THE BEHAVIORAL CAUSES OF REPRODUCTIVE SKEW IN COOPERATIVELY

POLYGYNANDROUS ACORN WOODPECKERS (*MELANERPES FORMICIVORUS*)

by

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B.A. August 2009, Hope College

A Thesis Submitted to the Faculty of Old Dominion University in Partial Fulfillment of
the Requirements for the Degree of

MASTER OF SCIENCE

BIOLOGY

OLD DOMINION UNIVERSITY
May 2015

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ABSTRACT

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Reproductive skew, the degree to which reproduction is shared among same-sex

individuals in a social group, is a pattern affected by ecological conditions, sociality,

cooperation, and the inter- and intrasexual behavior of individuals in complex animal

societies. Transactional and compromise skew models assume that high skew is the

product of dominance hierarchies among cobreeders, yet this has rarely been tested. Both

model types fail to incorporate the decisions of more than two individuals, generally

overlooking the effect of female behavior on male reproductive success in multi-male

groups, and are ineffective at predicting skew in larger groups characterized by more than

two same-sex cobreeders. To test these assumptions, I examined the potential behavioral

causes of reproductive skew in acorn woodpeckers (*Melanerpes formicivorus*), a

cooperative polygynandrous species that lacks dominance hierarchies among closely

related cobreeding males despite highly skewed paternity.

I quantified male mate-guarding behavior by measuring overall attendance time

and successful follows of breeding females prior to egg-laying to determine if these

behaviors resulted in a breeding hierarchy reflected by realized paternity. Mate-guarding

behavior of small (two-male) and large (three or more male) cohort groups was compared

to examine the effect of larger group sizes on reproductive skew. Moreover, the potential

effect of female behavior on male reproductive skew was examined by investigating female mating behavior in polyandrous social groups.

Reproductive competition among cobreeding males was high, as evidenced by consistently high attendance behavior throughout the fertile period of breeding females. Groups with three or more cobreeding males mate guarded for more days than groups with two cobreeding males. Attendance and following behavior were good predictors of reproductive skew in two-male groups, but did not predict paternity in groups with three or more cobreeding males. I hypothesized that this species may use tree cavities in which to copulate, and tested the prediction that the frequency and duration of tree cavity visits by breeding females with breeding males determined the realized paternity of the offspring of polyandrous groups. The timing and duration of cavity use behavior of males and females in this study closely resembled the timing and duration of copulation behavior in other polyandrous species. The cavity use behavior of females and males, however, was not a good predictor of realized paternity. The ways in which acorn woodpeckers agree with, and diverge from, the predictions of reproductive skew theory highlight both the potential insight derived by, and the limitation in scope of, this theory as a whole.

ACKNOWLEDGMENTS

The study presented here represents three years of dedicated research and collaboration with talented scientists, colleagues, field assistants, friends, and family. This research would not have been possible without the financial, academic, professional, and emotional support of a community of people. At the top of this list is my advisor, Dr. Eric Walters. I would like to express my gratitude to him for employing me as a field assistant straight out of college, for giving me the opportunity to work on multiple projects with him, and for taking a chance on me as his first graduate student. He provided me the opportunity and support to pursue this exciting research. He has been a friend and mentor, and has guided me through numerous challenges and successes with patience and aplomb. Thank you Eric.

Furthermore, many thanks to my committee members, Drs. Lisa Horth and Walter Koenig, for much-appreciated supervision throughout my graduate career. I am grateful for Dr. Horth's stern, and always accurate, advice. Her insight is spot-on, and her recommendations timely and astute. I am indebted to Dr. Koenig for his wealth of knowledge, experience, and expertise in the field of behavioral ecology, and the study of acorn woodpeckers in particular. His research with Dr. Walters provided the funding and empirical framework for this study. Also, many thanks to Dr. Joseph Haydock for his generous hospitality during the months I spent at Gonzaga University receiving training in genotyping from him and his undergraduate lab assistants. The parentage data presented here are the result of years of effort from the Haydock lab.

and excellent proof-reading skill. I would not have been able to accomplish this work

without the encouragement of all those I have listed here.

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CHAPTER I

INTRODUCTION

Reproductive skew is the degree to which reproduction is partitioned among two or more individuals of the same sex in a social group that cooperates to reproduce and/or rear young (Johnstone, 2000; Koenig et al., 2009). Reproduction that is shared equally is referred to as "low skew," while unequal sharing is "high skew." In many species, skewed parentage is a common feature of complex mating systems, such as polygamous species (species in which individuals are the social mate of more than one member of the opposite sex; Temrin & Sillén-Tullberg, 1994), or cooperatively breeding species (Mulder et al., 1994; Whittingham et al., 1997; Haydock & Koenig, 2002; Williams, 2004; Charpentier et al., 2005; Gilchrist, 2007; Nelson-Flower et al., 2011).

In cooperatively breeding species, individuals often care for offspring that are not directly related to them (Skutch, 1961; Cockburn, 1998; Koenig & Dickinson, 2004). When helpers, as they are known, forego reproduction to provision non-descendant individuals, reproduction becomes highly skewed toward the breeders (Clutton-Brock, 2002; Haydock & Koenig, 2002; Blackmore & Heinsohn, 2007; Koenig et al., 2011).

Distinct from cooperative breeding, reproductive cooperation (also referred to as cobreeding; Díaz-Muñoz, 2014), occurs when two or more individuals of the same sex cooperate to gain access to mating opportunities. This reproductive cooperation is the defining characteristic of cooperative polygyny (groups with one male and multiple females), cooperative polyandry (one female and multiple males), and cooperative polygynandry (multiple males and females). Moreover, reproductive cooperation can take many forms and can include males that participate in display coalitions to attract a mate,

as occurs in lekking wild turkeys (*Meleagris gallopavo*; Krakauer, 2005) and peafowl

(*Pavo cristatus*; Petrie et al., 1999). Male feral horses (*Equus caballus*) form competitive

coalitions that fight to gain access to females (Feh, 1999). In the alpine accentor

(*Prunella collaris*) and acorn woodpecker (*Melanerpes formicivorus*), multiple males and

females coexist and breed in social groups. These birds cooperate to raise the offspring of

multiple breeding birds of both sexes in the group (Davies et al., 1995; Koenig et al.,

1984). Species that cooperatively reproduce, by their very nature, often experience

greater variability in genetic parentage than do monogamous species (Li & Brown, 2000;

Gilchrist, 2007).

Due to the competition for parentage in animal societies characterized by high

skew, many species have evolved behavioral mechanisms by which individuals attempt

to increase their share of reproduction, safeguard future breeding opportunities, or gain

indirect fitness by helping close relatives breed successfully. In birds, males undertake

mate guarding to prevent female insemination by other males (Komdeur et al., 1999;

Chuang-Dobbs et al., 2001; Komdeur et al., 2007), engage in frequent copulation or

cloacal pecking to outcompete or displace sperm from other males (Davies, 1983; Davies,

1990; Hunter et al., 1992; Crowe et al., 2009), form dominance hierarchies to establish

relative access to mating opportunities (Lamprecht, 1986), or pursue extra-group mating

opportunities (Richardson et al., 2001; Hughes et al., 2003). Females destroy the eggs of

cobreeding females (Mumme et al., 1983; Koenig, Mumme, et al., 1995; Schmaltz et al.,

2008), form dominance hierarchies (Richardson et al., 2002; Dey et al., 2012), and

engage in extra-group copulations (Double & Cockburn, 2000).

The causes and consequences of skew are as varied as the species that are influenced by it. The field of reproductive skew theory was developed in an effort to determine common parameters that regulate reproductive success in animal societies (Vehrencamp, 1983; Nonacs & Hager, 2011). Skew theory is an area of study that aims to predict the ecological and social conditions under which individuals of the same sex will share (or not share) reproduction. By identifying the parameters that influence the share of direct and indirect fitness among individuals within animal societies, the ultimate goal of skew theory is to conceive a model through which the formation of social groups, and the evolution of sociality, can be explained (Reeve et al., 1998; Cant & Johnstone, 2000; Johnstone, 2000; Haydock & Koenig, 2003).

Originally conceived by Vehrencamp (1983), early skew models, called transactional models, are predicated on the notion that the allocation of reproduction is affected by group stability; these models are subdivided into "concessions" and "restraint" categories (Johnstone, 2000). In concessions models, one or more "dominant" individuals control the share of reproduction allotted to "subordinate" members, and the fraction of reproduction allocated is balanced against the risk of losing subordinate help if subordinates have no reproductive incentive to stay in the group (Vehrencamp, 1983; Reeve & Ratnieks, 1993; Reeve & Emlen, 2000). The fraction of reproduction apportioned to subordinates by dominants is called the reproductive concession. If a dominant individual affords too small a concession, subordinates have the option to leave the group, eliminating subordinate help provided to the dominant individual and disrupting group stability. In this model, dominants control the allocation of reproduction, while subordinates control group membership. Subordinates must therefore

weigh the potential reproductive success they will achieve in the group against their potential reproductive success if they choose the outside option and leave the group. If their chance of reproducing outside the group is high, the dominant must concede a larger share of reproduction to keep subordinates in the group, resulting in lower skew. Conversely, if a subordinate's chance of reproducing on its own is low, dominants only have to afford a small portion of reproduction to ensure group stability. When dominants and subordinates are closely related, the concession is predicted to be smaller due to the indirect fitness the subordinate gains when the dominant reproduces, resulting in higher skew (Clutton-Brock, 1998; Johnstone & Cant, 1999).

Restraint models make the opposite prediction: subordinates control the allocation of reproduction among members of the group, while the dominant members control group membership (Johnstone & Cant, 1999). Under these parameters, subordinate members must restrain the amount of reproduction they claim, lest the dominant members evict them from the group for monopolizing too large a share (Clutton-Brock, 1998; Johnstone & Cant, 1999). The subordinate's share of reproduction therefore represents a trade-off with the dominant to prevent the dominant from ejecting the subordinate from the group. Because the subordinate individual makes the decision about the partition of reproduction in this model, the predictions are reversed from concessions models. When dominant and subordinate members are close relatives, or the potential to reproduce successfully outside of a group is reduced by ecological constraints, or group productivity is high, the subordinate can claim a greater share before the dominant will risk losing fitness and disrupt the stability of the group by evicting the subordinate. As a result, reproduction is shared by dominants and subordinates more equally. When

dominant and subordinate members are not closely related, or the potential to reproduce

successfully outside of a group is greater, or productivity in the group is low, the

subordinate must restrain itself from claiming too great a share of reproduction because

eviction and loss of group stability has less effect on the fitness of the dominant under

these conditions, which results in high reproductive skew that favors the dominant

(Johnstone & Cant, 1999; Reeve & Keller, 2001). An advantage of this model is that it

can account for the possibility that a subordinate might acquire dominant status at some

point in the future. Such a prospect acts as an incentive for the subordinate to claim a

smaller share of reproduction in order to safeguard a place in the group until the change

in status can occur (Johnstone & Cant, 1999).

Both concessions and restraint models assume that all members of the group have

complete knowledge of the reproductive opportunity of the other members, and

dominants or subordinates (depending on the model) exert complete control over the

allocation of reproduction among the other members of the group (Reeve & Keller,

2001). Neither model, however, accounts for intra- or intersexual conflict between

members of a group if all individuals compete for a greater share of reproduction (Zink &

Reeve, 2005; Nonacs & Hager, 2011).

Following the introduction of transactional models, compromise models were

proposed in order to account for uncertainty on the part of group members as to the true

allocation of reproduction (Reeve et al., 1998; Johnstone, 2000). In compromise models,

instead of reproductive incentives balanced against group stability, reproductive success

is determined by the competitive ability of each individual, with each individual claiming

as much reproduction as possible against the ability of the other members of the group to

do likewise. Here, dominance is established according to competitive ability and effort. Group stability is not a factor in these models, though group productivity is significantly affected by conflict between group members. In a prevailing compromise model – the "tug-of-war" model – the more effort each member invests in competition, the lower the group productivity. The benefits gained from competition for each individual must therefore be weighed against the cost of intense competition that results in lower productivity affecting all group members (Reeve et al., 1998).

Concessions and restraint models put great emphasis on the importance of group stability on the reproductive success of its members. Compromise models account for conflict among members of the group, but are limited in terms of predictions about ultimate causes of skew in animal societies. Yet, all of these models make the same assumption that skew is determined by dominance hierarchies (Keller & Reeve, 1994; Kokko & Johnstone, 1999; Reeve & Keller, 2001). This is reflected in the universal practice of labeling individuals as "dominant" and "subordinate" in skew models.

The definition of dominance is extremely varied in the scientific literature. In concessions models, dominance takes the form of control over the reproduction of group members, while in restraint models, dominance is determined by controlling group membership. Compromise models define dominance according to the competitive ability of an individual to exploit a larger share of reproduction than other members of the group. Moreover, dominance can take the form of very different behavior according to the species being studied, and the definition of such behavior by the researcher (Drews, 1993).

Despite the ubiquity of this assumption, there have been relatively few studies in avian species that have explicitly tested if high skew is caused by the existence of a dominance hierarchy within social groups (Dawson & Mannan, 1991; Jamieson, 1997; Cant & Field, 2005). The lack of empirical tests of reproductive skew in dominance hierarchies is further complicated by the fact that most reproductive skew models exclusively address groups with only two cobreeders, in which one individual is the dominant and the other the subordinate (Keller & Reeve, 1994; Reeve & Keller, 2001). Limiting the breeding cohort to two individuals significantly simplifies the math in these models and clarifies the predictions they make. As a consequence, however, these types of models fail to accurately predict the complex behavior of cobreeding coalitions consisting of more than two individuals (Johnstone et al., 1999). Thus, polyandrous, polygynous, and polygynandrous species characterized by three or more same-sex cobreeders are overlooked by skew theory, despite the fact that these species have the potential to exhibit an intensification of the behavior predicted by skew models for smaller groups resulting from the greater number of cobreeders.

A second assumption consistently made in skew theory – which is most likely linked to the failure of most skew models to take into account a third individual – is that the distribution of paternity among cobreeding males is determined by the behavior of the males alone. In so doing, both transactional and compromise models often overlook the possibility that females may exert considerable influence on the allocation of reproductive skew in male cobreeding cohorts (Magrath & Heinsohn, 2000), as has been shown in brown jays (*Cyanocorax morio*; Williams, 2004).

The objective of the study presented here was not to test a specific model of reproductive skew, per se, but to qualitatively determine potential ways males and females behaviorally influence reproductive skew in a cooperatively breeding, socially polygynandrous species – the acorn woodpecker. In so doing, it was my goal to test the two predominant assumptions of reproductive skew theory: skew is determined by dominance hierarchies in social groups, and females do not significantly affect the distribution of paternity among cobreeding males. In Chapter II, I tested the effect of dominance hierarchies on paternity in polyandrous groups by determining if mate-guarding behavior predicts the reproductive skew of paternity. In Chapter III, I tested the assumption that females do not play a role in determining paternity in polyandrous groups by examining the relationship between female mating behavior during the fertile period leading up to egg-laying, and the distribution of paternity of the offspring produced in the resultant nests. Moreover, in both chapters I investigated the effect of larger male cohorts, consisting of three or more cobreeders, on reproductive skew and male and female behavior. Behavior and skew were examined in these groups to determine whether the predictions of reproductive skew theory remain accurate for larger groups.

CHAPTER II

THE EFFECT OF MATE GUARDING ON REPRODUCTIVE SKEW

INTRODUCTION

Mate-guarding behavior is defined as a close association between a male and a female in conjunction with the fertile period of the female, and it is a tactic frequently employed by males to prevent the female they are guarding from copulating with other males. It can occur before the female is fertile (precopulatory; Mumme et al., 1983a), during the fertile period (Morton, 1987; Gowaty et al., 1989; Møller & Birkhead, 1991; Hatchwell & Davies, 1992; Chuang-Dobbs et al., 2001; Komdeur, 2001; Low, 2006; Dias et al., 2009; Wilson & Swaddle, 2013), or after copulation has occurred (postcopulatory; Elias et al., 2014). Mate guarding is highly dependent on a male's ability to assess when a female becomes fertile and reaches peak fertility (Härdling et al., 2004), as well as the risk of potential sperm competition, which is competition between the sperm of two or more males to fertilize a female's eggs (Birkhead et al., 1992; Komdeur, 2001).

Mate guarding is commonly described as a proximate cause of reproductive skew among males. A male mate guards in order to prevent other males from fertilizing his mate's eggs, and by doing so, he insures his own paternity and biases skew in his favor (Komdeur et al., 1999; Chuang-Dobbs et al., 2001; Komdeur et al., 2007). Mate guarding of females by males is quantified relative to other activities, such as the trade-off between the time a male invests in guarding his mate, the time he must spend foraging, and the time he spends soliciting extra-pair copulations with other females (Parker, 1974; Chuang-Dobbs et al., 2001; Komdeur, 2001).

A shortcoming of the body of mate guarding research on avian species to date is that it has been disproportionately examined within the context of social monogamy (Birkhead, 1982; Gowaty et al., 1989; Chuang-Dobbs et al., 2001; Komdeur, 2001; Dias et al., 2009; Wilson & Swaddle, 2013). Relatively few studies focus on mate guarding in more complex mating systems, such as cooperatively breeding species characterized by variable numbers of male and/or female "helpers-at-the-nest" who participate in the care of offspring not their own (alloparental care; Skutch, 1935; Woolfenden, 1975). Even in cooperatively breeding species, mate guarding studies have concentrated on monogamous pairs because the majority of cooperatively breeding avian species are characterized by a monogamous pair and variable numbers of helpers (Legge & Cockburn, 2000; Koenig & Dickinson, 2004).

Mate guarding studies that examine avian species that participate in reproductive cooperation are even rarer (Mumme et al., 1983a; Hatchwell & Davies, 1992; Watts, 1998). Here I define reproductive cooperation, separate from cooperative breeding, as mating systems in which two or more individuals of the same sex cooperate to gain access to mating opportunities, also referred to as cobreeding (Díaz-Muñoz, 2014). Reproductive cooperation is sometimes a prominent feature in socially polyandrous, polygynous, or polygynandrous species, such as the Galapagos hawk (*Buteo galapagoensis*; Faaborg et al., 1995), pukeko (*Porphyrio porphyrio*; Jamieson et al., 1994), and acorn woodpecker (*Melanerpes formicivorus*; Koenig et al., 1984). Due to the lack of male cobreeders, monogamous males guard against extra-group males. When two or more males share a mate within the framework of a polyandrous mating system, the role of mate-guarding behavior is consequently more complex than it is in monogamous

species because polyandrous males are guarding against cobreeders, which are in some cases close relatives, in addition to males outside the group (Griffin, 2003; Andersson & Simmons, 2006).

Nonetheless, in many polyandrous species, cooperation between cobreeding males to reproduce has been theorized to benefit breeders through the indirect fitness gained when the males are closely related and therefore pass shared genes to their offspring (Hamilton, 1963, 1964; Clutton-Brock, 2002; Díaz-Muñoz et al., 2014). When cobreeding males are related, males that do not sire young are still able to accrue indirect fitness by not constraining the reproduction of a close male relative, and/or by caring for the offspring produced by a relative (Clutton-Brock, 2002). Cobreeding males can further benefit from the increased lifetime reproductive success and survivorship sometimes afforded by cooperating to reproduce, even when they are not closely related (Jamieson et al., 1994; Haydock & Koenig, 2003).

Mate guarding within the context of cobreeding among relatives represents a conflict between incurring direct fitness benefits through descendant offspring versus the indirect fitness benefits and overall group cohesion gained by not limiting the reproduction of cobreeders (Díaz-Muñoz et al., 2014). In some polyandrous and polygynandrous species, this conflict is dealt with by forming dominance hierarchies in which one or more individuals attain the majority of parentage (Eason & Sherman, 1995; Kokko & Johnstone, 1999; Cant & Field, 2005), while individuals lower in the pecking order achieve lower, or zero, reproductive success. Whether the "dominant" or "subordinate" individuals constrain the reproduction and group membership of the other individuals in the group is a subject of much debate, and forms the basis of reproductive

skew theory (Reeve et al., 1998; Johnstone, 2000; Nonacs, 2000). Both transactional and compromise models assume that individuals within a group form a dominance hierarchy in which a single individual, or group of individuals, affects the distribution of reproduction within the group (Johnstone, 2000; Reeve & Keller, 2001). Dominance is a relative term, dependent on the behavior of two or more individuals, and is typically established by an individual controlling the mating opportunities of cobreeders (Whittingham et al., 1997), individuals participating in repeated agonistic behavior with a consistent outcome (Drews, 1993), or by controlling the group membership of cobreeders (Cant et al., 2000).

There have been many studies that have examined the role of mate guarding within the context of mating strategies and evolutionary theory (Parker, 1974; Birkhead, 1979, 1982; Hatchwell & Davies, 1992; Wilson & Swaddle, 2013). Yet, few studies have tested explicitly if breeding hierarchies, as predicted by reproductive skew theory, determine genetic parentage within the framework of reproductive cooperation. This study represents an empirical test to investigate if a breeding hierarchy, established by mate-guarding behavior, truly influences the reproductive skew of polyandrous acorn woodpecker groups comprising two or more cobreeding males mated to a single female.

Acorn Woodpeckers

The mating system of acorn woodpeckers is characterized by family groups that vary from monogamous pairs to polygynous, polyandrous, and polygynandrous compositions (Haydock et al., 2001), and the majority of family groups throughout its range include non-breeding helpers of both sexes (Koenig et al., 1998). In California,

these family groups reside year-round in semi-permanent territories closely associated with oak-savannah habitat characterized by diverse oak species (MacRoberts & MacRoberts, 1976; Koenig et al., 1995b). Acorns make up a substantial portion of the acorn woodpecker diet, and this species spends a considerable amount of time and effort harvesting acorns in the fall and storing them in specialized storage trees, called granaries (Stacey & Ligon, 1987; Koenig et al., 2002). They excavate nest and roost cavities in trees within their territories (Hooge et al., 1999).

Acorn woodpecker helpers are almost exclusively offspring from previous nests that stay in their natal territory and participate in alloparental care (Koenig & Mumme, 1987; Hatchwell & Komdeur, 2000; Koenig & Walters, 2011). In some cases, the delay of dispersal lasts for several years, even though helpers reach sexual maturity within their first year (Koenig & Pitelka, 1981; Stacey & Koenig, 1990; Koenig et al., 2000; Koenig & Walters, 2011).

Moreover, cobreeding birds of the same sex are not random aggregations of birds, but related individuals, most typically close relatives such as sisters or mothers/daughters that nest jointly, brothers or fathers/sons that cobreed, as well as other combinations of uncles/nephews, aunts/nieces and cousins of varying degree that share breeding status (Hannon et al., 1985; Koenig et al., 1998; Koenig & Walters, 2011). Given this complexity, this species is ideal for examining how various combinations of same-sex breeders, particularly individuals that are closely related, compete for breeding opportunities while maintaining reproductive cooperation.

There is, for example, high competition among acorn woodpeckers to gain direct fitness through reproduction, as the chances are generally low for first-year birds to

acquire breeding status through dispersal or inheritance (Koenig et al., 2000). Only an estimated 56% of males and females that survive to their first spring eventually achieve breeding status (Koenig et al., 2000). Males, however, are five times more likely than females to inherit breeding status with their same-sex parent in their natal territory when the breeder of the opposite sex is replaced by an unrelated breeder from outside the group (Koenig et al., 2000; Haydock et al., 2001).

Predominantly, investigators of cooperatively breeding avian species have argued that the delay in dispersal of helpers is due to constraints on breeding vacancies and limited availability of prime breeding territories with optimal resources. In the case of acorn woodpeckers, these resources, termed "ecological constraints," include adequate acorn storage, food supply, and nesting/roosting cavities (Emlen, 1982; Vehrencamp, 1983; Stacey & Koenig, 1990; Hatchwell & Komdeur, 2000; Haydock et al., 2001).

When multiple birds of the same sex occur within a social group, as is the case when there are multiple cobreeders and helpers of the same sex in acorn woodpecker family groups, it could be expected that there is high competition among all same-sex individuals to reproduce, helpers and breeders alike. Yet Koenig et al. (1998) demonstrated that incest avoidance plays a significant role in determining who will reproduce. Despite the reduced chance that young birds will be able to fill a breeding vacancy in their first year, sexually mature helpers actively eschew breeding with the birds in their natal group when their opposite-sex parents are present (Koenig et al., 1998). This effectively avoids inbreeding depression, but also delays an individual's own reproduction for as many as five or six years (Koenig, 1987; Koenig et al., 1998; Haydock et al., 2001). Nonetheless, competition is still readily apparent in the fierce

power struggles that play out among helpers and breeders of different groups following breeding vacancies (Koenig et al., 1984; Hannon et al., 1985).

Among females, there is evidence of competition in both polygynous and polygynandrous groups, which are restricted to 2-3 breeding females. This competition is manifested in their egg-destruction behavior (Koenig et al., 1998). Egg-destruction occurs when one female of a joint-nesting pair is ready to begin laying eggs and the other female is not. The non-laying female will remove any egg from the nest cavity when she discovers it, thus delaying clutch initiation. Females can only lay one egg per day, so this behavior usually continues on subsequent days until the day before the egg-destroying female is ready to lay eggs herself (Koenig, Mumme, et al., 1995). Egg destruction also functions to prevent the initiation of two simultaneous nests within a single family group (Mumme et al., 1983b; Koenig, Mumme, et al., 1995).

Despite the fact that egg-destroying females are killing potential offspring that are closely related to them, this behavior ensures that a single female is not able to gain an advantage over her cobreeder by laying her eggs early, which would result in older, larger chicks than those eggs laid later. Accordingly, behavioral observation demonstrates that egg destruction results in synchronization of egg-laying, and ensures equal reproductive opportunities among joint-nesting females (Mumme et al., 1983b; Koenig, Mumme, et al., 1995; Koenig et al., 1998). Moreover, egg destruction results in a lifetime reproductive success in joint-nesting females that does not differ significantly from that of females who nest singly (Stacey & Koenig, 1990; Koenig, Mumme, et al., 1995), or may, in fact, result in a slightly higher lifetime reproductive success than singleton females (Mumme et al., 1983b).

Subsequent genotyping of the young from polygynous and polygynandrous acorn woodpecker groups confirmed the results garnered by behavioral observation: joint-nesting females share reproduction equally (Dickinson et al., 1995; Haydock et al., 2001). Paternity among cobreeding males, however, is not equal. In fact, paternity of the offspring in the majority of polyandrous nests is predominated by a single male and with no evidence of extra-group paternity (Haydock et al., 2001; Haydock & Koenig, 2002, 2003).

Past work has demonstrated that polyandrous males mate guard breeding females, while monogamous males generally do not (Mumme et al., 1983a). Yet despite many years of observation, there is still relatively little known about the behavioral mechanism by which male cobreeders partition reproduction among the two to five males typical of polyandrous groups (Haydock et al., 2003). Genetic analyses show the high reproductive skew typical of polyandrous acorn woodpecker group nests is not consistent among nests or years. This is true even when the composition of breeding birds remains unchanged (Haydock et al., 2001; Haydock & Koenig, 2003). Thus, the male with the majority of paternity often varies from nest to nest (Haydock et al., 2001; Haydock & Koenig, 2003).

In a study to determine the effect of limiting the potential for reproductive success on the behavior of males, Koenig (1990) removed single polyandrous breeder males from eight groups prior to egg-laying. These removals resulted in the destruction of four (50%) experimental nests following the release of the males back to their groups during incubation (Koenig, 1990). These results suggested that breeding males have a means of ensuring that they at least are competitive for paternity in a manner similar to joint-nesting females by destroying nests when access to the breeding female during her fertile

period is denied. Paradoxically, the high skew revealed by genotyping offspring of polyandrous groups (Haydock & Koenig, 2002, 2003) suggests the opposite pattern: in the majority of cases, one male was able to achieve disproportionately higher paternity compared to their cobreeders even though all males were present during the female's fertile period. Thus, competition for reproduction appears to be high among breeding males.

Polyandrous acorn woodpecker groups consist of variable numbers of males in the breeding cohort, and offspring produced by these groups are almost never sired by males outside of the social group (Haydock et al., 2001). This means, by definition, that mate guarding serves a different function for the males in these groups. Instead of protecting against extra-pair paternity, mate-guarding behavior represents within-group competition for paternity among closely related breeding males (Mumme et al., 1983a; Koenig et al., 1998). Again, this is reinforced by evidence that male acorn woodpeckers in monogamous pairs generally do not guard their mates (Mumme et al., 1983a).

By examining skew through the lens of compromise models, competition between males is thought to play a significant role in the way paternity is distributed among cobreeders (Reeve et al., 1998; Johnstone, 2000). I hypothesized that the more acorn woodpecker males mate guarded, the more likely they would father a greater proportion of offspring relative to other cobreeders in the group, and that inequality in mate-guarding behavior among cobreeding males would be reflected in a similar degree of skewed paternity. Thus, mate-guarding behavior likely forms the basis of breeding hierarchies in these groups. Moreover, as an extension of the Mumme et al. (1983a) study, which found that 2-male breeding groups mate guarded significantly more than

single-male groups, I hypothesized that males in groups with three or more cobreeding males would mate guard longer and with more frequency than males in 2-male groups, due to the increased competition caused by additional breeding males. These hypotheses are represented in the following three predictions:

1. Breeding males that mate guard more relative to their cobreeders will father more offspring than their cobreeders.

2. The duration of mate guarding will be longer in groups with three or more breeding males than groups with two breeding males, due to increased conflict caused by additional cobreeding males.

3. The proportion of successful follows and attendance time of males in 3+ male groups will be higher than that of males in 2-male groups.

I examined mate-guarding behavior using three years of observational data, and determined if mate-guarding behavior and reproductive skew differed according to the size of the male cobreeding cohort in a group. Finally, I tested the relationship between mate-guarding behavior and paternity based on the genetic parentage of offspring produced during the years mate-guarding behavior was observed.

METHODS

The population of acorn woodpeckers at the Hastings Natural History Reservation in Carmel Valley, California has been studied continuously and extensively since 1971.

Forty-four years of study have yielded a population that has been color-marked (N =

5,736 birds as of February 2015), from which blood samples from each individual caught

have been collected since 1985.

Because the composition of acorn woodpecker groups can change across years,

particularly during the breeding season, it was necessary to determine which groups at

Hastings were polyandrous. To accomplish this, the entire acorn woodpecker population

at Hastings was assessed at the beginning of each breeding season from 2009 to 2011 to

determine the breeding composition of each group. This was accomplished by visiting

every active territory on the Reservation in February and March in order to census each

group and determine group composition.

Acorn woodpeckers are cooperative breeders that live in social groups that often

include one or more non-breeding helpers of either sex. Helpers are identical in

appearance to breeders, their status can only be inferred by their relationship to opposite-

sex breeders. Breeding status is obtained by helpers in one of two ways: when one or

more individuals disperse to a new territory to fill a breeding vacancy or by inheriting the

natal territory should all opposite-sex breeders die or disperse (Hannon et al., 1985).

Incest is rare and thus breeders mate with all non-related members of the opposite sex

within the group (Koenig et al., 1998; Haydock et al., 2001).

Following the identification of polyandrous groups, these groups were visited at

least once every week to determine when mate guarding was initiated. Observations of

acorn woodpecker mate-guarding behavior in polyandrous groups were carried out

annually during the spring breeding season at Hastings during three years (2009-2011;

Table 1). The dates of onset, duration, and conclusion of mate guarding were recorded for

all nest attempts in 2010 and 2011. These data were not recorded in a consistent manner in the 2009 pilot year. In addition, the onset and duration of mate-guarding behavior was noted for thirteen nest attempts at nine groups in 2012 to supplement the data on the mean length and date of initiation of mate guarding in polyandrous groups, though mate-guarding behavior was not quantified during the 2012 breeding season (Table 2).

Once initiation of mate-guarding behavior was confirmed, the group was subjected to 3-9 observational watches (mean = 4). Watches were three hours in duration and were conducted on separate days during the mate guarding period. The length of time males spent mate guarding varied by group, ranging from 7 to 32 days. Consequently the total number of watches at each group varied according to the number of days the behavior persisted. Watches were conducted on non-consecutive days to distribute them as evenly throughout the mate guarding period as possible given the variable duration of the behavior across groups, and to facilitate observation of as many groups as possible when mate guarding happened concurrently at multiple groups.

Each family group at Hastings defends a discrete territory surrounding one or more granary trees where they store their acorns. The breeding birds were viewed near their territories from a canvas blind using a spotting scope and binoculars, and observations were recorded by dictation into a voice recorder. Observations were centered on the granaries and nest trees within each group's territory, where the birds spent the majority of their time.

Table 1. Nesting attempts for which attendance and following behaviors were observed at groups by year for 2009-2011. Only following behavior was observed at the group in bold.

Year	Nest No.	Group	No. Cobreeding Males
2009	1	**Cabin**	3
2009	1	Central Canyon	2
2009	2	Central Canyon	2
2009	1	Hay-Blom	2
2009	1	MacRoberts	3
2009	2	MacRoberts	3
2010	1	Central Canyon	2
2010	1	Dipsy	4
2010	1	Knoll	2
2010	1	MacRoberts	3
2010	2	MacRoberts	3
2010	1	Mike	3
2011	1	Mike	3
2011	1	Gate	2
2011	2	Gate	2
2011	1	Knoll	5
2011	2	Knoll	5
2011	1	Plaque	3

Table 2. Nesting attempts for which mate guarding initiation dates and durations were recorded in 2012.

Year	Nest	Group	Males
2012	1	ArfToo	2
2012	2	ArfToo	2
2012	1	Blompond	2
2012	2	Blompond	2
2012	1	Cavity	3
2012	2	Cavity	3
2012	1	Gate	2
2012	2	Gate	2
2012	1	Knoll	5
2012	1	Mike	2
2012	1	Middle Long Field 2	3
2012	1	Plaque	2
2012	2	Plaque	2

Mate guarding was quantified using a modification of the methods employed by Mumme et al. (1983a). The behavior was characterized by quantifying following behavior and attendance time. Successful follows were defined as the number of times the breeding female flew more than 15 m away from a breeding male and the male followed within 30 sec of her departure during a 3-hr observation period. This was compared to the number of times the male failed to follow the female during each watch for that group. Following behavior was expressed as a proportion of follows out of the total number of opportunities the male had to follow the female when she flew more than 15 m away during all observation periods. A male was considered to be guarding a female as long as the female was within 15 m of him and within his view.

Attendance time constituted the total amount of time each breeding male was within 15 m of the breeding female while both were in sight of the observer during a 3-hr observation period. Attendance was then expressed as a proportion of the total time the female and each male were within the observer's view during all 3-hr periods. The following and attendance behavior of males in 2-male groups and those of 3+ male groups were compared with Mann-Whitney *U* tests using SPSS software. The same test was used to compare the mate guarding duration, and the reproductive skew of the two types of groups.

Mate-guarding behavior data were standardized across groups relative to the first egg date (day 0) by plotting them according to days before (a negative number) and days after (a positive number) the first egg was laid. Following each behavioral observation, all tree cavities within the territory that the birds visited were checked for the presence of an egg by inserting a wireless camera into the cavity. Observations continued until mate-

guarding behavior ceased, which coincided with the onset of incubation around day 2 or 3, although some groups mate guarded longer.

21-day offspring were captured, banded, and bled using California Department of Fish and Game Scientific Collecting Permit SC-7368 (11 April 2012 to 11 April 2014), Federal Bird Banding Permit 21508 (15 April 2010 to 30 June 2013), and IACUC protocol 12-001 (issued 23 April 2012 to 23 April 2015). Parentage was assigned using the blood was sampled from the brachial vein of 21-day offspring using 22 microsatellite markers according to the methods employed by Haydock et al. (1996) and Haydock et al. (2001). Blood samples obtained from all adults and nests in 2009-2011 were used to analyze all possible parent pair combinations within the group, including helpers. Furthermore, genetic analyses also included any possible parent combinations using samples genotyped from the population as a whole.

To ascertain if there was a relationship between mate-guarding behavior and realized paternity, the males were ranked according to their overall attendance and following behavior. Ranks were established by averaging the proportions for attendance and following across all watches for a given nest attempt. A rank was given for attendance behavior, and a separate rank was given for following behavior. Males with the longest mean attendance and highest mean successful follows were ranked the highest. These ranks were then compared to each male's proportion of paternity in the resultant nest using a concordance correlation in SPSS to determine if there was concordance between following or attendance rank of males and their realized paternity.

RESULTS

Mate Guarding Initiation and Duration

Acorn woodpecker mate guarding begins in early April, peaks in May, and ends in June following the conclusion of egg-laying in second nests (Mumme et al., 1983a, Koenig et al., 1984). Mate guarding is not initiated synchronously across the population at Hastings, therefore during the breeding season all polyandrous groups were observed at least once every week to determine when each group began exhibiting the behavior. Mate-guarding behavior is readily evident and begins abruptly, demonstrated by males flying in close groups behind the breeding female, males spending 70-100% of their time in close proximity to the female (within 3-4 m), frequent visits to tree cavities, and increased vocalizations (Mumme et al., 1983a; pers. obs.).

A total of 18 nest attempts from 9 groups were observed during the 2009, 2010, and 2011 breeding seasons (Table 1). Manpower and time constraints did not allow the inclusion of all polyandrous groups within the population in this study, particularly when mate guarding occurred simultaneously across groups. Six nesting attempts were observed at four groups in 2009, six nesting attempts were observed at five groups in 2010, and six nesting attempts were observed at four groups in 2011 (Table 1). The timing and duration of mate-guarding behavior was documented for 26 nest attempts from the 2010, 2011, and 2012 breeding seasons (Tables 1 & 2), 18 of which were first nests and 8 were second nests. These data were not available from the 2009 breeding season. During 2010-2012, mate guarding initiation ranged from 15 Mar to 02 May (median = 17 Apr) for first nests. The range for second nests was 6 May to 13 Jun (median = 30 May). The latest record of birds mate guarding was 5 Jul at the Knoll group

during a final nest attempt, which was preceded by multiple failed nests in 2011. The mean duration of mate guarding for all nest attempts across these three years was 15.5 ± 7.1 days, with a median of 13.5 days.

Overall, the duration of mate guarding was significantly shorter for groups with two cobreeding males as opposed to groups with three or more males (Fig. 1; $U = 43.5$, $N = 26$, $P < 0.05$). Males in 2-male groups began mate guarding 10.6 ± 6.9 days, on average, before the female laid her first egg, while males in 3+ male groups began mate guarding 16.9 ± 9.3 days, on average, before the first egg date (Fig. 2).
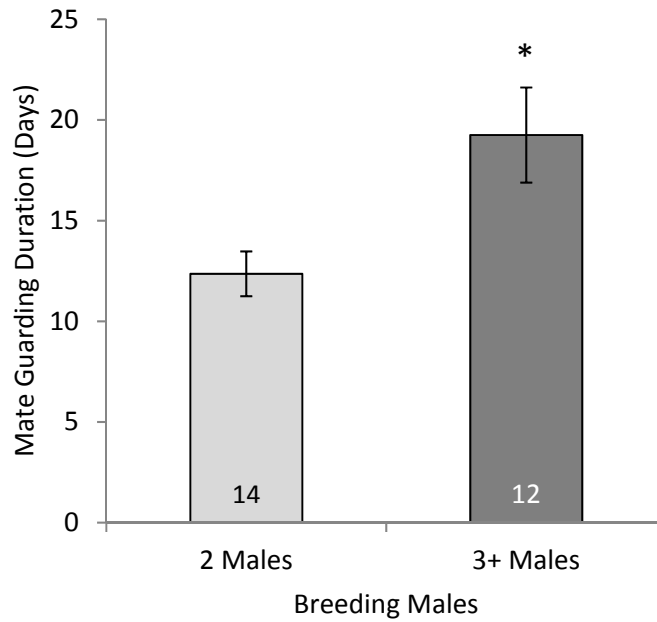
Figure 1. Mean mate guarding duration in days, with standard error bars and sample sizes, in groups with two males versus groups with three or more males during the 2010-2012 breeding seasons. The sample sizes represent the number of nest attempts for which mate-guarding behavior durations were recorded. Males in 3+ male groups mate guarded significantly longer than those in 2-male groups ($U = 43.5$, $N = 26$, $P < 0.05$).
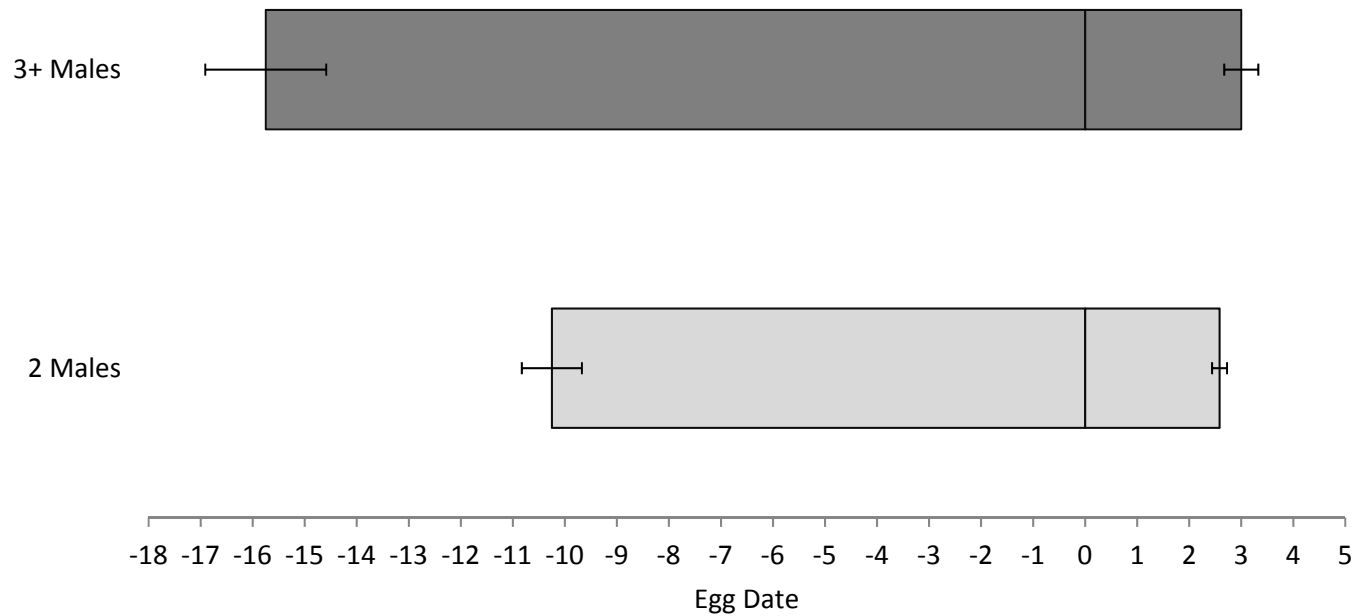
Figure 2. Mean duration of mate-guarding behavior by males in 2-male groups versus that of groups with three or more males, relative to the day in the laying cycle. Day 0 represents the first day a female laid an egg. Standard error bars are shown around the mean start and end dates of mate guarding for the two types of group.

Mate-Guarding Behavior

The proportional mean attendance across watches of 2-male groups was significantly higher than that of 3+ male groups (Fig. 3; $U = 133.0$, $N = 45$, $P < 0.05$) whereas the proportional mean following across watches of 2-male groups was not significantly different than that of 3+ male groups (Fig. 3; $U = 226.5$, $N = 48$, $P = 0.78$).

Mean attendance behavior by males began high (mean > 90%) as early as day -25 and remained so until approximately day -7 when mean attendance dipped as low as 66%, but then increased as the first egg date approached. Attendance eventually tapered off following day 3, which roughly coincided with initiation of incubation (Fig. 4). In contrast, the mean following behavior of males exhibited far more variability, and no clear pattern (Fig. 5).
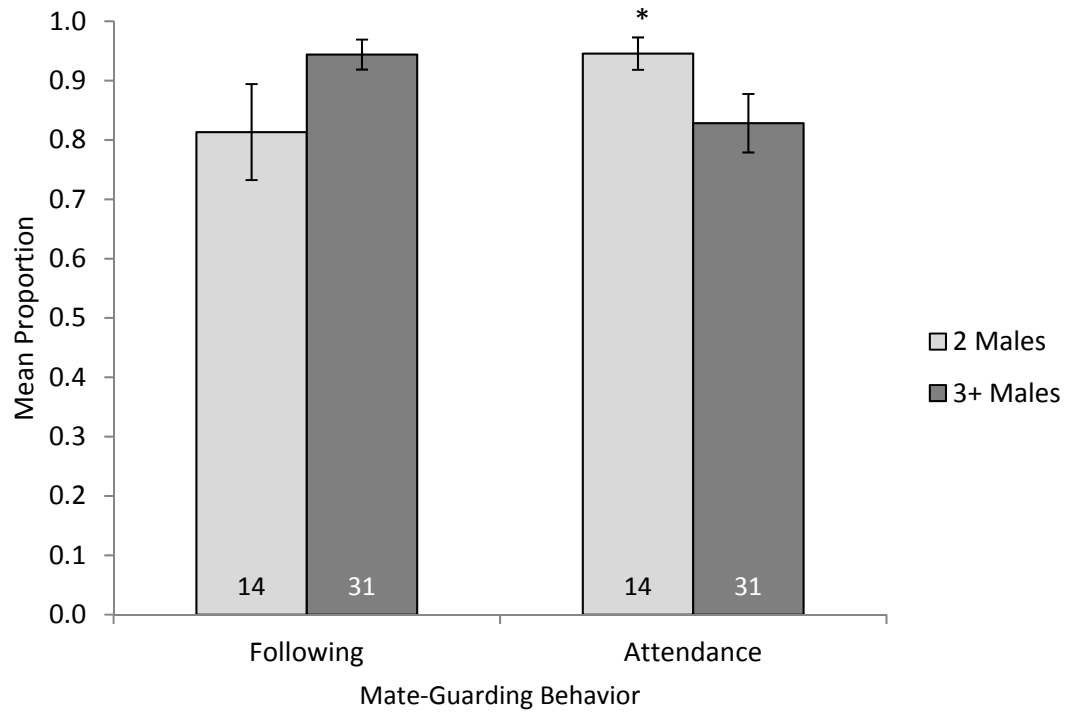
Figure 3. Proportional mean successful following and attendance of males in 2-male and 3+ male groups, showing standard error bars and sample sizes. The sample sizes represent the total number of males observed at all nest attempts according to group composition. Males in 2-male groups attended significantly more than males in 3+ male groups ($U = 133$, $N = 45$, $P < 0.05$), while there was no significant difference in following across group composition.
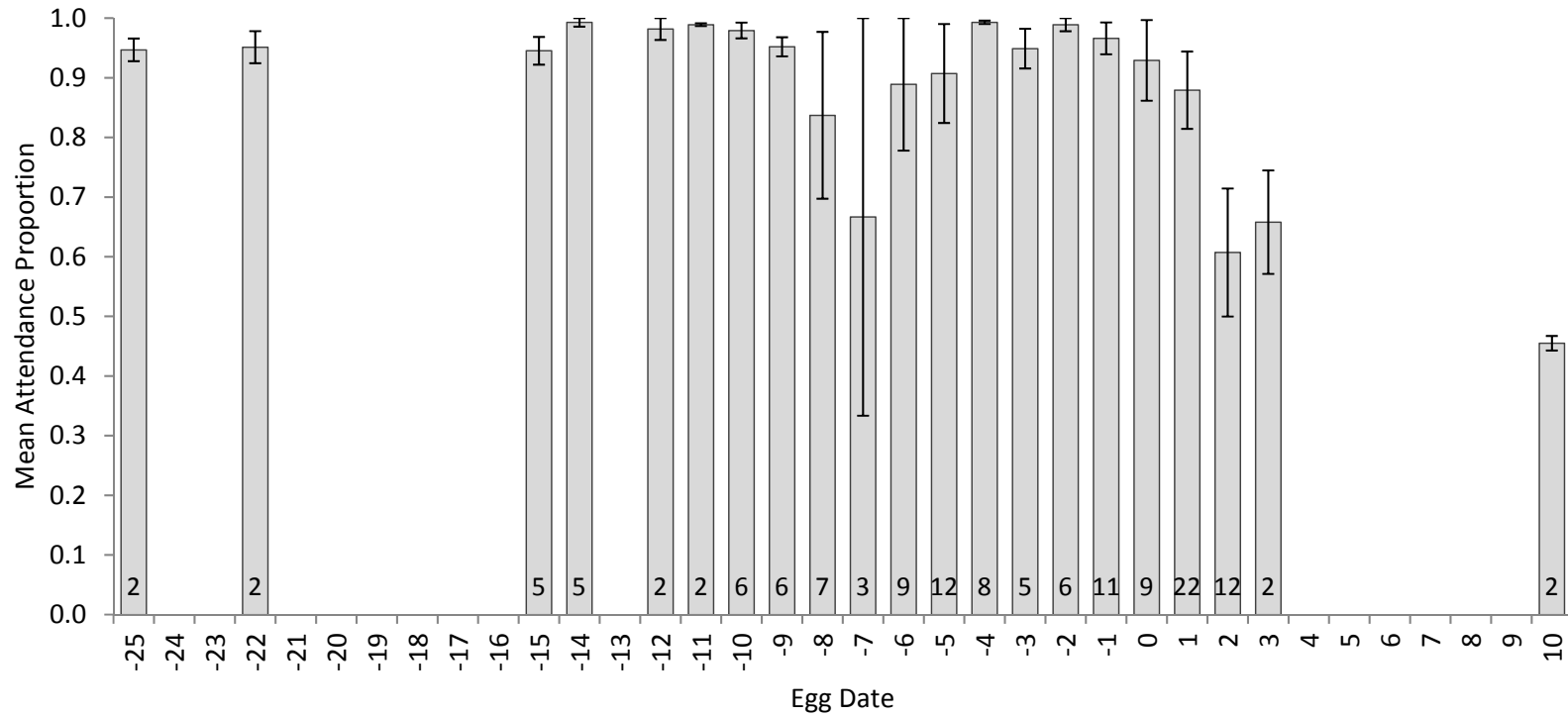
Figure 4. Proportional mean attendance relative to the day in the laying cycle (egg date). Day 0 represents the first day the female laid an egg. Standard error bars and sample sizes are shown. The sample sizes represent the number of males that were observed on each egg date. Days during which no observations were conducted are blank.
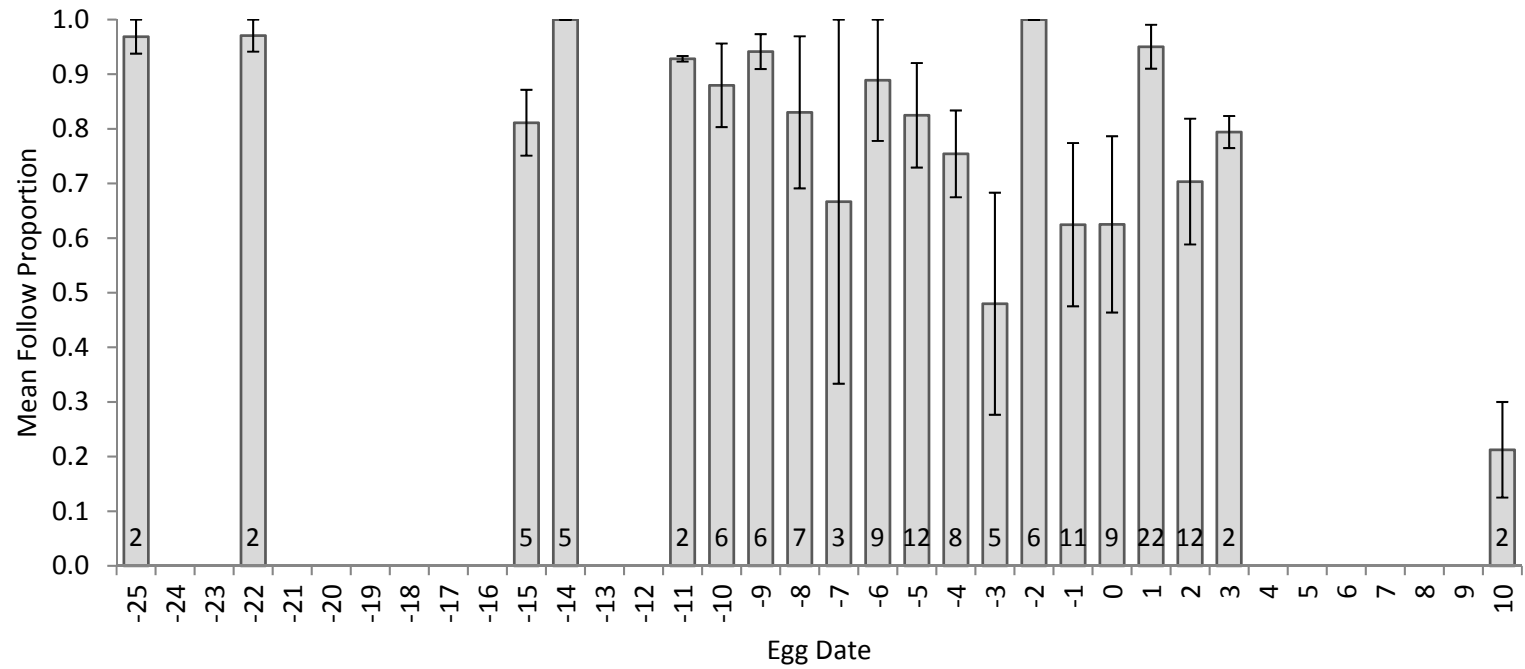
Figure 5. Proportional mean successful follows relative to the day in the laying cycle (egg date). Day 0 represents the first day the female laid an egg. Standard error bars and sample sizes are shown. The sample sizes represent the number of males that were observed on each egg date. Days during which no observations were conducted are left blank.

Paternity

Of the 18 nest attempts that were observed in this study, young successfully fledged from 14 nests (Table 3), yielding a total of 55 offspring that were genotyped. Out of these 14 nests, 12 produced 2 or more chicks. The mean number of chicks produced per nest was 3.9 ($N = 14$).

Reproductive skew of paternity for all nests in this study was determined by ranking the males according to their share of paternity for each nest. Males with the highest percentage of paternity in a nest were ranked α, males with the second highest percentage of paternity were ranked β, and males with the third highest percentage of paternity were ranked δ. Percentage of paternity was determined for the breeding males according to each individual nest, and the mean values indicate the mean percentage of paternity for males of that rank according to the number of offspring produced in each nest.

Paternity was highly skewed in nearly all nests (Fig. 6). In groups with 3-5 cobreeding males, the highest number of males to share paternity in a single nest was 3. Complete monopolization of paternity by one male occurred in 9 (64.3%) nests (high skew), paternity was skewed among males in 4 (28.6%) nests (moderate skew), and paternity was shared equally in only 1 (7.1%) of the 14 nests (no skew).

For 2-male groups, there was a very good strength of agreement between attendance rank and paternity rank ($r_c = 0.941$, $df = 9$, $P < 0.0001$). Similarly, in 2-male groups, there was a good strength of agreement between follow rank and paternity rank ($r_c = 0.857$, $df = 9$, $P < 0.01$). Though there was concordance between mate guarding and paternity in these groups, the overall mate guarding behavior and paternity in some

groups switched from nest to nest, as shown in the Central Canyon group (Table 4). In 3+ male groups, there was no significant concordance between attendance rank and paternity rank ($r_c = -0.052$, $df = 28$, $P = 0.55$), or follow rank and paternity rank ($r_c = 0.164$, $df = 28$, $P = 0.32$).

Table 3. Number of nests and offspring produced by males in 2-, 3-, 4-, and 5-male cohort groups.

No. Breeding Males	Nests	Offspring
2	4	21
3	7	24
4	1	4
5	2	6
Total	14	55
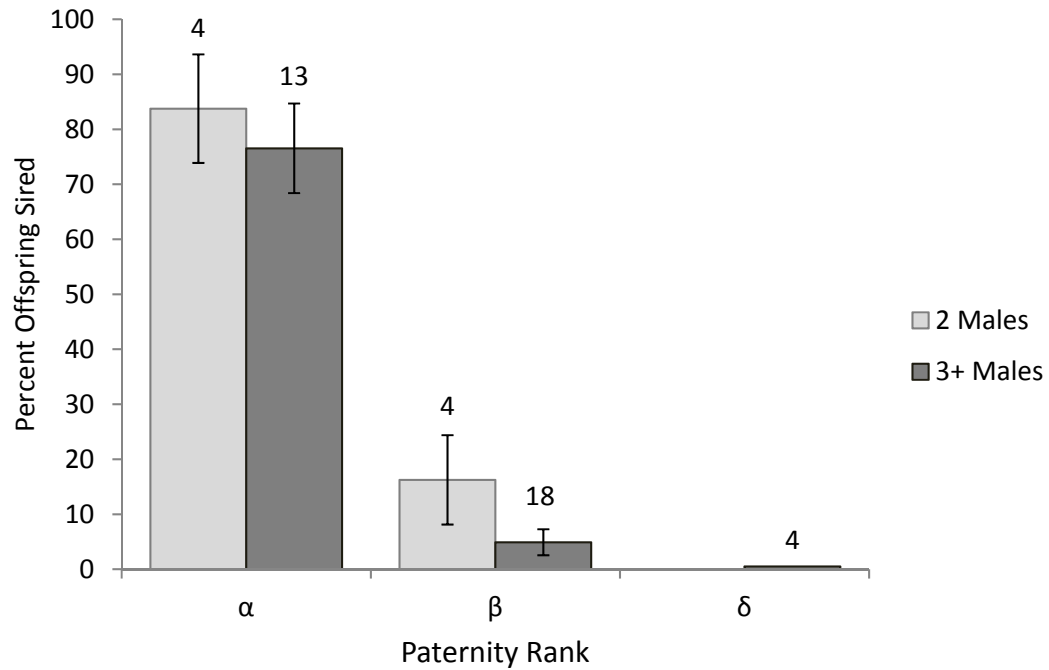
Figure 6. Mean percent offspring sired per nest, with standard error bars, by males in 2-male groups versus 3+ male groups relative to paternity rank during 2009-2011. Males ranked α had the highest percentage paternity, males ranked β had the second-highest percentage paternity, and males ranked δ had the lowest percentage paternity of the offspring in a nest. Sample sizes represent the number of males in each rank.

Table 4. Changes in paternity and mate guarding ranks for males 3327 and 4447 across three nests at the Central Canyon group during a two-year period. Nests 1 and 2 were in 2009, and nest 3 was in 2010. Where α = β, both males shared a rank.

Male	Nest	Paternity Rank	Attendance Rank	Follow Rank
3327	1	β	β	α=β
4447		α	α	α=β
3327	2	α	α	α
4447		β	β	β
3327	3	α	α=β	α=β
4447		β	α=β	α=β

DISCUSSION

Acorn woodpeckers represent an evolutionary enigma when viewed through the lens of reproductive skew theory. Both transactional and compromise models assume that dominance hierarchies exist in social groups wherein one or more individuals control the reproduction of other individuals within the group, or outcompete all others. Paternity in polyandrous acorn woodpecker groups is often skewed yet also inconsistent across nests, which is not predicted by either of these models. Perplexingly, even though the species has been studied for more than 40 years, no discernable social, behavioral or physiological correlate appears to predict reproductive skew or indicate any breeding hierarchy among breeding males (Haydock & Koenig, 2003; Koenig et al., 2011). Larger fledglings have been found to be dominant over smaller brood-mates (Stanback, 1994), yet this finding is not maintained when brood-mates reach maturity and share breeding status (Haydock & Koenig, 2003; Koenig & Walters, 2011). The present study postulates that the act of mate guarding in polyandrous and polygynandrous acorn woodpecker groups represents the effort to compete for, and mediate, access to the female relative to other cobreeding males, which in turn determines a type of ephemeral breeding hierarchy.

I confirmed that reproductive competition among males was high, as evidenced by the consistently high proportional mean attendance behavior throughout the fertile period of breeder females, regardless of the number of cobreeding males. High competition was further reflected in the significantly longer mate guarding duration of groups with three or more cobreeders compared with that of 2-male groups, revealing that an increase in the number of males is manifested as an increase in the length of time males will guard (Figs. 1 & 2). These findings indicate that the lack of a discernible

breeding hierarchy is not a result of indifference on the part of the males, which has been suggested for other polygynandrous species such as the pukeko (Jamieson & Craig, 1987).

Two possibilities are suggested by the significant difference in mate guarding duration across group composition. First, the increased competition caused by the extra males in 3+ male groups may be interfering with the ability of cobreeders to successfully copulate with the breeding female, thereby prolonging the time it takes for fertilization and laying to occur. Second, breeding females in 3+ male groups may indicate their receptivity to the males before they are fertile in order to obscure paternity, similar to long-tailed macaque females (*Macaca fascicularis*) whose period of sexual attractiveness to males is significantly longer than their period of fertility (De Ruiter et al., 1994). This pattern is thought to be an adaptation to reduce aggression among males and obscure a male's perception of paternity, thereby reducing the risk of infanticide (Engelhardt et al., 2004). Other advantages resulting from the obfuscation of paternity would be to encourage parental care from all male breeders (Møller & Birkhead, 1993), or to strengthen social bonds (Westneat et al., 1990). Paternity uncertainty to elicit parental investment has been demonstrated in barn swallows (*Hirundo rustica*; Møller, 1985) and house sparrows (*Passer domesticus*; Wetton & Parkin, 1991). The role breeding females play in influencing the copulation behavior and reproductive success of males in polyandrous groups is explored in greater detail in the following chapter.

The overall proportional attendance and, particularly, the successful proportion of follows by males in 2-male groups in this study were considerably lower than those reported by Mumme et al. (1983a) in their study of acorn woodpecker mate-guarding

behavior in 2-male polyandrous groups. The reason for the discrepancy in proportional attendance reported here versus that reported by Mumme may be due to a difference in sampling method: Mumme measured attendance by counting how often each male was in proximity to the breeding female in 5-min increments, while I continuously measured the total duration of time each male was in proximity to the breeding female during 3-hr observation periods. The cause of the discrepancy in following behavior across the two studies is less clear because I used the same method to measure following behavior as that used by Mumme.

Concessions (but not restraint or compromise) models predict that highly-skewed paternity is more likely to occur when cobreeding males are close relatives, due to the increased indirect fitness gained when group productivity is high (Vehrencamp, 1983; Reeve et al., 1998; Reeve & Emlen, 2000). All males in the breeding coalitions in this study were highly related to one another, and paternity in 64.3% of the nests were completely monopolized by a single male within each breeding cohort, representing high reproductive skew, as predicted by concessions models. This level of skew corroborates the degree of observed skew for cobreeding males reported by Haydock and Koenig (2003). Furthermore, the degree of skew was higher in groups with three or more cobreeding males than the skew in 2-male groups (Fig. 6).

Most importantly, I found that there was a high strength of agreement between mate-guarding behavior of males in 2-male groups and the relative reproductive success of each cobreeder, suggesting that males in these groups were able to exert some measure of control through competition over the distribution of paternity among cobreeders by mate guarding. Perhaps breeding hierarchies in these groups can be established by

guarding breeding females, as predicted by compromise models. Interestingly, contrary to expectation, the attendance behavior of males in 2-male groups was significantly higher than that of 3+ male groups (Fig. 1), perhaps due to the increased variability in mate-guarding behavior among males in 3+ male groups, though there was no significant difference in following behavior across the two types of groups (Fig. 1). The finding that males in 2-male groups stay in close proximity of breeding females significantly longer than males in 3+ male groups, combined with the discovery that there is a significant relationship between attendance behavior and reproductive skew in 2-male groups, suggests that males in smaller groups invest more in mate guarding. Perhaps these males invest more because doing so consistently results in greater direct fitness.

Yet the ability of a single male to prevent his cobreeders from mating with the female appears tenuous at best because subsequent nest attempts are sometimes characterized by a shift in the mate-guarding behavior of the males in the group, and a consequent change in reproductive skew among male cobreeders (Table 4). Haydock and Koenig (2002) posit that the high, variable skew in this species is most likely due to chance, determined on a clutch-by-clutch basis, and not by any particular characteristic or strategy of males in polyandrous groups. The relationship between mate guarding and paternity in 2-male groups in this study suggests otherwise. Yet the question still remains: if mate guarding influences the allocation of paternity in 2-male groups, why does the reproductive skew and mate-guarding behavior change across nests and years (Table 4)?

Unlike 2-male groups, there was no relationship between mate-guarding behavior and reproductive skew in 3+ male groups. The absence of a relationship between mate-guarding behavior and reproductive success in groups with large coalitions of males

indicates that this behavior does not determine dominance rank because males that mate guard the most were unable to influence the allocation of reproduction for themselves or among their cobreeders.

It is unusual for a species that exhibits high reproductive skew to lack a dominance hierarchy that determines the share of reproduction among members of social groups. Polyandrous species such as Arabian babblers (*Turdoides sqamiceps*; Zahavi, 1990; Lundy et al., 1998), pied babblers (*Turdoides bicolor*; Nelson-flower et al., 2011), white-winged trumpeters (*Psophia leucoptera*; Eason & Sherman, 1995), white-browed scrubwrens (*Sericornis frontalis*; Whittingham et al., 1997), and alpine accentors (Nakamura, 1998) are all characterized by high reproductive skew and a clear dominance hierarchy. Alternative causes of the variable high skew characteristic of large coalitions of polyandrous acorn woodpecker males could be incomplete control of reproduction by dominants and subordinates, which prevents the formation of a stable breeding hierarchy (Reeve et al., 1998). Another cause of acorn woodpecker skew could be short-term variation in long-term social queuing, which is represented by variation in breeding success across breeding seasons that nevertheless yields relatively equal lifetime reproductive success over multiple years for most cobreeders (Wiley & Rabenold, 1984; Heinsohn et al., 2000; Alberts et al., 2003; Cant & English, 2006; Buston & Zink, 2009).

The fact that males in 3+ male groups continue to mate guard despite evidence that this behavior has not been shown to predict paternity suggests that the increased number of males in these groups likely disrupts the ability of individual males to control access to the female. Yet incomplete control of reproduction among males cannot explain why the reproductive skew of offspring in 3+ male groups is higher than that of 2-male

groups (Fig. 6). If no male is able to control their share of paternity, the resultant skew would be predicted to be lower and proportionate to the number of males than that of 2-male groups. These results suggest a hidden mechanism that has yet to be determined that may be influencing the highly uneven distribution of paternity among males in groups with large breeding cohorts.

A factor not yet fully examined in this study is the behavior of the breeding females in polyandrous groups. Sexual selection theory posits that females stand to gain from competition among males, both on the behavioral and molecular (sperm competition) level (Jennions et al., 2000; Klemme et al., 2014). Thus, the lack of concordance between mate-guarding behavior and paternity in 3+ male groups could suggest some type of influence or manipulation by the female. This could be achieved by mating with specific males when she is fertile (Double & Cockburn, 2000), mating with other males outside her fertile period (Briskie, 1992), furtive copulation behavior that results in uncertainty of paternity on the part of the males (Gowaty et al., 1989), or increasing the difficulty for males to achieve successful copulations (Pizzari, 2001).

Additionally, sperm storage has been demonstrated in every avian species examined to date (Birkhead, 1998; Briskie, 1992; Johnsen et al., 2012), which suggests that sperm storage could potentially affect parentage for many species, particularly those that practice extra-pair copulation or cooperative reproduction. There have been, however, very few observations of copulations in acorn woodpeckers, despite hundreds of hours of surveillance (pers. obs.). Determining the role of sperm storage in this species is challenging given the dearth of direct observations of mating, which would clarify the

relationship between copulatory behavior during the fertile period of the female and the distribution of paternity.

Parentage lies at the intersection of mating behavior and genetics. Sperm competition, which is directly affected by both of these variables, as well as female choice, could play significant roles in determining paternity in acorn woodpeckers. Future research that compares the behavior of breeding birds with the sperm present on the resultant eggs, as described by Carter et al. (2000), could reveal a direct link between behavior and genetics in the young of polyandrous groups.

Mate guarding is energetically costly (Komdeur, 2001; Low, 2006). If this behavior does not accord direct fitness to males in large cohorts, what purpose could it serve? In Chapter III, I explore the possibility that females are affecting the outcome of paternity for cobreeding males. Just as the polyandrous dunnock (*Prunella modularis*) female adapts her copulation behavior with α and β males in order to enlist the parental assistance of both males (Hatchwell & Davies, 1992; Davies et al., 1996), acorn woodpecker females could play a role in determining the distribution of paternity in a way that safeguards the help of multiple mates. As demonstrated by Koenig (1990), female acorn woodpeckers can risk the destruction of an entire clutch of eggs by a male when that male is denied access to the female during her fertile period prior to, and during, egg laying. Females therefore gain from increasing the uncertainty of males as to the outcome of mating behavior. In the following chapter I investigate the ways in which female behavior could determine skew in this species.

CHAPTER III

THE EFFECT OF FEMALE CHOICE ON REPRODUCTIVE SKEW

INTRODUCTION

The role females play in determining the reproductive success of males has
historically been predicated on the Darwinian notion of "coy" females that choose males
based on fighting ability, ornaments, and courtship behavior (Darwin, 1871), thus
implying that males experience more selection pressure than females to reproduce.
During the mid-20th century, nearly 80 years later, male reproductive success was
hypothesized to be a function of the number of females with which a particular male was
able to mate successfully (Bateman, 1948). According to this paradigm, females were
thought not to increase their success as much as males when mating multiply because
females are constrained by the number of eggs they can produce and cannot engender
more offspring by mating with more males.

The concept of sperm competition in insects first appeared in 1970, wherein
competition was said to occur after copulation between the ejaculates of two or more
males to fertilize the ova within females (Parker, 1970). This concept broadened the
study of sexual selection to include selection pressure on females to not only choose the
highest quality mate, but to also choose whether to mate with more than one male, or, as
in the case of cryptic female choice, to influence which sperm fertilizes her eggs by
behavioral or physiological means after copulation has occurred (Eberhard, 1996;
Birkhead, 2000). Moreover, females have been shown to make choices about their
investment in offspring after fertilization has occurred according to their choice of mate,

such as investing less in egg-production when mated to a less attractive male
(Cunningham & Russell, 2000).

Female choice, which occurs both pre- and post-copulation, has a significant
effect on the fitness of both sexes (Møller, 1988; Eberhard, 1996; Kempenaers et al.,
1997; Burley & Foster, 2006). The ways in which females influence their own
reproductive success, as well as that of males, are typically subtler than the conspicuous
mating behavior and sexual characteristics of males, and have thus received far less
attention until recent years (Griffith et al., 2002; Westneat & Stewart, 2003). For
example, in a survey published in 1968, 93% of bird species were deemed monogamous
based on behavioral observations (Lack, 1968). In the years following, greater attention
on the behavior of females, as well as genetic testing of offspring, revealed 86% of bird
species exhibited varying degrees of extra-pair paternity, a finding that had previously
gone undetected (Griffith et al., 2002; Westneat & Stewart, 2003).

The last thirty years of avian research have been characterized by a tremendous
upsurge of interest in female choice and the selection pressures that affect it, remaining
the subject of heated debate to this day (Ah-King, 2011; Parker & Birkhead, 2013). The
majority of this research, however, has concentrated on the role of female choice within
the framework of a female-male pairing, and the ecological, social, physiological, and
genetic factors that motivate each sex to mate outside their social pairing (Arnqvist &
Kirkpatrick, 2005; Griffith et al., 2002). Comparatively, there have been fewer studies
that explore female choice in polyandrous mating systems, which are characterized by
larger social groups in which multiple males are the social mates of a single female.
Female choice in polyandrous mating systems has been studied in dunnocks (*Prunella*

modularis; Hartley & Davis, 1994), wattled jacanas (*Jacana jacana*; Emlen & Wrege, 2004), pukekos (*Porphyrio porphyrio*; Dey et al., 2012), brown jays (*Cyanocorax morio*; Williams, 2004), and relatively few other avian species. Most likely, this bias is due to the comparative scarcity of this type of mating system. For example, a current estimate places the prevalence of cooperative breeding at about 9% for all avian species (Cockburn, 2006), and only a fraction of cooperative breeders exhibit reproductive cooperation (Temrin & Sillén-Tullberg, 1994). Yet cooperative polyandry is an ideal system in which to study the direct effect of female behavior on male reproductive success, as well as the factors that influence female choice, because the social complexity that is characteristic of polyandrous groups engenders increased inter- and intrasexual conflict and selection pressure that may not be present in species that reproduce in pairs. Moreover, despite increased interest in female behavior, prevailing models of reproductive skew theory consistently fail to make predictions about the influence of female behavior on male reproductive skew, as discussed in Chapters I and II. To remedy these gaps in the literature, this study examines the effect of female mating behavior on male reproductive success using polyandrous acorn woodpeckers (*Melanerpes formicivorus*) as a focal species.

Male Mating Behavior

In oviparous – particularly avian – species, eggs and offspring often require a significant investment of parental care by both sexes in the form of incubation or provisioning (Møller & Thornhill, 1998; Liker & Székely, 2005). Consequently, there are numerous tactics males employ to ensure their paternity, given the cost of uncertain

parentage (Møller & Cuervo, 2000). Males may engage in frequent copulation with their mate, for example, to increase the number of sperm within the female to outcompete sperm from potential extra-pair copulations, particularly when the threat of kleptogamy is high (Hunter et al., 1992; Crowe et al., 2009). Males may also engage in copulations that coincide with peak female fertility on specific days and times in the day (Briskie, 1992; Akçay et al., 2011). Dunnocks employ cloacal pecking to induce mated females to expel the sperm of other males (Davies, 1983; Davies, 1990). In some species, males increase their territory defense (Tobias & Seddon, 2000), or increase their song output when their mates become fertile (Currie et al., 1998). Some males safeguard their paternity through dominance interactions with other males (Lamprecht, 1986). Many species mate guard to prevent extra-pair males from copulating with the female while she is fertile (Cheng & Burns, 1988; Gowaty et al., 1989; Harts & Kokko, 2013), as discussed in Chapter II.

Paternity assurance behaviors rely on the ability of males to successfully fertilize as many eggs as possible while also preventing other males from copulating with their mate(s) through mate guarding, territory defense, and dominance interactions. In addition, given the prevalence of extra-pair copulation and paternity in a large proportion of bird species, many paternity assurance behaviors have evolved as reproductive strategies in response to sperm competition (Davies, 1983; Birkhead et al., 1992; Michl et al., 2002; Wedell et al., 2002; Crowe et al., 2009). Sperm competition could play a significant role in determining paternity in many avian species because every species examined to date has been shown to possess sperm storage tubules within the female reproductive tract that enable the storage of sperm (Bakst, 1993; Birkhead & Møller, 1998; Sasanami et al., 2013). The ability of birds to store sperm considerably increases

the likelihood of sperm competition when a female mates with more than one male, even when copulations occur days or even weeks apart.

Much of the body of research centered on paternity assurance behavior has focused on the "anti-cuckoldry" – prevention of extra-pair paternity – aspect of socially monogamous pairs (Zeh & Zeh, 2003). More complex strategies are used by males and females in species that lek, mate promiscuously, exhibit convenience or sequential polyandry and polygyny, form complex cooperative polygynandrous groups, or simply live in colonies in which the maternity and paternity of offspring are more likely to be uncertain (Schleicher et al., 1997; Møller & Ninni, 1998). Paternity assurance in polyandrous species in which females form multiple pair bonds with males is often thought of as a trade-off relative to maintaining group stability in order to accrue benefits associated with breeding communally (Jamieson, 1997; Kokko & Johnstone, 1999). To do so, individuals offset maximizing individual fitness with minimizing conflict and increasing cooperation and care of offspring when multiple members of the same sex co-occur in cooperatively reproducing social groups, as predicted by transactional models (Jamieson, 1997; Kokko & Johnstone, 1999; Haydock & Koenig, 2003; Widdig, 2013).

Conflict between males in polyandrous and polygynandrous species can take the form of dominance interactions wherein one or more males impede or outright prevent the reproduction of subordinate males (Mumme et al., 1983; Clutton-Brock & Huchard, 2013). Males that have reduced or no opportunities to copulate with their social mate(s) in some cases provide little or no care for the offspring produced by the group in species such as the alpine accentor (Davies et al., 1996). Males denied access to the female(s) may destroy her offspring if they have little confidence of their own paternity (Koenig,

1990; Forstmeier et al., 2014). Furthermore, copulation rates among polyandrous species are generally quite high when compared to many monogamous species, which could be an adaptation in response to potential sperm competition (Davies, 1985; Jamieson & Craig, 1987; Briskie, 1992; Nakamura, 1998).

Female Mating Behavior

There have been many hypotheses postulating the potential benefits of extra-pair copulation for females. For example, according to the "sexy-son" hypothesis, females mated with less attractive males gain by mating with more attractive extra-pair males despite the risks associated with extra-pair copulation, resulting in sons that inherit more attractive secondary sexual characteristics (Weatherhead & Robertson, 1979; Johnsen et al., 1998). This concept has been expanded to the "sexy sperm" hypothesis, which posits that sperm competition results in male offspring with traits that increase fertilization efficiency, while also selecting for females who mate with multiple males (Keller & Reeve, 1995; Pizzari & Birkhead, 2002; Klemme et al., 2014). Females may copulate with extra-pair males to reduce the risk of unfertilized eggs if their mates are sterile (Walker, 1980; Sheldon, 1994; Keller & Reeve, 1995). Moreover, extra-pair copulations have been proposed to increase the genetic diversity of a female's offspring (Petrie et al., 1998), and to safeguard against genetic incompatibility (Johnsen et al., 2000; Griffith & Immler, 2009).

Extra-pair copulation isn't the only method by which females influence the reproductive success of their mates, and the viability of their offspring. Female mallards

(*Anas platyrhynchos*), for example, will invest more in offspring sired by high-quality

males by laying larger eggs, and will lay smaller eggs when mated to a less-preferred

male (Cunningham & Russell, 2000). Similarly, acorn woodpecker females have been

shown to lay larger clutch sizes when assisted by female helpers, thus counterbalancing

the increased cost of maternal investment against the benefits afforded by female helpers

in the form of provisioning young (Koenig et al., 2009).

For socially polyandrous species, as a consequence of the conflict that can be

generated by multiple mates, females sometimes incur energetic costs associated with

chasing, harassment, and forced copulations by breeding males (Hartley & Davies, 1994;

Castro et al., 1996). These costs may result in reduced female condition, decreased clutch

sizes, and the loss of offspring in cases where males destroy the clutch (Davies, 1985;

Koenig, 1990; Forstmeier et al., 2014; Liker et al., 2014). In fact, eggs from polygynous,

polyandrous, and polygynandrous acorn woodpecker groups have been shown to exhibit

significantly lower hatchability than those produced by monogamous pairs, most likely

due to interference during egg-laying and incubation (Koenig, 1982). Consequently, the

evolution of more aggressive or extreme tactics of paternity assurance among breeding

males could result in selection for female behavior that avoids the costs imposed by male

mating tactics (Chapman et al., 2003). Some females mate secretly (Double & Cockburn,

2000), solicit copulations with multiple males (Johnson & Burley, 1998), or, as in the

superb fairy-wren (*Malurus cyaneus*) engage in pre-dawn forays to mate outside of their

social group (Dunn et al., 1995; Double & Cockburn, 2000). All of these behaviors

increase uncertainty on the part of males as to their proportion of realized paternity, but

also function to elicit parental care from multiple males who have had access to the

female during her fertile period (Burke et al., 1989; Davies et al., 1996). Thus, females benefit directly by ameliorating some of the risks associated with polyandry while significantly influencing male reproductive success at the same time.

Acorn Woodpeckers

As discussed in Chapter II, acorn woodpeckers are a cooperatively breeding, polygynandrous species with a variable mating system. Polyandrous acorn woodpecker males mate guard intensely as early as 25 days before the female lays her first egg. Genetic analyses have revealed no extra-group paternity, which suggests that cobreeding males are guarding the female from copulating with the other males within the social group instead of males outside of the group (Haydock et al., 2001). Further, offspring produced by polyandrous groups exhibit highly skewed paternity (Chapter II; Haydock & Koenig, 2002, 2003). Though skew is high in individual nests, the male who fathers the most young in one nest does not necessarily sire the majority of the offspring in subsequent nests (Haydock & Koenig, 2002, 2003). In other words, the "reproductive winner" in polyandrous groups switches to different males from nest to nest, even when the group composition remains the same across multiple nests and years.

How, then, does the behavior of females and males influence the paternity of offspring in multi-male groups? In the previous chapter, I examined the role of mate-guarding behavior by males as a way of controlling access to the female, thereby skewing paternity in favor of the best guarders. I found that even though all males in polyandrous groups mate guard for weeks at a time, an energetically costly endeavor (Komdeur, 2001;

Low, 2006), this behavior only predicts paternity in 2-male groups, and fails to do so in 3+ male groups.

Acorn woodpeckers do not engage in loud, conspicuous copulation behavior like the cooperatively polygynandrous pukeko (Jamieson & Craig, 1987) or Galapagos hawk (*Buteo galapagoensis*; Faaborg & Bednarz, 1990), nor do they appear to copulate at the high rates characteristic of other polyandrous and polygynandrous species (Birkhead et al., 1987; Birkhead et al., 1993; Briskie, 1992). In fact, direct observation of a successful copulation in acorn woodpeckers is relatively rare. In a 3-yr study of mate-guarding behavior, Mumme et al., (1983a) observed a total of 18 nest attempts during which only eight attempted copulations were witnessed, two of which were deemed successful. Mumme et al.'s observations are consistent with my experience closely observing polyandrous groups over three breeding seasons. During more than 500 hours of observation, I witnessed 11 mating attempts, of which three appeared to involve cloacal contact. I observed that when a female gave her pre-mounting display, one of the breeding males would try to mount her and the other males would interfere by mounting both birds, flying into them, and generally physically forcing the male off the female, preventing cloacal contact.

Interestingly, I observed more same-sex mounting between breeding males during mate guarding (16 occurrences) than I saw attempted copulations between a breeding male and female (11 occurrences). Acorn woodpeckers have been observed engaging in "pre-roost mounting" in which all group members, including helpers and breeders of both sexes, mount each other prior to entering roost cavities for the night (MacRoberts & MacRoberts, 1976; Cockburn, 2004). It is unclear if cloacal contact is achieved through

this behavior because individuals mount each other extremely quickly, and same-sex mounting appears to occur as frequently as opposite-sex mounting, including reverse-sex mounting (pers. obs.). Moreover, pre-roost mounting appears to increase during the mate guarding period (Cockburn 2004). Perhaps pre-roost mounting and same-sex mounting during mate guarding is a result of the increase in hormones in males and females during the breeding season, or is an expression of dominance (Wagner, 1996). Moreover, same-sex mounting has been shown to be more common in polygamous birds (MacFarlane et al., 2007)). More research on this phenomenon would help clarify the origins of this behavior.

Why are so few successful copulations observed? Perhaps multiple copulations aren't necessarily required, especially if sperm can be stored for multiple days in order to fertilize all eggs. In domesticated fowl such as turkeys (*Meleagris gallopavo*), a single copulation has been shown to fertilize an entire clutch (Lake, 1975). Yet low copulation frequency is more common for socially monogamous species with small clutch sizes than for polyandrous species (Birkhead et al., 1987).

Although acorn woodpeckers do not engage in conspicuous copulation behavior, all polyandrous groups exhibit a marked affinity for tree cavities during the mate guarding period, which leads up to, and coincides with, the breeding female's fertile period (pers. obs.). This behavior is characterized by an increase in the number of times breeders land at cavity entrances, inspect cavities, enter cavities together, and excavate cavities. In this species, tree cavities are used year-round for nightly communal roosting and for nesting during the breeding season, hence all group territories contain one or more – sometimes as many as twenty – cavities for this purpose (Fig. 7; Hooge et al.,

1999). Throughout the year, all members of a group, including nonbreeding helpers of both sexes, participate in tree cavity excavation and maintenance (MacRoberts & MacRoberts, 1976; pers. obs.). In the 1-3 weeks leading up to egg-laying, however, maintenance and surveillance of the tree cavities in a group's territory is taken over by the breeding birds, while helpers are generally chased away from cavity entrances by the breeders throughout the day, though they are not prevented from communal roosting at night (pers. obs.).

Once mate guarding has begun, breeding females make numerous visits to tree cavities, enter them, and perch at the entrances. Breeding males similarly visit tree cavities often during this period, but the majority of the time they will only enter a tree cavity if a breeding female is nearby. In fact, the most common type of agonistic behavior I observed between breeding males during the mate guarding period occurred at cavity entrances, almost always when a breeding female was already inside the cavity (Fig. 8). This agonistic behavior consisted of males pecking each other on the head and neck, increased vocalizations, and physically forcing other males away from a cavity entrance when a breeding female was in close proximity. In the majority of cases, females entered tree cavities first, and were then followed by one or more males, though I observed some females enter cavities after a breeding male was already inside.
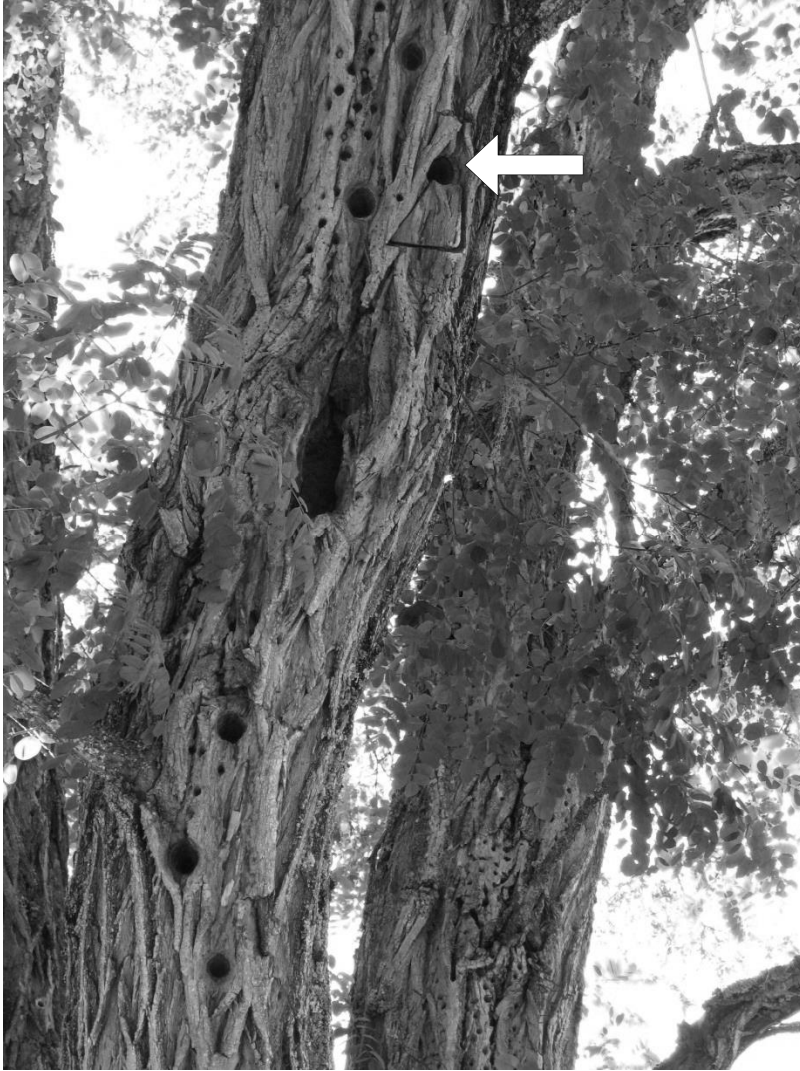
Figure 7. Tree cavities excavated by acorn woodpeckers in a black locust (*Robinia pseudoacacia*) tree in the "Knoll" group territory at the Hastings Natural History Reservation. This picture was taken in the spring of 2012. The cavity in the upper-right corner of the picture (indicated by the arrow) was a nest cavity for the group in previous years, and is distinguished by a triangular cut in the wood below the cavity entrance, which was used to remove nestlings to sample their blood, take measurements, and to attach color bands to their legs.

Figure 8. Grouping behavior of breeding males at an artificial nest cavity during the mate guarding period at a polyandrous social group named "Middle Long Field 2", which consisted of one breeding female and three cobreeding males. At the time this photograph was taken in April 2012, the breeding female was inside the cavity with a breeding male (who is looking out of the cavity entrance), while the remaining two males perched at the cavity entrance.

Agonistic behavior around tree cavities was common across all polyandrous groups I observed, which led me to hypothesize that this species could be mating within tree cavities. A literature review of the mating behavior of birds yielded only a single paper, Birkhead et al. (1987), that reports copulation behavior inside nest cavities, though they only report bird species that exhibit this behavior without any supporting data. Birkhead et al. hypothesized that some avian taxa are expected to copulate within nest cavities when predation risk is high. Paradoxically, they determined that colonially-nesting species, species that they suggest should be under *less* predation pressure, were more likely to mate within nest cavities than non-colonial cavity nesters, but again, a description of the data these observations are based on is unclear. Birkhead et al. argued that colonial nesters likely experience less predation than non-colonial nesters due to the presence of other birds nesting nearby, and concluded that predation risk, therefore, does not adequately explain cavity copulation behavior.

If copulations occur primarily inside a nest cavity, this would dramatically change the way males negotiate access to the female when she is fertile, and suggests ways in which females could control the timing and frequency of copulations in the presence of multiple breeding males within a social group. By copulating inside tree cavities, females might be able to exert greater control over the days and times during the laying cycle she mates, and the frequency with which she mates with males, thereby directly influencing the distribution of paternity among her offspring. Furthermore, mating within cavities may serve to hide copulatory activity from other breeding males. Doing so may enhance paternity uncertainty among males, which could in turn influence their parenting behavior.

Here I tested the hypothesis that female acorn woodpeckers copulate in tree cavities as a mating strategy to mitigate the costs associated with social polyandry. As a method to facilitate copulation, I predicted that the frequency with which breeding females entered tree cavities with breeding males, and the duration of time females spent within cavities with males during their fertile periods, would match the overall reproductive skew of paternity in polyandrous groups.

METHODS

This study was conducted in 2012 as part of a long-term project examining the life histories of acorn woodpeckers at the Hastings Natural History Reservation in Carmel Valley, CA, a study which began in 1968 and continues to the present day (MacRoberts & MacRoberts, 1976). During the spring of 2012, cavity use behavioral data were gathered from 13 nest attempts at nine polyandrous groups at Hastings.

Polyandrous groups were identified according to the methods described in Chapter II. Once they were identified, all polyandrous group territories were visited at least weekly beginning in early March to determine when mate guarding initiated. Mate-guarding behavior is characterized by breeding males remaining in close proximity (within 15 m) of the breeding female, following the breeding female every time she flies more than 15 m away, increased vocalizations by all group members, and increased activity in and around tree cavities by all breeding birds, as described in Chapter II. Once mate guarding was detected at a group, 3-hr cavity watches were conducted every two to three days until the birds stopped mate guarding, which generally coincided with the

onset of incubation about 2-3 days following clutch initiation, though some groups guarded longer.

Cavity watches involved the use of a spotting scope and a canvas blind centrally positioned within the territory of each group, and within view of all tree cavities in order to observe the birds at close range. In some cases, branches were minimally trimmed in order to improve the visibility of each cavity. In territories where all cavities were not visible from a single vantage point, two observers conducted watches simultaneously in order to record woodpecker behavior at all cavities. When mate guarding was confirmed at a group, a preliminary watch was conducted to determine which cavities the breeding birds visited. These cavities were given unique identification numbers that remained consistent throughout the breeding season, and cavity use behavior was recorded for each cavity.

Each watch lasted exactly 3 hrs, during which the focal tree cavities were observed continuously. Unlike the mate guarding study (Chapter II), in which the time of day watches were conducted was not standardized, the time that cavity watches were conducted at each group was randomly assigned from among four pre-determined start times (0600, 0900, 1200, and 1500 PST) in order to observe cavity use behavior at all points in the day in case there was temporal variation in the behavior (Briskie, 1992). Cavity use data were collected as follows:

1. The number of times each breeding bird landed at or moved within 15 cm of a cavity entrance.
2. The number of times each breeding bird entered a cavity

3. The duration of time each breeding bird remained in a cavity.

4. The number of times a breeding female went into a cavity with a breeding male.

5. The duration of time a breeding female spent in a cavity with a breeding male.

Data from #1-3 were used to measure the activity of the birds around tree cavities throughout the mate guarding period in order to determine when females and males started showing an interest in tree cavities. Data from #4-5 were used as a proxy for mating access. Males that spent more time in tree cavities with breeding females were assumed to be more successful at gaining mating access to the female than males that spent less time in the cavity with the female, given the absence of any observations of copulatory behavior outside of cavities. Each group was subjected to a minimum of four 3-hr watches conducted every 2-3 days during the mate guarding period. Following each watch, a camera was inserted into each cavity that the breeding birds had visited to determine if egg-laying had begun. Finally, parentage of all offspring from groups in this study was determined according to the same methods described in Chapter II. Again, 21-day offspring were captured, banded, and bled using California Department of Fish and Game Scientific Collecting Permit SC-7368 (11 April 2012 to 11 April 2014), Federal Bird Banding Permit 21508 (15 April 2010 to 30 June 2013), and IACUC protocol 12-001 (issued 23 April 2012 to 23 April 2015).

To determine if cavity use behavior, as a proxy for mating access, predicts paternity, the frequency with which a breeding female entered a tree cavity with a cobreeding male, and the duration of time females spent in tree cavities with each cobreeding male, was compared with each male's realized paternity in the resultant nest

using a concordance test. Cavity use behavior was analyzed by ranking the breeding

males according to the total number of times each male went into a tree cavity with a

breeding female across all watches for a group. Males with the most cavity visits with a

female were ranked α, males with the second-most cavity visits were ranked β, and so on.

A similar ranking system was used for the duration of time breeding females spent in tree

cavities with each breeding male. Males were then ranked according to the proportion of

paternity each achieved in the resultant nests. Males who sired the highest proportion of

offspring were ranked α, and so on. Cavity use ranks were thus compared with paternity

ranks through the use of concordance tests using SPSS.

RESULTS

Cavity Use

Both breeding males and females increased the frequency with which they visited

(landed within 15 cm of) tree cavities in their territories in the days leading up to the first

egg date (day 0). On average, this behavior increased on day -6, peaked on day 1, and

tapered off by day 3 for both sexes. The frequency that males landed at cavity entrances

closely mirrored the frequency that females landed at cavities (Fig. 9).

Moreover, all breeding females refrained from entering cavities with males during

watches until day -9, despite the fact that mate-guarding behavior in most groups had

initiated days, or even weeks, prior (Fig. 10). Cavity use behavior peaked on day -2,

tapered off by day 2, and then spiked again on day 3 (Figs. 10 and 11). According to

Koenig, Stacey, et al. (1995), incubation in monogamous and polyandrous acorn

woodpecker groups begins sporadically and increases gradually throughout egg-laying,

while full incubation is typically achieved on the day the penultimate egg is laid. For most groups, I observed that the birds began to exhibit an increase in incubation behavior (spending significantly longer periods of time in the nest cavity) by day 3, which is reflected in the spike in time females spent in nest cavities with males on that day (Fig. 11). As opposed to the activity of the birds during mate guarding, incubation was characterized by one bird entering the cavity, occasionally followed by a second bird that would sit at the cavity entrance, looking out for long periods of time (5+ min.). No cavity use data following day 3 were included in the analyses because breeding females and males were presumably using the nest cavities to incubate eggs rather than to mate.

There was no significant difference in the frequency with which females went into tree cavities with males in 2-male groups versus 3+ male groups (Fig. 12; $U = 73$, $N = 31$, $P = 0.126$). Females in 2-male groups, however, spent significantly more time in tree cavities with breeding males than females in 3+ male groups (Fig. 13; $U = 39$, $N = 31$, $P < 0.01$).
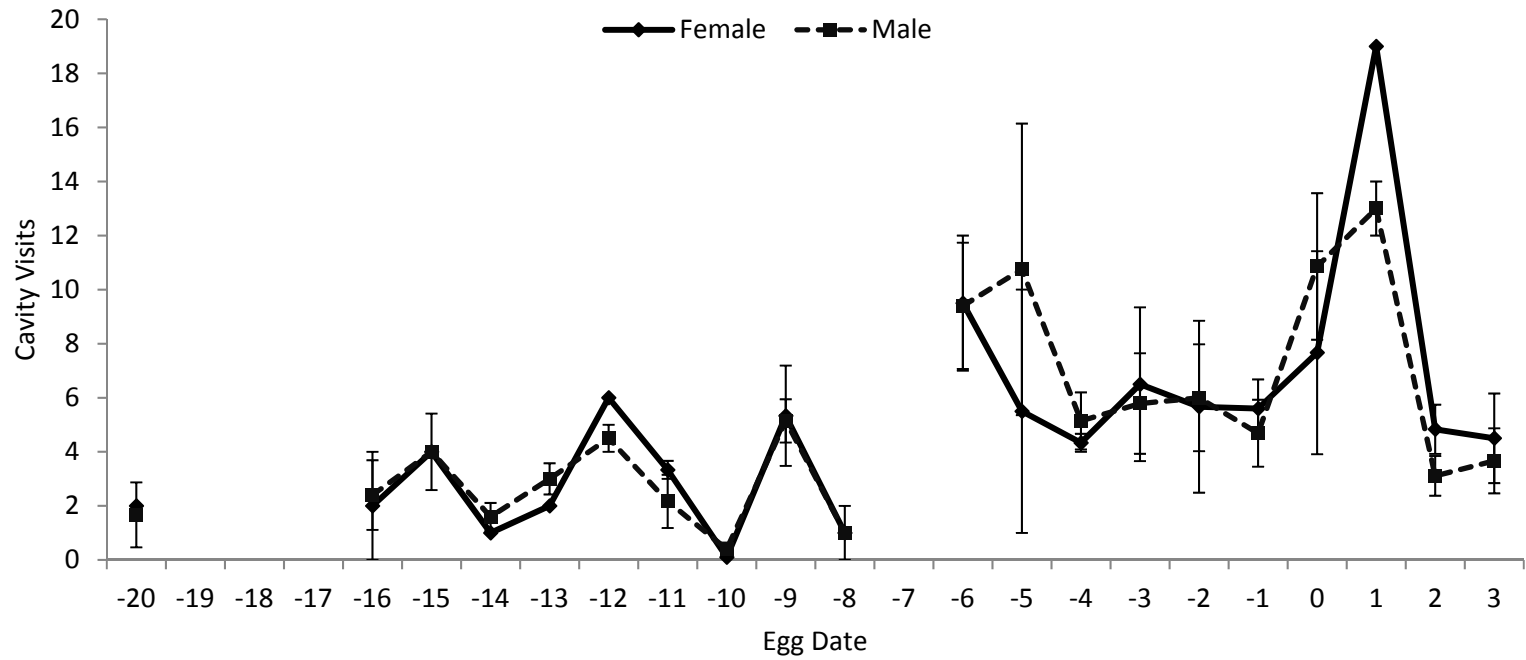
Figure 9. Mean cavity visit frequency (landing within 15 cm of cavity entrances) by breeding females (solid line) and breeding males (dashed line) during the mate guarding period relative to the day in the laying cycle (egg date). Day 0 represents the first day the female laid an egg. Days during which no observations were conducted are left blank. Standard error bars are shown.
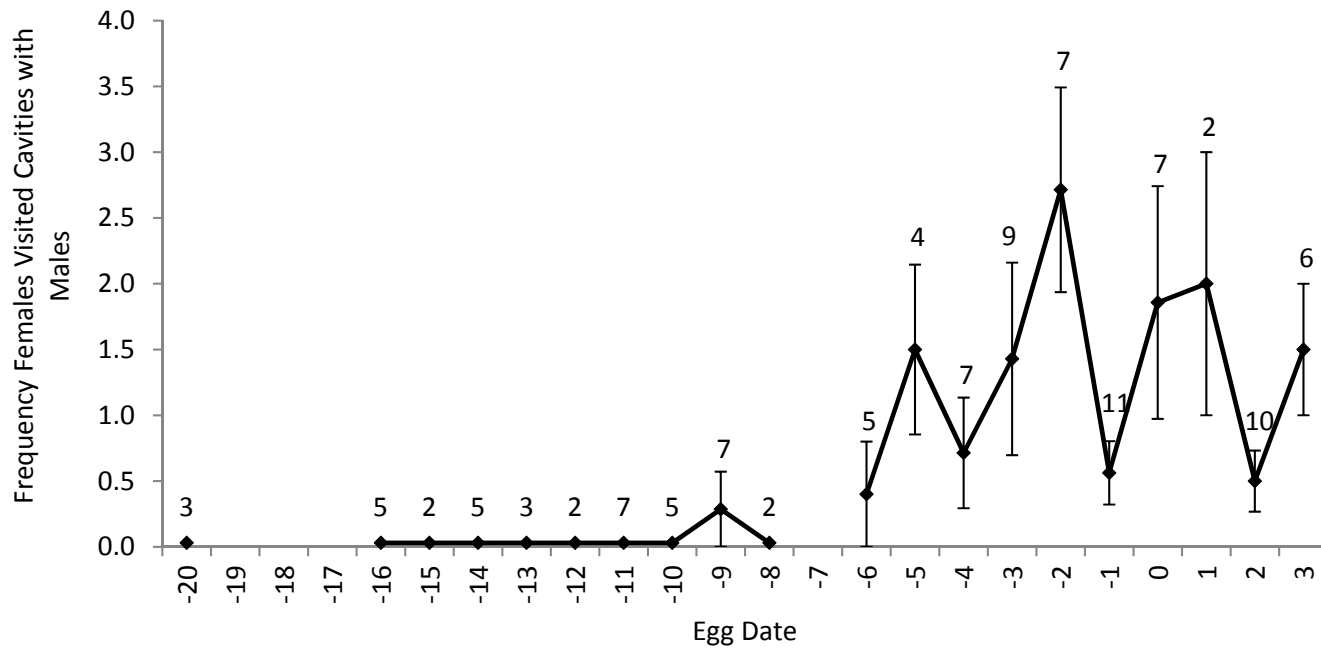
Figure 10. Mean frequency breeding females and males entered cavities together during the mate guarding period relative to the day in the laying cycle (egg date). Day 0 represents the first day the female laid an egg. Standard error bars are shown. Sample sizes appear above each datum, and represent the total number of males observed relative to the egg date. Days during which no observations were conducted are left blank.
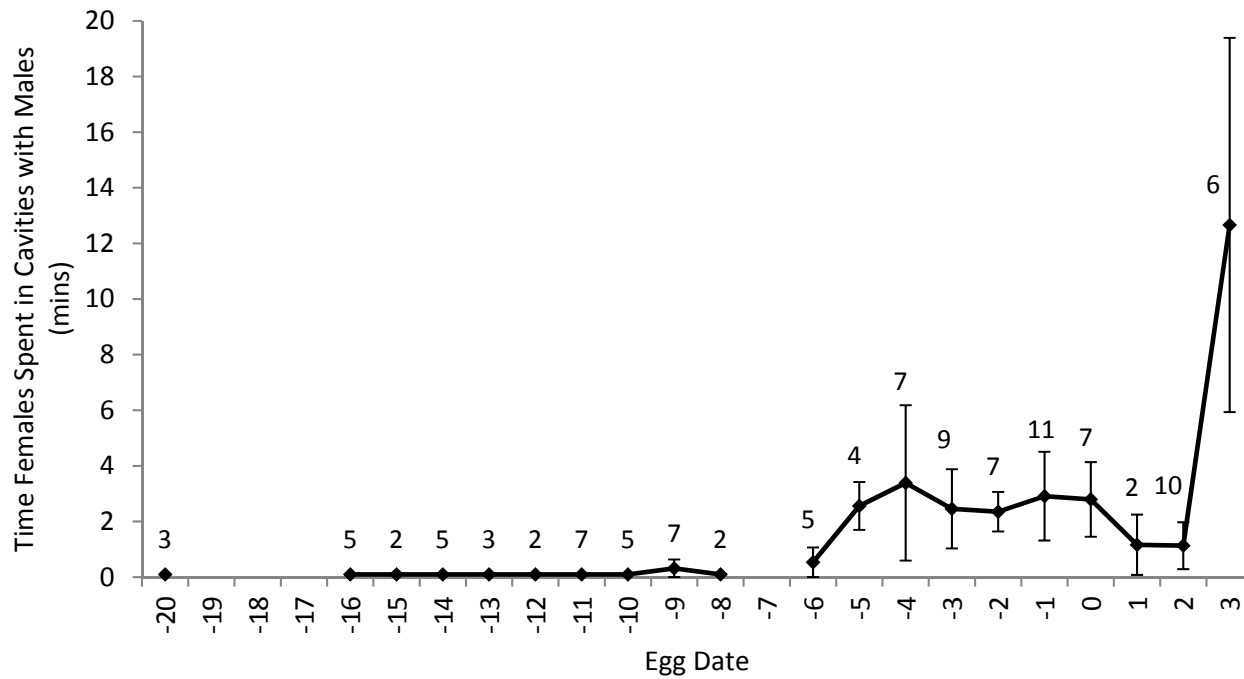
Figure 11. Mean time (min) breeding females spent in tree cavities with breeding males during the mate guarding period relative to the day in the laying cycle (egg date). Day 0 represents the first day the female laid an egg. Standard error bars are shown. Sample sizes appear above each datum, and represent the total number of males observed relative to the egg date. Days during which no observations were conducted are left blank.

Figure 12. Mean frequency breeding females went into tree cavities with breeding males relative to the number of males in the breeding cohort during the mate guarding period. Standard error bars and sample sizes are shown.
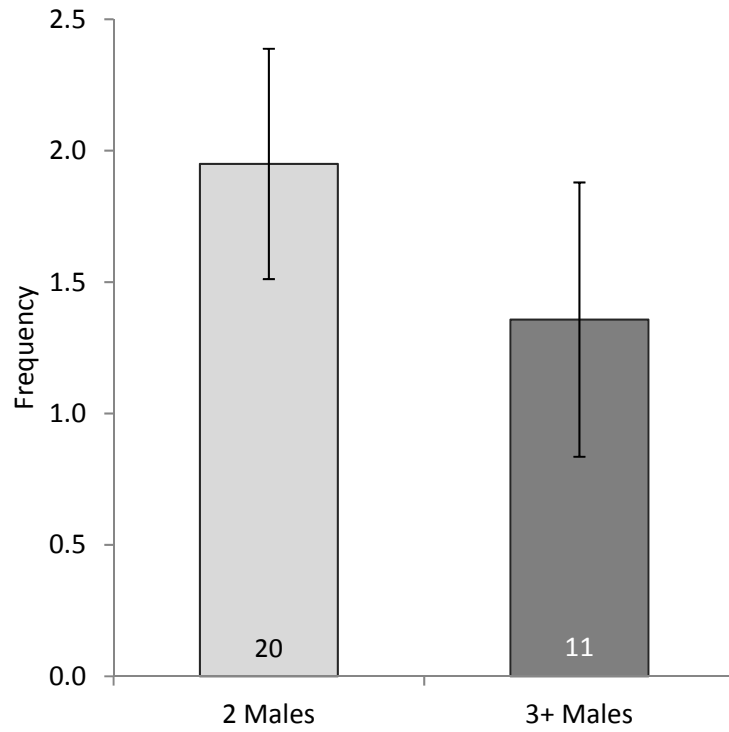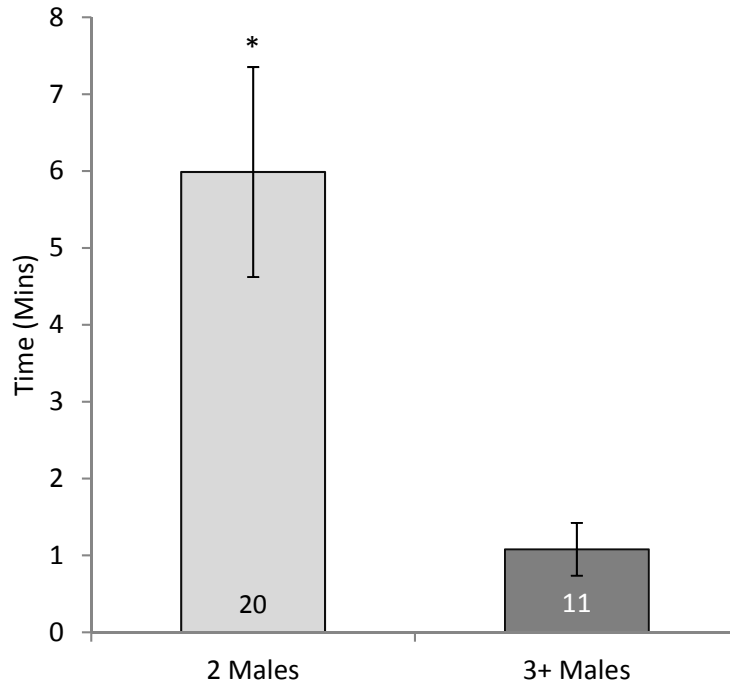
Figure 13. Mean duration of time (min) breeding females spent in tree cavities with males relative to the number of males in the breeding cohort during the mate guarding period. Females spent significantly longer durations of time in tree cavities with males in 2-male groups compared to 3+ male groups ($U = 39$, $N = 31$, $P < 0.01$). Standard error bars and sample sizes are shown.

Paternity

Of the 13 nests that were initiated as part of this study, 10 successfully produced offspring. Three nests failed due to the disappearance of eggs and/or nestlings caused by nest predation or failure to hatch. Of the 10 successful nests, 8 were produced by groups with two cobreeding males, and the remainder came from groups with 3+ cobreeding males. The total number of chicks yielded by all nests in this study was 27, and the mean number of offspring per nest was 2.7 ± 1.3 chicks.

In six nests, paternity of all of the chicks was assigned to a single breeding male. Both of the nests produced by the groups composed of 3+ males contained only a single chick. In four nests, paternity of all chicks could be attributed to one male when multiple nestlings were present. The remaining four nests that contained multiple offspring exhibited multiple paternity (Table 5).

There was no strength of concordance between the frequencies females went into cavities with breeding males and the realized paternity of the males in 2-male groups ($r_c <$ 0.01, $df = 15$, $P > 0.05$) or 3+ male groups ($r_c = 0.21$, $df = 7$, $P > 0.05$). Similarly, there was no strength of concordance between the duration of time females spent in tree cavities with males and the realized paternity of the males in 2-male groups ($r_c = -0.67$, $df = 15$, $P > 0.05$) or 3+ male groups ($r_c = 0.26$, $df = 7$, $P > 0.05$).

Table 5. Mean percent offspring sired by the first ranked (α) and second ranked (β) male per nest during 2012. Males were ranked relative to their relative success at siring young in a particular nest. *N* represents the number of males within each rank.

Male Cohort	Mean Percent Sired ± SE (*n*)	
(Mean *N* Offspring ± SE)	α	β
2 Males (3.13 ± 0.35)	75.56 ± 6.06 (9)	14.14 ± 6.67 (7)
3+ Males (1.00 ± 0.00)	100.00 ± 0.00 (2)	0.00 ± 0.00 (6)

DISCUSSION

From the perspective of an acorn woodpecker male in a polyandrous group, copulating with a female in a cavity likely reduces potential interference by other cobreeding males relative to copulation attempts that occur in view of those males. This is demonstrated by the high degree of mate-guarding vigilance reported in the previous chapter, as well as the high ratio of interrupted versus completed copulations observed in this species. All polyandrous breeding males mate guard in this species, a behavior that likely decreases the opportunities for successful mating attempts by any one male. Within the protection of a cavity, however, a male is presumably able to copulate with a female without interference.

From a breeding female's perspective, using cavities for mating could be a strategy to reduce the potential for injury or stress sustained by copulating in the presence of other cobreeding males given the frequency with which males in this species physically interfere with copulation attempts. For example, polyandrous female dunnocks that are chased excessively and harassed by multiple males during the mate guarding period tend to provision nestlings less, and this harassment is often correlated with reduced fitness in the form of infertile eggs (Davies, 1985). Additionally, a direct benefit of copulating within tree cavities may be a reduction in conflict among multiple breeding males. As described in Chapter II, because males spend a significant amount of time following and staying within close proximity to breeding females throughout the majority of their fertile periods, perhaps the only way for a female to copulate successfully with any male is to do so in a cavity. And because males are forced to wait for the female to

enter a cavity before they are able to copulate with her, aggressive interactions are aborted when the female fails to enter the cavity. According to my observations, pecking and jostling between males at cavity entrances typically occurs after the female has already entered the cavity. In this way, the behavior of females may disrupt dominance interactions among cobreeding males, which could explain why mate guarding does not predict paternity in 3+ male groups (Chap. II).

The peak in the distributions of both cavity-visit frequency and duration of time spent in cavities by breeding acorn woodpeckers in this study, which started on day -9 and tapered off by day 2 (Figs. 10 & 11), are highly reminiscent of the distribution of copulation frequency in other polyandrous and polygynandrous species, such as Smith's longspurs (*Calcarius pictus*; Briskie, 1992), dunnocks (Hatchwell & Davies, 1992), and alpine accentors (*Prunella collaris*; Nakamura, 1990). Across all groups, the frequency with which acorn woodpecker breeding females entered tree cavities with breeding males increased dramatically about nine days before females laid their first eggs, and peaked around the time first eggs were laid (Fig. 10). This was also reflected in the distribution of time females spent within tree cavities with breeding males (Fig. 11). In comparison, Smith's longspurs begin copulation around day -5, reach the peak number of copulations when the female lays her first egg, and then the rate tapers off by the time the female lays her penultimate egg around day 3 (Briskie, 1992). In dunnocks, males begin copulating with females around day -9, and continue to do so until the initiation of incubation, on day 3 (Hatchwell & Davies, 1992). Alpine accentors begin copulation around day -7, and conclude on day 2, around the time of clutch completion (Nakamura, 1990).

Thus, the pattern of cavity use behavior of acorn woodpeckers closely resembles the pattern of copulation frequency in other polyandrous species, which suggests that cavity use behavior could be a reliable proxy for mating access in this species. According to my findings, however, cavity use does not appear to predict reproductive skew in polyandrous acorn woodpecker groups. Nevertheless, the lack of a causal link between cavity use and paternity does not necessarily preclude the possibility that copulation behavior occurs within cavities. This study was hampered by small sample sizes caused by the lack of successful nests in groups with three or more cobreeders, as well as by the relatively small number of offspring produced per nest (mean offspring = 2.7 ± 1.3). Additional paternity data for such groups would be invaluable.

An alternative explanation for the observed cavity use behavior in this species is that females and males are entering tree cavities together in order to prepare the cavities for nesting, and to check for the presence of eggs once the breeding female begins to lay. In other polyandrous species, such as the dunnock, an egg in the nest has been shown to be a cue that the female is fertile, and results in an increase in copulation rate (Hatchwell & Davies, 1992). It follows that this might be an important cue for acorn woodpecker males as well, which is reflected in the increase in tree cavity visits around the time breeding females lay their first eggs (Figs. 9 & 10). More work needs to be done to determine what is actually occurring inside the nest cavities of polyandrous groups.

This study assumed that acorn woodpeckers, like other polygynandrous species, copulate at high frequency within tree cavities. The lack of concordance between cavity use and paternity suggests that this assumption may be false. In fact, the rarity of copulations observed in this species may be a clue. As mentioned previously, some avian

species require very few copulations to fertilize a clutch of eggs (Birkhead & Møller, 1992). If the breeding males in this species are only able to copulate with breeding females infrequently, the extremely uneven distribution of paternity in polyandrous and polygynandrous groups could be a product of chance, based on which male is nearest to the female in the event that she signals her receptivity, and copulation is completed without interruption by other males. Moreover, the effect of copulation interruption by other breeding males would most likely be greater in groups with three or more cobreeders, resulting in higher skew.

Finally, molecular methods to extract sperm from the perivitelline layer of eggs laid by a polyandrous female would determine the proportion of sperm contributed by each breeding male (Birkhead et al., 1994; Michl et al., 2002). Doing so could reveal how mating behavior is correlated with sperm competition and realized paternity. Furthermore, by comparing copulation behavior with the genetic identities of sperm present on the eggs laid by the female, one could test if factors such as sperm morphology and viability, or cryptic female choice play a role in determining reproductive skew in this species.

CHAPTER IV

CONCLUSIONS

All individuals vary according to a variety of properties that could include their fighting ability, physical traits, genetic predisposition, access to resources, attractiveness to potential mates, relatedness to others, gender, social status, and all the innumerable disparities between individuals that genetic and environmental variation can supply. As a consequence of these variables, it is inevitable that resources such as mating opportunities will not be shared equally. One member of a group can always be expected to claim a larger share, which creates a hierarchy of possession. Predicting who that individual will be based on reproductive skew theory, or some other physical/behavioral/genetic correlate, however, can be a challenging task.

In Chapter II, I tested the assumption that species in which reproduction is highly skewed form dominance hierarchies that influence each individual's share of reproduction. The mate-guarding behavior of cobreeding acorn woodpecker (*Melanerpes formicivorus*) males was quantified and compared with the paternity of nestlings in each social group in order to determine if cobreeding males form breeding hierarchies defined by each male's ability to guard breeding females. There was a significant strength of concordance between paternity and mate guarding (attendance and following) behavior in 2-male groups, but mate-guarding behavior failed to predict paternity in larger groups consisting of three or more cobreeding males, suggesting that breeding hierarchies break down in the presence of additional cobreeders.

Concessions models of reproductive skew theory predict high reproductive skew in groups consisting of close relatives. This prediction was corroborated by my finding that mate guarding in 2-male groups reliably predicts paternity. The model fails to predict skew, however, when applied to 3+ male groups. Compromise models predict that reproductive skew is a product of each individual's competitive ability relative to that of the other group members. Competition between acorn woodpecker males was evident in the significant increase of mate guarding duration in 3+ male groups compared to 2-male groups. The degree of reproductive skew in compromise models is determined by the relative competitive ability of the subordinate (Johnstone, 2000). Complete monopolization of paternity occurred in the majority of the nests in this study, indicating a high degree of skew, which in turn indicates subordinates had significantly weaker competitive ability. Yet this conclusion isn't supported by the fact that acorn woodpecker males who sire the majority of young in a nest often fail to do so in a second nest separated by only a matter of weeks – which functionally means the "dominant" and "subordinate" individuals in these groups change dramatically from nest-to-nest and year-to-year (Table 4). Does that mean their relative competitive abilities go through such drastic changes for each nest attempt as well? The mate guarding results garnered from the 3+ male groups seem to suggest a hidden variable at play.

In Chapter III, I tested the assumption made by many skew models that females do not influence the distribution of reproductive skew among cobreeding males. The tree cavity use behavior of breeding females during their fertile period was used as a proxy for mating access to test if female behavior affects the paternity of her offspring. The frequency and distribution of cavity use behavior by females across the laying cycle

closely resembled the frequency and distribution of copulation behavior of females in other polyandrous species. Yet this behavior did not predict the relative reproductive success of the male cobreeders in these groups. Contrary to my assumption that acorn woodpeckers engage in frequent copulation (albeit in tree cavities) because it is a common trait in polygynandrous species, the lack of concordance between cavity use and paternity, coupled with the high, variable skew characteristic of the majority of the nests, suggests females may actually be copulating extremely infrequently.

Future research of the mating behavior of acorn woodpeckers requires more direct experimental methods. The results from this study demonstrate the need to observe the behavior of males and females inside their tree cavities in order to directly quantify potential copulation behavior. To that end, I placed motion-sensing cameras in three artificial acorn woodpecker cavities at the Hastings Reserve in the spring of 2014, two of which were successfully adopted as nest cavities by the woodpeckers in those territories during that breeding season. The behavior of the birds in the weeks leading up to, and during, egg-laying was recorded, and the results from this preliminary study will be analyzed for future publication. Nest cameras allow a level of observational access never before possible in the study of this species. Placing cameras in the nests of monogamous, polyandrous, polygynous, and polygynandrous acorn woodpecker groups would reveal how the mating, incubating, and provisioning behavior of birds in these different group compositions differ from one other. This could in turn provide information about the proximate causes of the skewed paternity that characterizes polyandrous acorn woodpecker groups.

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Publications

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Brownson, A. C., Taank, V. K., Voegeli, V., & Walters, E. L. Design and construction of a novel web-streaming, motion-sensing nest monitoring system using Raspberry Pi micro-computers.

Awards

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Presentations

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