

DEMOGRAPHIC AND FITNESS CONSEQUENCES OF DELAYED DISPERSAL IN
THE COOPERATIVELY BREEDING ACORN WOODPECKER

By

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Abstract of Thesis Presented to the Graduate School
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DEMOGRAPHIC AND FITNESS CONSEQUENCES OF DELAYED DISPERSAL IN
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Cooperative breeding in birds occurs when more than two individuals provide care for a single nest. In many species, the additional adults present are offspring from a previous year who have delayed dispersal, and provision young who are non-descendant kin. Delaying dispersal and age of first breeding can influence the demography and fitness of individuals, but the fitness and demographic consequences of helping behavior are poorly understood. Using long-term data (1972-2004), I examined the demographic and fitness consequences of helping behavior in acorn woodpeckers *Melanerpes formicivorus*. Using a multi-state capture-mark-recapture framework, I found that the apparent survival of breeders was higher than helpers, and the survival of males was higher than females. Juveniles were much more likely to become helpers rather than breeders following fledging, and helpers were more likely to remain helpers rather than becoming a breeder. Both survival and transition rates varied annually and were positively influenced by the acorn crop. For fitness estimation, I focused only on

reproductive females who were banded as juveniles. Although helpers began reproduction significantly later and lived significantly longer than breeders, there was no significant difference in lifetime reproductive success or individual fitness between the two groups. However, birds that successfully bred at age 1 without helping had a significantly higher fitness than those who helped and successfully bred at age 2 or older. My results suggest that delayed dispersal and reproduction in the acorn woodpecker lead to a loss of fitness when conditions are favorable for successful reproduction. However, if constraints in the environment prevent an individual from breeding at age 1, helping is a viable option until reproduction is possible.

CHAPTER 1 INTRODUCTION

Cooperative breeding in birds occurs when more than two individuals provide care for a single nest (Brown 1987). Why some individuals provide care for young who are not their own has been of substantial interest to behavioral and population ecologists alike (reviewed in Stacey & Koenig 1990; Cockburn 1998; Koenig & Dickinson 2004). Recognized in 3.2% of the extant species of birds (Arnold & Owens 1998), cooperative breeding can manifest itself in a number of ways. Multiple males can share a single female mate (mate-sharing) and multiple females can lay eggs in the same nest (joint-nesting). Offspring can disperse and attempt to breed independently when they become sexually mature, or they can delay dispersal for a year or more and remain at home on their natal territory. Dispersing individuals may return home at a later time, may breed on their own, or may immigrate into another group of kin or non-kin. One of the most interesting aspects common to many cooperative breeding systems is helping behavior, which can generally be described as delayed reproduction past the point of sexual maturity and provisioning of young that are not direct descendants.

It has been suggested that a shortage of a critical resource constrains the availability of breeding territories and the ability of some individuals to reproduce successfully. This idea, referred to as the ecological constraints hypothesis, has been proposed as one cause of cooperative breeding (Koenig & Pitelka 1981; Emlen 1982). Often, the ecological constraint is a shortage of reproductive vacancies and can be associated with a lack of suitable nest cavities (Walters, Copeyon & Carter III 1992),

habitat (Woolfenden & Fitzpatrick 1984), or food-related resources (Koenig & Mumme 1987). Until a reproductive vacancy becomes available, helpers may remain on the natal territory and help raise younger siblings.

The acorn woodpecker *Melanerpes formicivorus* is a cavity nesting species common throughout the oak woodlands of western North and Central America, ranging from Oregon south to Colombia. In California the acorn woodpecker practices cooperative breeding, consisting of mate-sharing, joint-nesting and helping behavior, although the most common reproductive group is a monogamous pair (Koenig & Mumme 1987). Displaying one the most complex social systems of any vertebrate, the acorn woodpecker has been studied continuously since 1971 at Hastings Natural History Reservation in central coastal California (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987; Koenig, Haydock & Stanback 1998) and offers an opportunity to answer a number of questions related to cooperative breeding and helping behavior. The majority of demographic analyses regarding helping behavior were done several years ago (summarized in Koenig & Mumme 1987). Since then, many years of additional field data have been collected, and new techniques for estimating fitness and population dynamic consequences of social behavior have been developed.

My objectives were to investigate demographic and fitness consequences of helping behavior in the acorn woodpecker. In chapter 2 I investigated the effect of cooperative breeding and helping behavior on survival, probability of breeding, and realized population growth rate. I used multi-state and reverse-time capture-mark-recapture (CMR) modeling approaches to estimate the aforementioned parameters, to

investigate the influence of helping on these parameters, and to test specific biological hypotheses relevant to my study system.

In chapter 3 I investigated the effect of delayed dispersal (and thus delayed age of first reproduction) to help at home on individual fitness of female acorn woodpeckers. I estimated individual fitness using two methods: lifetime reproductive success (LRS), and individual fitness (λ , McGraw & Caswell 1996). I compared fitness of females who helped and those who dispersed as yearlings, allowing me to test for an effect of helping and delayed dispersal on individual fitness. I also compared helpers and dispersers that successfully bred at age 1 to investigate the fitness effects of variation in age of first reproduction which arises from differing dispersal strategies. Finally, I examined the effect of a number of social and environmental factors on individual fitness and its components.

The application of recently developed capture-mark-recapture techniques (multi-state models) and fitness estimation tools (λ) to long term data from the acorn woodpecker allowed me to address questions regarding cooperative breeding and helping behavior that were not possible when similar studies were conducted decades ago.

CHAPTER 2
DEMOGRAPHIC CONSEQUENCES OF DELAYED DISPERSAL IN THE
COOPERATIVELY BREEDING ACORN WOODPECKER

Abstract

Acorn woodpeckers (*Melanerpes formicivorus*) often delay dispersal and provision the offspring of close relatives. We investigated the demographic consequences of helping behavior using a multi-state capture-mark-recapture approach in Program MARK, and evaluated the influence of social and environmental factors on survival and breeding probabilities of acorn woodpeckers. Breeders survived better than helpers, and males survived better than females. Juveniles were much more likely to become helpers rather than breeders following fledging, and helpers were more likely to remain helpers rather than becoming a breeder. Both survival and transition rates varied annually. Group size and composition had a significant influence on survival of breeder males, breeder females and helper males. These social factors often had a negative influence on the likelihood a female would attain a breeding position, while not significantly influencing the same rates for males. The acorn crop positively influenced survival and probability of breeding. Realized population growth rate varied annually and was positively affected by both survival and transition probabilities. Survival of male breeders, which was strongly influenced by the size of the acorn crop, generally had the greatest influence on population growth rate.

Introduction

Social behavior influences survival, timing and probability of breeding, reproduction, dispersal, and population growth rate in many species of birds and mammals (Brown 1987; Stacey & Koenig 1990; Solomon & French 1996; Koenig & Dickinson 2004). However, the population dynamic consequences of social behavior are still not well understood. This is particularly true for cooperative breeding birds, in which more than two individuals participate in providing care for a single nest (Brown 1987).

One common characteristic of many cooperative breeding systems is the presence of helpers: individuals who delay dispersal, forego breeding and provide care for another individual's offspring (Emlen 1982, 1995). In some species, individuals may return to help a family member after dispersing and failing to breed as in the western bluebird *Sialia mexicana* and long-tailed tit *Aegithalos caudatus* (Dickinson, Koenig & Pitelka 1996; MacColl & Hatchwell 2002). In others, birds nest independently but establish territories near their parents and sometimes provision the young at both nests, as in Galapagos mockingbirds *Nesomimus parvulus* and western bluebirds (Curry & Grant 1990; Dickinson *et al.* 1996). Delayed dispersers can in some cases also stay without offering any help at the nest, as occurs in the Siberian Jay *Perisoreus infaustus* (Ekman, Sklepkovych & Tegelström 1994).

Delayed dispersal and helping behavior are often attributed to ecological constraints (Koenig *et al.* 1992; Hatchwell & Komdeur 2000) with constraints in some cases being so extreme as to cause helping behavior to be obligate (Boland, Heinsohn & Cockburn 1997). Depending on the suite of environmental and social factors experienced by an individual of dispersing age, the two possible strategies (disperse or stay) should confer differing fitness advantages to the individual. For example, Covas *et al.* (2004)

showed that when unlimited food was provided to colonies of social weavers the proportion of birds that helped decreased and more birds initiated independent breeding. Similarly, Walters *et al.* (1992) experimentally showed that red-cockaded woodpecker *Picoides borealis* helpers dispersed into suitable vacant territory when a key resource (a suitable nest cavity) was available, but generally remained at home and helped until nest cavities became available. Social factors, such as availability of mates, number of breeders on natal territory and group size and composition, may also affect an individual's dispersal decisions. When constraints on breeding are high, juveniles should be more likely to stay at home and help rather than disperse and breed independently (Koenig *et al.* 1992).

Individuals that provide help to relatives may increase their own inclusive fitness indirectly due to the promotion of shared genetic material (Hamilton 1964; Griffin & West 2002; Oli 2003). However, helping can have a positive or negative effect on the direct fitness of an individual. Survival and the probability that an individual will breed are two major components of fitness and population dynamics, and can be affected by delaying dispersal and remaining on the natal territory past the point of sexual maturity. Survival of non-breeders can be enhanced by familiarity with the natal territory, parental nepotism, or by group augmentation (Ekman, Bylin & Tegelström 2000; Kokko, Johnstone & Clutton-Brock 2001), while survival of breeders can be increased by the load-lightening associated with the presence of helpers or group augmentation (Kokko *et al.* 2001; Heinsohn 2004). By delaying immediate breeding, it is often possible to increase the likelihood of successful breeding through territory or mate inheritance, territory budding or by dispersing in coalitions of same-sex siblings (Woolfenden &

Fitzpatrick 1984; Hannon *et al.* 1985; Komdeur & Edelaar 2001; Dickinson & Hatchwell 2004). Changes in survival and the likelihood of breeding affect an individual's fitness and the growth rate of a population, and thus population dynamics. An understanding of how delayed dispersal and helping behavior influences probability of survival and breeding, and of the influence of environmental and social factors on these rates, is necessary for discerning the fitness and population dynamic consequences of helping behavior in cooperative breeding systems.

Here we apply multi-state capture-mark-recapture (CMR) models (Williams, Nichols & Conroy 2002) to 33 years of data to investigate the survival and population dynamic consequences of delayed dispersal and helping in the cooperatively breeding acorn woodpecker *Melanerpes formicivorus*. Specifically, we ask the following: Do non-breeding helpers and breeders have different survival probabilities? Are there sex-specific differences in survival (within helpers and breeders, and overall) or the probability of becoming a breeder or helper after fledging? Which social and environmental factors influence survival and probability of becoming a breeder? Finally, we used Pradel's (1996) reverse-time CMR model to estimate and model the realized population growth rate and investigate the effect of variation in survival and probability of breeding on the growth rate.

Methods

Study Species

The acorn woodpecker is a cooperative breeding bird common in oak woodlands of the Pacific coast. Breeding groups range from single monogamous pairs up to 15-member mixed groups of breeders and non-breeding helpers of both sexes (Koenig & Mumme 1987). Helpers are almost always offspring from prior years. Both breeders and

helpers contribute to territory defense, food storage, and care of young (Mumme, Koenig & Pitelka 1990).

Exhibiting one of the most complex social systems of any vertebrate, the acorn woodpecker is opportunistically polygynandrous, often practicing both mate-sharing and joint-nesting within the same group (Koenig & Mumme 1987). Mate-sharing occurs when 2-4 males, usually brothers or a father and son(s), compete for reproductive access to 1-3 females, usually sisters or a mother and daughter(s). Joint-nesting occurs when multiple females synchronously lay eggs in a common nest. The latter occurs in 22% of groups, while mate-sharing by males occurs in slightly over half (54%) of groups. However, the most common breeding system, making up 23.5% of all groups, is a monogamous pair (Koenig & Mumme 1987; Koenig & Stacey 1990). Incest is rare; a genetic analysis by Haydock *et al.* (2001) found that only 14 of 400 (3.5%) offspring apparently resulted from incestuous breeding. In general, the high costs of inbreeding depression (estimated to be at least 1.2-1.8 lethal equivalents per individual) select against helpers breeding with related group members (Koenig *et al.* 1998; Koenig, Stanback & Haydock 1999). Helpers disappear at a higher rate than breeders, at least in part because of dispersal outside the study area (Koenig *et al.* 2000).

The apparent limiting factor (or critical resource, cf. Walters (1990) for successful breeding acorn woodpeckers in California is an acorn storage tree or granary (Koenig & Mumme 1987). Members of the group drill and maintain holes in a tree throughout the year, collecting acorn mast and storing it in the granary. Larger granary sizes allow the food stores to last through the winter, enabling earlier nesting, larger clutches, and higher nesting success in the spring (Koenig & Mumme 1987; Koenig & Stacey 1990).

Study Area

The study site is located on Hastings Natural History Reservation in the Santa Lucia mountain range in Monterey County, California. Elevation ranges from 450 to 920m. Summers are hot and dry, while winters are cool and wet with infrequent snow. Common trees in the study area include five species of oak: coast live oak (*Quercus agrifolia*), canyon live oak (*Q. chrysolepis*), blue oak (*Q. douglasii*), black oak (*Q. kelloggii*), and valley oak (*Q. lobata*), along with California sycamores (*Platanus racemosa*), willows (*Salix* spp.), California buckeye (*Aesculus californica*), and madrone (*Arbutus menziesii*). The plant communities in acorn woodpecker habitat include foothill woodland, savanna-grassland, and riparian woodland. Acorn woodpeckers are most frequently found in generally open areas with a dense ground cover of grasses and few shrubs (Koenig & Mumme 1987).

Field Methods

Acorn woodpeckers at Hastings Reservation have been individually marked and their survival and reproduction have been monitored since 1971 (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987; Koenig & Stacey 1990; Koenig *et al.* 1999). Nestlings were banded between 20-25 days after hatching; fledging occurs at approximately 30-32 days (Weathers, Koenig & Stanback 1990). Breeding status of adults (helper or breeder) was determined indirectly based on the history and known relatedness of birds. Generally, birds immigrating into a group were assumed to be potential breeders, whereas offspring remaining from prior years were generally classified as non-breeding helpers. However, when all breeders of the opposite sex disappeared and were replaced by unrelated individuals, offspring were assumed to

inherit breeding status within their natal territory (Koenig & Mumme 1987; Haydock *et al.* 2001). Further details on field methodology are given in Koenig & Mumme (1987).

Each fall starting in 1980, the acorn crop of the five *Quercus* species was estimated. For each tree, the number of acorns counted in 15 s by each of two observers was tabulated. Each count value was log-transformed and the mean value was calculated and used as an index of the acorn crop (hereafter, acorn crop or AC) (Koenig *et al.* 1994a; Koenig *et al.* 1994b).

Group size and composition of each group was determined in the spring of each year. The number of breeding males, breeding females, helper males and helper females was determined for each group (details in Koenig & Mumme 1987).

Survival and Transition Probabilities: Estimation and Modeling

A multi-state CMR model was constructed separating birds into juvenile (J), helper (H), and breeder (B) stages. A bird was considered a juvenile from banding (just prior to fledging) until the following spring breeding season (1 March). Juvenile woodpeckers had several potential options available to them. They could remain on the natal territory past the point of sexual maturity and help, they could disperse to fill a breeding vacancy (either within or outside of the study area), they could inherit breeding status on their natal territory, or they could die. After becoming a helper, an individual could die, continue to help, or become a breeder (either within the group, following the death of the opposite-sex breeder, or by dispersing to another group to fill a reproductive vacancy). Breeding birds could continue breeding (either in the same group or after moving to another group), die, or (rarely) revert to becoming a helper.

Following Williams *et al.* (2002), we define Φ_i^{rs} as the probability of being alive and in state s at time $i + 1$, given that the bird was alive in state r at time i . The recapture probability, p_i^r , is the probability that a bird alive in state r at time i is captured or observed after banding. Both Φ_i^{rs} and p_i^r assume that survival and transition between i and $i + 1$ and capture at i depend only on the state at time i .

The parameter Φ_i^{rs} is the product of both survival and probability of transition between states (Eq. 17.30 of Williams *et al.* 2002):

$$\Phi_i^{rs} = S_i^r \Psi_i^{rs},$$

where S_i^r is the probability that an animal in state r at time i survives and remains in the study population until time $i + 1$, and Ψ_i^{rs} is the probability that an animal is in state s at time $i + 1$, given that it was in state r at time i and survived until $i + 1$ and remained in the study area (Williams *et al.* 2002). It is important to note that, due to the finite study area, birds that disappeared could either have died or dispersed outside the study area.

Therefore, these estimates are apparent survival, and should not be interpreted as true survival, especially in the case of helpers, a large fraction of which are known to disperse. Similarly, transition probabilities for helpers becoming breeders are to an unknown extent compromised by the probability of dispersal, as only the fate of individuals remaining in the study area could be determined. In contrast, although breeders do sometimes disperse (Haydock and Koenig, unpublished data), apparent survival for breeders is likely to closely reflect actual survival. Additionally, for a given state, the transition probabilities sum to 1 (i.e. $\sum_s \Psi_i^{rs} = 1$).

In our analysis, we have three states, juvenile, helper and breeder. For example, Ψ^{JB} is the probability that a juvenile bird in a given year will be a breeder one year later, and Ψ^{HH} is the probability that a helper in one year will remain a helper the next year. By definition, a juvenile bird at i cannot be a juvenile at $i + 1$, as it must become either a helper or breeder. Therefore, $\Psi^{JJ} = 0$. Additionally, birds cannot return to the juvenile stage. Thus, $\Psi^{HJ} = \Psi^{BJ} = 0$.

We excluded from analyses individuals that were banded as fledglings but did not survive the winter. Because we included only those birds that survived to the first spring following fledging, all juveniles included in the analyses became either a helper or a breeder. Juvenile survival was thus set to 1.

We estimated the goodness of fit (GOF) for our multi-state model using Program U-CARE (Choquet *et al.* 2003). With two sexes (male, female), three strata (juvenile, helper, breeder) and 33 capture occasions, our data file was too large for Program U-CARE to handle. Because of the large number of states in our model, we were unable to use the standard Arnason-Schwarz (AS) multi-state model and instead used TEST 3G and M of the Jolly-Move (JMV) model, as implemented in U-CARE. This is a reasonable approach to GOF of the Arnason-Schwarz (AS) multi-state model, because the JMV model is unlikely to show significantly greater fit to the data than the AS model (Cooch & White 2005). Further details regarding JMV and AS models are available in Pradel, Wintrebert & Gimenez (2003).

We implemented the multi-state model using Program MARK (White & Burnham 1999). For model comparison we used Akaike's Information Criterion (AIC), which considers both the deviance of the model and the number of estimated parameters to

provide a parsimonious description of how well the models explained variation in the data when compared to one another (Burnham & Anderson 2002; Williams *et al.* 2002). A difference in AIC_c values (ΔAIC_c) of less than two indicated that the models were similarly supported by the data. A moderate difference in model support was shown when $2 < \Delta AIC_c < 7$, and strong support when $\Delta AIC_c > 10$. We used the most parsimonious model (lowest AIC_c) to examine survival and transition estimates.

Using the most parsimonious model, we investigated the effect of environmental and social factors on survival and breeding probability by modeling the logits of survival and transition rates as linear functions of the factors. Values of all environmental and social factors were scaled such that value ranges from 0 to 1. The relationship between the survival or transition rate and a covariate was considered significant if the 95% confidence interval of the slope parameter of the linear model (β) did not include 0 (Williams *et al.* 2002).

Pradel's (1996) reverse-time CMR model, implemented in Program MARK, was used to estimate and model the realized population growth rate (λ). For model selection and parameter estimation, we used the same methodology as for the multi-state model. For the Pradel's model, our interest was in the overall growth rate of the population, and the breeding status of birds (juvenile, breeder, helper) was therefore ignored. We used Program RELEASE, implemented in Program MARK (White & Burnham 1999), to estimate GOF for the general Pradel's model.

Results

Our dataset spanned 33 years (1972-2004) and included data for 1570 individual acorn woodpeckers (845 males and 725 females). We included 1218 birds banded as juveniles (690 males, 528 females), and 352 birds banded as adults (155 males, 197

female). Only juveniles that were present in the population during their first spring were included in our analysis.

The fully time-dependent multi-state model of survival, recapture, and transition probabilities, $\{S^J(s^*t) S^H(s^*t) S^B(s^*t) p^J(s^*t) p^H(s^*t) p^B(s^*t) \Psi^{JB}(s^*t) \Psi^{HB}(s^*t) \Psi^{BB}(s^*t)\}$, fit the data poorly ($\chi^2_{105} = 219.9$, $P < 0.0001$). The variance inflation factor, \hat{c} , was 2.09, indicating over-dispersion (Lebreton *et al.* 1992). Therefore, we used calculated \hat{c} to aid in parameter estimation and model comparison.

The most parsimonious model (Model 1, Table 2-1) differed from the second and third most parsimonious models (Model 2 and 3, respectively, Table 2-1) by ΔQAIC_c of 0.25 and 1.13, respectively, indicating that these 3 models were practically identical. Model 1 included an additive effect of sex and time in all parameters except recapture probability of breeders and helpers, probability of transitioning from breeder to helper, and by definition, all fixed parameters, which were constant across time and sex (Table 2-1). Recapture (p) rates for helpers and breeders were equal and constant across time and sex. The transition rate between breeder and helper was constant across time and sex. As the most parsimonious model, we used Model 1 in further analyses.

Recapture probability (the probability of being seen again after banding, assuming an individual is still alive) for helpers and breeders was high (0.958, 95% CI: 0.947, 0.975). Juvenile recapture was fixed to zero (Table 2-1). Survival rates showed temporal variation and differed between sexes and breeding status. The apparent survival was higher for males than females, and higher for breeders than helpers (Table 2-2). Apparent breeder survival was approximately 10% higher than that of helper, and male survival was 8% higher than female survival. The difference between male and female survival

was most pronounced among helpers, where males survived at a rate nearly 12% higher than female helpers. Survival probability of helpers of both sexes exhibited greater temporal variation than that of breeders (Figure 1).

Juvenile acorn woodpeckers were roughly 4-7 times more likely to become helpers than breeders following fledging, but this differed between sexes. Juvenile males had a higher probability than juvenile females of becoming a breeder in the study area in the spring after fledging (Table 2-3). Additionally, helpers were approximately twice as likely to remain helpers the following year as becoming breeders, with females having a slightly higher probability of remaining helpers. Once an individual became a breeder, the probability of it returning to the helping stage was very low and similar for the two sexes (Table 2-3).

Using the most parsimonious model (Model 1, Table 2-1), we investigated the effects of environmental and social factors on survival and transition probabilities. Survival of male breeders (S^{BM}) was positively influenced by the acorn crop, size of storage facilities and group size. The effect of group size was due to both the number of breeders and the number of helpers, since both positively influenced survival (Table 2-4). Survival of female breeders (S^{BF}) was positively influenced by acorn crop, storage holes and group size. The group size effect on the survival of breeder females was due to number of helpers in the group (especially helper males). Survival of male helpers (S^{HM}) was positively influenced by storage holes and group size, which was due to the number of helpers (specifically helper males), but was unaffected by the annual acorn crop. Survival of female helpers (S^{HF}) was positively affected by only the acorn crop, showing no influence of any social factor (Table 2-4).

The probability of a male breeding in his second year (the year following his juvenile year, Ψ_M^{JB}), was not significantly influenced by any social or environmental factor (Table 2-5). The same probability for females was negatively influenced by the number of breeders in the group (both the number of breeding males and females), while it was positively influenced by the acorn crop. Females, however, were less likely to become breeders (Ψ_F^{JB}) if there were more breeders in their natal group and more likely to become a breeder if the acorn crop was good. Male helpers were more likely to become breeders (Ψ_M^{HB}) when the acorn crop was good and less likely when there were more helper females in the group. Female helpers were less likely to become breeders (Ψ_F^{HB}) in larger groups (which was due to the number of helpers, specifically helper females), and also more likely when the acorn crop was better (Table 2-5).

The fully time-dependent Pradel's model, $\{\Phi(s * t) p(s * t) \lambda(s * t)\}$, fit the data poorly ($\chi^2_{139} = 475.4, P < 0.0001$), and a variance inflation factor (\hat{c}) of 3.42 was used to aid parameter estimation and model comparison. The most parsimonious model included constant capture probability (p), additive effect of sex and time on survival (Φ), and time effect on realized population growth rate (λ). A competing model that differed in QAIC_c by 1.23 (Δ QAIC_c) showed an additive effect of sex and time on λ (Model 2, Table 2-6). Because the Δ QAIC_c was less than 2, there was no support for a difference between the two models, indicating that the sex effect on λ was negligible. Although there was no significant difference between the two models, we chose the one yielding the smallest QAIC_c value (Model 1, Table 2-6), $\{\Phi(s + t) p(.) \lambda(t)\}$. The realized annual population growth rate ranged over time from 0.598 (95% CI: 0.530, 0.674) to 1.547 (95% CI: 1.296, 1.846, Figure 1).

We investigated the influence of the underlying survival and transition probabilities on λ , and found that all probabilities had a significant positive influence on λ . Survival of male breeders (S^{BM}) generally had the greater influence on λ ($\beta = 2.023$; 95% CI: 1.433, 2.612), followed by S^{BF} ($\beta = 1.718$; 95% CI: 1.225, 2.212), S^{HM} ($\beta = 1.654$; 95% CI: 1.810, 2.128) and S^{HF} ($\beta = 1.450$; 95% CI: 1.035, 1.865). Among transition probabilities, Ψ_M^{HB} had the highest influence on λ ($\beta = 0.443$; 95% CI: 0.301, 0.585), followed by Ψ_F^{HB} ($\beta = 0.442$; 95% CI: 0.301, 0.582), Ψ_F^{JB} ($\beta = 0.369$; 95% CI: 0.221, 0.517), and Ψ_M^{JB} ($\beta = 0.334$; 95% CI: 0.200, 0.469). The regression coefficients and confidence intervals for the transition probabilities Ψ^{JH} and Ψ^{HH} , were of equal magnitude, but opposite sign of Ψ^{JB} and Ψ^{HB} , respectively for the corresponding sexes.

Discussion

In cooperatively breeding birds, there are costs as well as benefits associated with a bird's decision to stay and help vs. disperse and attempt to breed independently (Brown 1987; Dickinson & Hatchwell 2004; Ekman *et al.* 2004). For example, survival of philopatric individuals is often higher than that of dispersers due to factors such as territory familiarity (Ekman *et al.* 2004). A bird's decision to disperse or stay and help can also influence its probability of breeding. Survival and breeding probability are key components of fitness, and the effect of dispersal decisions on these demographic parameters can have important population dynamic consequences.

In our analyses, helpers had lower apparent survival than breeders, and thus permanently disappeared with much greater frequency. However, this is clearly because many disappearing helpers are dispersing to fill reproductive vacancies outside of the study area (Koenig *et al.* 2000). Although breeder dispersal does occur (Haydock and

Koenig unpublished manuscript), apparent survival of breeders is relatively close to the real survival rate due to the fact that once an individual begins breeding at a site, it generally stays there until death or some catastrophic event occurs (Koenig & Mumme 1987). Of the 1570 individuals included in our analysis, 352 were banded as adults, the majority of which were immigrants from outside of the study area. Assuming that emigration equals immigration, 35.7% of helpers disappearing are filling breeding vacancies outside of the study area (Koenig *et al.* 2000). Therefore, both the survival rate and probability of attaining a breeding position for helpers were likely biased low. The dispersal confound also exists for female acorn woodpeckers, who, like many avian species, tend to disperse further than males (Greenwood 1980; Koenig *et al.* 2000).

Koenig and Mumme (1987), in a previous analysis of the Hastings population (1973-1986), estimated annual survival of breeding males to be 0.824 and breeding females to be 0.712. Our estimates (0.756 for breeding males and 0.714 for breeding females) were similar to the extent that the earlier estimates fall within the 95% confidence intervals (Table 2-2).

Koenig & Mumme (1987) hypothesized that the higher mortality of female breeders is attributable to increased energetic expenditure by females associated with egg laying and incubation, nest care, and territory defense. Additionally, the higher number of males banded as juveniles that remained in the study area reflects male-biased natal philopatry, while the higher number of females banded as adults (many of which immigrated into the study area) reflects female-biased dispersal. This male-biased philopatry is likely a major source of the apparently higher survival of helper male acorn woodpeckers (Koenig *et al.* 2000).

In many systems, it is not possible to differentiate between individuals that permanently emigrate from the study area and those that die. The confounding of dispersal and survival is almost a universal problem (Koenig, Van Vuren & Hooge 1996). Walters' (1990) work on red-cockaded woodpeckers has probably been the closest to avoiding the problem in a cooperative breeder. Survival rates of red-cockaded woodpeckers were similar to acorn woodpeckers: 0.76 for breeding males and 0.68 for breeding females, but the survival of helper males was slightly higher than that of breeders (0.78 compared to 0.76, Walters 1990)

Juvenile birds that survived their first breeding season were much more likely to become a non-breeding helper than to attain a breeding position in the study area. Males were almost twice as likely as females to become a breeder in the study area following their first year. We offer two possible explanations for the higher breeding probability for males. First, cobreeding among males is more common, and dispersing coalitions of brothers were more successful at competing for breeding positions following a vacancy (Hannon *et al.* 1985). Thus, a larger number of helper males will generally fill a given number of vacancies than helper females. Secondly, male-biased philopatry typically leads to more males remaining in the study area and attaining breeding positions than females (Koenig *et al.* 2000).

A woodpecker that remained a helper for the year following fledging was roughly twice as likely to become a breeder as a juvenile (compare Ψ^{JB} and Ψ^{HB} for both sexes, Table 2-3). But because the helper stage includes birds of varying age, the increased Ψ^{HB} probability is likely an effect of age. Once an acorn woodpecker obtains a breeding position, however, it rarely reverts to helper status (Haydock and Koenig unpublished

manuscript), in contrast to species in which “redirected helping” by failed breeders is common, such as long-tailed tits and western bluebirds (Dickinson *et al.* 1996; MacColl & Hatchwell 2002). Analysis of populations with redirected helping would likely yield significant Ψ^{BH} values.

Previous work has shown the acorn crop to be strongly correlated with reproductive success, territory stability, and breeder survival in acorn woodpeckers (Koenig & Mumme 1987; Koenig & Stacey 1990). Therefore it was not surprising that the size of the acorn crop had a significant influence on survival and transition probabilities of acorn woodpeckers. For breeders, acorn production increased annual survival of both sexes. For helpers, however, only the survival of females was significantly influenced by acorn production. In years with large acorn crops, juveniles (females) and helpers (males and females) had a higher probability of attaining a breeding position. Thus, more birds breed during years with bumper acorn crops, in much the same way that Ural owls *Strix uralensis* take advantage of the vole cycle, and begin breeding at different ages depending on food availability (Brommer, Pietiainen & Kolunen 1998).

Using granary size (the number of storage holes available for acorn storage) as a proxy for territory quality, Koenig & Mumme (1987) found no relationship between territory quality and breeder survival. However, we found a positive influence of the number of storage holes on the survival of breeders of both sexes, and male helper survival. Larger granaries allow groups to take advantage of larger acorn crops, leading to increased food availability in the winter (Koenig & Mumme 1987). Interestingly, however, territory quality had no direct effect on the likelihood of a juvenile or helper

becoming a breeder. The dispersal decisions of western bluebirds are influenced by site quality (Kraaijeveld & Dickinson 2001; Dickinson & McGowan 2005), but we found no direct relationship between territory quality and dispersal. However, because territory quality increases survival, it could indirectly increase the probability of breeding for acorn woodpeckers because longer lived birds have more opportunities to breed. Long-lived species place greater value on future reproduction (Stearns 1992), and this could be one possible explanation for the high survival characteristic of cooperative breeding species (Ekman *et al.* 2004).

Koenig & Mumme (1987) found that survival of male breeders increased with group size, number of breeders, and number of helpers, but found no relationship between the survival of female breeders and any group size or composition measurement. We found that group size and composition had a strong positive effect on survival of both sexes, with both the number of breeders and helpers positively influencing survival of breeder males, and number of helpers positively influencing survival of breeder females. Such increased survival in larger groups offers support for the group augmentation hypothesis, which states that if larger groups confer increased survival, it benefits all group members (especially breeders) to recruit and maintain larger groups (Brown 1994; Kokko *et al.* 2001). The presence of helpers in a group can increase the survival of breeders due to the reduction in breeder workload (Khan & Walters 2002; Heinsohn 2004), in addition to simply increasing group size and thus diluting the effects of predation.

The realized population growth (λ) fluctuated annually in a manner similar to the survival probability of adult birds. Although the breeding probabilities had a significant

influence on λ , their influence on λ was generally less than those of survival probabilities, consistent with the observation that growth rates of fairly long-lived birds were more sensitive to survival parameters than reproductive parameters (Stahl & Oli in press). Survival of breeder males, which had the strongest impact on the population growth rate, was higher in years of larger acorn crops. This reinforces the importance of the role of the acorn crop for group stability and individual survival (Hannon *et al.* 1987).

For delayed dispersal to be maintained, benefits of delayed dispersal must balance or exceed associated costs (Ekman *et al.* 2004). This study suggests that acorn woodpeckers that delay dispersal and help have a lower apparent survival than breeders. Even if we consider that death and disappearance are not separable outcomes, and assume that survival is equal (Walters 1990), helpers are unlikely to be fully compensated, at least directly, for helping (Dickinson & Hatchwell 2004). The delayed start of reproduction is likely to reduce direct fitness (McGraw & Caswell 1996; Oli, Hepp & Kenamer 2002; Oli & Armitage 2003), but some other component of fitness may be compensating individuals who follow this strategy. Helpers are certainly gaining indirect fitness by assisting related breeders such that inclusive fitness of helpers is comparable to those that disperse and breed (Hamilton 1964). MacColl & Hatchwell (2004), using Oli's (2003) methodology for estimating inclusive fitness, showed that for long-tailed tits with zero lifetime reproductive success (LRS), a non-zero fitness was possible through helping. However, inclusive fitness consequences of cooperative breeding still remain poorly understood. Earlier work by Koenig & Mumme (1987) found that males delaying dispersal and helping may have a significantly longer reproductive lifespan and a higher LRS than those who dispersed in their first year to begin breeding. Females that delay

dispersal and help, however, had a shorter reproductive lifespan and lower LRS than first-year dispersers, with only the latter being significant (Koenig & Mumme 1987). A thorough examination of the inclusive fitness consequences of delayed dispersal and helping behavior is clearly desirable.

Table 2-1. Quasi-likelihood adjusted AIC differences (ΔQAIC_c) for five models of the survival, recapture, and transition probability in relation to sex and status for acorn woodpeckers (1972-2004).

Number	Model	ΔQAIC_c	QAIC _c Weight	Number of Parameters
1	$S^J(.) S^H(s+t) S^B(s+t) p^J(.) p^H = p^B(.) \Psi^{JB}(s+t) \Psi^{HB}(s+t) \Psi^{BH}(.)$	0	0.407	129
2	$S^J(.) S^H(s+t) S^B(s+t) p^J(.) p^H(.) p^B(.) \Psi^{JB}(s+t) \Psi^{HB}(s+t) \Psi^{BH}(.)$	0.25	0.360	130
3	$S^J(.) S^H(s+t) S^B(t) p^J(.) p^H = p^B(.) \Psi^{JB}(s+t) \Psi^{HB}(s+t) \Psi^{BH}(.)$	1.13	0.231	128
4	$S^J(.) S^H(t) S^B(s+t) p^J(.) p^H(.) = p^B(.) \Psi^{JB}(s+t) \Psi^{HB}(s+t) \Psi^{BH}(.)$	11.19	0.002	128
5	$S^J(.) S^H(s+t) S^B(s+t) p^J(.) p^H(.) p^B(.) \Psi^{JB}(s+t) \Psi^{HB}(s*t) \Psi^{BH}(.)$	36.44	0.000	155

The symbols used in this table are defined as follows: S = survival; p = recapture rate; Ψ = transition rate; J = juvenile; H = helper; B = breeder; Ψ^{JB} = juvenile to breeder transition (the effect was the same for juvenile to helper); Ψ^{HB} = helper to breeder transition (the effect was the same for remaining a helper); Ψ^{BH} = breeder to helper transition (the effect was the same for remaining a breeder); (t) = time effect, no sex effect; $(s+t)$ = additive effect of sex and time; $(s*t)$ = interactive effect of sex and time; $(.)$ = constant parameter, no effect of sex or time. Parameters that had fixed values, and were thus constant $(.)$ by definition, were as follows: $S^J(1)$, $p^J(0)$, $\Psi^{JJ}(0)$, $\Psi^{HJ}(0)$, and $\Psi^{BJ}(0)$. The complementary parameter for each transition probability experienced the same effect (i.e. Ψ^{HB} and Ψ^{HH} both experienced sex and time effects).

Table 2-2. Estimates of apparent survival rates (S) for male, female, breeder and helper acorn woodpeckers (1972-2004) based on Model 1 (Table 2-1). Mean values (95% CI) are given.

	Male	Female	Overall
Helper	0.695 (0.452, 0.849)	0.577 (0.327, 0.771)	0.636 (0.389, 0.810)
Breeder	0.756 (0.587, 0.862)	0.714 (0.531, 0.835)	0.734 (0.559, 0.849)
Overall	0.725 (0.519, 0.855)	0.644 (0.427, 0.802)	-

Table 2-3. Transition probabilities (Ψ) between juvenile, helper and breeder stages for acorn woodpeckers (1972-2004) in relation to sex based on Model 1 (Table 2-1). Mean values (95% CI) are given, with M = male, F = female.

		To:	
From:		Breeder	Helper
Juvenile	M	0.212 (0.067, 0.515)	0.787 (0.485, 0.932)
	F	0.130 (0.037, 0.392)	0.870 (0.608, 0.963)
Helper	M	0.365 (0.158, 0.617)	0.635 (0.383, 0.842)
	F	0.344 (0.143, 0.601)	0.656 (0.399, 0.857)
Breeder	M	0.995 (0.987, 0.998)	0.005 (0.002, 0.013)
	F	0.995 (0.987, 0.998)	0.005 (0.002, 0.013)

Table 2-4. Influence of social and environmental factors on apparent survival rate of acorn woodpeckers (1972-2004). Regression coefficients (β) are given with 95% CI (significant effects are shown in **bold**). S^{HM} = survival of helper males; S^{HF} = survival of helper females; S^{BM} = survival of breeder males; S^{BF} = survival of breeder females.

Covariate	S^{HM}	S^{HF}	S^{BM}	S^{BF}
Group size	0.094 (0.010, 0.177)	-0.032 (-0.125, 0.061)	0.205 (0.104, 0.306)	0.146 (0.026, 0.267)
Breeders	0.069 (-0.030, 0.169)	-0.055 (-0.161, 0.052)	0.080 (0.002, 0.158)	0.040 (-0.052, 0.132)
Helpers	0.088 (0.014, 0.162)	0.010 (-0.070, 0.091)	0.210 (0.099, 0.322)	0.144 (0.022, 0.267)
Breeder males	0.057 (-0.040, 0.154)	-0.041 (-0.144, 0.062)	0.058 (-0.012, 0.127)	0.074 (-0.021, 0.168)
Breeder females	0.085 (-0.014, 0.184)	-0.056 (-0.159, 0.046)	0.081 (-0.004, 0.166)	-0.016 (-0.099, 0.066)
Helper males	0.076 (0.009, 0.144)	0.016 (-0.068, 0.100)	0.173 (0.065, 0.282)	0.124 (0.004, 0.244)
Helper females	0.064 (-0.011, 0.139)	-0.005 (-0.076, 0.067)	0.144 (0.046, 0.243)	0.088 (-0.022, 0.198)
Acorn crop	0.376 (-0.079, 0.831)	0.528 (0.047, 1.010)	0.420 (0.013, 0.826)	1.04 (0.580, 1.498)
Storage facilities	0.191 (0.090, 0.291)	0.062 (-0.041, 0.165)	0.135 (0.039, 0.231)	0.127 (0.008, 0.247)

Table 2-5. Influence of social and environmental factors on transition probabilities of acorn woodpeckers (1972-2004). Regression coefficients (β) are given with 95% CI (significant effects are shown in **bold**). Symbols used are as follows: Ψ_M^{JB} = transition probability from juvenile to breeder (male); Ψ_F^{JB} = transition probability from juvenile to breeder (female); Ψ_M^{HB} = transition probability from juvenile to breeder (male); Ψ_F^{HB} = transition probability from juvenile to breeder (female). The β -values and 95% CI for Ψ^{JH} and Ψ^{HH} were of equal magnitude but opposite sign of Ψ^{JB} and Ψ^{HB} , respectively, for each sex.

Covariate	Ψ_M^{JB}	Ψ_F^{JB}	Ψ_M^{HB}	Ψ_F^{HB}
Group size	-0.008 (-0.260, 0.144)	-0.052 (-0.263, 0.159)	-0.079 (-0.176, 0.019)	-0.166 (-0.318, -0.015)
Breeders	-0.026 (-0.166, 0.114)	-0.354 (-0.635, -0.074)	-0.063 (-0.178, 0.051)	-0.101 (-0.263, 0.060)
Helpers	-0.037 (-0.182, 0.108)	0.097 (-0.061, 0.256)	-0.068 (-0.155, 0.020)	-0.174 (-0.312, -0.035)
Breeder males	0.019 (-0.102, 0.140)	-0.293 (-0.553, -0.033)	-0.027 (-0.139, 0.084)	-0.069 (-0.225, 0.087)
Breeder females	-0.100 (-0.258, 0.059)	-0.317 (-0.590, -0.044)	-0.101 (-0.217, 0.014)	-0.123 (-0.279, 0.033)
Helper males	-0.033 (-0.163, 0.097)	0.077 (-0.077, 0.231)	-0.019 (-0.097, 0.060)	-0.174 (-0.315, -0.032)
Helper females	-0.029 (-0.179, 0.121)	0.074 (-0.078, 0.226)	-0.111 (-0.202, -0.020)	-0.118 (-0.237, 0.002)
Acorn crop	0.637 (-0.205, 1.478)	1.514 (0.439, 2.588)	1.009 (0.359, 1.659)	1.547 (0.699, 2.395)
Storage facilities	0.031 (-0.091, 0.152)	-0.205 (-0.454, 0.043)	0.008 (-0.096, 0.112)	-0.163 (-0.333, 0.008)

Table 2-6. Quasi-likelihood adjusted AIC differences ($\Delta QAIC_c$) for five models of the realized population growth of acorn woodpeckers (1972-2004) using Pradel's reverse-time capture-mark-recapture model. Symbols are as follows: Φ = survival, p = recapture, and λ = realized population growth rate. Sex effect is noted (s), time effect is noted (t), additive effect of sex and time is noted ($s + t$), and a period (.) indicates the constant value of the parameter.

Number	Model	$\Delta QAIC_c$	QAICc	
			Weights	Parameters
1	$\Phi (s + t) p (.) \lambda (t)$	0	0.63	66
2	$\Phi (s + t) p (.) \lambda (s + t)$	1.22	0.34	67
3	$\Phi (t) p (.) \lambda (t)$	6.67	0.02	65
4	$\Phi (t) p (.) \lambda (s + t)$	8.72	0.01	66
5	$\Phi (s + t) p (.) \lambda (s)$	104.35	0	36

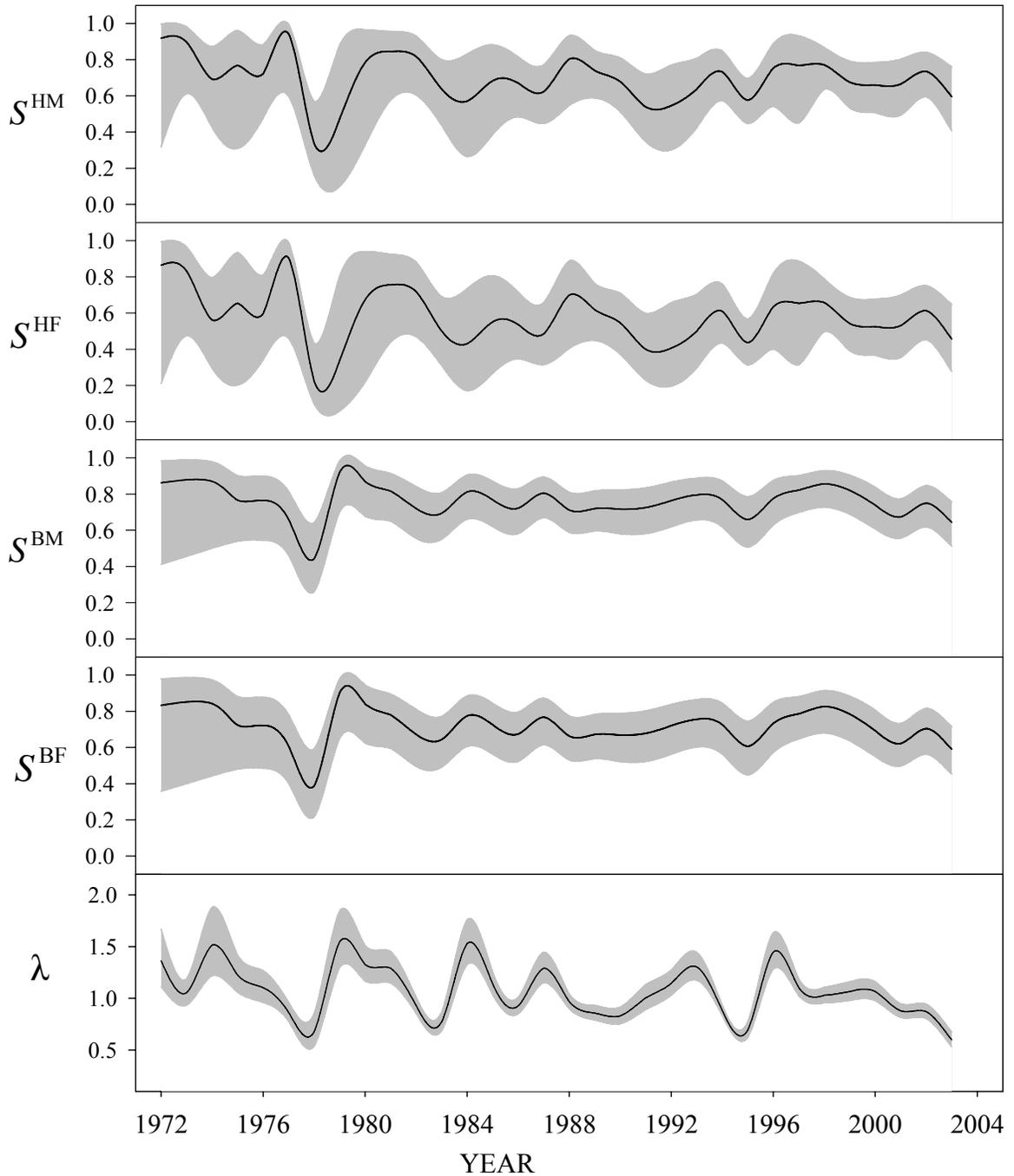


Figure 1: Annual variation in survival of acorn woodpeckers (1972-2004). Mean rates (black lines) are shown with 95% confidence interval (gray shade) for male and female helpers (S^{HM} and S^{HF} , respectively) and male and females breeders (S^{BM} and S^{BF} , respectively). Estimates are based on Model 1 (Table 2-1) and are compared to realized population growth rate (λ).

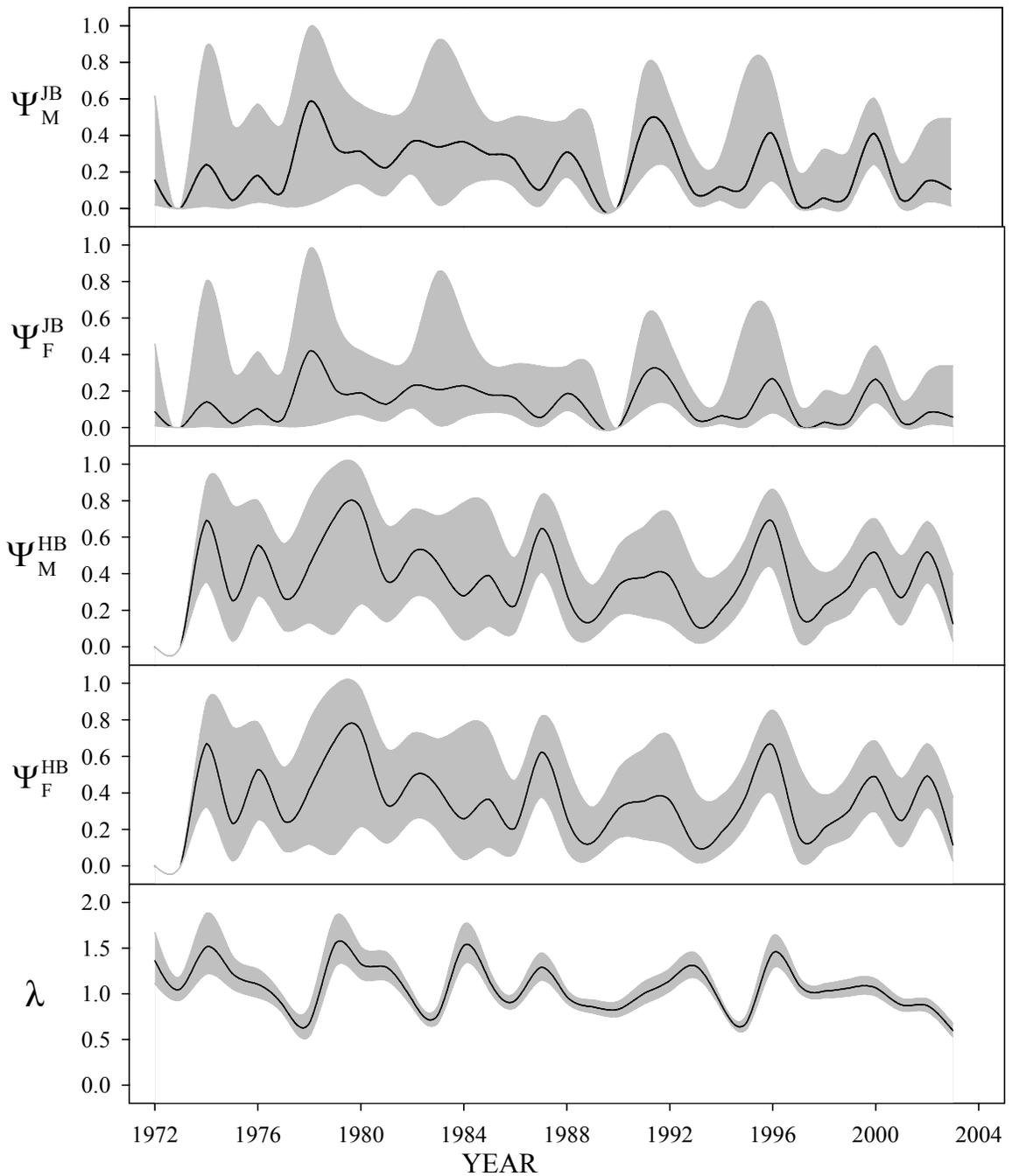


Figure 2: Annual variation in transition probabilities of acorn woodpecker (1972-2004). Mean rates (black line) are shown with 95% confidence interval (gray shade) for the transition from juvenile to breeder stages for males (Ψ_M^{JB}) and females (Ψ_F^{JB}), and from helper to breeder stages for males (Ψ_M^{HB}) and females (Ψ_F^{HB}). Estimates are based on Model 1 (Table 2-1) and are compared to realized population growth rate (λ).

CHAPTER 3
FITNESS CONSEQUENCES OF DELAYED REPRODUCTION IN A
COOPERATIVE BREEDER: DOES HELPING HELP?

Abstract

Cooperative breeding in birds occurs when more than two individuals provide care for a single nest. In many species, the additional adults present are offspring from a previous year who have delayed dispersal, and provision young who are non-descendant kin. Delaying dispersal and age of first breeding can potentially influence fitness, but fitness consequences of helping behavior are poorly understood. Using long-term data (1972 - 2004), we examined the fitness consequences of helping behavior in acorn woodpeckers *Melanerpes formicivorus*. Although helpers began reproduction significantly later and lived significantly longer than breeders, there was no significant difference in lifetime reproductive success or individual fitness between the two groups. However, birds that successfully bred at age 1 without helping had a significantly higher fitness than those who helped and successfully bred at age 2 or older. Our results suggest that delayed dispersal and reproduction in the acorn woodpecker leads to a loss of fitness when conditions are favorable for successful reproduction. However, if constraints in the environment prevent an individual from breeding at age 1, helping is a viable option until reproduction is possible.

Introduction

Cooperative breeding in birds occurs when more than two individuals provide care for a single nest (Brown 1987). Frequently, helpers are offspring from a previous nest who have delayed dispersal, and provide care for their siblings from a later clutch (Cockburn 1998). Previous studies of the possible costs and benefits of helping indicate that fitness benefits of helping are often lower than loss of fitness from not breeding independently (Reyer 1984; Woolfenden & Fitzpatrick 1984; Komdeur & Edelaar 2001; MacColl & Hatchwell 2002; Dickinson & Hatchwell 2004). One likely reason for the reduced fitness is a delayed onset of reproduction, which can profoundly influence fitness (Cole 1954; Lewontin 1965; McGraw & Caswell 1996). Early reproduction generally allows an individual to begin propagating its genes sooner than delayed reproduction (e.g., Oli *et al.* 2002; Oli & Armitage 2003), but doing so can have detrimental effects if survival, growth or reproductive potential is compromised (e.g., Pyle *et al.* 1997).

If delayed age of first reproduction reduced fitness, why would an individual delay reproduction and help? One explanation is that constraints in the environment limit individuals' ability to successfully breed immediately upon reaching sexual maturity; helping is a strategy that enables some birds to make the best of a bad situation (Koenig & Pitelka 1981; Emlen 1982; Koenig *et al.* 1992). In many cooperatively breeding birds, a critical resource (such as suitable habitat, a food related resource or a breeding cavity) is often necessary for successful breeding, and the absence of this resource can lead to a shortage of breeding positions (Woolfenden & Fitzpatrick 1984; Koenig & Mumme 1987; Walters *et al.* 1992).

The acorn woodpecker *Melanerpes formicivorus* is a cavity nesting species and a common inhabitant of the oak woodlands of California (Koenig & Mumme 1987; Koenig

et al. 1995). Practicing opportunistic polygynandry in addition to helping behavior, the cooperatively breeding acorn woodpecker exhibits one of the most complex social systems of any vertebrate, with group size ranging from a single pair to a mixed group of up to 15 breeders and helpers. Territorial inheritance is rare, yet many individuals delay dispersal for one year or more and help on their natal territory (Koenig & Mumme 1987).

Using long-term (1972-2004) life-history data, we investigated the fitness consequences of helping behavior in female acorn woodpeckers. Specifically, we addressed the following questions: (1) Does helping (and delayed age of first reproduction) reduce fitness? Specifically, do helpers have lower fitness compared to birds that disperse and breed without helping? (2) What social and environmental factors influence fitness? (3) If helpers have lower fitness than breeders, why does helping persist?

Methods

Study Species and Study Site

The acorn woodpecker is a cooperatively breeding, cavity nesting species that ranges throughout the oak woodlands of California and possesses one of the most complex social systems of any vertebrate (Koenig & Mumme 1987). The reproductive system of this species is opportunistic polygynandry, a mix of mate-sharing (multiple males compete for mating opportunities with one or more females) and joint-nesting (multiple females breed with one or more males and lay their eggs in a single nest). Group size and composition range from a monogamous pair to a 15-member mixed group of breeders and non-breeding helpers of both sexes (Koenig & Mumme 1987). Both breeders and helpers contribute to territory defense, food storage, and care of young (Mumme *et al.* 1990).

In parts of their range, acorn woodpeckers construct granaries, or storage trees, in which they store acorn mast, food that supplements their diet of sap and flying insects (MacRoberts & MacRoberts 1976; Koenig & Mumme 1987). These granaries are a critical resource, allowing territories to be maintained year-round and may serve as an alternative to winter fattening when food is more scarce (Koenig *et al.* 2005). Groups with acorn stores remaining in spring experience earlier nests and higher reproductive success than those without stored acorn mast (Koenig & Mumme 1987; Koenig & Stacey 1990).

This study took place at Hastings Natural History Reservation in central coastal California. Plant communities at Hastings include foothill woodland, savanna-grassland, and riparian woodland. Common trees in the study area include five species of oak: coast live oak (*Quercus agrifolia*), canyon live oak (*Q. chrysolepis*), blue oak (*Q. douglasii*), black oak (*Q. kelloggii*), and valley oak (*Q. lobata*), along with California sycamores (*Platanus racemosa*), willows (*Salix* spp.), California buckeye (*Aesculus californica*), and madrone (*Arbutus menziesii*). Acorn woodpeckers are mainly found in open areas, nesting in oaks and sycamores, with a dense ground cover of grasses, and few shrubs (Koenig & Mumme 1987).

Field Methods

Intensive research on acorn woodpeckers at Hastings Reservation began in 1971 (MacRoberts & MacRoberts 1976) and continues to date (Koenig & Mumme 1987; Koenig *et al.* 2000; Haydock & Koenig 2003); data collected during 1972-2004 were used in this study. The majority of natural cavity nests (located 2 - 20m up in trees) were located and checked, and groups were censused to determine membership. Birds were individually marked with leg bands as nestlings 20-25 days after hatching or as soon as

possible if immigrating as adults. Group size and composition (number of breeders and helpers) were determined by observation and the known relationship of group members based on banding record (Koenig *et al.* 1998; Koenig *et al.* 1999). Further details on field methodology can be found in Koenig & Mumme (1987).

Each fall starting in 1980, the acorn crop of the five *Quercus* species was estimated. For approximately 250 oak trees, the number of acorns counted in 15 s by each of two observers was recorded. Each count value was log-transformed and the mean value was calculated and used as an index of annual acorn crop (hereafter, acorn crop or AC) (Koenig *et al.* 1994a; Koenig *et al.* 1994b).

Estimation of Fitness

Although there is a significant amount of reproductive skew among breeding male acorn woodpeckers (Haydock & Koenig 2003), the egg destruction behavior of joint-nesting females enforces hatching synchrony and leads to equal parentage of fledglings by breeding females (Mumme, Koenig & Pitelka 1983; Haydock *et al.* 2001). Therefore, to estimate the number of young fledged per female, we divided the number of young fledged for a group by the number of breeding females in the group. Survivorship was determined by repeated visits to each group, and by monitoring the territory until all group members were seen (Koenig & Mumme 1987). For the purposes of this analysis, because we only focus on individuals who successfully reproduced at least once in their lives, birds disappearing were treated as dead.

We used two measures of individual fitness. First, we calculated the lifetime reproductive success (LRS) as the total number of offspring produced by a female during her lifetime (Clutton-Brock 1988; Newton 1989). A second measure of individual fitness (λ) was estimated using the methods of McGraw & Caswell (1996). This fitness measure

represents the rate at which an individual's genes are propagated if the vital rates remain the same (McGraw & Caswell 1996). A population projection matrix for each individual was constructed, with age-specific annual fertility rates (estimated as one half times the number of offspring produced by a female per year) on the first row of the matrix, and survival probability of 1 along the lower sub-diagonal until age of last reproduction. The dominant eigenvalue of the matrix is the estimate of individual fitness (λ). All fitness calculations were done using MATLAB.

Statistical Analysis

We used a t-test to compare mean fitness of individuals that helped as yearlings to those that did not. Because some individuals may attain a breeding position at age 1 but fail to breed, we also used t-tests to compare the fitness of helpers to individuals who dispersed and bred successfully at age 1, and to those who dispersed at age 1 but did not successfully reproduce until age 2 or older.

Effect of Social and Environmental Factors on Fitness

We investigated the influence of social and environmental factors on both LRS and λ . Social factors included group size (the number of adults in the group), the number of male, female and total helpers, and the number of male, female and total breeders. Environmental factors included the acorn crop of the previous fall (potentially still present in the spring), the acorn crop of the current fall, and the number of storage holes in the group's granary (an estimate of territory quality). We collected data for each social and environmental variable in three ways: the year the individual was born, the year the individual began breeding and the average over the individual's lifespan (Koenig & Mumme 1987).

We used step-wise variable selection procedure in multiple linear regression to identify variables significantly influencing LRS or λ (System) 2002). Then, using only those variables selected by the stepwise variable selection procedure, we fitted a multiple linear regression with LRS (or λ) as response variable and the aforementioned social and environmental variables as predictors.

Results

We had lifetime survival and reproductive data for 498 females that were banded as juveniles and were resighted at least once during or after their first potential breeding season. We excluded individuals who were still alive (last seen in 2004) and those that never successfully reproduced within the study area. Therefore, all analyses were based on 141 females (61 potential breeders and 80 potential helpers).

On average, female acorn woodpeckers lived 4.35 ± 0.25 yrs, began breeding between at age 2.39 ± 0.11 , reproduced 2.55 ± 0.19 times, and had a mean post-maturation survival (numbers of years survived beyond the age of first reproduction) of 1.96 ± 0.22 yrs (Table 3-1). The mean LRS was 6.90 ± 0.65 and mean individual fitness (λ) was 1.27 ± 0.04 . The longest lived individual (female 787) in our study lived 16yr, and had the largest LRS (37.75), although not the highest λ (1.54, compared to the maximum of 2.62). This individual did not help in its first year, and first successfully reproduced at age 1.

Lifetime reproductive success and fitness were strongly correlated with each other, and both fitness measures were strongly correlated with lifespan, post-maturation survival, lifetime number of reproductive events and mean number of young fledged (Table 3-2). Neither measure of fitness was significantly related to age at first reproduction (α). Only two fitness components showed a significant and positive

relationship with α : lifespan and mean young fledged. Lifespan and reproductive lifespan were positively correlated with one another, as well as with number of reproductive events, and mean young fledged.

Comparing the fitness components and fitness of females that delayed dispersal and helped for at least one year (helpers; $n = 80$) to those that dispersed and attempted to breed at age 1 (potential breeders; $n = 61$), we found the following (Table 3-1). Helpers began breeding at around age 3, which was significantly delayed compared to potential breeders. Helpers outlived potential breeders, living about 1.5 yr longer. There was no significant difference between helpers and potential breeders in terms of post-maturation survival, number of reproductive events, mean young fledged per reproductive event, lifetime reproductive success or individual fitness (λ).

Because some individuals disperse but fail to successfully reproduce at age 1, we also compared helpers to those individuals who successfully reproduced at age 1 (“breeders,” $n = 44$). As expected, helpers began reproduction significantly later (3.09 compared to 1.0, $p < 0.05$) but lived longer than the breeders (5.08 compared to 3.20, $p < 0.05$). Birds that began breeding at age 1 had a significantly larger individual fitness (λ) than helpers (1.43 compared to 1.21, $p < 0.05$). Neither LRS nor any other component of fitness differed significantly between the two groups.

Comparing helpers to those potential breeders who dispersed and acquired a breeding position but failed to successfully reproduce until age 2 or older, the only measure of fitness or fitness component that differed significantly between the two groups was lifespan, with helpers living 1.2 yr longer (5.08 compared to 3.88, $p < 0.05$). Neither measure of fitness, nor any other component of fitness differed. Dispersers who

bred at age 1 had higher fitness than those who dispersed at age 1 but failed to breed until age 2 (1.43 and 1.18, respectively, $p < 0.05$).

Of 29 candidate social and environmental variables considered, the stepwise variable selection procedure selected five variables as having significant influence on λ : the acorn crop the year before birth (AC), the granary size on the territory when the individual was born (GBirth), granary size the year the individual began breeding (GBreed), the average granary size over the individual's lifetime (GLife), and the number of breeding females in the group the year the individual began breeding (BF). A multiple linear regression model with these variables included explained 44.3% of the variation in λ ($\lambda = 1.80094 - 0.25147AC - 0.00012GBirth - 0.0027GBreed + 0.000518GLife - 0.19782BF$; $R^2 = 0.443$, $p < 0.0009$). None of the social or environmental variables considered significantly influenced LRS.

Discussion

Two of the most interesting characteristics of cooperative breeding systems are offspring retention and helping behavior. Instead of dispersing when they are capable of breeding independently, many individuals stay at home for 1 yr or more and help to raise siblings. Helping is generally considered a route to lower fitness, and helpers attempt to, but rarely do, recoup the loss of fitness due to foregoing reproduction and remaining at home (Dickinson & Hatchwell 2004).

The acorn woodpecker follows one of two routes upon reaching sexual maturity. Individuals can delay breeding for one or more years and help raise non-descendant kin, the path of so-called helpers. Alternatively, individuals can disperse and attempt to breed as soon as they are sexually mature at age 1 (potential breeders). In this study, helpers had a delayed age of first reproduction and a longer lifespan but neither measure of

fitness, nor any other component of fitness differed significantly between helpers and potential breeders. However, it is important to note that some individuals disperse and gain a dominant position in a group, but for some reason (e.g. no mate, poor acorn crop, predation) fail to successfully fledge any young at age 1. Thus, we compared fitness and its components of birds who successfully reproduced at age 1 (“breeders”) to those who delayed dispersal and helped; this comparison should better elucidate the fitness consequences of helping and delayed of first reproduction. Females that successfully reproduced at age 1 had higher fitness (λ) compared to those who stayed home and helped. In other words, dispersing and breeding is advantageous if the individual can successfully reproduce at age 1, otherwise there is no difference in fitness for helpers or breeders. There was no difference in LRS between the two groups. However, LRS may not adequately quantify fitness because it only considers the amount of reproduction and ignores the timing of reproduction, which can also substantially influence fitness (McGraw & Caswell 1996; Oli *et al.* 2002). Consequently, inferences based on λ may be more appropriate (McGraw & Caswell 1996; Oli *et al.* 2002; Oli & Armitage 2003).

One obvious consequence of helping is that reproduction is delayed. Early work proposed that a delayed age of first reproduction could reduce fitness (Cole 1954; Lewontin 1965). Recent comparative life history studies of birds and mammals found that Cole’s prediction strictly holds in species characterized by early maturity and high reproductive rates (Oli & Dobson 2003; Stahl & Oli in press); this conclusion is consistent with findings of several empirical studies that have examined the effect of age at first reproduction on fitness. In the wood duck, for example, individuals beginning reproduction at an earlier age had a greater individual fitness than those who delayed age

of first reproduction (Oli *et al.* 2002), indicating that fitness benefits of early reproduction outweigh associated costs (e.g. Reznick 1985). In the goshawk, a species characterized by late age of first reproduction and low fecundity, individuals who delayed maturity had higher fitness than those who began breeding earlier (Krüger 2005).

Using LRS as a measure of fitness, Koenig & Mumme (1987) and Koenig & Stacey (1990) found no significant difference in fitness between acorn woodpeckers of either sex that helped and those who reproduced without helping. Consistent with findings of Koenig & Mumme (1987) and Koenig & Stacey (1990), we found no significant difference in LRS between helpers and breeders. When λ was used as a measure of fitness, however, we found that delayed reproduction due to helping is costly in acorn woodpeckers, with significantly lower fitness for females that helped for one or more years compared to those who bred as yearlings.

If helping is a route to lower fitness, why has it been maintained in the system? We offer three possible explanations, which are not mutually exclusive: (1) ecological conditions prevent some individuals from beginning to breed at sexual maturity, (2) females are more successful at dispersing and attaining a breeding position with a sister, and (3) inclusive fitness benefits.

Ecological constraints have been proposed as the cause of cooperative breeding, especially offspring retention (Koenig & Pitelka 1981; Emlen 1982). In cooperative breeding systems, a critical resource is often necessary for a family unit to exist. In the case of acorn woodpeckers, the critical resource is the granary (Koenig & Mumme 1987). Without a tree in which to store acorns, a family unit may not persist and therefore ecological constraints may influence delayed dispersal, helping behavior and an average

age of first reproduction over a year past the point of sexual maturity. Acorn woodpeckers invest a considerable amount of time constructing and maintaining their granary much in the same way red-cockaded woodpeckers *Picoides borealis* must invest considerable effort creating cavities in live trees (leading to delayed dispersal and reproduction in a number of males Walters *et al.* 1992). In red-cockaded woodpeckers, males typically begin reproduction between 2 - 3yrs of age (for comparison, as female helpers are rare Walters 1990). Another cooperative breeder that has been intensively studied, the Florida scrub-jay *Aphelocoma coerulescens* generally breeds for the first time at age 2, with only 3 females breeding at the age of sexual maturity (1yr) in 18 years of study (Woolfenden & Fitzpatrick 1990). Individuals remaining at home must wait for a breeding vacancy to become available, and it can be advantageous to disperse with siblings and compete as a unit for vacancies (Hannon *et al.* 1985).

Up to 30 helpers from surrounding territories vigorously compete for reproductive vacancies; the winners of such “power struggles” are often larger groups consisting of same-sex sibling units (Koenig 1981; Hannon *et al.* 1985). Therefore, sisters (or brothers) dispersing together were more likely to attain a breeding position when one became available, and remaining at home past the point of sexual maturity may be advantageous if it increases a female’s chances of successfully dispersing with and competing alongside a sister for a breeding vacancy. Joint dispersal leads to approximately one half of all joint-nesting occasions (Koenig & Mumme 1987; Mumme, Koenig & Pitelka 1988).

Because helpers in this system were nearly always related to at least one of the breeders (most often both breeders are the helper’s parents) and therefore the young they provision, helpers are most certainly accruing indirect fitness benefits (Koenig &

Mumme 1987). Helper presence has been shown to increase reproductive success and survival of group members (Koenig & Mumme 1987; Stahl, Koenig & Oli unpublished manuscript). Therefore the inclusive fitness totals of helpers are most certainly likely to be higher than our direct fitness estimates, and may lead to helping being advantageous in some or all situations.

Stacey & Ligon (1987; 1991) showed that acorn woodpecker helpers remaining on high quality territories had higher LRS and survivorship. Both the acorn crop and territory quality positively influence survival, probability of breeding and reproductive success in acorn woodpeckers (Koenig & Mumme 1987; Stahl *et al.* unpublished manuscript), and this study has shown direct effects on individual fitness were also apparent. Using granary size (number of storage holes) as a proxy for territory quality, we found that birds breeding on higher quality territories over their lifetime had higher fitness. The most important social effect on fitness was that joint-nesting females had lower λ than females nesting alone. This result is consistent with that of Mumme *et al.* (1988) who found that the lifetime reproductive success of joint-nesting females was less than or equal to that of singly nesting individuals, despite increased survival and territory dominance resulting from co-breeding.

Three caveats must be mentioned. First, the results presented in this manuscript are only for females, and may not apply to males. Males are the more common helping sex and co-breed more often than females joint-nest (Koenig & Mumme 1987). Unlike females, parentage in males often significant skewed (Haydock *et al.* 2001; Haydock & Koenig 2003). Second, breeders typically occupy a territory continuously once they begin breeding, and are therefore more likely to remain in the study area than helpers (Haydock

& Koenig unpublished manuscript; Stahl *et al.* unpublished manuscript). Because of this we only have fitness estimates for those helpers who remained in the study area, and the fitness of those leaving the study area to fill breeding vacancies could possibly be different than those remaining in the study site (Koenig *et al.* 2000). Third, we have only considered the direct fitness of individuals and our estimates must therefore be seen as conservative. Indirect fitness benefits could possibly make up for the cost of delayed dispersal. Future work should employ the methodology of Oli (2003) to accurately quantify the inclusive fitness that Hamilton (1964) suggested.

In conclusion, helping in the acorn woodpecker is a route to lower fitness, but only if dispersers successfully reproduce at age 1. If the prospects of successful reproduction look grim, staying at home can be worthwhile. Females breeding on territories with larger granaries had higher fitness. The only obvious social factor that affected fitness was that joint-nesting females suffered reduced fitness. At least in the acorn woodpecker, helping is maintained due to constraints placed on individuals in terms of limited reproductive vacancies. Helpers are possibly attempting to make due by accruing inclusive fitness benefits and/or waiting to disperse with siblings, which increases the likelihood of attaining a breeding position (Hannon *et al.* 1985).

Table 3-1. Fitness components and measures of fitness for female acorn woodpeckers (1972-2004) that were banded as juveniles, were recorded at least once after their first possible breeding season, and reproduced at least once. Means (SE) and ranges are shown. A t-test was used to compare helpers (N = 80) and potential breeders (N = 61), helpers and breeders that first reproduced at age 1 ($\alpha = 1$; N = 44), and helpers and breeders that first reproduced at age 2 or older ($\alpha \geq 2$; N = 17); $P < 0.05$ indicates statistical significance.

Fitness Measure/Component	All females	Helpers vs. Potential Breeders			Helpers vs. Breeders			
		Helper	Potential Breeders	<i>P</i>	$\alpha = 1$	<i>P</i>	$\alpha \geq 2$	<i>P</i>
Age at first reproduction (α)	2.39 (0.11)	3.09 (0.14)	1.48 (0.11)	<0.05	1.00 (0)	<0.05	2.70 (0.16)	0.08
Lifespan	4.35 (0.25)	5.08 (0.32)	3.39 (0.36)	<0.05	3.20 (0.47)	<0.05	3.88 (0.43)	<0.05
Post-maturation survival	1.96 (0.22)	1.99 (0.28)	1.92 (0.36)	0.88	2.20 (0.47)	0.67	1.18 (0.43)	0.21
Reproductive events	2.55 (0.19)	2.58 (0.24)	2.52 (0.30)	0.89	2.77 (0.39)	0.65	1.88 (0.36)	0.21
Lifetime reproductive success (LRS)	6.90 (0.65)	7.21 (0.84)	6.50 (1.01)	0.59	7.21 (1.31)	1.00	4.66 (1.24)	0.19
Individual fitness (λ)	1.27 (0.04)	1.21 (0.03)	1.36 (0.07)	0.06	1.43 (0.10)	<0.05	1.18 (0.05)	0.72
Mean young fledged per event	2.42 (0.09)	2.55 (0.13)	2.26 (0.12)	0.10	2.23 (0.15)	0.13	2.31 (0.18)	0.41

Table 3-2. Correlation between fitness components and measures of fitness for female acorn woodpeckers (1972-2004) that were banded as juveniles, were recorded at least once after their first possible breeding season, and reproduced at least once. The two measures of fitness were lifetime reproductive success (LRS) and individual fitness (λ). Age at first reproduction is represented as α . The Pearson correlation coefficient is given above, and the p-value below ($p < 0.05$ indicates a significant relationship between the two variables, $N = 141$).

	LRS	λ	α	Lifespan	Post-maturation survival	Reproductive events
λ	0.618 <.001	-				
α	0.058 0.494	-0.146 0.083	-			
Lifespan	0.837 <.001	0.390 <.001	0.441 <.001	-		
Post-maturation survival	0.903 <.001	0.509 <.001	-0.015 0.856	0.891 <.001	-	
Number of reproductive events	0.921 <.001	0.531 <.001	-0.037 0.665	0.857 <.001	0.974 <.001	-
Mean young fledged per event	0.566 <.001	0.674 <.001	0.325 <.001	0.423 <.001	0.306 <.001	0.305 <.001

CHAPTER 4 CONCLUSIONS

Group living can affect the fitness and population dynamics of social animals. In cooperative breeding birds, some individuals delay reproduction and assist in raising young that are not their own direct descendants, whereas others disperse and attempt to breed independently when they attain sexual maturity (Cockburn 1998). Direct benefits of delayed dispersal and/or helping behavior can include increased survival (e.g., Ekman *et al.* 2000) and territory acquisition via budding (Woolfenden & Fitzpatrick 1984; Komdeur & Edelaar 2001). An individual can gain indirect fitness by helping aids kin (Hamilton 1964). However, because delayed reproduction is a characteristic of helping, this behavior can also have fitness costs. Despite decades of research, the fitness and population dynamic consequences of cooperative breeding are poorly understood.

In this thesis I investigated both the fitness and demographic consequences of cooperative breeding and the strategy of delayed dispersal and reproduction for helpers in the cooperatively breeding acorn woodpecker. Applying recently developed techniques for estimating survival and fitness to a long-term data set, my results were based on robust calculations.

In chapter 2, I investigated the demographic and population dynamic consequences of helping behavior and cooperative breeding and found that survival and breeding probabilities of acorn woodpeckers differed depending on sex, status and year. The apparent survival (the probability of surviving and remaining in the study area) of helpers was lower than breeders. However, this difference was likely biased towards

breeders as they are more likely to remain in the study area; many helpers that disappeared were filling reproductive vacancies outside the study area. Males (both helpers and breeders) survived at a greater rate than females. Juvenile males, when compared to females, were nearly twice as likely to become breeders immediately after their first year of life. For both sexes, though, the most common strategy was to delay dispersal and help for at least one year.

A number of social and environmental factors influenced the survival and breeding probabilities. Acorn woodpeckers were more likely to survive and also had a higher probability of becoming a breeder in years when the acorn crop was high. Larger granaries (i.e., better quality territories) also positively influenced survival, but surprisingly had no effect on breeding probability. Group size and composition both increased survival of group members. The realized population growth rate (λ) varied annually and was most influenced by survival, followed by breeding probabilities. Because the acorn crop positively influences survival and probability of attaining a breeding position, the changes in realized growth rate reflect the variation in the annual acorn crop.

In chapter 3, I examined the fitness consequences of helping behavior. Although individual fitness of helpers did not differ from that of potential breeders (individuals that dispersed as yearlings without helping), female acorn woodpeckers that successfully reproduced at age 1 had a significantly higher individual fitness (λ) than those that helped and delayed age of first breeding until age 2 or later. This difference was due to a delayed onset of reproduction for helpers. Furthermore, yearling dispersers who did not

successfully reproduce until age 2 or later did not have a significantly greater fitness than helpers (who also did not begin breeding until age 2 or later).

Four factors significantly influenced λ : the acorn crop prior to birth, two measures of territory quality (lifetime average, and year of first reproductive event), and the number of co-breeding females in the group when the individual began breeding. Females living on higher quality territories showed higher fitness, but individuals who shared reproduction with other females suffered a fitness loss.

In conclusion, my study has shown that helping in acorn woodpeckers generally is a route to lower fitness if dispersers successfully reproduce as yearlings. However, if successful reproduction is not possible staying at home is the next best strategy. In years with large acorn crops, more birds are able to acquire breeding positions within a group and fitness is increased on territories with larger granaries in which to store these acorns. When the acorn crop fails, the likelihood of breeding is significantly decreased and staying at home is suitable in the face of such constraints. These inferences are made based only on direct fitness, and the results may differ if inclusive fitness were considered. Therefore, inclusive fitness calculations should be a main target for future research in this and other cooperative breeding systems.

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BIOGRAPHICAL SKETCH

Justyn Stahl was born on September 13, 1980, in Alton, Illinois. He is the oldest son of Ralph and Bette Stahl. After graduating from Alton High School in 1998, he moved to Miami, Florida, to attend the University of Miami where he received his bachelor's degree in biology in 2002. He then spent two field seasons working on prothonotary warblers in Southern Illinois. He moved to Gainesville, Florida, and the University of Florida in the fall of 2003.