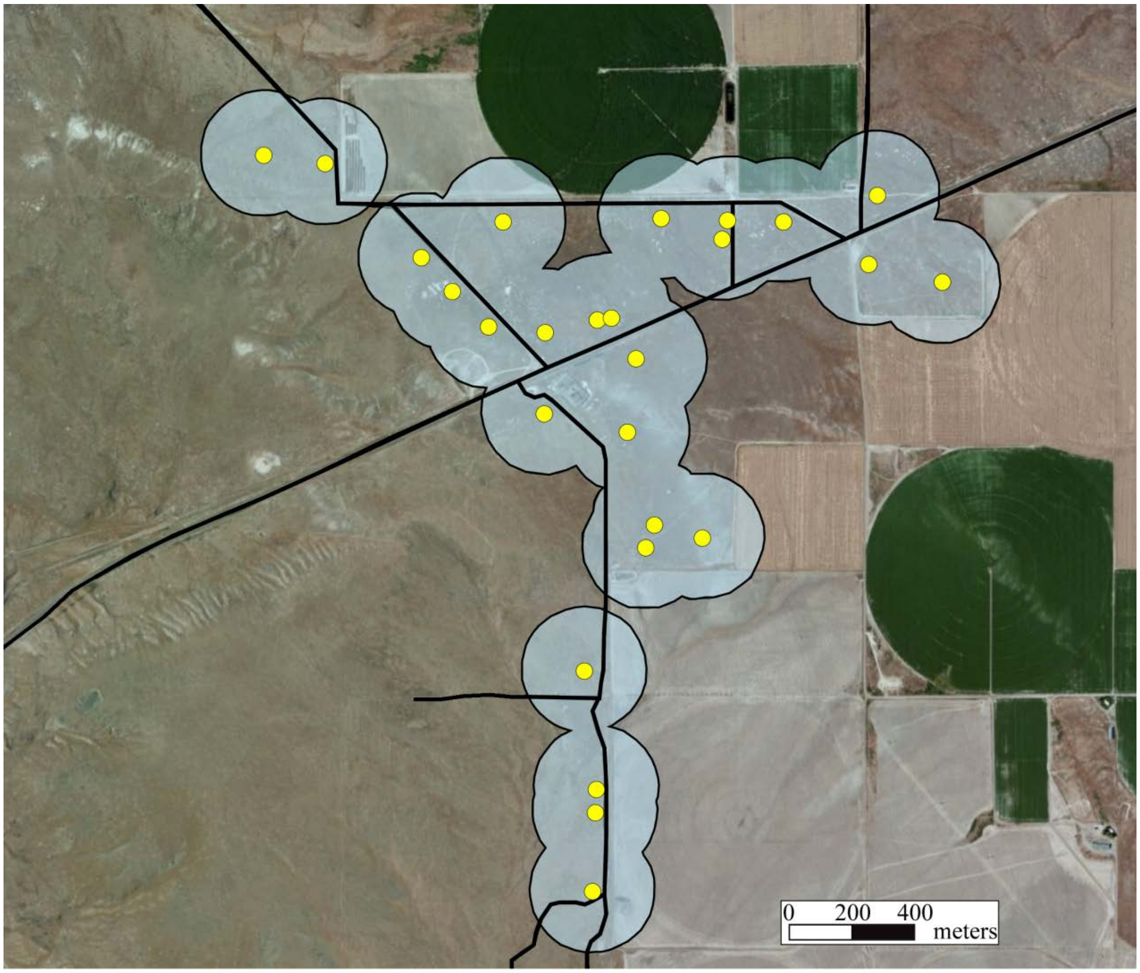


Figure 1.1. Area map showing nesting density of western burrowing owls in a portion of the Morley Nelson Birds of Prey National Conservation Area near Grand View, Elmore County, Idaho during the 2012 breeding season. Circles represent 200-meter buffers around each owl nest. I describe this nesting aggregation as “semi-colonial.”

A.

Timing Is Everything Hypothesis

Parasitic egg added during laying	Host **rejects** early added egg
Parasitic egg added during incubation	Host **accepts** late added egg

B.

Three's a Crowd Hypothesis

Clutch size increases by one egg	Host **rejects** because of increase in clutch size
Clutch size remains the same	Host **accepts** because clutch size does not change

C.

Odd Man Out Hypothesis

Dissimilar Parasitic Egg	Host **rejects** the dissimilar parasitic egg
Similar Parasitic Egg	Host **accepts** the similar parasitic egg

Figure 1.2. Prediction matrices of research hypotheses. Predictions of the Timing is Everything Hypothesis for the effect of nesting stage (timing) on host response to parasitic egg addition (A), predictions of the Three’s a Crowd Hypothesis for host response to change in clutch size (B), and predictions of the Odd Man Out Hypothesis for host response to dissimilar and similar sized parasitic eggs.

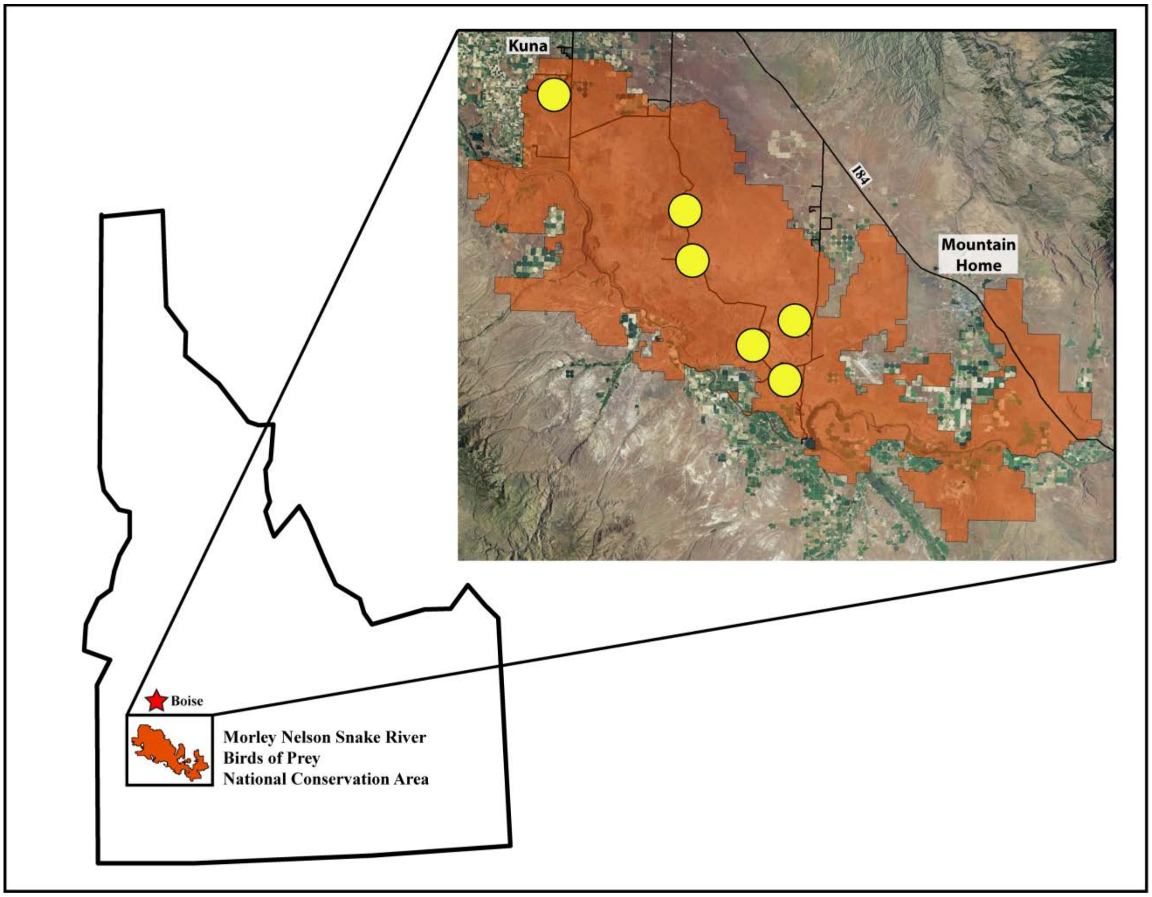
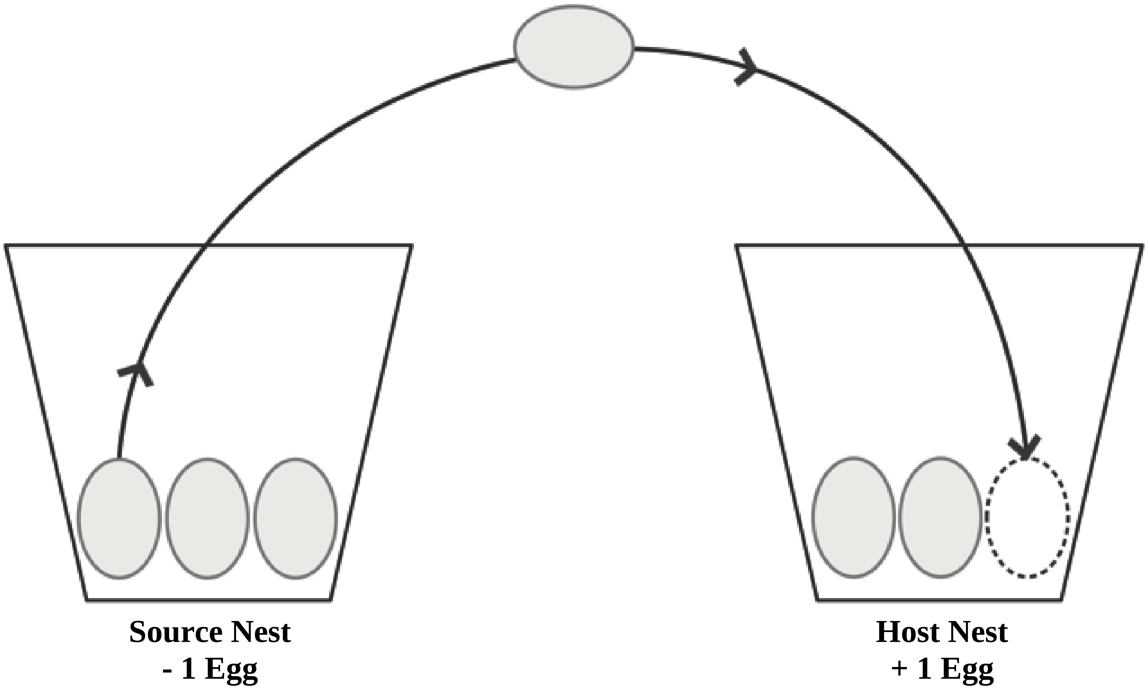


Figure 1.3. Vicinity map showing the location of the Morley Nelson Birds of Prey National Conservation Area (NCA) within southwestern Idaho. Each yellow circle represents the regions in which I examined burrowing owl nests in 2012 and 2013.

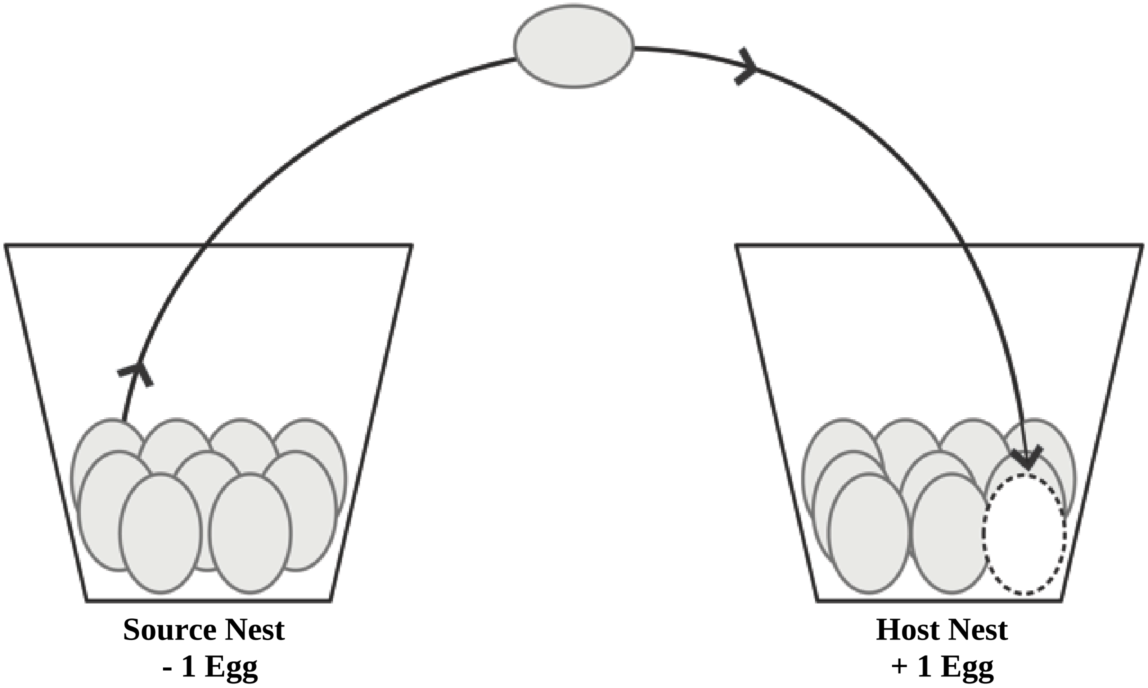
A.

Laying Addition



B.

Incubation Addition



C.

Laying Reciprocal

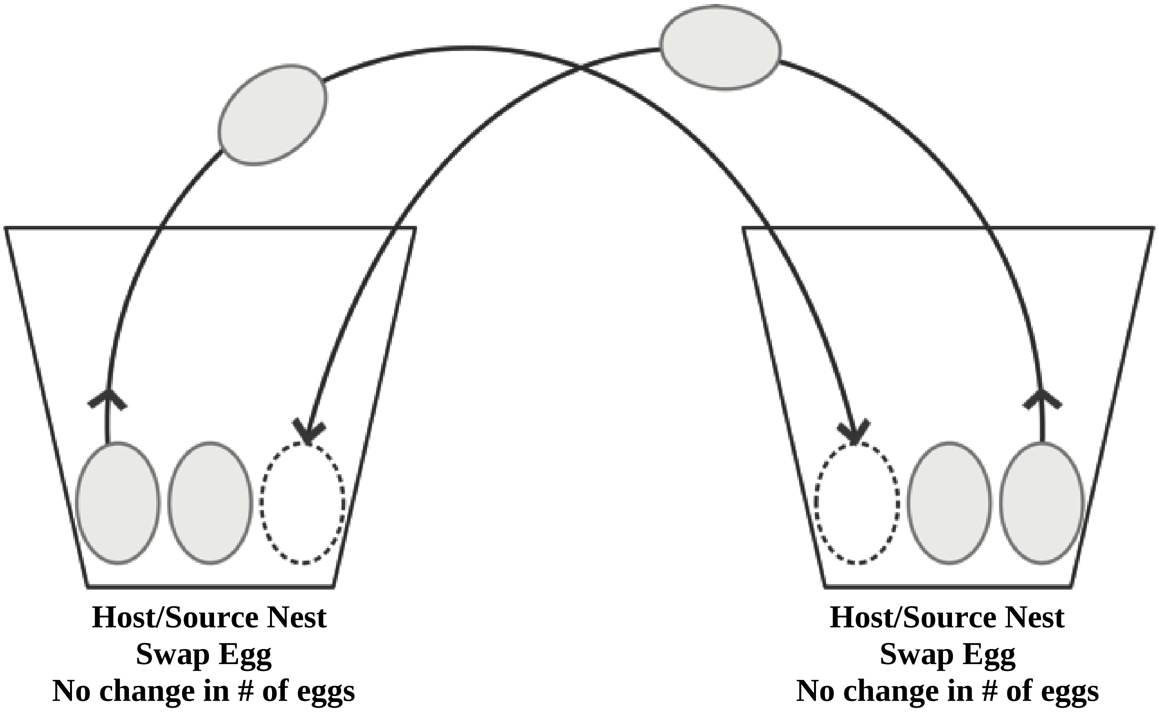


Figure 1.4. Illustrations depicting how I conducted clutch manipulations to record the behavioral responses of host burrowing owls whose nests were subjected to experimental conspecific brood parasitism. One burrowing owl egg was removed from a source burrowing owl nest and then introduced into host nests. (A) I added the source egg to a burrowing owl nest during the host females' normal laying period, or (B) after the host female had completed her clutch and initiated incubation. (C) Source eggs were reciprocally swapped between two burrowing owl nests during the females' normal laying period.

Table 1.1. Number of host rejections and acceptances after I added a single egg into burrowing owl nests during the host's laying period (*n* = 11), during the incubation period (*n* = 11), and when reciprocally swapped between nests during the laying period (*n* = 12) in southwestern Idaho, USA during the breeding seasons of 2012 and 2013.

	Number of Nests		
Treatment	**Reject**	**Accept**	**% Rejected**
Laying Addition	**3**	8	27.3
Incubation Addition	0	11	0.0
Laying Reciprocal	**3**	9	25.0
Control	0	17	0.0
Total	**6**	**45**	**13.3**

Table 1.2. **Table of nest fates (i.e., accept or reject) for burrowing owls relative to differences between the average volume of host eggs and the volume of the parasitic egg added to their nest in southwestern Idaho, USA during the 2012 and 2013 breeding seasons. Negative values represent parasitic eggs that were smaller than the average host egg, whereas positive values indicate larger parasitic eggs.**

Year	Nest Name	No. of Eggs Averaged*	Mean Volume of Host's Eggs	Volume of Parasitic Egg	Treatment	Volume Difference (mm^2)	Fate
2012	Missile 5	3	273.50	356.67	Reciprocal	-83.17	Accept
	Missile 3	4	345.87	410.03	Reciprocal	-64.16	Accept
	Cinder 9	8	356.45	412.03	Incubation	-58.58	Accept
	Tadpole NW 1	7	382.17	417.52	Reciprocal	-35.03	Accept
	Corner 3	2	337.00	348.50	Laying	-11.50	Accept
	Baja 10	11	382.53	362.99	Incubation	19.32	Accept
	Mt. View 4	4	358.34	334.27	Laying	24.06	Accept
	Bennett 1	6	386.54	361.40	Laying	25.14	Accept
	Trailer 4	5	399.07	372.25	Laying	26.82	Accept
	Sub S 2	5	375.37	341.16	Laying	34.36	Accept
	Delta 2	6	402.53	377.99	Reciprocal	36.92	**Reject**
	Sub E 2	9	371.74	327.97	Incubation	43.76	Accept
	Missile 4	4	384.41	329.45	Reciprocal	54.95	Accept
	Missile 1	5	335.40	269.28	Reciprocal	66.12	**Reject**
	Delta 3	9	389.91	314.45	Incubation	75.45	Accept
	Mt. View 1	9	366.46	269.26	Incubation	97.20	Accept
2013	Trailer 1	3	347.96	434.01	Laying	-86.05	**Reject**
	Nic W 3	10	342.65	423.96	Incubation	-81.31	Accept
	Boggs 1	2	280.01	352.16	Laying	-72.15	Accept
	Mt. View 1	6	344.83	405.26	Reciprocal	-60.43	Accept

Year	Nest Name	No. of Eggs Averaged[*]	Mean Volume of Host's Eggs	Volume of Parasitic Egg	Treatment	Volume Difference (mm^2)	Fate
	Sub E 2	6	290.23	352.00	Incubation	-61.77	Accept
	Bennett 1	9	298.67	358.01	Reciprocal	-54.81	Accept
	Bennett 2	8	374.70	424.41	Incubation	-49.71	Accept
	Baja 5	3	316.52	353.62	Reciprocal	-37.10	Accept
	Baja 1	8	319.23	356.03	Incubation	-36.80	Accept
	Missile 5	5	346.61	376.05	Laying	-29.44	**Reject**
	Baja W 1	8	330.36	347.03	Incubation	-16.67	Accept
	Sub S 1	6	354.01	347.03	Laying	6.97	Accept
	Baja 9	5	343.70	333.17	Reciprocal	10.53	**Reject**
	Sub SE 1	7	369.73	335.37	Laying	34.37	Accept
	Mt. View 3	3	415.89	355.82	Reciprocal	60.07	Accept
	Delta 1	6	364.21	287.22	Reciprocal	76.98	Accept
	Baja 4	3	402.08	316.80	Laying	85.28	**Reject**
	Corner 3	8	463.03	364.96	Incubation	98.08	Accept

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[*] total number of host eggs present in the nest prior to the addition of the parasitic egg (i.e., not including those eggs that may have been laid following the experimental parasitism).

Table 1.3. Nest fate (i.e., accept or reject) as a function of treatment[*] and within-clutch variation (SD) of host egg volumes (mm^2) during the 2012 and 2013 breeding seasons in southwestern Idaho, USA.

Year	Nest	Treatment[*]	Host Intraclutch SD (mm^2)	Fate
2012	Missile 1	Reciprocal	28.31	**Reject**
	Missile 4	Reciprocal	23.55	Accept
	Missile 3	Reciprocal	23.19	Accept
	Sub E 2	Incubation	23.07	Accept
	Sub S 2	Laying	21.18	Accept
	Delta 2	Reciprocal	18.76	**Reject**
	Corner 3	Laying	14.71	Accept
	Trailer 4	Laying	13.84	Accept
	Mt. View 1	Incubation	13.02	Accept
	Baja 10	Incubation	12.22	Accept
	Delta 3	Incubation	10.57	Accept
	Bennett 1	Laying	9.85	Accept
	Cinder 9	Incubation	6.63	Accept
	Tadpole NW 1	Reciprocal	6.58	Accept
	Missile 5	Reciprocal	4.63	Accept
	Mt. View 4	Laying	4.02	Accept
2013	Baja 5	Reciprocal	27.23	Accept
	Baja 9	Reciprocal	26.72	**Reject**
	Delta 1	Reciprocal	24.44	Accept
	Baja W 1	Incubation	21.16	Accept
	Sub S 1	Laying	18.66	Accept
	Mt. View 3	Reciprocal	18.08	Accept
	Nic West 3	Incubation	17.64	Accept
	Baja 1	Incubation	16.28	Accept
	Bennett 2	Incubation	16.13	Accept
	Mt. View 1	Reciprocal	16.01	Accept
	Baja 4	Laying	16.00	**Reject**
	Corner 3	Incubation	15.77	Accept
	Boggs 1	Laying	15.34	Accept
	Sub SE 1	Laying	15.04	Accept
	Missile 5	Laying	11.76	**Reject**
	Bennett 1	Reciprocal	11.08	Accept
	Sub E 2	Incubation	10.60	Accept
	Trailer 1	Laying	6.17	**Reject**

[*] Treatment categories: (1) Laying: addition of a parasitic egg during the host's laying period, (2) Incubation: addition of a parasitic egg during the host's incubation period, and (3) Reciprocal: reciprocal swap of a parasitic egg with one of the host's own eggs during the laying period.

Figure 1.5. Photo of a nest where the host burrowing owls rejected the parasitized clutch of eggs (top), and then re-nested (bottom) within the same burrow chamber during the 2012 breeding season in southwestern Idaho, USA.

Table 1.4 Nest attendance for male and female burrowing owls at parasitized (*n* = 5) and control (*n* = 4) nests in southwestern Idaho, USA during the breeding seasons of 2012 and 2013.

Treatment	Nest Name	No. of Nestlings	Male Nest Attendance (min/hr)	Female Nest Attendance (min/hr)
Parasitized	Baja 10	11	15.73	24.75
	Corner 3	7	11.25	28.58
	SubE 2	6	21.45	28.44
	SubS 2	8	14.18	20.98
Control	Cinder 9	3	5.97	23.21
	Baja 9	8	18.58	39.18
	Delta 2	6	16.52	34.04
	Missile 2	6	28.97	36.35
	SubS 1	8	10.34	19.51

Figure 1.6. Photo of two dissimilar eggs taken from the same burrowing owl clutch in southwestern Idaho, USA during the 2013 breeding season. The bottom egg is longer and more pointed than the top egg.

Table 1.5. Number and percent of total prey deliveries by adult male and female burrowing owls in southwestern Idaho, USA during the breeding seasons of 2012 and 2013 captured by nest cameras during crepuscular periods (i.e., dawn and dusk) for the first 17 days after nestlings hatched.

	Nest Name	Treatment	No. of Male Prey Deliveries	Male %	No. of Female Prey Deliveries	Female %
Invertebrates	Delta 2	Control	1	100	0	0
	Sub S 1	Parasitized	3	100	0	0
	Corner 3	Parasitized	6	67	3	33
	Sub E 2	Parasitized	13	62	8	38
	Missile 2	Control	1	33	2	67
	Sub S2	Control	1	33	2	67
	Baja 9	Control	5	16	26	84
	Baja 10	Parasitized	1	12	7	88
	Cinder 9	Parasitized	0	0	0	0
Vertebrates	Cinder 9	Parasitized	12	100	0	0
	Sub S 1	Parasitized	18	95	1	5
	Sub S2	Control	21	95	1	5
	Baja 10	Parasitized	22	88	3	12
	Delta 2	Control	6	86	1	14
	Sub E 2	Parasitized	29	85	5	15
	Baja 9	Control	40	82	9	18
	Corner 3	Parasitized	31	79	8	21
	Missile 2	Control	0	0	1	100

Figure 1.7. Two photos of typical behavior for male (♂) and female (♀) burrowing owls in southwestern Idaho, USA during the breeding seasons of 2012 and 2013. I analyzed nest camera data from the crepuscular periods (i.e., dawn and dusk) during 17 consecutive days after the nestlings had hatched to assess provisioning rates and patterns of nest attendance. (A) Female owl standing near the nest burrow entrance while the male is present at the satellite burrow. (B) Female owl holding vertebrate prey (Perognathus sp.) recently delivered by the male.

CHAPTER TWO: RESPONSES OF FEMALE BURROWING OWLS TO ALTERATIONS IN CLUTCH SIZE: ARE BURROWING OWLS DETERMINATE OR INDETERMINATE EGG-LAYERS?

Abstract

Using field experiments, I examined the egg-laying response of female western burrowing owls (*Athene cunicularia hypugaea*) to clutch size manipulations during the 2012 and 2013 breeding seasons in southwestern Idaho. To assess laying determinacy of burrowing owls, I altered female clutch size by removing or adding one egg during the laying period. At the time of egg removal or egg addition, the resident female had between one and five of her own eggs present in her clutch. I removed one egg each from nine burrowing owl nests (removal nests) and then immediately transferred each into nine other nests (addition nests). The end result was that I reduced clutch size for females by one egg at some nests and likewise increased clutch size by one egg at other nests. I compared the size of completed clutches of both removal and addition nests to the size of completed clutches at control nests that I visited a similar number of times but where no eggs were permanently added or removed. Mean clutch size at removal nests did not differ from controls. On the other hand, mean clutch size at addition nests was significantly larger than clutch size of control nests. These findings suggest that female burrowing owls responded to the removal of an egg by laying a replacement, yet they did not curtail laying in response to the addition of an egg to their nest. Thus, female burrowing owls in my study area may be described as removal indeterminate and

addition determinate. These results have implications for understanding burrowing owl nesting biology, and they also may provide insight into how laying determinacy can facilitate conspecific brood parasitism or mitigate its costs in this species.

Introduction

The cause of the variation in avian clutch size has long fascinated biologists (Craig 1913, Cole 1917, Lack 1954, Skutch 1967, Klomp 1970). Whereas for some species, the number of eggs laid is constant (Cuthbert 1945, Poulsen 1953, Richdale 1950, Rice and Kenyon 1962, Harris 1964, Feare 1976, Snyder and Hamber 1985), for others clutch size may vary within species-specific limits (Kluyver 1951, Davis 1958, Beukeboom et al. 1988). Clutch size variability can be attributed to a number of factors that operate external to the individual. For instance, clutch size varies in relation to nesting habitat (Drent and Daan 1980, Hogstedt 1980, Ball et al. 2002), nest predation (Skutch 1949, Slagsvold 1984, Lima 1987, Martin 1995, Martin et al. 2000, Farnsworth and Simons 2001, Travers et al. 2010), latitude (Jetz et al. 2008, Griebeler et al. 2010), nesting-population density (Both et al. 2000), and laying date (Meijer 1990, Haywood 1993). The question of why birds lay as many eggs as they do can be approached by investigating both the proximate and ultimate factors underlying the regulation of clutch size.

Ultimate Control of Clutch Size

In birds, clutch size is the most important factor in determining reproductive success in that it establishes an upper limit for the number of offspring that can be produced in any single bout of reproduction (Williams 1966, Thomson et al. 1998). The "optimal" clutch size should maximize an individual's lifetime fitness by balancing future reproductive potential with current reproductive costs. Most hypotheses regarding the evolution of an optimal clutch size originate with Lack (1947, 1954, 1966), who hypothesized that clutch size is ultimately determined by the greatest number of offspring for which the parents can adequately provide food, assuming that individuals seek to maximize their reproductive output for each breeding attempt. This reasoning suggests that the largest clutch size that can be supported will be determined by environmental quality or the amount of food available. Offspring from over-sized broods may become undernourished and experience lower survival when compared to the offspring of smaller broods. Thus, if clutch size is heritable, genotypes producing maladaptive clutch sizes will be selected against, and the final result will be that the modal clutch size will be the most productive (Klomp 1970). According to Lack's hypothesis, starvation of offspring should not only occur in over-sized broods but also in those that are of average size when conditions are poor and/or parents are unable to find enough food. The practice of initiating incubation prior to clutch completion, with the result that eggs hatch asynchronously and likely giving some offspring an adventitious head start, may facilitate the adjustment of brood size to the current food supply (Lack 1954). For example, in years when food is not limited, there may be an opportunity to fledge additional young that would have likely suffered increased mortality in those years when food was scarce (Lack and Lack 1951, Ingram 1959).

Although Lack's hypotheses remain influential, his original idea has been extended to incorporate one of the fundamental tenets of life-history theory, i.e., that current reproduction comes at a cost of future reproduction (Perrins 1965, Williams 1966, Charnov and Krebs 1974). For this reason, a smaller clutch may be favored to the most productive when the short-term benefit of a greater number of fledglings is balanced by long-term costs to future reproductive success (Stearns 1976, Boyce and Perrins 1987, Nur 1986). In addition, further emphasis has been placed on the significance of individual variation in parental quality, such that each individual female is capable of adjusting her clutch size to her own unique circumstances so as to maximize her fitness (Perrins and Moss 1975, Hogstedt 1980, Pettifor et al. 1988).

Proximate Control of Clutch Size

The group of ovarian follicles that complete the rapid growth phase of development undergo yolk deposition and eventually ovulation. The anterior pituitary gland secretes the gonadotrophic hormones follicle stimulating hormone (FSH) and luteinizing hormone (LH), which regulate the growth and development of ovarian follicles (Farner and Wingfield 1980, Sharp et al. 1990). In some species, the number of follicles that initially respond to gonadotrophin secretion at the onset of laying is equal to the final clutch size (Cole 1917, Klomp 1970). In these species, external stimuli, such as the number of eggs present in the nest, have no influence on follicular development such that clutch size is determined independent of any extrinsic cues. The precise mechanism regulating clutch size in such determinate egg layers remains largely unknown (Klomp 1970, Haywood 1993). However, one hypothesis is that the number of eggs laid is predetermined by an endogenous, genetically encoded signal; that is, clutch size is determined by mechanisms that regulate the initial recruitment of ovarian follicles (Williams 2012, Haywood 2013).

In other species, the number of follicles stimulated by gonadotrophic hormones is greater than the number of eggs laid, and control of clutch size arises from sensory information gained through external stimuli. In these species, follicular growth and development occurs asynchronously, resulting in a hierarchy of small yolky follicles (3-8 mm in diameter in Warren hens, *Gallus domesticus*) and large yolky follicles (8-40 mm in diameter; Gilbert et al. 1983). Typically, large yolky follicles complete the yolk deposition phase and undergo ovulation, whereas small yolky follicles, which are highly susceptible to undergoing atresia, will likely be resorbed. In species that have a 24-h laying interval, a cohort of small yolky follicles is recruited each day for rapid growth from a quiescent pool of slow-growing follicles (Lofts and Murton 1973, Johnson and Woods 2007, Haywood 2013). From each cohort, only one small yolky follicle is destined to undergo ovulation, while the rest undergo atresia. Thus, in the absence of any extrinsic cues signaling for the disruption of follicular growth, indeterminate layers will lay supra-normal clutches (Haywood 1993). Thus, clutch size in indeterminate layers is regulated by the initial disruption of follicular growth, which may further inhibit the recruitment of additional follicles. Furthermore, clutch size is not ultimately predetermined by a maximum number of follicles, nor is it determined by mechanisms that regulate follicle recruitment. Rather, clutch size is proximately controlled by an inhibitory cue that likely originates from external stimuli (Williams 2012).

In birds, the transition from egg-laying to incubation behavior is generally modulated by increasing blood plasma concentrations of the pituitary hormone, prolactin (Lea et al. 1981, El Halawani et al. 1984, Hall et al. 1986). For example, injection of exogenous prolactin into laying females induces incubation and interrupts egg-laying

(Riddle et al 1935, Opel and Proudman 1980). Prolactin operates at the level of the ovary to directly inhibit growth of small yolky follicles (Zadworny et al. 1989). As denervation of the brood patch (Hall 1987) and egg or nest removal (Etches et al. 1979, Goldsmith et al. 1984, Lea and Sharp 1989) both decrease plasma prolactin levels, the rise and maintenance of high levels of prolactin has been linked to tactile information gained by contact of the brood patch with the growing number of eggs in the nest (Klomp 1970). The increase of prolactin at the onset of incubation and its role in disrupting follicular growth and development suggests that it may be involved in the control of clutch size in indeterminate layers (Haywood 1993).

Laying Patterns in Birds

Birds can be placed into two groups depending upon their response to alterations in clutch size while laying. In some birds, clutch size is predetermined and limited by the number of large yolky follicles that develop in the ovary prior to the start of laying. Cole (1917, 1930) defined this group of birds as “determinate” egg-layers. Neither the addition nor the removal of eggs during the laying period will affect the total number of eggs laid.

In other species, the number of eggs a female is capable of producing is not predetermined and can be influenced by external factors present at the time of laying. Cole (1917, 1930) defined these birds as “indeterminate” egg-layers. Removal of eggs during laying delays the onset of incubation and stimulates an indeterminate female to recruit additional ovarian follicles; this extends the laying period and females effectively replace the lost eggs. When eggs are added to the clutch of an indeterminate female, further follicular development is inhibited and/or existing follicles are resorbed, and egg-laying ceases early.

Because natural egg removal and addition could occur independently (e.g., through nest predation and brood parasitism, respectively; Kennedy and Power 1990), a bird does not have to be both removal and addition indeterminate to be described as an indeterminate egg-layer. A species may be removal indeterminate and addition determinate, or removal determinate and addition indeterminate. If a species of bird has the ability to adjust clutch size in either direction (i.e., prolong laying in response to egg removal, or curtail laying in repose to egg addition), then that species must be indeterminate to some degree (Holcomb 1971). Thus, the ability to prolong laying in response to egg removal is referred to as removal-indeterminate, whereas the ability to curtail laying early when clutch size is increased is referred to as addition-indeterminate (Kennedy and Power 1990). Failure to adjust clutch size in response to either egg removal or addition is referred to as removal-determinate and addition-determinate, respectively.

While laying determinacy has been examined in more than 100 avian species (Kennedy 1991, Haywood 1993, Haywood 2013), it has not been established in western burrowing owls (*Athene cunicularia hypugaea*). However, several facets of burrowing owl natural history suggest that they may be indeterminate egg-layers. In his review of laying determinacy, Kennedy (1991) described several traits that seem to be correlated with indeterminate laying. In general, species that lay relatively large clutch sizes tend to be indeterminate, whereas species that have small clutches tend to be determinate. Burrowing owls lay large clutches of up to 14 eggs (Poulin et al. 2011), so this trait is more consistent with indeterminate laying. Furthermore, clutch size in burrowing owls can be highly variable (4 - 14 eggs, Poulin et al. 2011), which is a characteristic that is also associated with species that lay indeterminately (Kennedy 1991).

The objective of my study was to determine whether burrowing owls are determinate or indeterminate egg-layers. To answer this question, I analyzed clutch size data from a larger experiment that included clutch manipulations (Chapter One). I removed or added one egg from burrowing owl nests during the female's normal laying period and compared the final clutch size to clutch size of un-manipulated, control nests to examine the egg-laying response of female burrowing owls. Because of their relatively large and variable clutch size, I expected that burrowing owls might respond to clutch size manipulations in an indeterminate manner. If burrowing owls are indeed indeterminate egg-layers, I expected that females would adjust their clutch size to compensate for egg removal by laying an additional egg to replace the one that was taken (Figure 2.1). Likewise, if burrowing owls are indeterminate, under conditions of egg addition, I expected female burrowing owls to respond by taking the added egg into consideration when making their clutch size assessment and consequently lay one fewer of their own eggs (Figure 2.1; Haywood 1993, Kennedy 1991).

Study Area and Methods

Study Area

During the 2012 and 2013 breeding seasons, I studied western burrowing owls within the Morley Nelson Birds of Prey National Conservation Area (NCA) in southwestern Idaho (Figure 1.3). The NCA covers approximately 2,430 km^2 (about 1,962 km^2 of which is public land) in Ada, Elmore, and Owyhee counties. Congress established the NCA in 1993 (Public Law 103-64) to provide for the conservation, protection, and enhancement of raptor populations and habitats (Sharpe and van Horne 1998). The Snake River Canyon is the dominant geologic feature, flowing through 130 km of the southern and western portions of the NCA. The topography of the surrounding river plain above the canyon is flat to rolling, with rocky outcrops and a few isolated buttes. Elevation within my focal study area ranged from 877 - 914 m. Precipitation averages 31.7 cm annually, with 12.1 cm occurring during the breeding season (March through July). During the breeding season, average daily temperatures increase from 5.5^{o} C in March to 23.1^{o} C in July (N.O.A.A. 2002).

While some native shrub-steppe habitat remains, range fires and human disturbances have converted large portions of the NCA to exotic annual grasslands. Once covered by expansive shrub-lands, burned and other highly disturbed areas are now dominated by invasive plants such as cheatgrass (*Bromus tectorum*), Russian thistle (*Salsola kalil*), and tumble mustard (*Sisymbrium altissimum*; Hironaka et al. 1983, USDI 1996). The study area also contains BLM-managed rangelands, agricultural fields, several paved and dirt roads, a few homes, and the Orchard Combat Training Center (a military training area used by the Idaho Army National Guard). Agricultural areas grow primarily sugar beets, corn, grain, alfalfa, beans, and potatoes. Cattle and sheep grazing also occur within portions of the NCA, primarily during winter (USDI 1996, Moulton et al. 2005).

There are approximately 350 artificial burrows (deployed in clusters of 2 or 3 artificial burrows per nest-site location; Smith and Belthoff 2001) within the NCA available to burrowing owls for nesting or roosting (Belthoff and Smith 2003, Moulton et al. 2006). Since 1997, burrowing owl nesting pairs have occupied 30-60 of the artificial burrows in the NCA each year (Belthoff and Smith 2003, Belthoff, unpublished data). Distributions of burrowing owls at both natural and artificial nests vary from high density, with up to six neighbors nesting within 400 m of a focal nest, to very low density where many kilometers separate nesting pairs (Welty 2010, Welty et al. 2012). For the purpose of my study, only artificial nest sites were considered for experimentation, although I monitored both natural and artificial burrows during each breeding season. Using artificial burrows allowed me to accurately count, measure, and mark eggs; record the date of egg laying, incubation, and hatching; and capture and mark adult and juvenile burrowing owls.

Locating and Capturing Burrowing Owls

Surveillance for burrowing owl pairs began in mid-March and continued through mid-May in each year. I visited all existing artificial burrow sites at least twice during each breeding season to check for evidence of burrowing owl use. I considered a nest site occupied if I observed an owl repeatedly or signs of use (e.g., whitewash, pellets, dung) at the burrow entrance. I inspected nests every 7-14 days and checked for eggs to confirm the presence of a nesting pair.

To capture adult burrowing owls, I employed one of the following methods: one-way wire basket trap placed at the entrance of the nest burrow (described in Smith 1999), bow-net baited with a mouse (*Mus musculus*), or by hand directly from the chamber of the artificial burrows. I captured juvenile burrowing owls by hand directly from the nesting chamber, although I occasionally captured some juveniles using a one-way basket trap.

Measuring and Marking Owls

Upon capture, I measured the following for each owl: mass (to the nearest g using a 300-g Pesola spring scale), relaxed wing-chord length, tail length, and tarsus length (all to the nearest 1 mm using a metric ruler). In addition, I measured the culmen (to the nearest 0.01 mm using digital calipers) and also measured the length of the emerged primary feathers (from end of shaft to tip of emerging feather) for juveniles. These measurements are standard in my study area and are collected as part of long-term research and monitoring of the local burrowing owl population.

Because males do not incubate, I classified adult owls with brood patches as females (Martin 1973, Poulin et al. 2011). From a distance, I was also able to identify the sex of some pairs of owls based on plumage color differences (males are typically lighter during the breeding season). I was unable to determine the gender of juvenile burrowing owls because they are generally monomorphic in both size and plumage (Poulin et al. 2011). Using venipuncture of a wing vein, I collected 300 µl of blood from adult owls and 100 µl of blood from juvenile owls for use in other studies. Each owl received a U.S. Geological Survey aluminum leg band (size 4). In addition, adult owls received three colored plastic leg bands arranged in a unique combination so they could be easily identified in the field.

Clutch Manipulation Experiments

For examination of laying determinacy, I took advantage of manipulations conducted as part of a larger study designed to answer questions surrounding conspecific brood parasitism (CBP; Chapter One). In 2012 and 2013, I performed clutch size manipulations at 44 burrowing owl nests and monitored 17 un-manipulated control nests as part of that experiment. The investigation of CBP required that some of the clutch manipulations take place after the onset of incubation (*n* = 22). Several studies in other avian species revealed that final clutch size is determined several days prior (typically 3 – 5 days) to the laying of the last egg and is often preceded by an increase in prolactin hormone (Haftorn 1985, Meijer 1990, Beukeboom et al. 1988). To the best of my knowledge, there is no published literature describing the reproductive hormones that regulate clutch size in burrowing owls. Thus, for the purpose of my study, the only nests I included in the analysis of laying determinacy were those at which I manipulated clutch size during laying when a female's clutch size was between one and five eggs.

To facilitate clutch size manipulations, I excavated the nesting chamber for each nesting pair to check for eggs. If no eggs were present on my first visit to a nest, I continued to monitor the nest until I found eggs. Once I found eggs in a nest, I visited the nest weekly until the clutch was complete, and every 7-14 days thereafter. On the first and all subsequent visits, I marked new eggs with a small amount of indelible ink and measured egg width and length to the nearest 0.01 mm with stainless steel digital calipers. All eggs were handled to determine if they had been incubated. If eggs were cool to the touch and lacked noticeable shell pigmentation that often accumulates from incubation, I considered them non-incubated; if the eggs felt warm, I considered them incubated. For all nests, I recorded the date and number of eggs present at each visit and whether incubation had started. To control for any potential effects of human disturbance, I created a set of control nests. I recreated all of my activities at the control nests but did not permanently remove or add any eggs.

Egg Removal and Addition

I ascertained laying determinacy of burrowing owls in two ways. At some nests, I removed one egg from a clutch where incubation had not commenced and then immediately transferred it to another occupied nest site that was at a similar stage of development (Figure 2.3). At these nests, I added the egg that I had recently taken from the removal nest, and placed it in the center of the clutch. Thus, clutch size at removal nests was reduced by one egg, while clutch size at addition nests was increased by one egg. Egg-laying by focal females continued after removal/addition. When I ultimately found the same number of eggs in a given nest for two consecutive weeks, I recorded that number as the final clutch size. Furthermore, after the initial egg removal/addition, I continued to examine the eggs so I could be certain that they were being incubated and that the nest had not been abandoned. I ultimately achieved n = 11 removal nests, n = 11 addition nests, and n = 17 control nests. To establish laying determinacy, I compared the completed clutch sizes of removal and addition nests to the completed clutch sizes of un-manipulated control nests. Because the important comparison is the final number of eggs that are present in the female's nest when she makes her clutch size assessment, I compared the final clutch sizes of removal nests to control nests when not including the egg that I removed and the final clutch sizes of addition nests to control nests while including the egg that I added.

Timing of Manipulation

At most experimental and control nests, I was unable to determine the exact date of clutch initiation. However, by backdating from a known clutch size given a laying interval of 1.5 days (Olenick 1990), I approximated clutch initiation date. To illustrate, if

I found two eggs on my first visit to a nest, I assumed that those two eggs were laid 1.5 days apart. As a result, I would estimate the clutch initiation date to be 3 days prior to my present visit. I approximated clutch completion date by applying the same method, only this time in reverse. Once I had an estimate of the date that a given female laid her last egg, I could then approximate the number of days that a female was still laying eggs after I had manipulated her clutch. This information was useful in establishing whether the time interval from clutch manipulation to last-egg laid was sufficiently long for a female to be able to respond to egg removal or addition.

Data Analysis

I performed Wilcoxon Signed Rank tests to examine the egg-laying response of female burrowing owls to clutch size manipulations. I used a nonparametric test because clutch sizes were not normally distributed. I compared the completed clutch sizes of removal and addition nests to the completed clutch sizes of un-manipulated controls. I used a significance level of alpha < 0.05, and report means ± SE. I performed all analyses using JMP Pro 10 Statistical Software (SAS Institute, Inc., Cary, NC).

Results

In 2013, two nesting pairs deserted their clutch in the week following the addition of an egg (Chapter One). As a result, I could not be certain of the final clutch size at those nests and therefore excluded them from analysis. Two additional nests from 2013 were excluded because I discovered that the manipulation took place too late into the laying cycle. In 2012, one removal nest was abandoned; however, this occurred 16 days after the clutch was completed so I included it in the analysis. It is impossible to know for sure, but I believe that it is likely that either one or both of the adult owls at this nest suffered predation, because it is unusual for adults to abandon nests this late into incubation otherwise (pers. observ.). At the treatment nests, the clutch manipulations occurred 10.4 ± 0.72 days (Range 6 - 17 days) before the female laid her final egg. I ultimately included nine removal nests and nine addition nests in my analysis of laying determinacy.

Egg Removal

Removal of an egg from burrowing owls nests did not cause owl pairs to abandon their nest. Not including the egg I removed, completed clutches at removal nests (8.3 ± 0.44 eggs, n = 9) did not differ significantly in size from un-manipulated control nests (8.8 ± 0.18 eggs, n = 17; Wilcoxon ranked sums: Z = -0.77, DF = 1, P = 0.44, Figure 2.4).

Egg Addition

For three nests not included in these results, the augmented clutch was abandoned soon after the addition of a conspecific egg (see Chapter One). Clutch size at addition nests (10.7 ± 0.66 eggs, n = 9) was significantly larger than the clutch size in control nests (8.8 eggs ± 0.18, n = 17; Wilcoxon ranked sums: Z = 2.74, DF = 1, P = 0.0061, Figure 2.4). For this analysis of addition determinacy, the added egg was included in the calculation of final clutch size.

Discussion

In some species of birds, the number of eggs that are produced can be influenced by external and/or internal cues at the time of laying (Klomp 1970). Those species that can alter their clutch size in response to proximate cues are indeterminate egg-layers, whereas those species that cannot are determinate egg-layers. For instance, some species of gulls (Larus sp.) are indeterminate, and they use tactile information gained from contact between their brood patch and the number of eggs present in their nest to inform their clutch size decisions (Winkler and Walters 1983). Similarly, species within the order Galliformes also prolong laying after egg removal, but they use visual cues to make their clutch size decisions (Steen and Parker 1981). As clutch size is an important determinant of reproductive success, different species of birds have evolved specific laying strategies (i.e., determinate and indeterminate laying patterns) so that they can maximize their lifetime fitness.

Responses to Clutch Manipulations

My results suggest that burrowing owls within my study area responded to the removal of an early-laid egg by producing a replacement, whereas they were unable or unwilling to respond to the early addition of an egg by curtailing their own laying. Based on these behavioral responses, burrowing owls can be classified as removal indeterminate and addition determinate egg-layers. These results are consistent with the behavior of pied flycatchers (*Ficedula hypoleuca*), which is also a species that is removal indeterminate and addition determinate (Kern et al. 2000). In addition to burrowing owls, there are two additional species of owl that have been classified as indeterminate: barn owls (*Tyto alba*; Durant et al. 2004), and snowy owls (*Bubo scandiacus*; Parmelee 1992). In a small study of captive bred barn owls, the removal of the first and all subsequent eggs induced a female to lay 18 consecutive eggs (Y. Handrich, pers. observ. cited *In* Durant et al. 2004). Snowy owls demonstrate extreme flexibility in the number of eggs that they produce, which is largely attributed to the dramatic differences in annual environmental conditions and food supply (Parmelee 1992). Similar to snowy owls, food availability also limits clutch size in barn owls (Mikkola 1983, Taylor 1994). In contrast, supplemental feeding experiments found that food abundance does not influence clutch size in burrowing owls (Wellicome et al. 2013). I did not investigate these factors during my study, but clutch size variation in burrowing owls may be related to age and individual quality (Wellicome 2000), lay date (Wellicome 2000, Rosenberg and Haley 2004), and depredation (i.e., reduced clutch size when re-nesting; Catlin and Rosenberg 2008).

Although it is not fully known when egg removal must occur for burrowing owls to respond in an indeterminate manner, my methods were efficacious in eliciting this response. I removed an egg from nests when females had laid 1-5 eggs. In some species, females will lay substantially more than one replacement egg, provided that the removals begin with the first laid egg (Brockway 1968, Gilbert et al. 1983, Rohwer 1984, Frumkin 1988, Arnold and Rohwer 1991). European kestrel (*Falco tinnunculus*) females lay additional eggs when their clutch size is reduced early in laying, but only if the removals are initiated before the females start spending half of their time incubating (Beukeboom et al. 1988, Meijer 1990). Often prolactin levels steadily increase as the female spends more time incubating, and thus prolactin may proximately regulate clutch size by suppressing the growth and development of additional ovarian follicles (Lea et al. 1981, El Halawani et al. 1984, Hall et al. 1986, Zadworny et al. 1989, Meijer 1990). If and to what extent prolactin influences clutch size in burrowing owls is not known, nor is it known what happens to prolactin concentrations throughout the egg-laying and incubation periods.

Adaptive Benefits of Laying Patterns

There is still some debate as to why certain species of birds are determinate egg-layers and others are indeterminate egg-layers. For burrowing owls, removal indeterminacy could be an adaptive behavior that enables them to replace eggs that are lost as a result of predation or nest destruction (e.g., collapse, flooding). Nest predation in burrowing owls is one of the primary causes of nest failure (Green and Anthony 1989, Desmond et al. 2000, Moulton et al. 2006). Burrowing owls may be more susceptible to nest predation because they nest below ground (Wellicome and Haug 1995, Sleno 2000), yet other studies have shown that avian predators such as the prairie falcon (*Falco mexicanus*), red-tailed hawks (*Buteo jamaicensis*), and great horned owl (*Bubo virginianus*) also pose a substantial predation threat. In this case, indeterminate laying is unlikely to be an adaptive benefit in these instances because avian predators typically pose a threat to burrowing owl offspring post-hatch (Clayton and Schmutz 1999). Green and Anthony (1989) found that predation was responsible for 20% of nest failures and that American badgers (*Taxidea taxus*) were responsible for 90% of the nests lost. In other studies, the overall rate of nest predation has been reported to be even higher (16 – 54%; Desmond et al. 2000). In the event of a predation event, the ability to lay indeterminately would be beneficial especially if the loss of eggs occurs early in the laying period. This ability would allow the female to replace any eggs that were lost or could help the female to quickly re-nest (Parsons 1976). Indeed, for some bird species, re-nesting after predation can increase lifetime productivity (Martin et al. 1989, Hipfner 2001). Thus, given that predation is one of the primary causes of nest failure in burrowing owls, and that the results of my study demonstrate that burrowing owls replace an egg that is removed early in laying, removal indeterminate behavior likely provides some burrowing owls with a selective advantage that allows them to produce a complete clutch following a loss of at least one egg due to nest predation or other natural causes.

Similarly, indeterminate laying may be beneficial to nesting females who lose eggs during laying because they abandon or bury a partial clutch in response to brood parasitism. For example, if a nest is parasitized early in laying and the residents abandon or bury the corrupted clutch, an indeterminate female could avoid an unfavorable lag in egg-laying and instead produce a full complement of eggs without delay. Indeed, burrowing owls in my study area may have responded to experimental brood parasitism in much the same way (see Chapter One). In four cases, soon after rejecting the experimentally parasitized clutch, the resident female re-nested within the same or in a nearby artificial burrow, thereby avoiding any negative effects of delayed nesting. Therefore, removal indeterminate behavior in burrowing owls could also be adventitious if their nest is parasitized (and later rejected) early on in the laying cycle.

Interestingly, indeterminate laying could also provide a fitness advantage for the brood parasite. For example, a female bird who parasitizes the nest of a conspecific but also has a nest of her own could avoid a potentially maladaptive clutch size reduction, provided that she is able to prolong laying (i.e., lay indeterminately) until she has a full complement of eggs in her own nest (Kendra et al. 1988). Conversely, a determinate egg-layer would be unable to avoid sacrificing clutch size in her own nest. If a determinate female laid some eggs parasitically, each egg she lays in another female’s nest would result in one fewer egg in her own nest. Therefore, it is possible that indeterminate laying behavior in burrowing owls could benefit a female if she laid eggs in her own nest, but she also laid some eggs parasitically.

For the hosts of conspecific brood parasites, indeterminate laying could be a disadvantage. If a host female responds to the addition of an egg in an indeterminate way and incorporates the added parasitic egg into her clutch, she may lay fewer of her own eggs. For the indeterminate female, reducing clutch size to account for the parasitic egg would likely decrease her reproductive success. In contrast, an addition-determinate female would not incur the cost of a decreased genetic contribution to her own clutch, and instead she would incur an additional nestling. However, oversized broods could result in a decrease in nestling survival resulting from increased competition for limited parental resources, and an increase in the likelihood of being detected by a predator (Klomp 1970). Intriguingly, a determinate female who is parasitized could potentially avoid the costs of an oversized brood by laying one of her own eggs elsewhere. Thus, it is possible that a single occurrence of brood parasitism could result in a domino effect, effectively triggering a series of parasitic egg-laying among many females.

The results I reported in Chapter One indicated that conspecific brood parasitism may be a component of burrowing owl reproductive behavior because females responded to experimental parasitism by abandoning clutches in some cases. Given that burrowing owls in my study area may be removal indeterminate, it is possible that females who are parasitized and reject a partial clutch of eggs could avoid the costs of a reduced clutch, enabling them to re-nest and resume laying a new clutch of eggs. Also, female burrowing owls could avoid decreasing their own clutch size if they are brood parasites themselves. Furthermore, a determinate response to brood parasitism could be a potential defense strategy for the hosts of brood parasites. In this case, an addition-determinate female could avoid curtailing her own laying in response to the addition of a parasitic egg.

Conclusions

The goal of my research was to determine if burrowing owls are determinate or indeterminate egg-layers. Although extensive investigations have been carried out on their general nesting ecology, no previous study describes the response of female owls to clutch size alterations during laying. My empirical findings that show that burrowing owls may be removal indeterminate and addition determinate egg-layers provide new understanding of burrowing owl reproductive behavior.

Furthermore, my results may provide insight into a strategy for endangered species conservation. Western burrowing owls have experienced significant population declines in portions of their range; they are considered endangered in Canada, threatened in Mexico, and a species of special concern in nine states in the U.S. (Klute et al. 2003). If there were ever the need or desire to supplement the clutch size of wild burrowing owls through captive breeding, it may be possible to remove one egg from the nests of captive breeding pairs, and then introduce single eggs into the nests of wild burrowing owls. My results based on field experiments suggest this method of egg donation would be unlikely to cause a maladaptive clutch size for both the captive and wild pairs. That is, if burrowing owls are removal indeterminate, the captive pair would replace the egg that was removed. Also, if burrowing owls are addition determinate, the addition of an egg to the nest of the wild owls would not cause the host female to handicap her own reproduction by curtailing laying. However, based on my experiments on CBP (see Chapter One), I suggest that captive laid-eggs be added to wild owl nests very soon after the onset of incubation by the host female. This timing would be unlikely to result in rejection and nest abandonment (Chapter One), and it would ensure that the donated egg hatches near the time of the rest of the clutch.

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Predicted Female Response to Clutch-size Alterations

	Determinate	**Indeterminate**
Egg removal	**does not** lay replacement egg	**lays** replacement egg
Egg addition	**does not** curtail laying early	**curtails** laying early

Figure 2.1. Predicted female responses to clutch size alterations.

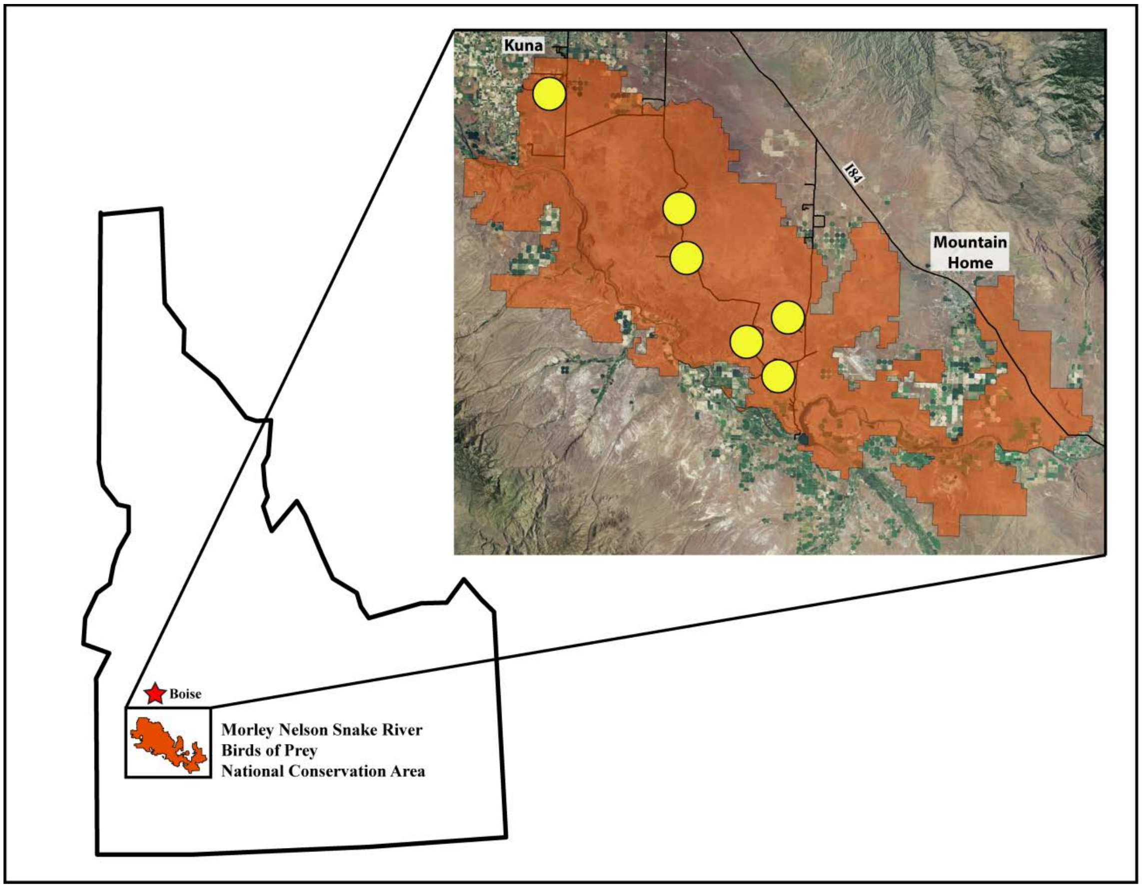

Figure 2.2. Vicinity map showing the location of the Morley Nelson Birds of Prey National Conservation Area (NCA) within southwestern Idaho. Each yellow circle represents the regions in which I examined burrowing owl nests in 2012 and 2013.

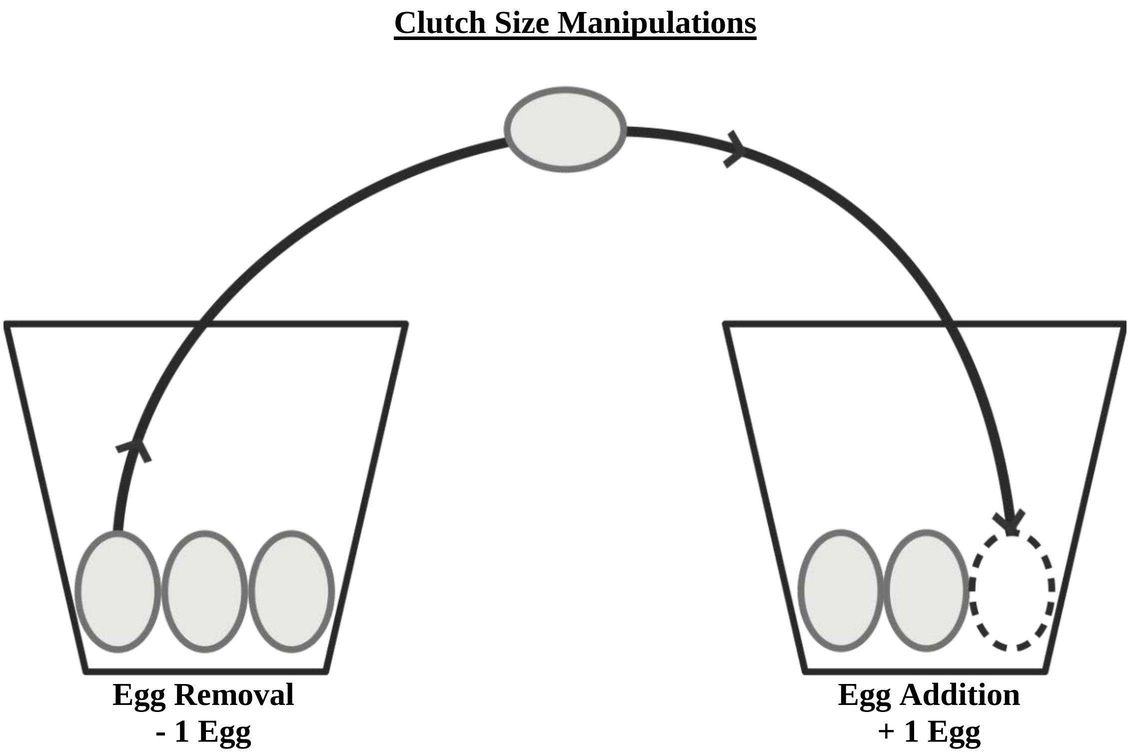

Figure 2.3. **Illustrations depicting how manipulations were conducted to record the egg-laying behavior of female burrowing owls whose clutches were increased or decreased in size by one egg in southwestern Idaho, USA. In each case, one burrowing owl egg was removed from (*n* = 9) nests and then introduced to (*n* = 9) burrowing owl nests during the normal laying period.**

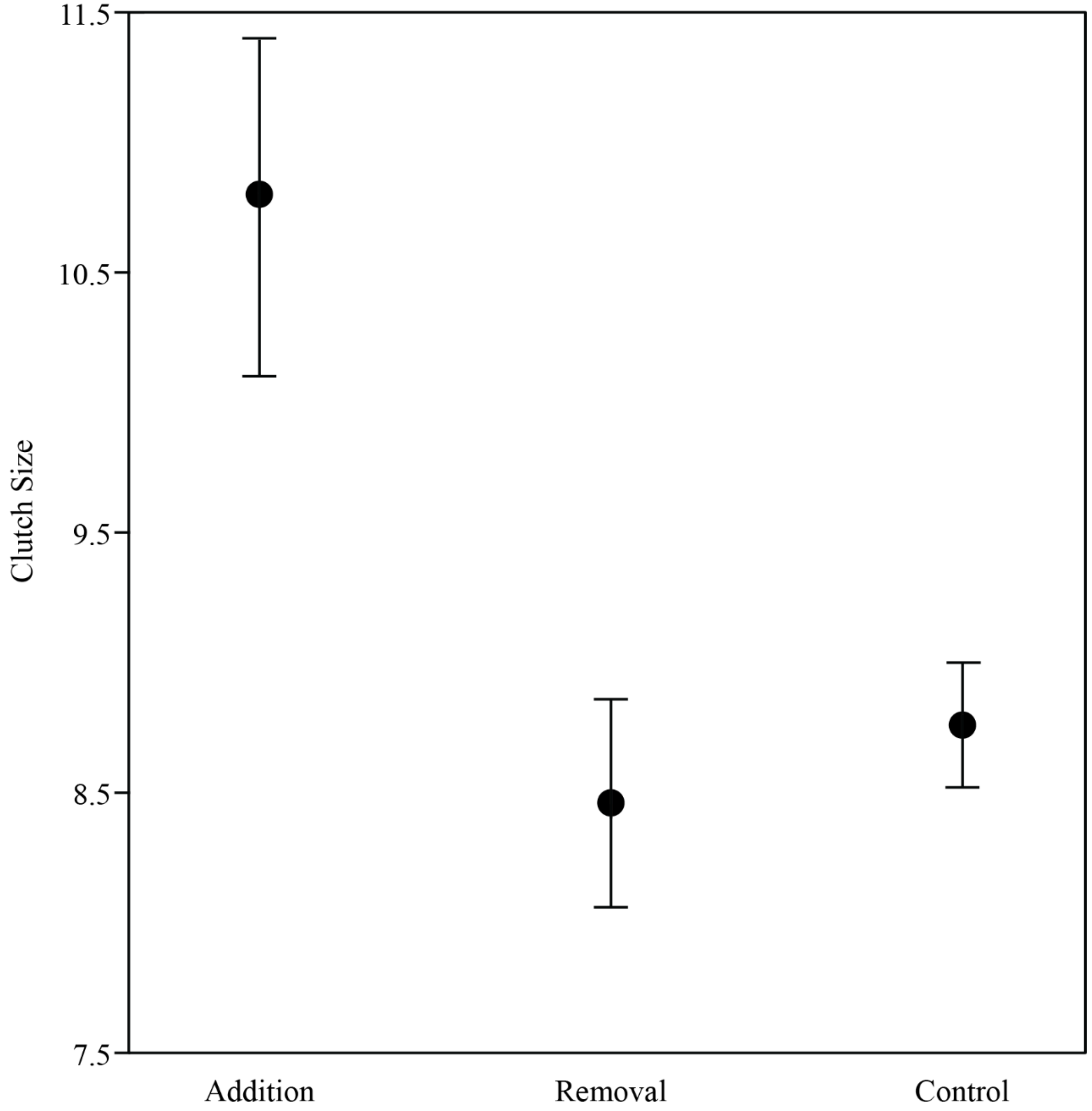

Figure 2.4. Mean ± SE size of completed clutches at nests where one egg was added (*n* = 9) or removed (*n* = 9) during the laying period in relation to completed clutch sizes at control nests (*n* = 17) during the 2012 and 2013 breeding seasons in southwestern Idaho, USA. Completed clutch sizes at addition nests include the egg that was added, whereas completed clutch sizes at removal nests does not include the egg that was removed.

APPENDIX

Appendix 1. Prey weights for each prey species, family, or order used for calculating biomass of prey items observed in still images from nest cameras monitoring burrowing owl behavior in southwestern Idaho, 2012 – 2013 (Moulton 2003).

SPECIES	COMMON NAME	MASS	REFERENCE
Mammals:			
Spermophilus mollis	Pauite Ground Squirrel	177g	Steenhof 1983
Thomomys townsendii	Townsend Pocket Gopher	200g	Steenhof 1983
Perognathus parvus	Great Basin Pocket Mouse	15g	Smith and Murphy 1973
Dipodomys ordii	Ord's Kangaroo Rat	53g	Steenhof 1983
Reithrodontomys megalotis	Harvest Mouse	12g	Smith and Murphy 1973
Peromyscus maniculatus	Deer Mouse	17g	Smith and Murphy 1973
Mus musculus	House Mouse	19g	Steenhof 1983
Microtus montanus	Montane Vole	38g	Smith and Murphy 1973
Unidentified Rodent		15g	Mean weight of mouse sp.
Reptiles:			
Pituophis melanoleucus	Gopher Snake	202g	Steenhof 1983
Sonora semiannulata	Western Ground Snake	9g	Steenhof 1983
Invertebrates:			
Arachnida	Scorpion	1.5g	Smith and Murphy 1973
	Windscorpion	1.0g	Smith and Murphy 1973
Orthoptera	Grasshopper	0.62g	Olenick 1990
	Cricket	0.5g	Moulton 2006
Unidentified Orthoptera		0.5	Smallest Orthopteran weight
Unidentified Coleoptera		0.23	Moulton 2003

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