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Beyond Age and Stage: Consequences of Individual Variation in Demographic Traits

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy Integrative Biology
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DEDICATION

I dedicate this dissertation to Blake, my partner of over 11 years, my parents Jay and Lisa, my PhD adviser Gordon A. Fox, my master's adviser Joseph Veech, and to Jim and Sehoya Cotner, without whom I wouldn't be where I am today.

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ABSTRACT

Within natural populations, individuals vary in their propensity to grow, survive and produce offspring. Additionally, fates of individuals are often correlated and non-independent as a result of shared genes, rearing environment or both. Variation in demographic traits can change population dynamics over time. The effects of variation in individual growth rate on population growth rate, net reproductive rate and generation time are examined, along with quantifying the sources of variation in survival of a long-lived cooperatively breeding bird, the Florida Scrub-Jay (*Aphelocoma coerulescens*). I built a 2 stage population model with two growth phenotypes, fast and slow, and simulated all parameter values using R 3.3.1. Variation in individual maturation rate changes population dynamics, especially in the presence of phenotypic correlation between parents and offspring in growth phenotype. I used Cox Proportional Hazard models with a covariance structure derived from a kinship matrix using the R packages survival and kinship2. Survival of juvenile Florida Scrub-Jays is strongly dependent on kinship, or the degree of relatedness between individuals, in addition to body mass, social structure of the natal territory, natal territory quality and environmental conditions of the rearing period. Breeder Florida Scrub-Jay survival is mainly structured by group size, kinship, yearly variation in environmental conditions and territory quality.

CHAPTER ONE

Introduction

Variation in the rate at which individuals grow is common in nature and has been documented across several taxa, especially fish and vascular plants (Pfister and Stevens 2002; Fujiwara et al. 2004; Huss et al. 2007). For example, in natural plant populations, individuals can vary greatly in size and rate of growth, even among plants of the same age (Weiner 1988; Stoll et al. 1994). In fish populations, there can be high variability in sizes even within a cohort that grew up in the same time and place (Ricker 1958; Huss et al. 2007). Growth and development depend on genetic variation, resource availability, environmental conditions, and biotic interactions, resulting in plastic growth and variable growth rates among individuals (Weiner 1998; Pfister and Stevens 2002; Monro and Marshall 2014). Furthermore, size is often positively correlated with fitness, so the rate at which individuals grow is likely to be an important life history trait (Pfister and Stevens 2002; Fujiwara et al. 2004; Dmitriew 2011). For example, in salmonids and other bony fish species, female size is positively related to egg and clutch size (Morita and Takashima 1998; Huss et al. 2007). Annual plants that are bigger at the end of the growing season produce more seeds than slower growing conspecifics (Espeland and Farrell 2010). Variation among individuals in growth rate can change the distribution of individual sizes or the size structure, within the population (Stoll et al. 1994; Pfister and Stevens 2003). Due to the relationship between individual size, and size-dependent traits related to fitness, population growth could be influenced by growth variation among individuals.

Phenotypic plasticity has been long recognized as a common feature in plants. This plasticity may lead to differential growth among individuals within plant populations, and individuals of the same age can have very different sizes and may grow at very different size-specific rates. This variation in growth can change the size structure of the population. If reproduction and survival are correlated with body size, an altered size structure could change the population growth rate due to changes in reproduction and survival within the population (Zuidema et al. 2009). As one might expect, they found that the fast growers contributed more to the population growth rate than slow growers (Zuidema et al. 2009). This raises the question of how heterogeneity in ontogenetic growth rate generally affects population growth rate.

Age and stage-based matrix projection models are popular and useful tools, but the assumption of standard stage-based models is that individuals transition between stages at constant rates (Caswell 2001). Recently, researchers have recognized that ignoring variation in growth or maturation time among individuals can result in misleading conclusions about population growth, net reproductive rate and generation time, and sensitivities to population growth rates (De Valpine 2009; Acker et al. 2014; De Valpine et al. 2014; Vindenes and Langangen 2015). In response, frameworks for matrix and integral projection models have been introduced that incorporate variation in individual growth rate and development time (De Valpine 2009; De Valpine et al. 2014; Vindenes and Langangen 2015). The approach of De Valpine et al. (2014) is a general approach to incorporate stochastic development times, meaning individuals spend variable amounts of time in a stage, in population models. Including variable stage durations in population models can change the conclusions of the models, especially in the sensitivities and elasticities of parameters to the asymptotic growth rate (De Valpine 2009; De Valpine et al. 2014). Vindenes and Langangen (2015) developed a framework for matrix and

integral projection population models for discrete and continuous traits, respectively, that can account for individual variation traits related to fitness. Furthermore, these modeling frameworks allow a researcher to consider different mechanisms of inheritance for these traits and include this in population models (Vindenes and Langangen 2015). They examined the effects of ignoring variation in the life history among individuals in a stage-age structured model and found that the asymptotic population growth rate was similar for the model that included heterogeneity and the model without. However, the estimates of other demographic outputs including the net reproductive rate and the transition rates differed between models (Vindenes and Langangen 2015). De Valpine et al. (2014) also found that including variation in maturation time in models resulted in the same long-term population growth rate, but different sensitivities and elasticities. However, under some circumstances the population growth rate can change when variation in development times is included in a population model. For example, De Valpine (2009) incorporated variable stage durations into a population model of medflies and found that increased heterogeneity in stage durations increased the asymptotic population growth rate. Thus, there evidence that heterogeneity in growth or development time can impact the asymptotic population growth rate and population dynamics.

Here, we built a simple model to examine the basic relationship between heterogeneity in ontogenetic growth and population growth rate. Simple, heuristic models have use in exploring such basic relationships and understanding the underlying structure. Here, we examine the consequences of heterogeneity in the rates at which individuals grow using a model of an iteroparous population. Specifically, we built a simple model incorporating heterogeneity in maturation age that allows us to ask i) How does the long-term population growth rate (λ), depend on the amount of growth heterogeneity? ii) How much of this change in λ is due to

change in net reproductive rate R_0 , and how much to change in generation time T ? iii) How does the phenotype correlation between parents and offspring affect population dynamics when there is heterogeneity in growth rate?

Methods and Results

We built a deterministic, density-independent matrix model to examine heterogeneity in growth. The model has two stages (juvenile and adult) and two phenotypes, with differing maturation rates for "slow" and "fast" developers; thus this is the simplest model that can incorporate ontogenetic growth heterogeneity. The life-cycle graph for this model is shown in Figure 1. Juvenile survival rate is S , and the fraction maturing to adulthood is γ_s or γ_f , respectively, for slow and fast individuals. Adults of both types survive at rate P , and survivors produce F offspring each year. The proportion of offspring entering into each phenotypic class depends on the parent-offspring phenotype correlation, ϕ . This correlation can be positive or negative because it represents the phenotypic, not genetic, correlation. Kendall et al. (2011) found that parent-offspring correlation in survival phenotype changed the magnitude of increase of the population growth rate.

We parameterize the model to allow a single parameter to measure heterogeneity: we add or subtract σ from the mean individual growth transition rate γ where:

$$\begin{aligned}\gamma_s &= \gamma - \sigma \\ \gamma_f &= \gamma + \sigma\end{aligned}\quad (1)$$

to hold for all values of γ and σ . Because of the relationship in eq. (2), all values of σ are constrained by the value of γ , and must be interpreted in the context of γ .

$$0 < \gamma < 1$$

$$0 < \sigma < \min(\gamma, 1 - \gamma) \quad (2)$$

to hold for all values of γ and σ . Because of the relationship in eq. (2), all values of σ are constrained by the value of γ , and must be interpreted in the context of γ .

Analytical Results

The eigenvalues and eigenvectors of this model can be written analytically, but because there are four classes, these expressions require solutions to quartic equations – which do not lend themselves to biological insight. Thus, we consider one special case of the model that does permit some analytical insight. This involves a special value of the parent-offspring correlation ϕ . When $\phi = 1$, there is perfect correlation between parents and offspring in phenotype, so this scenario represents a monotypic population.

Consider the case of the simple case where we consider the individual maturation rate, γ , juvenile survival, s , and fertility, F . Let $\alpha = 1 - \gamma$ where $s\alpha$ is the fraction of individuals that persist in the juvenile stage and the maturation rate for individuals is equal to γ . (Figure 1). Then, the asymptotic population growth rate is

$$\lambda = \frac{1}{2} \left[\rho + \sqrt{\rho^2 + 4S(F\gamma - P\alpha)} \right] \quad (3)$$

Where $\rho = P + s\alpha$. Examination of eq. (3) shows that $\partial\lambda/\partial\sigma > 0$ in cases where fertility, F , is non-negative. Therefore, $\partial\lambda/\partial\sigma > 0$ must be true for the range of values that make the model biologically realistic. In this case where $\phi = 1$, the slow individuals will disappear and only the population with the fast phenotype will persist.

$$\frac{\partial \lambda}{\partial \sigma} = \frac{1}{2} \left[s + \frac{4(F-P)s + 2s(P+s\alpha)}{2\sqrt{(P+(s\alpha)^2 + 4s(F(\gamma+\sigma) - P\alpha))}} \right] \quad (4)$$

In the case of a monotypic population, increasing γ always increases λ . (Figure 2).

Graphical representations show that net reproductive rate also increases as γ increases in this scenario while generation time, T , decreases with γ , although the pattern is notably different from λ and R_0 (Figure 2). Now, if we consider this monotypic population example to be a case where there is a perfect parent/offspring correlation ($\phi = 1$) and σ represents a standard deviation from the average growth rate, heterogeneity in growth causes the fast type to dominate the population. Conceptually, this represents two “sub-populations” of each phenotype with no cross between them. In this case, the fast individuals have a growth rate of $\gamma + \sigma$, and increasing σ always increases the growth rate at any value of γ (eq. (4)).

Numerical Results

We wanted to understand the how individual maturation rate and σ depend on the parent-offspring correlation, where parents can produce each type of offspring. To consider more general cases than simply $\phi = 1$, we calculated λ numerically using R (3.1.3, (R Core Team 2015) for the range of possible values of γ and σ (eq. ((2))). We also considered nine values of juvenile survival probability from 0.1 to 0.9 in 0.1 increments. We fixed fertility, F , and adult survival probability, P . We considered 21 values of ϕ ranging from 1 to -1 in increments of 0.1. For each unique combination of values of γ , σ , and ϕ , we estimated the dominant eigenvalue and

used the R popbio library (Stubben and Milligan 2007) to estimate generation time (T) and net reproductive rate (R_0). This estimate of T is derived from the approximation $T \approx \log R_0/r$ (Caswell 2001), and should be interpreted as the average age difference between parents and offspring. Because of this approximation, variation in λ can be due to variation in R_0 or T .

The effect of σ on λ depends strongly on the value of the parent-offspring phenotype correlation ϕ (Figure 3). From the analytical results, we know that when $\phi = 1$, increasing γ and σ always increases λ (eq. (3)&(4), Figure 3). When $\phi = 0$, there is no correlation between parent and offspring in growth phenotype and parents produce half of each type on average. In this case, increasing σ decreases λ at any value of γ (Fig. 3). Likewise, for $-1 \leq \phi < 0$, the same pattern holds, where increasing σ decreases λ . However, the effect of σ on λ changes from negative to positive when ϕ is roughly equal to 0.3 for small values of γ . As ϕ approaches 1, σ increases λ at all values of γ , the average growth rate from the juvenile stage to the adult stage. The pattern of change in λ as a function of ϕ and σ is similar across S , the probability of juvenile survival (Figure X). The population growth rate becomes larger as S increases, but the general pattern across σ and ϕ does not differ significantly between values of S .

The effect of σ on net reproductive rate, R_0 , follows a similar pattern to that of λ where R_0 depends on σ and the parent offspring phenotypic correlation ϕ (Figure 4). As is the case with λ , R_0 increases with σ as ϕ becomes positive and large (Figure 4). Likewise, when ϕ is zero or negative, R_0 decreases as σ increases. The relationship between R_0 and σ changes from negative to positive as ϕ approaches 0.5 for all values of γ (Figure 4). As γ increases, the relative change of R_0 across σ becomes smaller, in other words, the slope is less steep when $\gamma \geq 0.7$ (Figure 4). As S increases, R_0 increases and similar to the results for the asymptotic growth rate, the pattern of change in R_0 across σ and λ is similar for all values of S from 0.1 to 0.9 (Figure X).

Generation time (T), defined here as the average age difference between parents and offspring (Caswell 2001), is much less variable across the combinations of g , σ and ϕ than λ and R_0 (Figures 3 - 5). When the average growth rate γ is small (< 0.1) the generation time is the largest ranging from 10 to 6 years. The slope of the change of T across σ is steepest at $\gamma = 0.1$ (Figure 4). The slope continues to flatten as γ increases. When $\gamma \geq 0.5$, T is similar across the range of σ and ϕ (Figure 4). If γ is high enough (about 0.5), even negative parent offspring phenotype correlations result in a generation time roughly equal to 4 time steps, which is what T equals when γ and $\phi = 0.9$, a high growth probability and strong positive parent offspring phenotype correlation. Generation time decreases as the average growth rate increases, but the magnitude of change across γ and σ is small when $\gamma \geq 0.5$ (Figure 5). Similar to the results of λ and R_0 , the juvenile survival probability S does not strongly affect the results (Figure X).

To further investigate the pattern of generation time across our simulated values of all parameters, we estimated the expected age at first reproduction for each phenotype, fast and slow, as a function of γ and σ . This gives an estimate of the mean time to maturity for each phenotype. Estimating the expected age at first reproduction involves adding a new absorbing state to the life cycle called “reproduced-before-dying”. Next, we built a new transition matrix where individuals can be absorbed into this new state (see Caswell 2001 pp. 124-126 for the full procedure). This quantity depends on the probability of transition for individuals based on probabilities of survival and maturity, thus the parent-offspring phenotype correlation does not affect the mean age at first reproduction for either phenotype. The relationship between σ and the expected age at first reproduction is negative for the fast phenotype and positive for the slow phenotype (Figure 5). The mean age at first reproduction increases faster for the slow phenotype than it decreases for the fast phenotype. Here, the survival probability of juveniles, S , affects the

mean age at first reproduction. As S increases, the mean age at first reproduction increases, along with the variance and the range (Figure 6). The mean age at first reproduction is lower for the fast phenotype than the slow phenotype at any value of $\sigma > 0$, γ and S . On average, individuals of the slow phenotype are older at first reproduction than fast individuals.

Thus far, we have focused on the asymptotic or long-term dynamics of the population by estimating the asymptotic growth rate λ , or the dominant eigenvalue of the projection matrix. To understand transient dynamics, we estimated the damping ratio for each combination of γ , σ , and ϕ . The damping ratio is the ratio of the dominant eigenvalue to the second eigenvalue. This value tells us how long it takes for a population to reach the stable age or stage distribution. As with the results for the asymptotic dynamics, the damping ratio depends on σ and ϕ . The damping ratio increases as σ increases for a monotypic population, or when there is perfect correlation in phenotype between parents and offspring, $\phi = 1$. (Figure 7). In other words, with increasing variation in growth, there is an increase in the rate at which the population reaches the stable stage distribution. The direction of this relationship changes as ϕ gets smaller. When $\phi = 0.5$, increasing σ decreases the damping ratio, meaning that increased variation around γ slows the rate at which the population converges to the stable distribution. The change in the magnitude of the damping ratio as σ increases is not large, however (Figure 7). S , the probability of juvenile survival, does not affect the results (Figure X).

Discussion

Growth variation is common in natural populations but is often ignored in population models for ecological inference and application (de Valpine 2009). Using the simplest growth model possible with two stages, we have shown that the asymptotic population growth rate depends on the probability of growing to the adult stage and heterogeneity in this trait.

Interestingly, the parent-offspring phenotype correlation strongly affects the results. If there is perfect correlation between growth phenotype of parents and offspring ($\phi = 1$), or a monotypic population, increasing the individual growth rate increases the population growth rate. In this case, the individual growth rate is always increased with added heterogeneity in growth (eq. (3)). However, in natural populations, there is a physiological limit to how fast individuals can grow where they cannot grow faster and faster each generation in perpetuity. Additionally, all offspring are unlikely to match their parents' growth phenotypes exactly, the case of a perfect correlation between parents and offspring ($\phi = 1$)

Beyond this scenario of perfect correlation, in cases where $1 > \phi \geq -1$, this parent-offspring phenotype correlation affects population growth rate and net reproductive rate through adults producing different frequencies of each type of offspring, where the value of ϕ determines those frequencies. Positive correlations mean a higher proportion of offspring with the same growth phenotype of the parent, whereas negative correlations produces the opposite. The proportion of each phenotype in the population will affect the long term growth rate because each phenotype matures at a different rate, thus individuals will reach the reproductive stage at variable times at different values of the correlation. Therefore, the distribution of growth phenotypes for each generation as determined by ϕ will determine the asymptotic growth rate and the net reproductive rate.

For example, in our two growth type population model, growth rate heterogeneity has a positive relationship with the asymptotic population growth rate when the parent-offspring correlation is sufficiently positive (Figure 3). In this situation, fast parents produce more fast than slow offspring on average. Increasing growth rate heterogeneity makes the fast juveniles faster, or more likely to transition to the reproductive stage, thus increasing the asymptotic growth rate.

While it is true that slow parents will produce more slow than fast offspring when the phenotype correlation is positive, the contribution to the population growth rate of the extra fast juveniles outweighs the negative contribution of the slow juveniles since increasing heterogeneity will make these individuals slower, and fewer and fewer will reach reproductive stage.

The relationship between growth heterogeneity and population growth rate is negative when there is no correlation between parents and offspring in growth phenotype (Figure 3). Any variation in individual growth rate will decrease the population growth rate. When there is no correlation between parents and offspring in growth phenotype ($\phi = 0$), parents will produce equal frequencies of offspring of each type, on average.

How do positive and negative phenotypic populations come about in natural populations? Consider a simple example of a sedentary species where individual growth phenotype is largely determined by the microsite conditions. Assume microsites are evenly distributed across the landscape and the young disperse into available microsites with equal probability. Because the microsite determines the growth phenotype, offspring may or may not match the parents' phenotype due to chance because of equal probability of landing in any given microsite. Of course, habitats are not checkerboards and dispersal is unlikely to be random in many real-world cases so this simple example is not realistic. However, we can more easily imagine scenarios where positive or negative phenotype correlations between parents and offspring could arise from maternal effects, dispersal patterns and distribution of microsites.

Generation time, however, is not strongly affected by the parent-offspring phenotype correlation (Fig. 5). Generation time is only large when the average probability of growth is small, and it quickly declines as growth probability increases. The relative homogeneity in generation time across the variation in growth rate (σ) could be due to very few slow juveniles

surviving to maturity. The mean age at first reproduction increases more rapidly for slow individuals than it declines for fast individuals with heterogeneity in growth (Figure 6). Thus, slow individuals will take a much longer time to reach maturity, and overall fewer of them will reach this stage than the fast individuals because due to heterogeneity. Therefore, the weighted mean of the generation times is dominated by the fast individuals.

In our model, we only considered two growth types that do not change throughout the life cycle for simplicity. In natural populations, there are likely to be several growth phenotypes and these could be transient, meaning occurring only in some time steps. Individuals could experience growth spurts from an influx of nutrients or a gap opening in the canopy for example, but it may only have temporary effects on growth. In these cases, the dynamics of the population could be very different or more complex.

The effects on growth rate heterogeneity on the population growth rate can be compared to the effects of heterogeneity in survival and reproduction. In the absence of a parent-offspring correlation, heterogeneity in reproduction has no effect on the population growth rate (Kendall et al. 2011). However, when a parent-offspring correlation is added to the model, positive correlations increase the population growth rate with increased variation in reproduction while negative parent-offspring phenotypic correlations decrease it. Growth rate heterogeneity in our model has similar effects on population growth rate with both positive and negative parent-offspring phenotypic correlations. Survival heterogeneity, however, has a different effect. It leads to cohort selection even with no correlation between parents and offspring which increases the population growth rate. When the parent offspring phenotypic correlation is added to the model, survival heterogeneity increases the population growth rate, even with a negative parent offspring correlation (Kendall et al. 2011). The results here show that increasing the variance in

growth rate increases population growth rate, but only under some circumstances depending on mean age to maturity and the parent offspring correlation.

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Figures

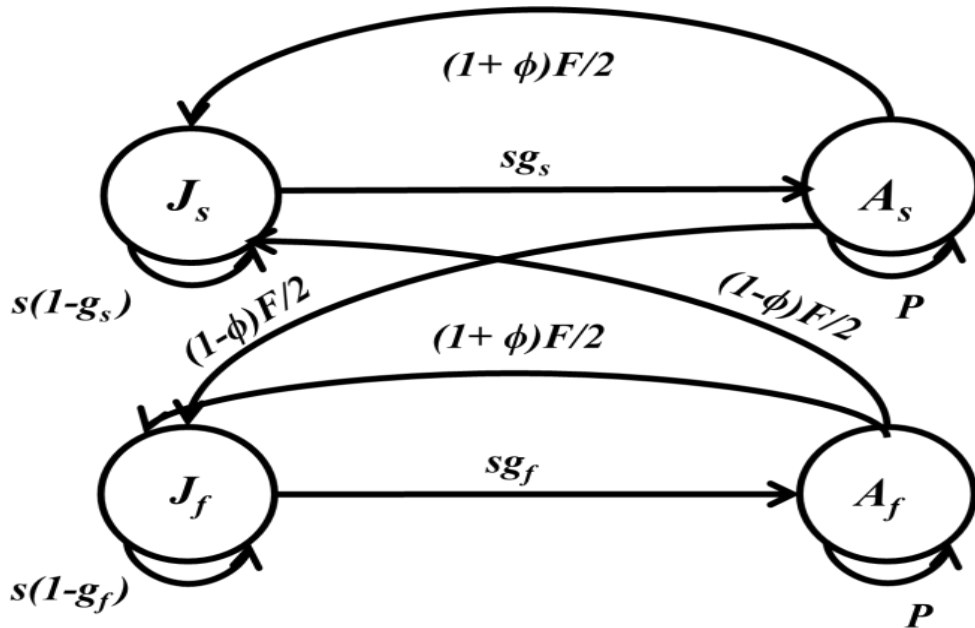


Figure 1.1. Life cycle diagram for a two-stage plant population with two types of individuals according to growth phenotype, fast and slow. Adults of each type can contribute offspring to both slow and fast phenotypic classes.

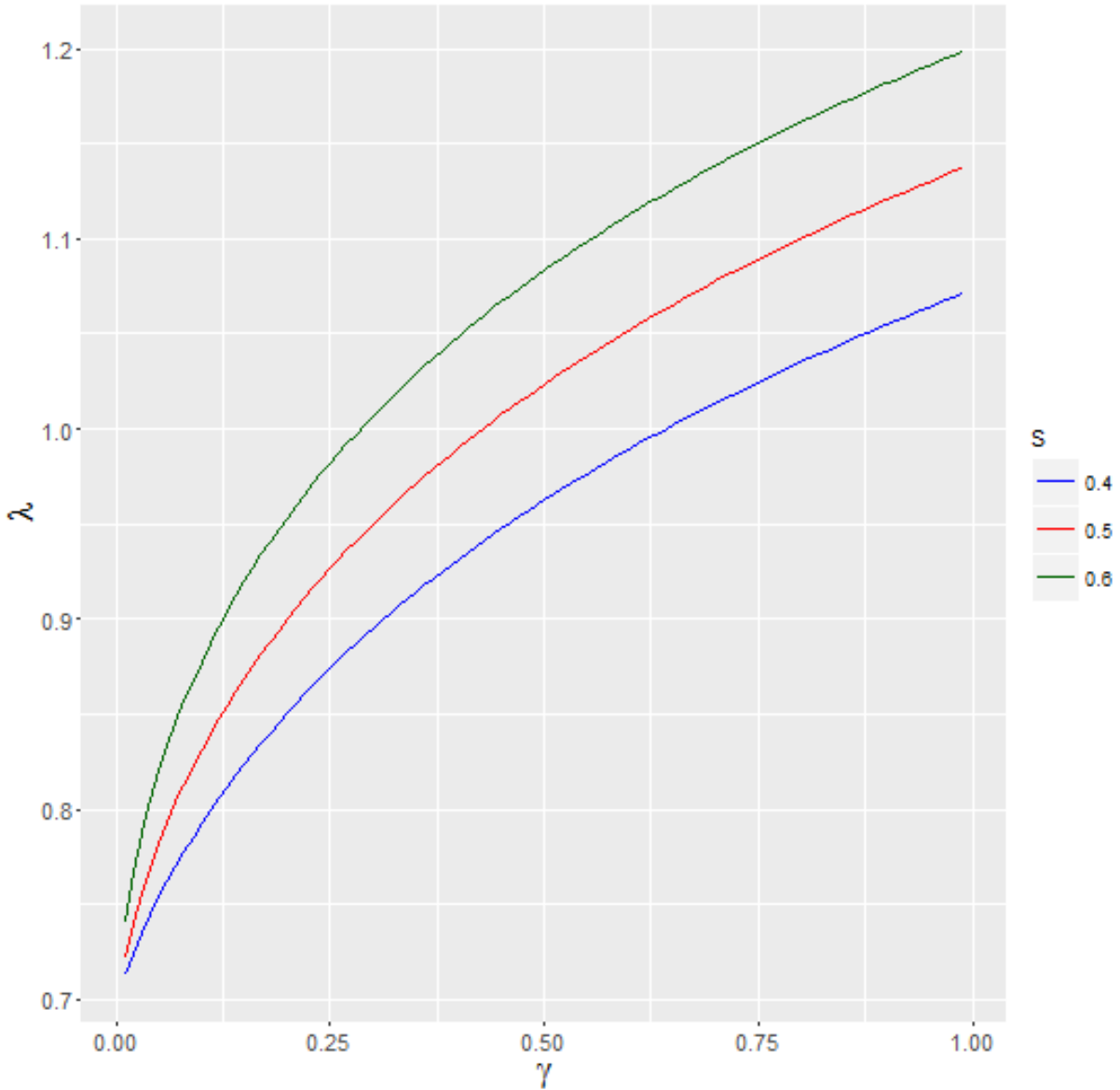


Figure 1.2. Long-term population growth rate λ as a function of γ , the mean individual maturation rate in a monotypic population or where $\phi = 1$, over three values of juvenile survival probability.

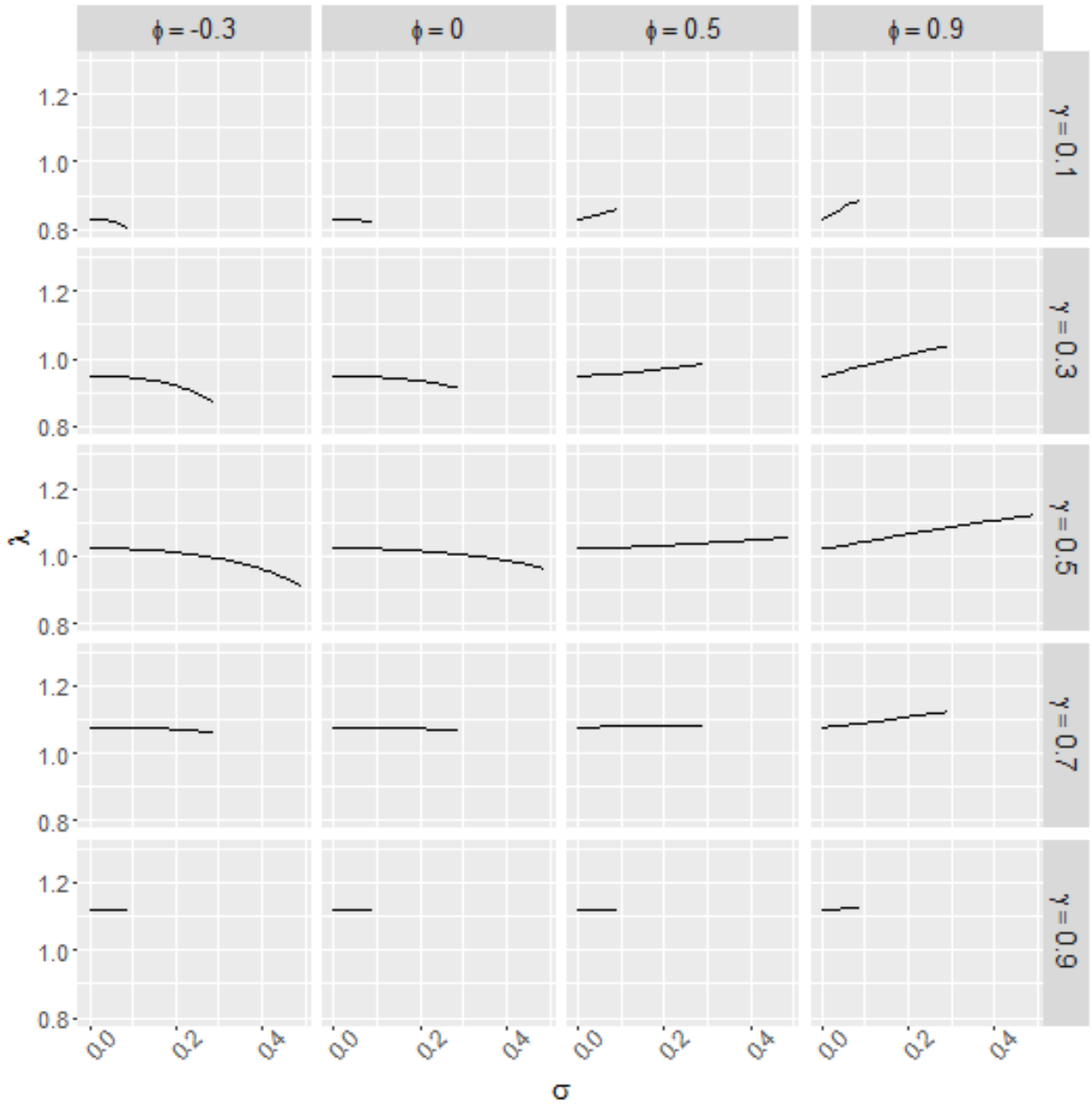


Figure 1.3. The asymptotic population growth rate, λ , as a function of the variation in growth rate σ , the average growth rate γ , and the parent-offspring phenotypic correlation ϕ . S is fixed at 0.5, where on average, half of the juveniles will survive during each time step. The line segments for the five values of γ are of differing lengths due to the conditions in Eq. 2 where σ cannot exceed the value of γ . Each subsequent figure shares this feature.

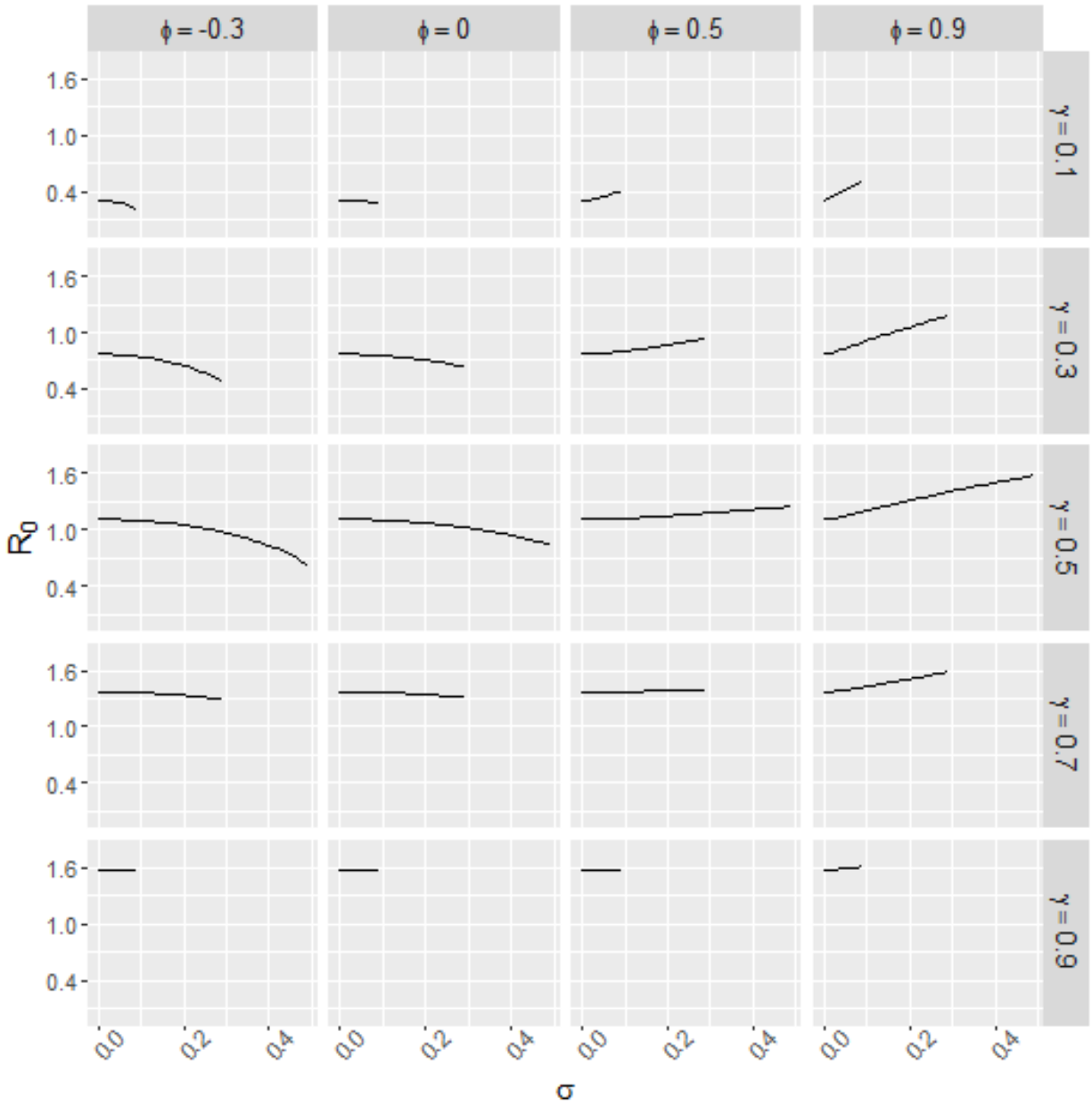


Figure 1.4. Net Reproductive Rate, R_0 , as a function of variation in growth rate σ , the average growth rate γ and the parent-offspring phenotypic correlation ϕ .

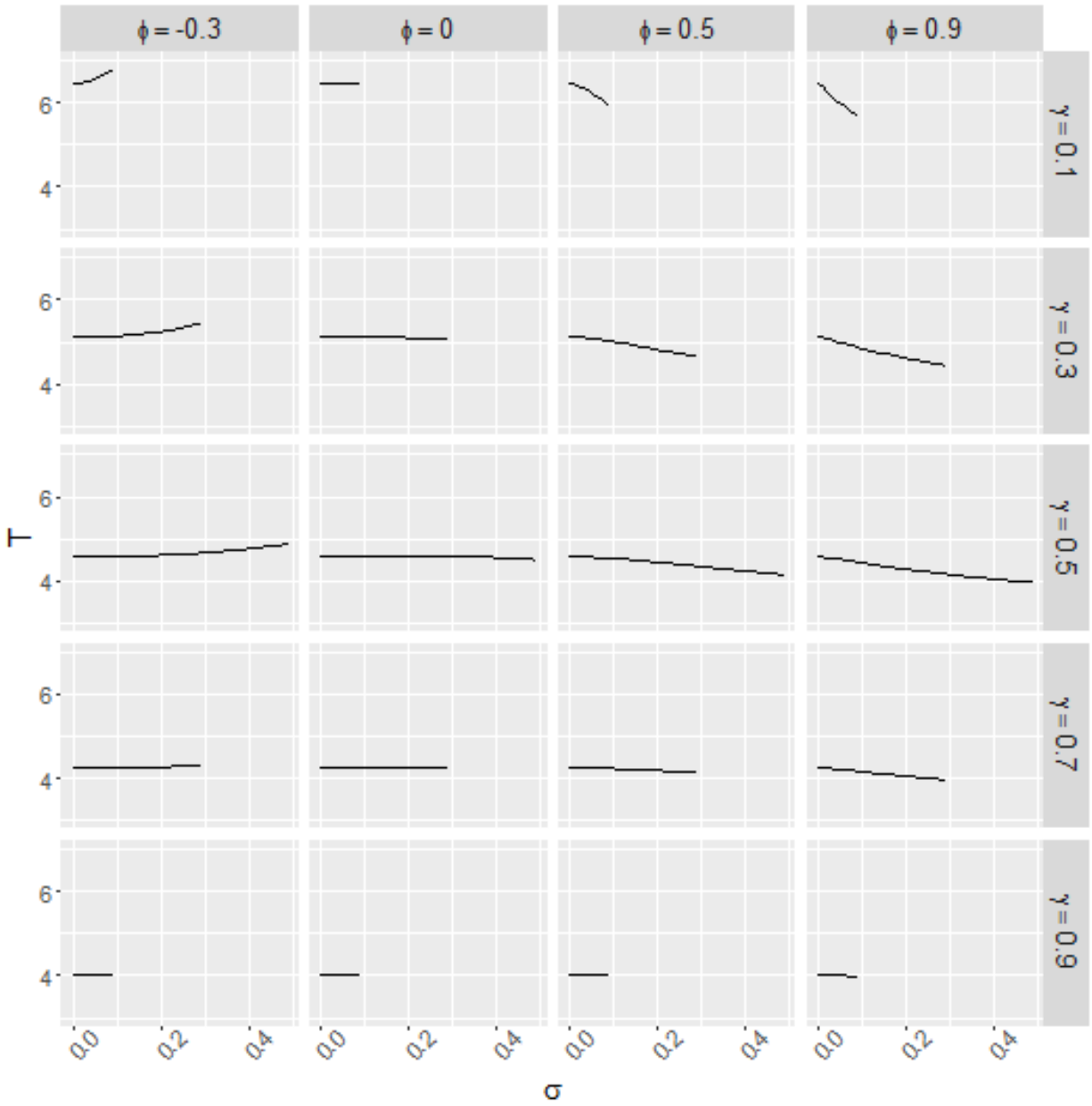


Figure 1.5. Generation time, T , as a function of variation in growth rate σ , the average growth rate γ and the parent-offspring phenotypic correlation ϕ .

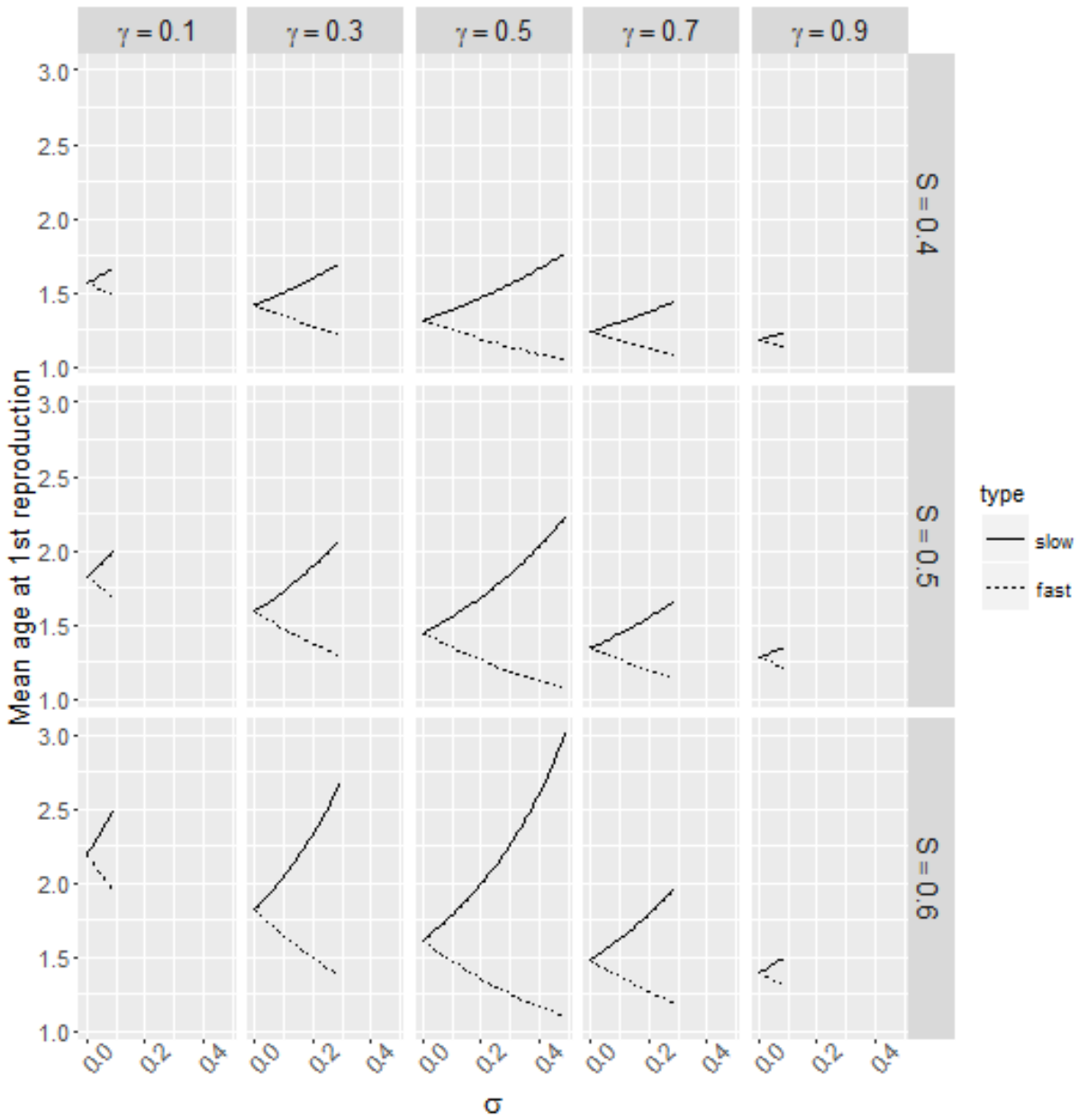


Figure 1.6. Mean age at first reproduction for each phenotype as a function of variation in growth rate σ , juvenile survival probability S , and γ , the average growth rate from the juvenile to adult stage.

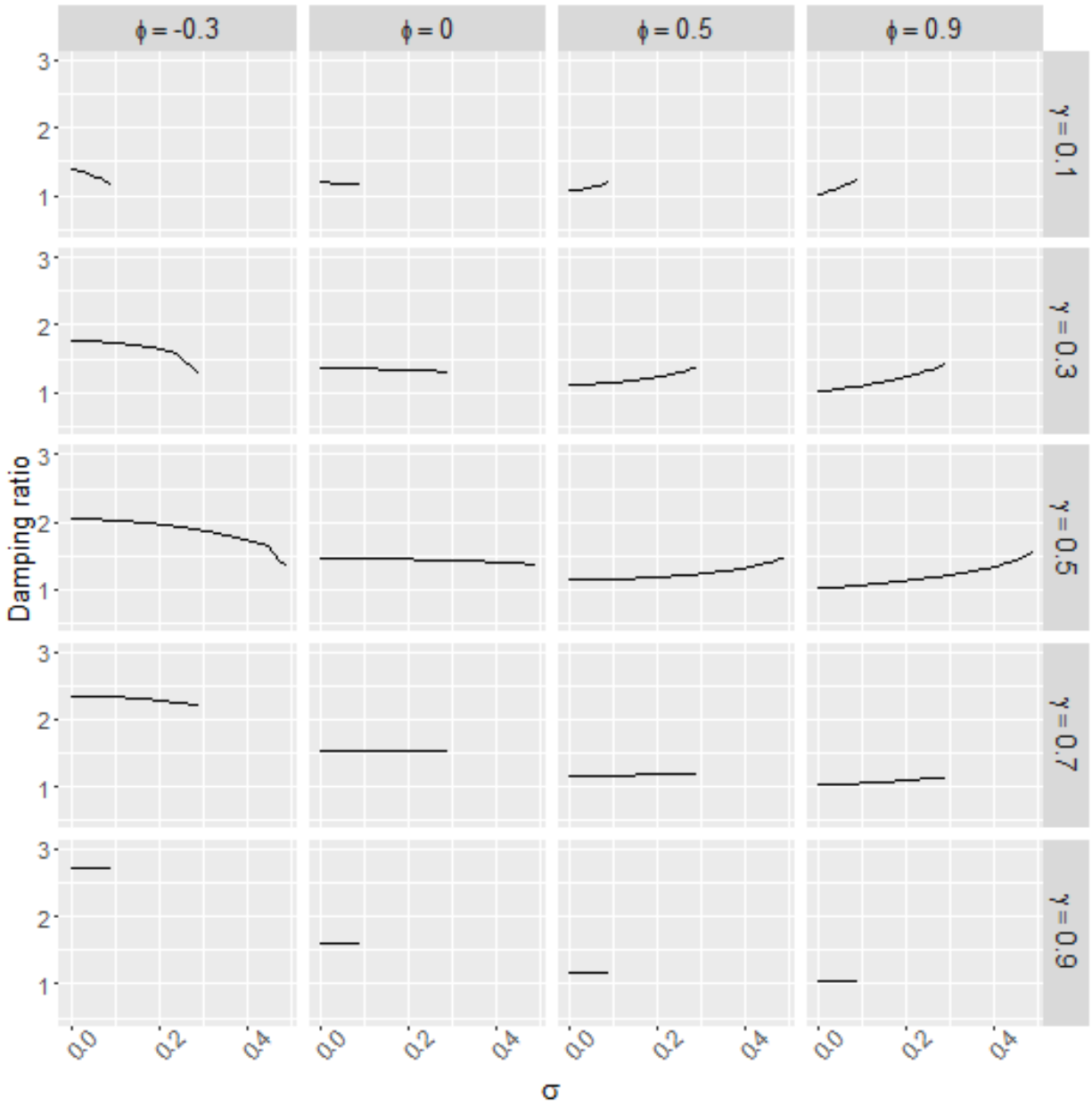


Figure 1.7. Damping ratio, or the ratio of the first and second eigenvalues, as a function of variation in growth σ , the average growth rate and the parent-offspring phenotypic correlation ϕ .

CHAPTER TWO

Introduction

Survival probability of offspring during the juvenile stage can affect recruitment of breeders into a population, potentially affecting population growth rate (Gaillard et al. 1998; Ringsby, Sæther & Solberg 1998; Oli & Armitage 2004; Sergio et al. 2010; Dehnhard et al. 2014). Even in long-lived organisms that produce large numbers of offspring, such as forest trees, there is evidence of recruitment limitation (Clark et al. 1999). Additionally, this trait is recognized as an important fitness component that can shape life-history (Stearns 1979; Reid et al. 2003; Reid et al. 2010). Juvenile survival probability as a function of early life conditions has been shown to have short and long-term fitness benefits or costs in several taxa, including long-lived herbivorous mammals and birds (Gaillard et al. 2000; Reid et al. 2010; Mumme et al. 2015; Plard et al. 2015). For example, juvenile survival of Audouin's gulls is strongly affected by early life conditions, including density and weather conditions (Payo-Payo et al. 2016). These benefits and costs can subsequently affect survival and reproductive output, changing population-level processes over time (Lindström 1999; Gaillard et al. 2003). Therefore, quantifying juvenile survival and examining the mechanisms underlying variation in this trait could improve our understanding of the contribution of juvenile survival to population growth rate over space and time.

Several processes are known to affect offspring survival, although the relative importance of each mechanism varies can vary among habitats, life history strategy and taxa. Genotype, density-dependence, resource availability, environmental conditions, maternal effects, parental quality, birth order within a clutch and behavior (e.g. Clutton-Brock et al. 1987; Gaillard et al.

1998; Gaillard, Festa-Bianchet & Yoccoz 1998; Coulson et al. 2001; Gaillard et al. 2003; Crespin et al. 2006) all affect survival of young both within and among birth cohorts. Environmental conditions and resource availability often vary over time and individuals born in different years are likely to experience different environments. Cohort effects result when there is variation in demographic traits among individuals born in different years, as a result of the conditions experienced during the birth year (Gaillard et al. 2003).

Beyond cohort effects, closely related individuals such as siblings can have similar phenotypes and demographic fates due to shared genes, maternal effects and litter/brood effects, collectively known as “family effects” (Gaillard et al. 1998). For example, Roe deer fawn siblings have similar growth rates and over-winter survival compared to unrelated fawns (Gaillard et al. 1998). Likewise, first-year survival of cheetah cubs is more similar among siblings than unrelated cubs, primarily due to “litter effects” (Pettoreli and Durant 2007). Growth rate and survival of blue mussel larvae were found to be affected by family lineage in laboratory conditions, with families responding differently to growing conditions (Yund and McCartney 2016). Family effects are one mechanism that can generate variation in demographic traits among individuals within age and stage classes, called demographic heterogeneity, which can change population growth rate through changing the demographic variance (Kendall et al. 2011).

The structure of kinship, or the degree of genetic relatedness, over space and time has been shown to affect demographic rates in both social and solitary species (Lamben & Yoccoz 1998; Pope 2000; Støen et al. 2005; Newman et al. 2016). For example, the role of kin structure on microtine vole population dynamics has been well documented (Lamben & Krebs 1993; Lambin & Yoccoz 1998). Survival of juvenile voles and recruitment rate are affected by spatial kinship structure where juvenile survival is higher when mothers are in kin clusters (Lamben &

Yoccoz 1998). Due to the effects of kinship on demography, family effects are considered to be an important component to population dynamics.

Here, we take advantage of a 34 year data set on a marked population of Florida Scrub-Jays (*Aphelocoma coerulescens*) to decompose some of the contributions to variation in juvenile survival, most importantly the variation due to kinship or lineage. Florida Scrub-Jays are cooperative breeders restricted to scrub-dominated habitats with periodic fire in peninsular Florida (Woolfenden & Fitzpatrick 1984). Family groups consist of a monogamous breeding pair, juveniles and 0-6 non-breeding adult helpers that raise young on year-round territories. Florida Scrub-Jay offspring delay dispersal until ages 2 or 3, on average. Helpers have been shown to increase fitness of juveniles by provisioning young and providing additional watchers for predators, the main source of mortality of young jays (Woolfenden and Fitzpatrick 1984, Mumme 1992). Snakes and *Accipiter* hawks are the primary predators of Florida Scrub-Jays, with the former a larger threat to jays in the nestling and fledgling stages. Scrub-jays have a sentinel system where group members trade watching for threats and foraging. Larger groups provide more watchers and increase the probability of detecting a predator (Woolfenden & Fitzpatrick 1984; Fitzpatrick and Woolfenden 1988; Mumme 1992). Pairs residing in territories with low to medium height scrub oaks (*Quercus sp.*) with sandy openings produce more fledglings than pairs on lower quality territories, on average (Breininger & Oddy 2004).

Juveniles are sedentary during the first year of life and do not disperse until after one year of age. Thus, young scrub-jays can be relatively easily tracked throughout the first year of life, providing a good source of data for estimating survival with little or no heterogeneity in re-sighting probability. Furthermore, fledglings hatched on the study site are of known parentage as immigrants that become breeders are trapped and banded (Woolfenden & Fitzpatrick 1984). By

the mid-eighties, over half of the breeders in the population were of known parentage. Offspring can easily be assigned parentage because Florida Scrub-Jays are behaviorally and genetically monogamous, as demonstrated by genetic analyses of three Florida Scrub-Jay populations (Quinn et al. 1999; Townsend et al. 2011).

In a previous study of the same marked population of Florida Scrub-Jays, Fox et al. (2006) found that parent and territory identity were good predictors of survival of breeding Florida Scrub-Jays, indicating that some aspect of familial relationships are important in structuring survival in this species. A kinship matrix can be estimated from this population's pedigree and use it to estimate variance components in survival due to kinship, or the degree of relatedness with other individuals in the population (Pankratz, de Andrade & Therneau 2005; Anderson et al. 2007). We can take advantage of this extensive pedigree of a wild vertebrate population to estimate variance in survival due to kin structure or relatedness, which gives us an ability to gain insight that is difficult to do in many populations due to lack of required data. Unlike many previous studies considering kinship structure in demography, we make use of a modeling approach that estimates the variance in survival time due to genetic correlations among individuals. This approach considers an individual's degree of relatedness to all other individuals, instead of just parent or family identity.

We examined how the physical and social conditions of the natal territory and kinship affect mortality risk in hatch-year Florida Scrub-Jays. We considered brood size, nestling mass, fledgling number, the presence of helpers, and territory quality represented by total size, the area of oak scrub and total area in the 2-9 year fire return interval as possible predictors. We addressed four main questions regarding the pattern of juvenile survival of Florida Scrub-Jays. How variable is survival probability of Florida Scrub-Jays from fledging to one year old among

years? What is the relationship between the social and physical conditions of the natal territory and probability of survival to the pre-breeding stage? Does parental quality as measured by age and experience change the probability of juvenile survival? How much variance in expected survival probability is due to family or lineage?

Methods

Study Area and Population

The data come from a banded population of Florida Scrub-Jays under continuous study since 1969 at Archbold Biological Station (hereafter, “Archbold”) located in Highlands County, Florida (27.10° N, 81.21° W). The area is characterized by oak-dominated scrub in well-drained soils with periodic fire. The methods of data collection are described in detail elsewhere (Woolfenden & Fitzpatrick 1984; Mumme et al. 2015). In short, each spring all territory boundaries are mapped and every nest is monitored until failure or fledge. All nestlings are banded and weighed at 11 days post hatch then recaptured and weighed as juveniles at approximately 90 days old. Each territory with at least one fledgling is visited weekly during the breeding season from fledge date until all juveniles are recaptured. Additionally, there are monthly censuses of all scrub-jays in each territory throughout the entire year.

Territory boundaries are mapped each breeding season during April and May using aerial photography as outlined by Woolfenden & Fitzpatrick (1984). The maps are digitized using ArcGIS (ESRI, Redlands, California, USA). The study area is composed of 5 m² cells in a grid. Controlled burns take place throughout the study tract within burn units of various fire return intervals. As a result, Florida Scrub-Jay territories can encompass multiple burn units. Since the start of the study, the monitored area has increased as Archbold has acquired adjacent properties. Thus, there are some territories where the scrub-jays were banded and censused, but the territory

lacks data on composition. For analyses examining the effect of territory quality in terms of size and structural composition, we used a smaller data set including fledglings where there is data available that describe quality at the natal territory (N = 1583).

Statistical Analyses

We defined the juvenile survival period as commencing when individuals fledge, typically 15-20 days post-hatch, to 365 days post-fledge, when individuals transition to the pre-breeder stage at one year old. We first estimated cumulative survival during all years and for each year using the standard non-parametric Kaplan-Meier method (N = 2492). For all subsequent analyses, we used semi-parametric Cox proportional hazard and Cox mixed effects models. These models are semi-parametric because the baseline hazard does not have to be specified. These models focus on the hazard function, or the risk of mortality, instead of the survival function. The hazard function describes the instantaneous probability of an occurrence of an event, which in this case is death. However, we can obtain the probability of survival from the hazard function (Therneau & Grambsch 2000; Rodriguez 2007).

Cox models are appropriate for time-to-event data, such as time to death, and can accommodate censored data (Therneau & Grambsch 2000, Fox 2001; Fox et al. 2006). We are interested in the distribution of event times within a follow-up period. If an event is not observed during follow-up, either from not experiencing the event or individuals dropping out of a study, all we know is that the event time is greater than the follow-up time (Fox 2001). The only censored individuals in these data were still alive as of April 2016. As juveniles, Florida Scrub-Jays stay within in their natal territories and individuals do not disperse before turning one year old. Thus, there is very little heterogeneity in re-sighting probability, so Cox regression models are appropriate for these data.

An extension of the Cox model is the addition of random effects, which can account for correlation among individuals (Therneau et al. 2003; Therneau 2015). In this case, the random effects are shared frailties. Frailty refers to excess risk in survival time, where some individuals are more frail than others, and will experience an event sooner than more robust individuals (Therneau & Grambsch 2000; Wienke 2010; Govindarajulu et al. 2011). Frailty terms modify the hazard function for individuals within groups that share some characteristic, such as families or birth cohorts. Model forms are shown in Appendix 1 of the Supplemental Information.

Before 1999, birds were sexed behaviorally; thus, the known-sex birds are individuals that survived to maturity when males and females begin to exhibit sex-specific behaviors (Woolfenden & Fitzpatrick 1984; Mumme et al. 2015). Many of the individuals that died before one year old prior to 1999 are of unknown sex. Since then, the sex of nestlings has been determined via blood samples taken during the nestling stage. To determine if survival during the first year is different between the sexes, we estimated survival probability using the standard non-parametric Kaplan-Meier method using data on fledglings from 1999 to 2015 (N = 1562). We also fit a Cox proportional hazard model and a parametric accelerated failure time (AFT) model with a Weibull error distribution using sex as a covariate. AFT models using a Weibull error distribution are have proportional hazards; they are more powerful than Cox proportional hazard models and so using them in this way permits us to find smaller survival differences between sexes than the Cox models. Unfortunately the theory for modeling random effects in AFT models is more poorly developed than for Cox models, so we do not use them for other purposes.

We considered cohort or birth year, population density, brood size, number of fledglings within the natal brood, nestling mass (g), helpers, and parental age and experience as predictors

of mortality hazard of hatch-year Florida Scrub-Jays ($N = 2492$). Cohort year was considered first as a factor with 34 levels, then as a random term in mixed effects models. We used total number of jays divided by the number of breeding territories at each April's census as an estimate of population density. Helpers were modeled in two ways: presence/absence and as the number of helpers present ranging from 0 to 6. We also considered an interaction between year as a factor and the presence/absence of helpers. Some breeders are of unknown age so the sample size for models with these terms is smaller ($N = 2164$). Age of breeders is their known age in years or an estimated minimum age. Breeder experience is measured as the number of years previously bred, starting with zero for the first year bred. We added quadratic terms and an interaction for age and experience for both mothers and fathers to test for non-linearity.

We considered territory size, area of oak scrub and area of the territory in the 2 – 9 year fire return interval as indicators of territory quality with a smaller data set ($N = 1583$) that excludes fledglings reared in territories without this information. As expected, all three are highly correlated; thus, we performed a principal component analysis. All three variables were scaled and centered before performing the PCA. The first principal component accounted for 72% of the variance and reflects the linear combination of all three territory variables. There is a strong positive relationship between all three territory variables (Figure S1), so we used territory size as the predictor for territory quality for easier biological interpretation. We transformed territory size by standardizing whereby the values are in terms of standard deviations.

We tested the proportional hazard assumptions for each model by plotting the scaled Schoenfeld residuals and a chi square test (Therneau and Grambsch 2000). We ranked model fit using Akaike's information criterion (AIC) where models within 2 AIC units were considered to

have similar support. We retained the predictors from the best fitting Cox proportional hazard models as fixed effects in the Cox mixed effects models.

We considered cohort or birth year and pedigree/kinship as random effects or frailty terms for the Cox mixed effects models. The frailty terms are estimated from a Gaussian distribution with a mean of 0 and a variance-covariance matrix Σ that describes the structure of correlations between individuals (Therneau, Grambsch, & Pankratz 2003; Pankratz, de Andrade & Therneau 2005). Here, we used a kinship matrix of marked birds in the population as the variance-covariance structure among individuals. Using a covariance structure in models of survival from the kinship matrix is preferable to the shared frailty approach of Fox et al. (2006), because members of a family are not treated uniformly but instead the shared frailties are estimated from the degree of genetic relatedness. We constructed a pedigree object in R from the complete pedigree based on parental data using the package kinship2 1.6.4 (Therneau & Sinnwell 2015). We then used this pedigree to estimate the kinship matrix for individuals in the population. All analyses were performed in R 3.3.2 (R Development Core Team, 2016).

Results

From 1981 – 2015, the average proportion of survivors one year post-fledge is 0.38 ± 0.11 (standard deviation) with a median of 0.4 (Figure 1). The Kaplan-Meier survival estimates for hatch year males and females overlap at the very beginning of the period and begin to separate over time (Figure 1). However, the difference between the curves is slight. The 95% confidence intervals for the Kaplan Meier survival estimate overlap for males and females (Figure 1). The estimated coefficient for sex (male) in the Cox model indicates that males have a lower hazard relative to females, however the coefficient is not distinguishable from 1. Not surprisingly, then, the reduction in deviance from the null model (baseline hazard only) is one

unit and not significant with a chi-square distribution test ($\chi^2 = 2.04$, $p = 0.15$). However, the estimated coefficient for sex is significant in the parametric accelerated failure-time model. The model with sex as a predictor is a better fit given the data than the null model. The reduction in log likelihood is significant according to a chi-square test (deviance = 5.5, $p = 0.02$).

The hazards are approximately proportional for all covariates. The best fitting proportional hazards models include year modeled as a factor, nestling mass (g) and helpers (Table 1). Mother breeding experience, population density and brood size are also included in the best supported models (Table 1). The coefficients for each birth year are a mix of positive and negative where some cohorts have an increased risk relative to others and vice versa. Likewise, the year by helper interaction terms are a mix of positive and negative estimated coefficients. However, the AIC for this model is several units larger than the best fitting model (Table 1).

All best supported proportional hazard models include birth year as a predictor (Table 1). Mixed effects models with year as the only random effect have similar support to the proportional hazards models with year as a factor based on the reduction in deviance (Table S1). However, mixed effects models with two random terms, kinship and year, have more support than models with one random effect (Table S1). The estimated variance component for kinship is very large; juvenile scrub-jays have a 77-90% greater or lesser relative risk of dying than the average risk whereas birth year accounts for a 25-30% change in risk relative to individuals hatched in an average year (Table 2).

In addition to kinship and birth year, the models with the most support include nestling mass (g), helpers, and mother experience as fixed effects (Table 3). Models with brood size and population density as additional fixed effects have similar support according to AIC (Tables 1 & 3). Nestling mass significantly affects mortality risk of hatch year Florida Scrub-Jays where a

one gram change in mass from the mean nestling mass (45.19 g) reduces or increases the relative mortality risk by about 3% (Figure 2). One or more helpers present changes the relative risk of juveniles by approximately 15% relative to individuals without any helpers present while each helper decreases the relative risk by 6% (Figure 3). Experience and age of the mother, but not that of the father, affects mortality risk of hatch-year scrub-jays (Figure 4). We found no support for a quadratic term representing mother experience. Increasing territory size decreases relative risk for hatch year birds. Density and relative risk have a positive relationship, where increasing the total number of jays per total territory number increases risk relative to the mean density (Figure 5). Territory size and relative risk are negatively correlated. A change in territory size by one standard deviation from the mean territory size changes the relative risk by 15% (Figure 6).

Discussion

First-year survival of Florida Scrub-Jays (*Aphelocoma coerulescens*) is strongly structured by family lineage, or kinship. There is a large spread of mortality risk among individuals due to kinship, where some individuals will experience an 77 - 90% reduction or increase in risk relative to the mean (Table 2). Thus, there is a strong familial effect on mortality risk during the first year of life. Due to the nature of the study, these data are observational so we cannot estimate heritability of juvenile survival. The effect of kinship includes both genetic and non-genetic components, including maternal effects, parent behavior, social structure and territory quality. Maternal effects can manifest in several ways, from egg development, provisioning of young and overall conditions on the natal territory (Blount et al. 2001; Van De Pol et al. 2006).

Hatch year Florida Scrub-Jays generally have high mortality during the first year, where on average, 40% of fledglings survive the first year (Figure 1). However, the proportion of jays

surviving throughout the first year is highly variable over the period from 1981 – 2015 (Figure S1). The number of fledglings produced each year, the input, is itself highly variable with the mean fledglings per pair ranging from 0.34 to 1.82 per year (Figure S3). Precipitation, disease prevalence, fluctuations in predator numbers, and abundance of arthropods during the breeding season, the main source of food for nestlings and fledglings, can change from year to year, with some years deviating substantially from the average. Food availability, predator density and the ability of adults to detect predators could directly and indirectly affect post-fledgling survival (Naef-Daenzer et al. 2001; Eggers et al 2005; Eggers et al. 2006).

According to the Cox model and the Kaplan-Meier estimate, there are no substantial differences in male and female survival (Figure 1), although the parametric accelerated failure time model suggests that there are differences in male and female survival. The reduction in deviance from the null model is significant according to a chi-square test (deviance = 5.5, $p = 0.02$). It's possible that differences begin to emerge as young jays reach independence due to their social hierarchy where males dominate females (Woolfenden & Fitzpatrick 1977). Sex-based differences in survival probability are expected to manifest during the pre-breeder stage, where female survival is expected to be lower than males due to the dispersal behavior of Florida Scrub-Jays. On average, females disperse sooner and farther than males (Woolfenden & Fitzpatrick 1984). This behavior may make females more likely to encounter unfamiliar territory, which could increase their mortality risk. Juveniles are much more sedentary, although they do move around to neighboring territories as they reach nutritional independence and approach the pre-breeder stage (personal observation). Females may go on farther forays than males near the end of the juvenile period as individuals transition to adults, perhaps leading to slight differences

in mortality risk in the Kaplan-Meier estimates at one year post-fledge (Figure 1) and the results of the AFT model.

Nestling body mass is directly influenced by food availability and parents' ability to deliver food. The number of brood mates can determine food intake and affect body mass. Models with brood size as a predictor have similar support to models without it according to AIC (Tables 1, 3 & 4), but the predictor itself is not significant ($z = 0.04$, $P = 0.90$). Predator abundance may indirectly affect body mass through the effects on the foraging behavior of adults, which could affect how much food is delivered to offspring. Post-fledging survival of great and coal tits is dependent on body mass and timing of breeding, where predator abundance sharply increases as the breeding season progresses (Naef-Daenzer, Widmer & Nuber 2001).

Body mass is an important trait in determining post-fledgling survival in several avian species, where juvenile mass is positively correlated with survival (Ringsby, Sæther & Solberg 1988; Naef-Daenzer et al. 2001; Perlut & Strong 2016). The positive relationship between mass and juvenile survival is not limited to birds or even animals. Plard et al. (2015) found that juvenile survival of Roe deer is strongly affected by early growth which is directly and indirectly influenced by birth date and precipitation, both reflections of resource availability. For numerous plants species there is a well-known relationship between size and survival, where growth rate can be highly plastic to growing conditions (Horvitz & Schemske 2002; Callaway, Pennings & Richards 2003).

Mumme et al. (2015) estimated survival probability during the fledgling and juvenile stages and found survival probability in the first days post-fledge to day 30 is affected by brood size, nestling mass, group size and territory quality. After day 30, survival is affected most strongly by nestling mass then juvenile mass, which are positively correlated (Mumme et al.

2015). None of the other covariates that affected survival from day 15 to day 30 or nestling mass were significant in models of survival after day 30, nor predicted acquisition of a breeding territory. Juvenile mass, however, was positively associated with the probability of becoming a breeder (Mumme et al. 2015). Similarly, we found that nestling mass strongly affects mortality risk in juvenile Florida Scrub-Jays, with larger birds having a lower mortality risk compared to lighter birds (Figure 2). All best supported models include nestling mass (Tables 1, 3 & 4). Unlike Mumme et al. (2015), we found an effect of helpers and natal territory quality on survival from fledge to one year old (Figs. 2 & 4). We did not consider juvenile mass in our analyses because fledglings have to survive to 90 days post-hatch to have a measurement of juvenile mass.

Presence of one or more helpers can decrease mortality risk by 15% relative to individuals with no helpers at the natal territory, while each additional helper reduces risk by about 5% (Figure 3). Helpers can increase juvenile survival indirectly by providing food to nestlings and directly through predator detection and mobbing behavior. Because helpers are usually offspring from previous years, successful pairs will have larger group sizes and can further increase annual reproductive success. Furthermore, additional group members aid in territory defense and could help expand territory size. Group living can confer advantages in predator detection and some cooperatively breeding species, including Florida Scrub-Jays, have developed sentinel systems for maximizing foraging efficiency while lower predation risk (Woolfenden & Fitzpatrick 1984; Clutton-Brock et al. 2001). However, there can be complex interactions between social and physical conditions of territories whereby non-breeder helpers and juveniles can compete for resources and confer a fitness cost if territories are small with a low oak composition (Mumme et al. 2015). Our results suggest that there is an interaction

between helpers and year, where presence of helpers decreases mortality risk in some years, but increases mortality risk in other years (Table S1). There are likely complex interactions between climatic conditions, resource availability and the effects of helpers on survival from fledge to one year old. Helpers may increase survival of young in years when resources are abundant, but become competitors to offspring in years with resource stress.

Previous breeding experience of mothers, but not fathers, influences first-year survival of Florida Scrub-Jays (Figure 3). Within each experience level, juvenile mortality risk increases with age, but offspring of more experienced mothers at any given age have lower relative risks (Figure 3). Offspring of mothers that are young and experienced are expected to have a lower mortality risk, all else being equal. For example, a 4 year old mother with 2 years of previous breeding experience is better than a 4 year old mother with 1 year of previous breeding experience, from the perspective of the offspring (Figure 3). Experienced mothers may be better at provisioning young, detecting predators or both. Fathers with previous breeding experience could be better parents than first-time fathers in terms of behavior, although we did not find an effect of father age or experience on first-year survival of juveniles. Within experience levels, fledglings of older females have higher mortality risks than those of younger females (Figure 3). Perhaps we found an effect of mothers due to reproductive senescence of females or some other aspect of a mother's phenotype that changes with age and translates to higher mortality of offspring. Wilcoxon et al. (2013) found that young and old female Florida Scrub-Jays produce fewer fledglings than middle-age females, but they did not find evidence for age-related changes in the amount of reproductive hormones in females. In contrast, they did not detect an effect of male age on fledgling production, but there was an age effect on hormones (Wilcoxon et al.

2013). Males and females may have different costs to reproduction, and this could partially explain our results.

Population density has a negative effect on survival of fledglings and juveniles, potentially due to more competition for resources or disease risk (Figure 5). Florida Scrub-Jays are susceptible to vector-borne diseases and bacterial infections (Wilcoxon, Boughton, & Schoech 2010), and with a higher density, disease may spread more easily. We used a simple measure of density, the total number of jays divided by the number of territories. The results indicate that some measure of abundance is important for juvenile survival. A more biologically meaningful measure of density could be the number of individuals in adjacent or neighboring territories. Some processes may take place over a large scale that affects the whole study site while others may operate at a smaller scale, at the level of territories or a cluster of territories.

Territory size negatively affects hazard where a larger territory decreases mortality risk (Figure 6). Individuals residing in territories one standard deviation larger than the average can experience a 15% reduction in mortality risk (Figure 6). Larger territories are more likely to have a greater area of oak scrub and a mosaic of burn patches than smaller territories. Optimal territories for Florida Scrub-Jays consist of scrub oaks of low to medium height oaks (1- 3 m) and sandy patches for caching and foraging interspersed throughout the territory (cite). Scrub oaks (*Quercus sp.*) provide several important functions in the Florida Scrub-jay life cycle including nesting sites, cover from predators and acorns, which are an important autumn food resource (Woolfenden & Fitzpatrick 1984). The extent of oak cover and height is directly influenced by fire. The optimal habitat for Florida Scrub-Jays in terms of reproductive success occurs between 2 and 9 years post fire, where pairs produce more fledglings than in overgrown or very recently burned habitats (Breininger & Oddy 2004).

For birds, the post-fledgling period is considered to be an important stage in the life cycle because survival during this period can affect the size of the future breeding population and subsequently affect population growth rate (Ringsby, Sæther & Solberg 1998; Cox et al. 2014; Dehnhard et al. 2014). In passerines, survival rates of juveniles varies across species and habitats (Naef-Daenzer, Widmer & Nuber 2001; Cox et al. 2014, Dehnhard et al. 2014). Age, habitat quality, cohort effects, food availability, population density, sex and parent age were the main mechanisms examined in a review across several studies of post-fledgling survival in mainly forest passerine species (Cox et al. 2014). Here, in addition to kinship and group size, we found that Florida Scrub-Jay juvenile survival is influenced by many of these mechanisms, most importantly body size, parent experience and population density (Tables 1 – 3; Figures 2 – 6).

A common method for estimating survival is to use capture-mark-recapture in the Cormack-Jolly-Seber framework using the program MARK. While this is a widely-used and sound method for estimating re-sighting probability and apparent survival probability, the Cox regression model framework allows us to easily model risk of mortality as a function of several covariates with the additional advantage of including shared frailty terms. The CMR method is especially useful for species with long-distance dispersal and/or low philopatry due to its ability to use heterogeneity in recapture probability in estimates of survival probability. Due to the sedentary behavior of Florida Scrub-Jays, we can skip the step of estimating heterogeneity in capture/re-sighting probability of incorporating it into models of mortality risk. Furthermore, we can use the kinship matrix for the population as the correlation structure among individuals to estimate variance components among families, easily implemented in R 3.3.3 (R project).

We have demonstrated that first-year survival of Florida Scrub-Jays has a family component consisting of both genetic and non-genetic components. Kinship structure has a

strong effect on mortality risk, where individual risk can be up to 90% greater or smaller than the average risk due to the degree of relatedness to other individuals. Additionally, there is substantial year to year variation in first-year survival of Florida Scrub-Jays, and future research may consider if there is variation among families or lineages in performance of different year types. For example, some families could do better in wetter years while others produce more offspring or have greater offspring survival in drier years.

This study highlights the importance of family effects, specifically kinship, on demographic parameters. Models of the Cox family are widely used in medicine and epidemiology, but rarer in ecological studies. As far as we know, this is the first study to show that juvenile survival is structured by kinship or lineage in this species, and the first to use mixed effects Cox models with kinship as the correlation structure to estimate demographic rates in a natural, non-human population. The consequences of kinship in reproductive success and population growth rate could be profound due to its effect juvenile survival which can limit recruitment. Given our results, future demographic research should consider family effects, particularly kinship where the data are available, and focus data collection efforts on pedigrees or parental information.

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Tables

Table 2.1. Results of model selection analysis for Cox Proportional Hazard models of first-year survival of Florida Scrub-Jays (*Aphelocoma coerulescens*) as a function of biological and social conditions of the natal territory for 34 consecutive birth cohorts from 1981 - 2015 (N = 2492).

Mass refers to nestling mass (g), helpers refers to the presence or absence of 1 or more helpers.

Population density is estimated as the total number of scrub-jays per the total number of breeding territories each April. Birth year is modeled as a factor with 34 levels.

Model	K	AIC	Δ AIC
Mass + Helper + Birth Year	37	22323.54	0.00
Mass + Helper + Brood Size + Birth Year	38	22325.46	1.92
Mass + Helper + Density + Birth Year	38	22325.54	2.00
Mass + Helper + Density + Brood Size + Birth Year	39	22327.46	3.92
Mass + Birth Year	36	22335.50	11.96
Mass + Helper + Year + Helper X Birth Year	72	22355.34	31.80

Table 2.2. Estimated relative risk for the frailty terms, kinship and birth year, from the best-fitting Cox mixed effects models of Florida Scrub-Jay (*Aphelocoma coerulescens*) mortality risk from fledge to one year old. The random effects or frailties are modeled as a Gaussian distribution with a mean of 0 and a variance matrix Σ that represents the correlation structure among individuals. The relative risk can be estimated by $\exp(\sqrt{Variance})$. The models shown here are fit from different data sets. The data for the first model excludes territory size (N = 2164), while the second model includes territory size, which is not available for all territories (N = 1583).

Model	Term	Relative Risk
Mass + Helper + Density + Mother Experience + Kinship + Birth Year	Kinship	0.90
	Birth Year	0.29
Mass + Helper + Density + Territory Size + Kinship + Birth Year	Kinship	0.75
	Birth Year	0.32

Table 2.3. Results of model selection analysis for Cox mixed effects models of first-year survival of Florida Scrub-Jays (*Aphelocoma coerulescens*) as a function of biological and social conditions (N = 2164). Mass refers to nestling mass (g) while helpers refers to the presence or absence of helpers. Experience is a count representing the number of years previously bred. Both kinship and birth year are random effects drawn from a Gaussian distribution with a mean of zero and variance Σ . The variance-covariance matrix for kinship is derived from the kinship matrix, or degree of relatedness to all individuals in the population.

Model	K	AIC	Δ AIC
Mass + Helper + Density + Mother Experience + Kinship + Birth Year	6	19084.41	0.00
Mass + Helper + Density + Kinship + Birth Year	5	19085.77	1.36
Mass + Helper + Density + Mother Experience + Brood Size + Kinship + Birth Year	7	19086.31	1.90
Mass + Helper + Mother Experience + Kinship + Birth Year	5	19088.82	4.42
Mass + Helper + Kinship + Birth Year	4	19090.49	6.08
Mass + Helper + Mother Experience + Brood Size + Kinship + Birth Year	6	19090.77	6.36
Mass + Helper + Brood Size + Kinship + Birth Year	5	19092.49	8.08

Table 2.4. Results of model selection analysis for Cox mixed effects models of first-year survival of Florida Scrub-Jays (*Aphelocoma coerulescens*) as a function of territory size and social conditions (N = 1583). Helper was modeled as a binary variable to represent presence/absence of 1 or more helpers. Territory size was standardized.

Model	K	AIC	Δ AIC
Mass + Helper + Density + Territory Size + Kinship + Birth Year	6	13277.08	0.00
Mass + Helper + Density + Kinship + Birth Year	5	13277.78	0.70
Mass + Helper + Territory Size + Kinship + Birth Year	5	13278.80	1.71
Mass + Helper + Kinship + Birth Year	4	13279.33	2.24
Mass + Helper + Brood Size + Kinship + Birth Year	5	13281.25	4.17
Mass + Kinship + Birth Year	3	13282.68	5.59

Figures

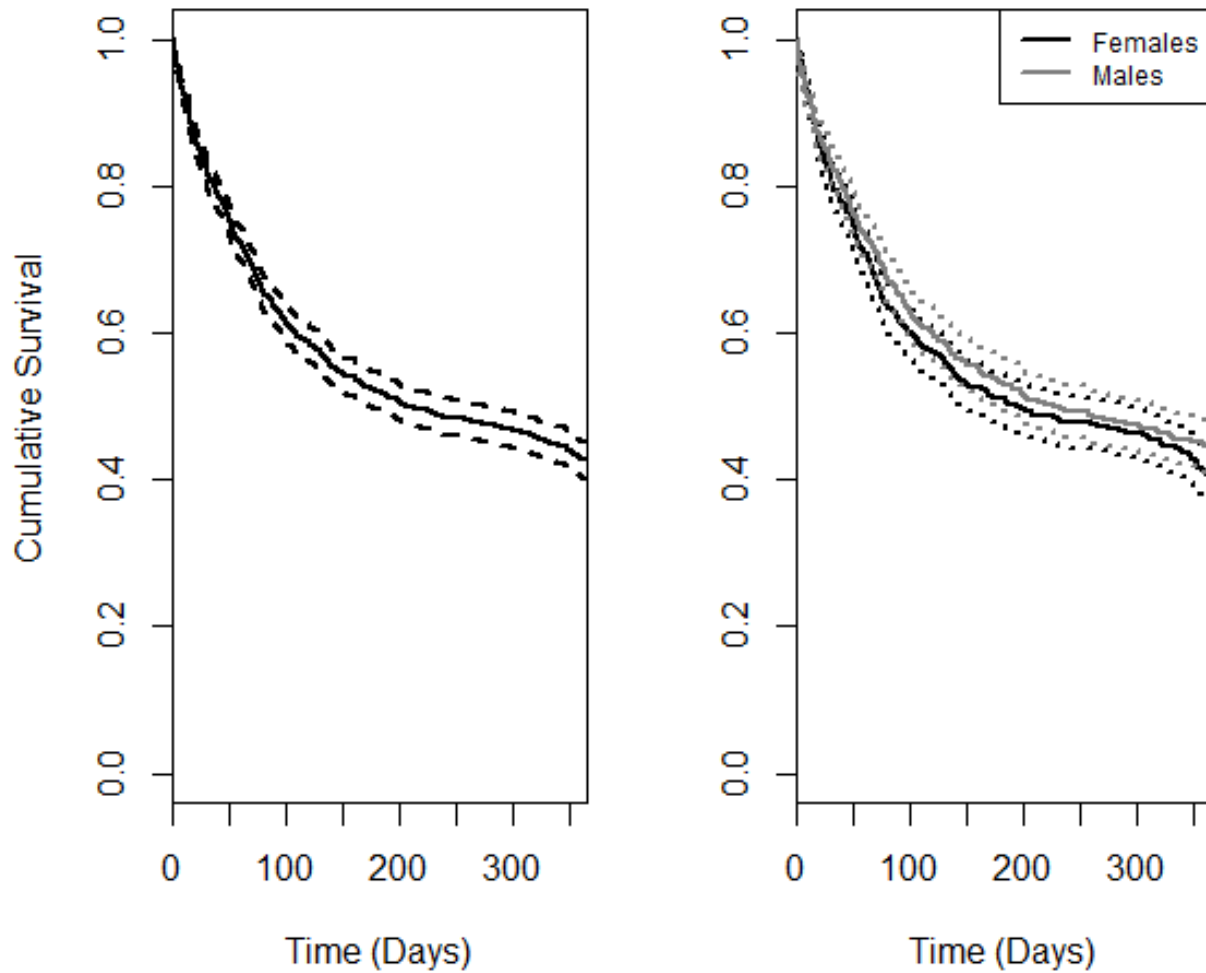


Figure 2.1. Left: Kaplan-Meier estimate of survival probability of Florida Scrub-Jays (*Apelcoma coerulescens*) from fledge date to one year old across all cohorts from 1981 – 2015 (N = 2492). Right: Kaplan-Meier estimates of survival probability for male and female fledglings from 1981 – 2015 (N = 1562). Dashed lines are the upper and lower 95% confidence intervals.

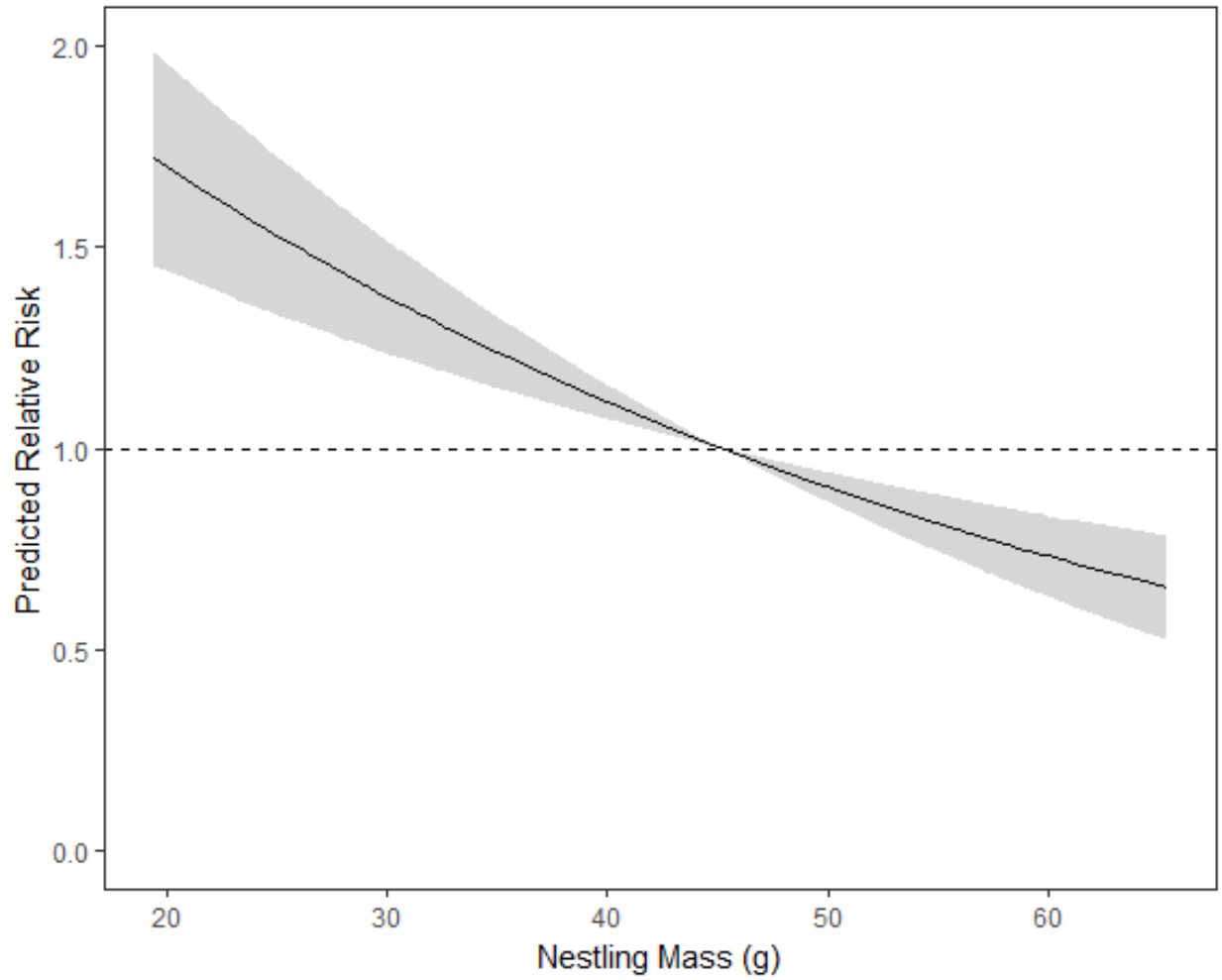


Figure 2.2. Predicted relative risk of mortality from fledge (15 – 20 days post-hatch) to one year old as a function of nestling mass (g) in juvenile Florida Scrub-Jays. The dark gray ribbons represent the upper and lower 95% confidence intervals.

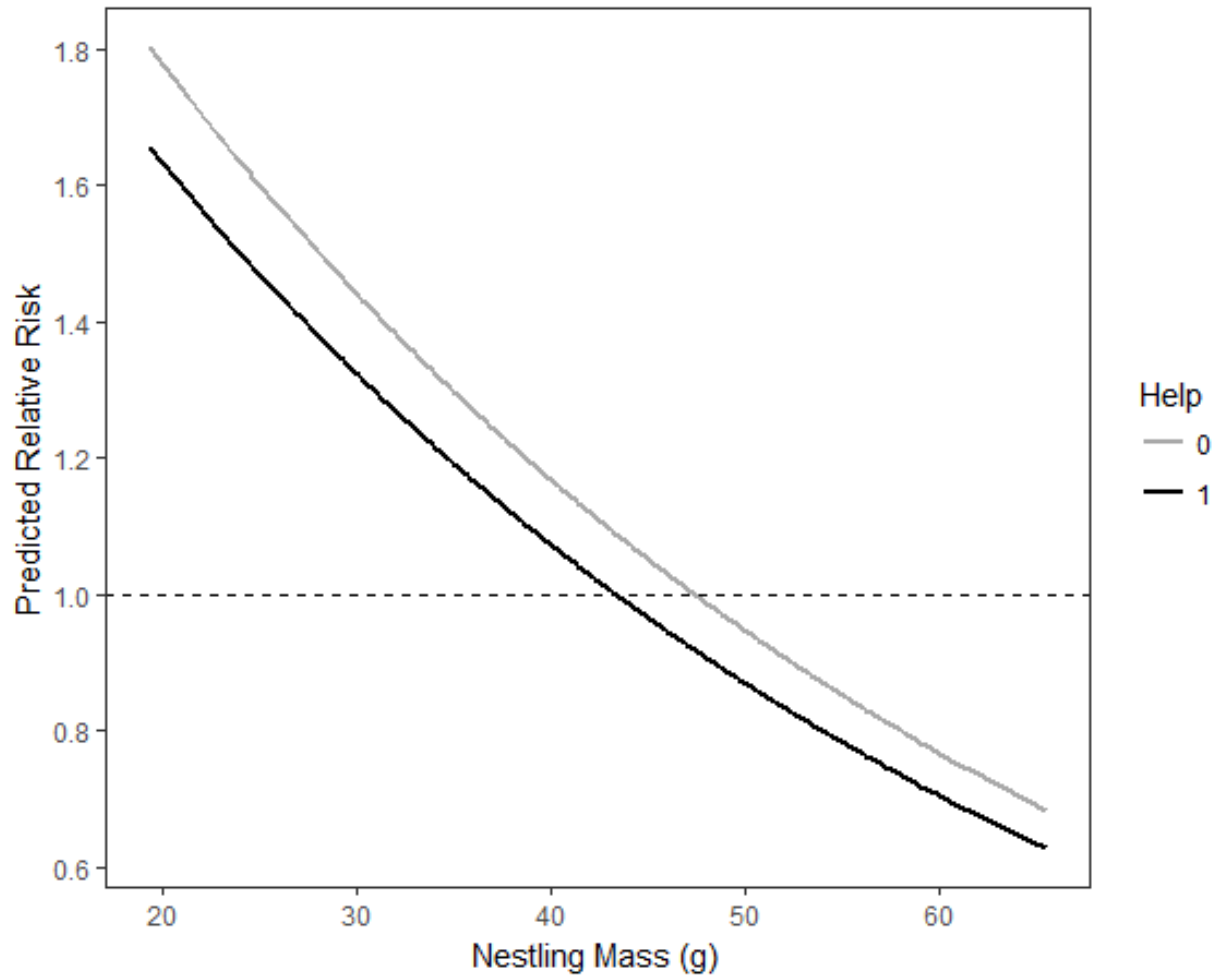


Figure 2.3. Predicted relative risk of mortality of Florida Scrub-Jays during the first year of life as a function of the number of helpers present at the natal territory (N = 2492). The dark gray ribbons represent the upper and lower 95% confidence intervals.

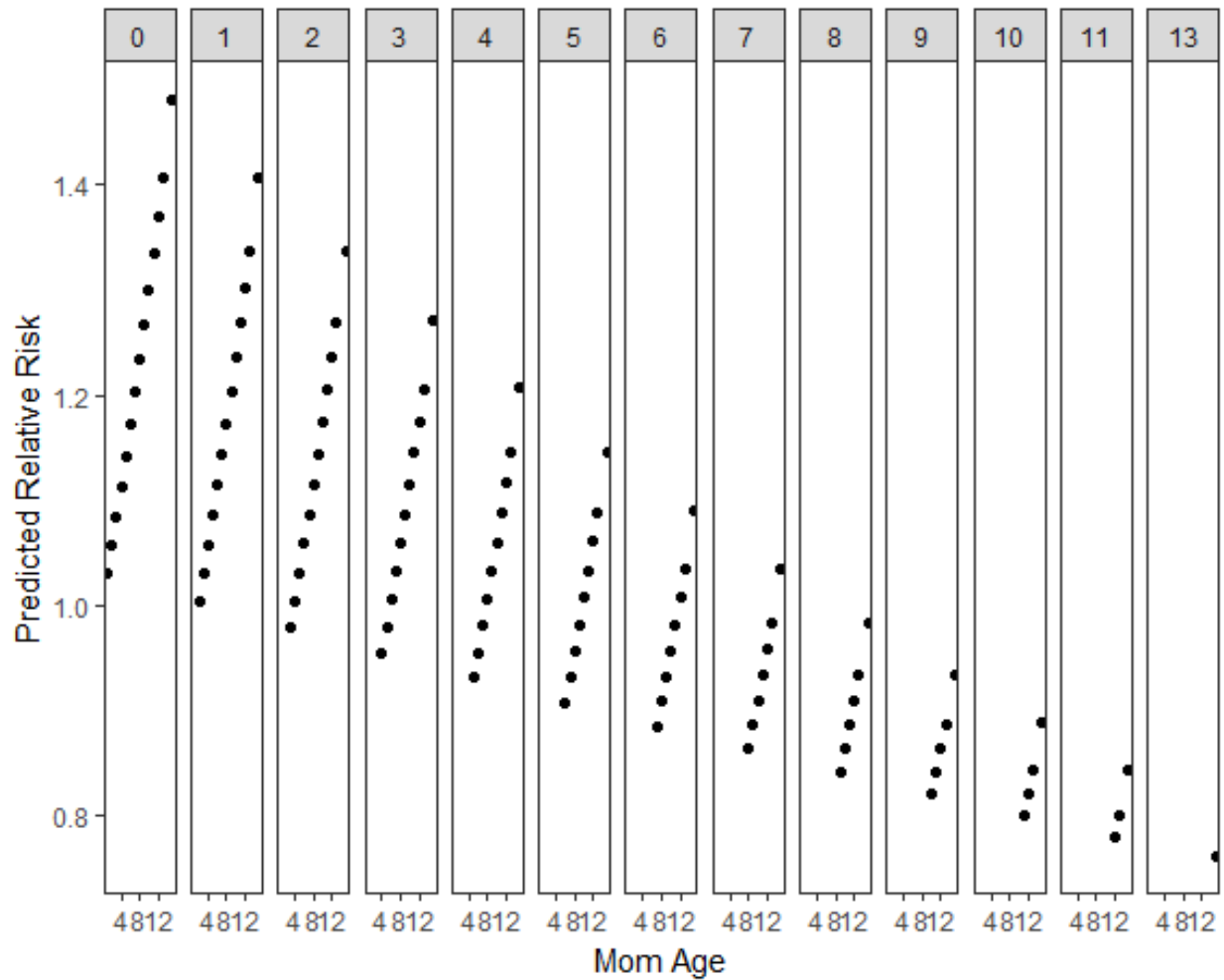


Figure 2.4. Predicted relative mortality hazard of Florida Scrub-Jays during the first year as a function of mother age and experience for all years from 1981 – 2015. Each vertical panel represents the number of previous years bred, or years of breeding experience. The distribution of mothers' ages is on the x axis within each panel.

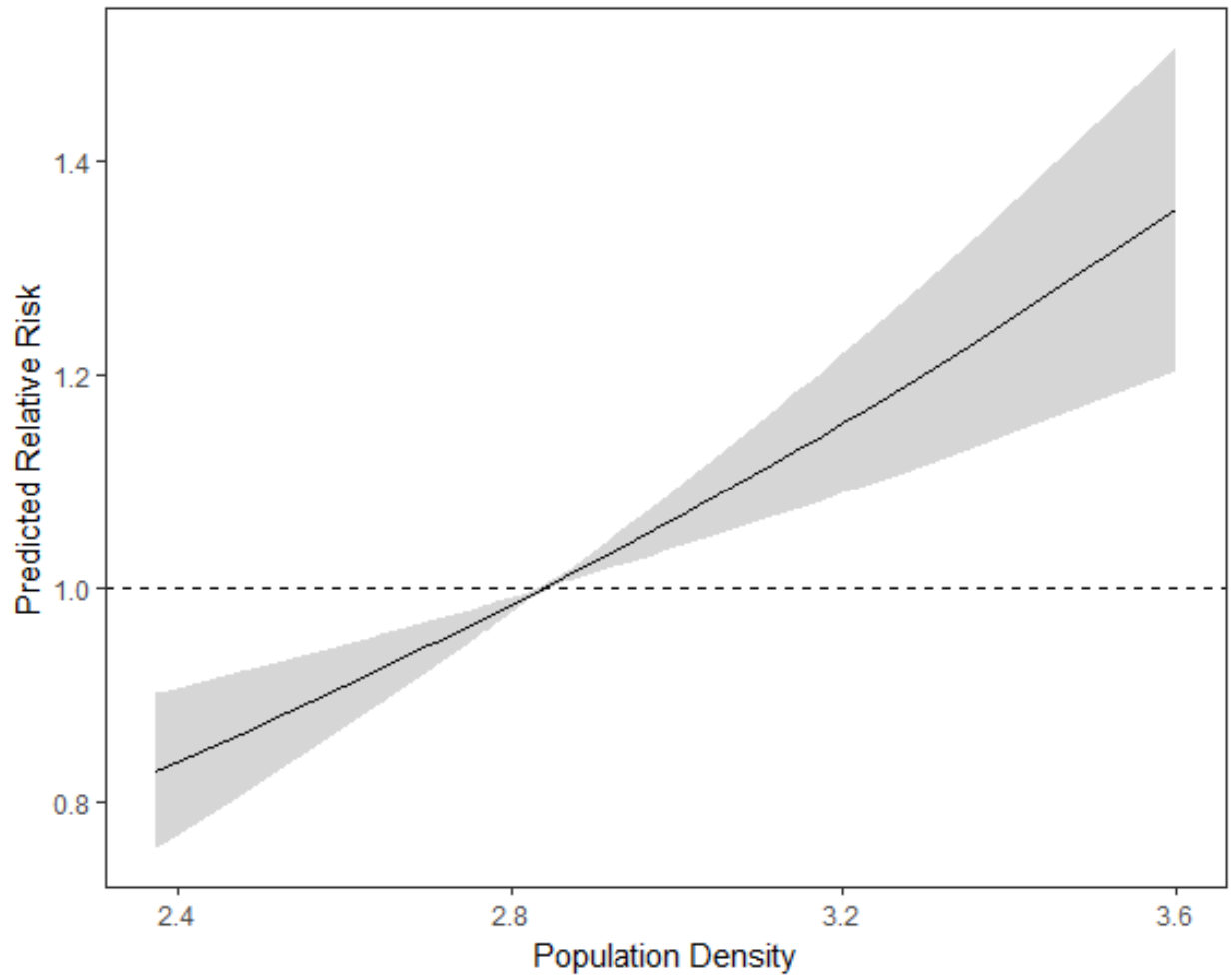


Figure 2.5. Predicted relative risk as a function of population density measured as the total number of birds divided by the total number of territories in April each year.

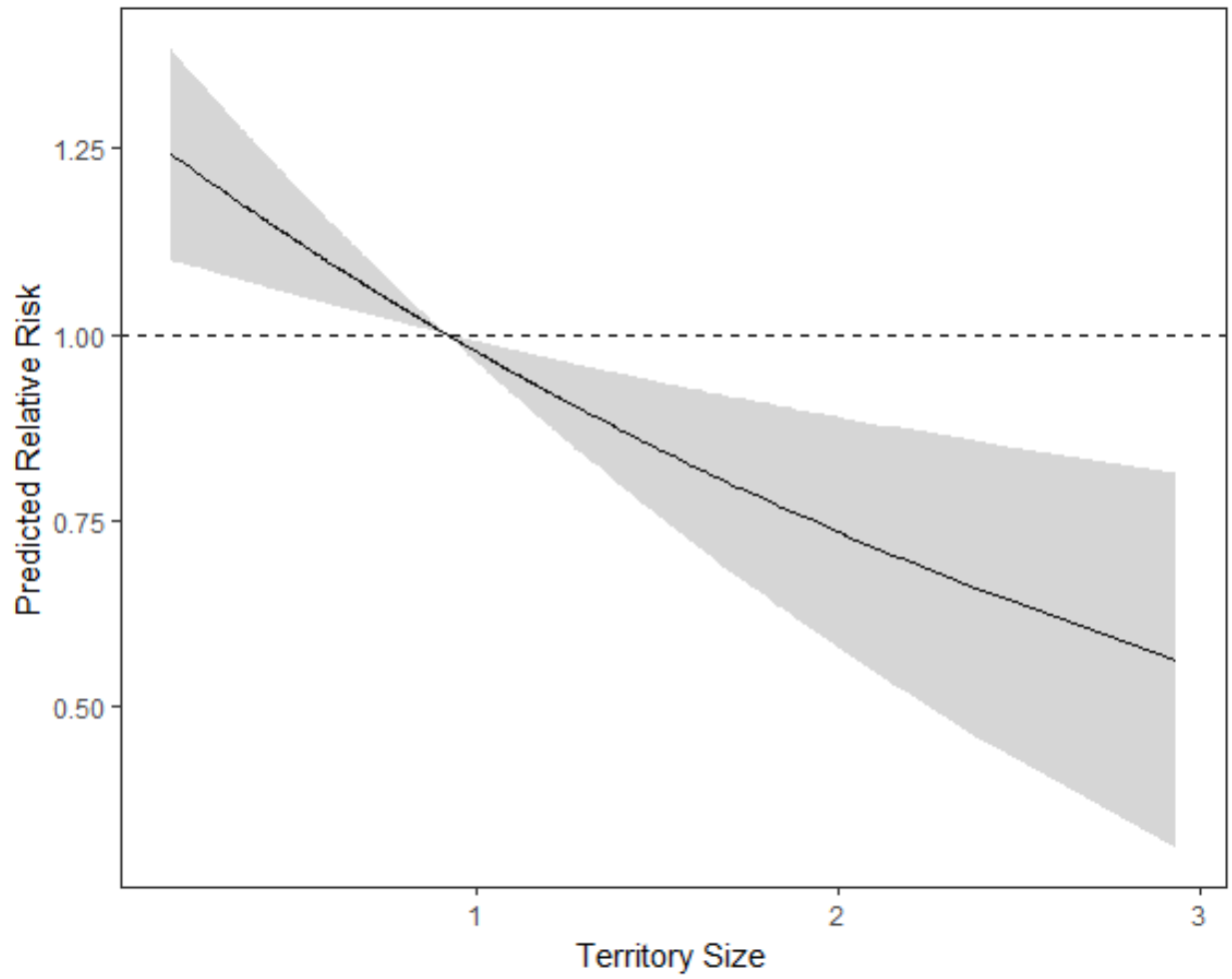


Figure 2.6. Predicted relative risk of mortality as a function of territory size in terms of standard deviations ($N = 1583$).

CHAPTER THREE

Introduction

It has been long recognized that individuals within a population differ in demographic traits, although generally these differences are attributed to sex, age or stage class. Thus, classic population models allow for different demographic rates among these groupings. For example, survival probabilities of juveniles is often lower than mature individuals (Reid et al. 2010; Plard et al. 2015). An assumption widely used in estimating demographic rates is that all individuals within an age or stage class are expected to be homogeneous in this trait. However, over the past few decades, there has been much interest in understanding how phenotypic variation among individuals within these categories can affect estimates of population level parameters, in which rely on growth and transition probabilities (Cam et al. 2012; Plard et al 2015; Vindenes and Langangen 2015).

A substantial body of theoretical research has shown that within-cohort variability in survival can lower the extinction risk in populations (Conner and White 1998; Kendall and Fox 2003) and, if it is persistent throughout the lives of individuals, increase the population growth rate (Kendall et al. 2011). Covariance among individuals in phenotypic traits that affect survival probability reduces the effect of demographic stochasticity, increasing population viability (Kendall and Fox 2002). Variation in traits that affect demographic performance - henceforth "demographic traits" - results from genetic variation, environmental conditions, and their interactions. Phenotypic covariance can be a result of shared environment through cohort and

family or maternal effects. Fates of siblings can be correlated, for example (Gaillard et al. 1998; Pettorelli and Durant 2007) thus, individuals within shared environments are not independent, and we can potentially predict demographic rates as a function of measured traits and unobserved differences among individuals (Kendall and Fox 2002). Phenotypic traits related to fitness are considered to be unobserved or latent and modeling approaches have been developed to incorporate these individual differences in models of fitness components (Cam et al. 2016).

Related individuals, such as siblings or parents and offspring, are correlated through shared genes in addition to maternal or sibling effects. Kinship is a specific type of family effect in the sense that it describes the degree of genetic relatedness among individuals. Kin structure has been shown to influence demographic traits with consequences at the population-level (Lambin et al. 1998; MacColl et al. 2000; Pope 2000). The relationship between kinship and fitness has been well-studied in social species of several taxa (Armitage 1987; Clutton-Brock et al. 2001; Clutton-Brock 2002; Griffin and West 2003). Kin structure across space can also arise in solitary species, often as a result of dispersal behavior and kin recognition, and it can influence survival and reproductive success (Lambin and Yoccoz 1998; Støen et al. 2005). For example, recruitment of red grouse males is dependent on spatial kin structure where family groups occupy territory clusters (MacColl et al. 2000). Thus, kinship is likely to be important in structuring demography in several species, both social and solitary species, and is worth consideration in the estimation of survival and reproductive success.

In this study, we take advantage of 35 year data set of a marked population of Florida Scrub-Jays (*Aphelocoma coerulescens*) to examine the effects of kinship on breeder survival. In a previous study of this population, Fox et al. (2006) found that parent and territory identity were good predictors of breeder survival and provided better fits given the data than models without

those predictors. These results suggest that some aspect of family is important in determining survival of breeding Florida Scrub-Jays (Fox et al. 2006). This species is cooperatively breeding where offspring delay dispersal and help raise young, usually their siblings or half-siblings (Woolfenden and Fitzpatrick 1984). Family groups consist of a breeding pair, juveniles and 0-6 adult helpers that are generally offspring of one or both breeders residing in year-round territories defended from other families (Woolfenden and Fitzpatrick 1984). Florida Scrub-Jays are habitat specialists restricted to oak (*Quercus sp.*) scrub habitats with sandy soils and periodic fire. Their territories provide all their life history needs including food and nesting sites (Woolfenden and Fitzpatrick 1984). Helpers generally disperse by age three; natal dispersal is local although females typically disperse farther and earlier than males (Woolfenden and Fitzpatrick 1984).

The sedentary behavior of Florida Scrub-Jays facilitates re-sighting of individuals over time and offspring can easily be assigned parentage. Florida Scrub-Jays are socially and genetically monogamous, offspring resulting from extra pair copulations is extremely rare (Quinn et al. 1999; Townsend et al. 2011; Chen et al. 2016). Thus, there is an extensive pedigree of this population where over half the breeders were of known-parentage by the mid-1980s. Due to the cooperative behavior and the presence of helpers that can increase fitness of breeders, this data set offers us a rare opportunity to examine the consequences of kinship on demographic traits.

Unlike many previous studies considering kinship structure in demography, we make use of a modeling approach that estimates the variance in survival time due to genetic correlations among individuals (Pankratz et al. 2005). This approach considers an individual's degree of relatedness to all other individuals, instead of just parent or family identity. In the modeling

approach of Fox et al. (2006), frailty terms were used to describe the intra-group correlation in hazard, or the instantaneous risk of dying. The hazard of each group is adjusted based on properties of that group. The shared frailty approach used in Fox et al. (2006) treats each member of a group equally in terms of hazard, so that all members of a family are modeled as having the same hazard. Because of this limitation, Fox et al. (2006) restricted their analyses to groups of individuals with very similar relatedness, such as maternal families. Since then, methods have been developed that permit incorporation of an entire pedigree in the shared frailty model: a kinship matrix is used to describe the correlation structure among individuals in the population (Pankratz et al. 2005; Therneau 2015). This is biologically more realistic and permits improved estimates of hazards and of their components.

Due to social structure and cooperative breeding system, using these approaches can give us insight into some of the consequences of cooperative breeding. The presence of related individuals such as helpers can increase survival of breeders by offsetting costs of reproduction (Clutton-Brock 1988; Paquet et al. 2015). For example, female breeder survival of sociable weavers is positively correlated with the presence of helpers that feed offspring (Paquet et al. 2015). Here, we expand upon the research of Fox et al. (2006) using data from the same marked population of Florida Scrub-Jays but additional 3 years of data and extensive pedigree data for the population. In our analyses, we model dependence among individuals with data from a pedigree of all marked birds in the population beginning in 1978 until the completion of the breeding season in 2016.

We built Cox proportional hazard models and shared frailty models to address the following research methods. What is the expected survival for a breeder, and how much variation is there from year to year? How does survival probability change with age, experience, group

size and territory quality? How much variance is there among families and cohorts? Does fledgling production change breeder survival probability? If so, is there a negative or positive effect of fledgling production on annual survival probability?

Methods

Study Area and Population

All data are derived from a marked population of Florida Scrub-Jays residing at Archbold Biological Station (hereafter, “Archbold”), Highlands County, Florida (27.10°N, 81.21°W). This population has been under continuous study since 1969. Detailed methods are described elsewhere (Woolfenden and Fitzpatrick 1984; Mumme et al. 2015). Briefly, all nestlings hatched on the study tract are banded and weighed at 11 days old then recaptured and weighed as juveniles around 90 days post-hatch. All immigrants that disperse into the study area from nearby scrub are captured and banded. The data consist of known and unknown-age breeder Florida Scrub-Jays from 1981 to 2016 (N = 994). The first breeding cohort considered here is from 1981, meaning all individuals in the data set were classified as breeders for the first time in 1981 or later. The population was supplementally fed prior to this time, so we do not consider data prior to 1981. The pedigree includes individuals back to 1978 to include the parents the breeding cohorts of the 1980’s. Unknown age birds are individuals that have dispersed into the study tract from nearby scrub habitats. There are a greater number of unknown age females (N = 187) than males (N = 123), which is consistent with dispersal patterns in this species.

Territory boundaries are mapped each breeding season during April and May using aerial photography as outlined by Woolfenden & Fitzpatrick (1984). The maps are digitized using ArcGIS (ESRI, Redlands, California, USA). The study area is composed of 5 m² cells in a grid. Controlled burns take place throughout the study area in different return intervals ranging from 2

to 60+ years. Thus, Florida Scrub-Jay territories can encompass multiple burn units. Since the start of the study, the monitored area has increased as Archbold has acquired adjacent properties so there are some territories where the scrub-jays were banded and censused, but the territory lacks data on composition. For analyses examining the effect of territory quality in terms of size and structural composition, we used a smaller data set including breeders where there is data available that describe quality at the breeding territory (N = 480).

Statistical Analyses

We initially estimated median survival using the non-parametric Kaplan-Meier method (cite) across all breeding cohorts from 1981 to 2016. We also estimated survival for each breeding cohort and for males and females separately. Breeding cohort refers to individuals that bred for the first time in the same year. For the remainder of the analyses, we used the Cox family of regression models to analyze mortality risk throughout the breeding lifespan. Cox models are appropriate for time to event data and can accommodate censored data (Therneau and Grambsch 2000). Right censored data result when the event of interest does not occur during the observation period, or the individual exits the study or observation period before an event occurs. In this case, all we know is that the event time exceeds the observation time (Fox 2001).

The breeding lifespan begins when birds are classified as a breeder ($t = 0$) to death or right censorship. Individuals still alive as of the monthly census in April 2016 were right-censored (i.e., their death dates are unknown but greater than the April 2016 census). Individual scrub-jays transition to the breeding stage once they lay or sire an egg and they remain in that stage till death, regardless of breeding success. Individuals enter this stage at different ages, but typically Florida Scrub-Jay adults become breeders at age 2 or 3 (Figure 1). Immigrants that dispersed into the study area are of unknown age but they are at least one year old. Breeders are

faithful to their established territories and it is very unlikely for breeders to disperse off the study tract (Woolfenden and Fitzpatrick 1984). Breeders do not disperse; if they move, it is to a nearby territory (McDonald et al. 1996) Thus, when a breeder disappears from the monthly censuses, it is overwhelmingly likely that it is dead: no breeder has ever disappeared for longer than one census and been resighted, and no breeder has ever been found breeding elsewhere in the region (Woolfenden and Fitzpatrick 1984; McDonald et al. 1996; Mumme 2000).

We first fit standard Cox proportional hazard models (Therneau and Grambsch 2000) to estimate survival probability with sex, breeding cohort, and age at first breeding as covariates. Breeding cohort year was modeled as a factor in the proportional hazard models. Cox models can be extended to cases where hazards are not proportional over time or where covariate values are updated during the entire follow-up time (Therneau and Grambsch 2000; Thomas and Reyes 2014). The follow-up time is split into intervals where the value of covariates is recorded at the beginning of the interval and stays the same until the start of the next interval, when the covariate value is updated. Individuals enter each interval until censorship or death. These models require that the time intervals are specified, although they do not need to be equally spaced (Thomas and Reyes 2014).

For the time-varying Cox models, we use an interval of one year, or until death. Territory size, group size, age and fledgling number change at the beginning of each time interval. Group size was measured as the number of adults present at the breeding territory at each April census. We considered territory quality with a smaller data set ($N = 480$) excluding breeders residing in territories without this information. Territory size, amount of oak scrub and amount of territory in the 2 – 9 year fire return interval all reflect territory quality. All three are positively correlated so we performed a principal component analysis. The first principal component represented all

three variables and accounted for 72% of the variance so we used territory size for easier biological interpretation. We transformed territory size by standardizing whereby the values are in terms of standard deviations.

Finally, we fit Cox models with mixed effects, which are equivalent to shared frailty models (Therneau and Grambsch 2000; another). Frailty refers to excess risk in survival time, where some individuals are more frail than others, and will experience an event sooner than more robust individuals (Therneau & Grambsch 2000; Wienke 2010; Govindarajulu et al. 2011). Frailty terms modify the hazard function for individuals within groups that share some characteristic, such as families or birth cohorts. The frailty terms in Cox models are estimated from a Gaussian distribution with a mean of 0 and a variance-covariance matrix Σ that describes the structure of correlations between individuals (Therneau, Grambsch, & Pankratz 2003; Pankratz, de Andrade & Therneau 2005). Nest year or current year was included as a random term instead of a fixed effect or factor as described above.

An additional advantage of using mixed effects or frailty models is incorporation of a kinship matrix constructed from a pedigree. Using a covariance structure in models of survival from the kinship matrix is preferable to the shared frailty approach of Fox et al. (2006), because members of a family are not treated uniformly but instead the shared frailties are estimated from the degree of genetic relatedness. We constructed a pedigree object in R from the complete pedigree based on parental data using the package kinship2 1.6.4 (Therneau & Sinnwell 2015). We then used this pedigree to estimate the kinship matrix for individuals in the population. All analyses were performed in R 3.3.2 (R Development Core Team, 2016).

Results

The breeding lifespan is highly variable among cohorts for Florida Scrub-Jay breeders with similar means and variances for both sexes (Figure 1). The standard deviation in breeding life span is nearly as large as the mean for males and females (3.35 ± 3.08 & 3.32 ± 2.85 , respectively). The pooled estimate of cumulative survival from the Kaplan-Meier survival estimates show, on average, half of a breeder cohort has died after 2 years of breeding (Figure 2). Breeder survival does not differ between the sexes until later ages, and then only slightly (Figure 3). The coefficient for sex (male) in the Cox model is negative but not significant ($\exp(\beta) = 0.92$, $z = -1.10$, $p = 0.27$).

Hazards are approximately proportional for males and females until near the maximum breeding lifespan, where female survival is lower than males (Figure 3). Age at first breeding is positively correlated with mortality risk during the breeding lifespan where the older the individual at time of first breeding, the higher the mortality risk relative to jays breeding for the first time at younger ages (Figure 4). The best fitting proportional hazard models include age at first breeding and sex (Table 1). The best fitting time-varying model was a mixed effect model with age at 1st breeding and group size as fixed effects and nest year as a random effect (Table 2). Models with sex and current age as an additional fixed effects and kinship have similar support (Table 2). Fledge number is not a significant predictor of mortality hazard ($\exp(\beta) = 1.02$, $z = 0.81$, $p = 0.42$) and it is not included in the best fitting models, as determined by AIC (Table 2). Group size and mortality risk are negatively correlated, where each additional group member decreases risk by 7% (Figure 5). Territory size and mortality risk are negatively correlated, where a one standard deviation increase in territory size leads to a 10% decrease in risk. There is support for the interaction term between group size and territory size with a

positive relationship between the interaction and hazard ($\exp(\beta) = 1.17$, $z = 1.96$, $p = 0.050$, Table 3).

The best fitting model of the set with territory size includes nest year only with no fixed effects (Table 3). Territory size and group size are included as fixed effects in models within two AIC units of the best-fitting (Table 3). Kinship is included as an additional random effect in the top fitting models (Table 3). The estimated variance component for kinship varies drastically between models without territory size ($N = 812$) and models with territory size as a predictor ($N = 480$) (Table 4). The estimate for nest year is different for each set of models, but difference is not nearly as large as the difference in estimates for kinship (Table 4). Kinship changes risk from 2 to 31% relative to the average mortality risk, depending on the model set (Table 4). Breeders have a 20-29% increase or reduction in risk due to current nest year, relative to the risk of individuals in an average year.

Discussion

We found that kinship affects mortality risk where the spread of risk is up to 31%, meaning that risk can be up to 31% larger or smaller relative to the mean risk (Table 4). However, in models including territory size, the estimated variance for kinship is low (Table 4). The estimated relative risk is only 2%. This might appear to be a large discrepancy between estimates, but it merely reflects the fact that in this observational study kinship is not separable from territory. Due to the nature of the study and observational data, the effects of kinship include both genetic and non-genetic components. We found a distinct effect of kinship from territory size in the fledgling and juvenile stages; the estimates for the kinship variance components were much higher, even when territory size was included. The relative risk estimate was 77% from models with territory size, and 90% in models without (Feichtinger et al.). Fox et

al. (2006) found that territory identity reduced model deviance more than a homogenous survival model, as did maternal and paternal identity. The dispersal behavior and territory acquisition strategies of this species could result in a kin structure across space. Males can inherit their natal territory or they can bud a breeding space from the natal territory (Woolfenden and Fitzpatrick 1984). These two strategies can result in related individuals in adjacent territories. Studies of different taxa have shown that dispersal patterns result in kin clusters, and this spatial arrangement of kin can influence reproductive success and survival, as demonstrated for microtine voles (Lambin and Yoccoz 1998), howler monkeys (Pope 2000), red grouse (MacColl et al. 2000), and brown bears (Støen et al. 2005). Group size also impacts mortality risk in precisely the way one might expect for a cooperative breeder: larger groups have lower hazard (Figure 5). Helpers can potentially increase survival of breeders by lowering the cost of reproduction for breeders by bringing reducing provisioning effort of the parents (Hatchwell 2009). Paquet et al. (2015) found that helpers increase survival of breeder female sociable weavers, but decrease the survival of males, although this effect diminishes with age. Non-breeding adult Florida Scrub-Jays participate in territory defense and anti-predator behavior in addition to feeding nestlings. Florida Scrub-Jays have a sentinel system whereby group members trade foraging with watching the territory for intruders and predators (Woolfenden and Fitzpatrick 1984). From our analyses we cannot tease apart the effects of reducing provisioning effort and predator detection on breeder survival, but it's likely that both mechanisms are important.

Pre-breeders are generally offspring of one or both breeders, so larger groups are a result of past reproductive success. These families may be able to hold on to larger, high quality territories whereby survival of nestlings is a function of kinship, brood size, group size, and

territory size mediated through nestling and juvenile body mass (Mumme et al. 2015, Feichtinger et al.). Increasing territory size by one standard deviation above the average decreases mortality risk by 10%. Large territories likely have more resources, including food, nesting sites and open areas from fire that provide places to forage.

Cooperatively breeding species are of special interest in studies of kinship and demography because of the relationship between helping behavior and fitness. In these systems, there are mature individuals called helpers that help raise offspring of related or non-related individuals (Paquet et al. 2015). There is a large body of literature on kin selection, indirect and direct fitness benefits of helping and the evolution of cooperation (e.g. Clutton-Brock 2002; Hatchwell 2009; Griffin and West 2003). Hamilton (1969) proposed that helpers accrue indirect fitness benefits by increasing survival and reproductive success of related individuals. Recently, there is interest in the direct benefits of helping (Clutton-Brock 2002; Griffin and West 2002).

Age at first breeding, year, and kinship structure survival during the breeder stage of Florida Scrub-Jays. Individuals generally start breeding at ages 2 or 3, with very few breeding at 1 year and few waiting for longer than 3 years post-fledge (Figure 1). Entering the breeder stage at an older age increases hazard, although it is not clear if being an older breeder is inherently riskier, or if the mortality risk is higher simply because older first time breeders are closer to the expected lifespan. Males and females have similar mortality risk until around 8 years breeding, or approximately 10 or 11 years old. (Figure 2). Females may senesce faster than males at old ages and, there is some evidence of female reproductive senescence in the species (Wilcoxon et al. 2013), but the sample size is small since so few jays survive for more than 10 years. This is the first use of a pedigree for estimating survival in a wild population.

Fledgling number does not have much impact on breeder survival (Table 2), but we used an interval of one year in our analyses. It's possible that there is a cost of reproduction on survival, especially for females, but this cost diminishes throughout the year. For future analyses, we could split the year into smaller time intervals, such as months, to further explore this hypothesis.

We found that variation in survival of breeders is mainly driven by year to year variability in environmental conditions, and family identity, with an effect of group size, age at first breeding and territory size. Disease prevalence, abundance of predators, and climatic conditions such as precipitation are some of the environmental conditions that can vary year to year and influence survival of breeders. Drought may result in food stress, lowering survival, whereas precipitation may increase arthropod abundance, an important food resource, and increase survival. However, increased rainfall may also increase the abundance of disease vectors. Florida Scrub-Jays are susceptible to viral and bacterial infections, with periodic epidemics of vector-borne diseases such as avian malaria or encephalitis occurring on the study tract (Wilcoxon et al. 2010). Thus, there is likely a non-linear relationship between precipitation and survival. Future analyses could consider precipitation during different parts of the year (winter and summer, for example) as a predictor to further explain variation in breeder survival.

Individual heterogeneity can be especially pronounced in small populations with a noticeable effect on population growth rate, net reproductive rate and generation time (Conner and White 1998). Florida Scrub-Jays are a federally Threatened species that has experienced a sharp decline in numbers due to development and habitat degradation, particularly fire suppression. These birds are habitat specialists with short-distance dispersal. Habitat connectivity has been lost and it has been estimated their numbers have declined by 90% since the beginning

of the twentieth century (Root 1998). Thus, ignoring unobserved variation could bias population level estimates of this species. Future research can investigate the effects of variation in breeder survival due to kinship on estimates of population dynamics and viability.

We have demonstrated that Florida Scrub-Jay breeder survival is a function of yearly environmental variation, kinship, age, group size and territory size. When territory quality is not considered, kinship has a strong effect on breeder survival, where mortality risk can increase or decrease by 31% from the degree of relatedness to other individuals in the population. However, this effect is diminished when territory size is included. This may indicate a kinship structure over space closely tied to territory, where related individuals occupy adjacent territories. Yearly variation strongly affects survival of breeders, and future research may consider variation among families or lineages in performance of different year types. This study highlights the potential importance of kinship in determining demographic rates of a cooperatively breeding species. Future research should focus on disentangling the effect of territory and kinship on survival of breeding Florida Scrub-Jays.

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Tables

Table 3.1. Model selection of Cox proportional hazard models for mortality risk of male and female Florida Scrub-Jay (*Aphelocoma coerulescens*) breeders from 1981 – 2016 (N = 994). Age refers to the minimum age at first breeding. Individuals hatched on the study tract are of known age, but most immigrants to the population are assigned a minimum age, usually 2 years old. Cohort refers to breeding cohort, or the first year bred.

Model	K	AIC	ΔAIC
Age at 1 st breeding	1	9912.89	0.00
Age at 1 st breeding + Sex	2	9913.79	0.90
Age at 1 st breeding + Sex + Breeding Cohort + Sex X Age	38	9931.20	18.31
Age at 1 st breeding + Breeding Cohort	36	9933.01	20.12
Age + Sex + Breeding Cohort	37	9934.12	21.23

Table 3.2. Model selection for time-varying Cox models with random effects (N = 812). Group size is a count of individuals present at the territory at the April census each year. Age refers to current age, as opposed to age when breeding for the first time. Nest year is the current breeding year. Kinship and nest year are random terms derived from a Gaussian distribution with a mean = 0 and a covariance matrix Σ .

Model	K	AIC	Δ AIC
Age at 1 st breeding + Group Size + Nest Year	3	9391.36	0.00
Age at 1 st breeding + Group Size + Sex + Nest Year	4	9391.84	0.48
Age at 1 st breeding + Group Size + Age + Nest Year	4	9392.51	1.15
Age at 1 st breeding + Group Size + Nest Year + Kinship	4	9392.73	1.37
Age at 1 st breeding + Group Size + Sex + Nest Year + Kinship	5	9393.62	2.26
Age at 1 st breeding + Group Size + Age + Nest Year + Kinship	5	9393.97	2.61
Age at 1 st breeding + Group Size + Fledge Number + Nest Year + Kinship	5	9394.17	2.81

Table 3.3. Model selection for mixed effects Cox models with time-varying covariates of mortality risk of breeder Florida Scrub-Jays in territories where there is information on territory composition (N = 480). Kinship and nest year are random effects derived from a Gaussian distribution with a mean = 0 and a covariance matrix Σ . The kinship matrix derived from the population's pedigree is used as the covariance structure. Nest year is the current year.

Model	K	AIC	Δ AIC
Nest Year	1	5087.87	0.00
Age 1 st breeding + Territory Size + Nest Year	3	5089.55	1.69
Age 1 st breeding + Group Size X Territory Size + Nest Year	5	5089.65	1.79
Age 1 st breeding + Group Size + Nest Year	3	5089.78	1.91
Nest Year + Kinship	2	5089.87	2.00
Age 1 st breeding + Territory Size + Kinship + Nest Year	4	5091.55	3.69
Age 1 st breeding + Group Size X Territory Size + Nest Year + Kinship	6	5091.78	3.91

Table 3.4. Relative risk estimates for the random effects or shared frailty terms for the best supported model with kinship as a random term with a territory quality variable (N = 480) and without (N = 812). Age at 1st breeding, group size and territory size are fixed effects. Relative risk can be estimated from exponentiation of the standard deviation of the variance component $\exp(\sqrt{Var})$.

Model	Term	Relative Risk
Age at 1 st breeding + Group Size + Kinship + Year	Kinship	0.31
	Nest Year	0.29
Age at 1 st breeding + Territory Size + Kinship + Nest Year	Kinship	0.02
	Nest Year	0.20

Figures

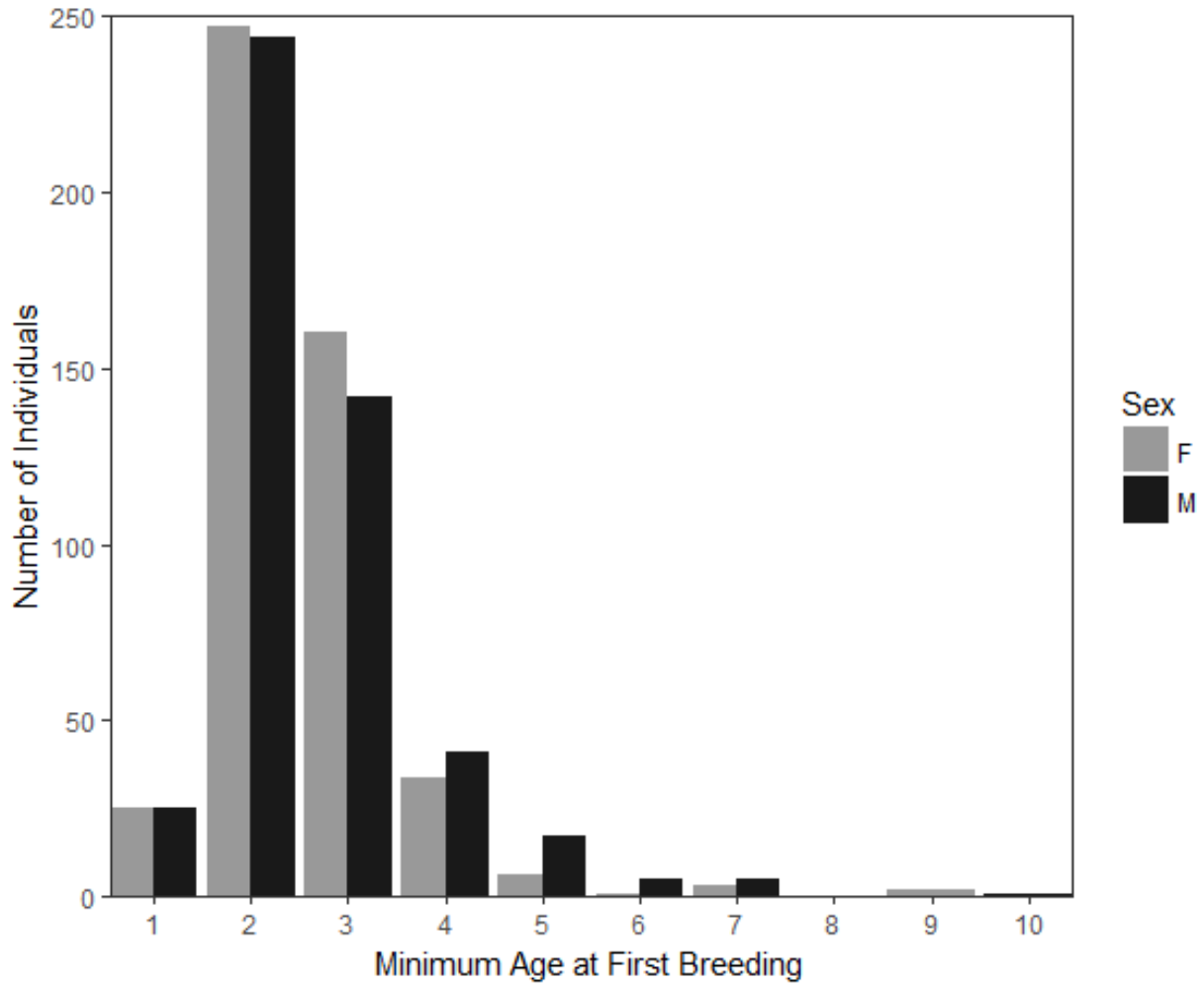


Figure 3.1. Distribution of ages at first breeding for male and female Florida Scrub-Jays from 1981 to 2015 (N = 958) at Archbold Biological Station. Some breeders in the population have dispersed into the study tract and therefore the exact age is unknown.

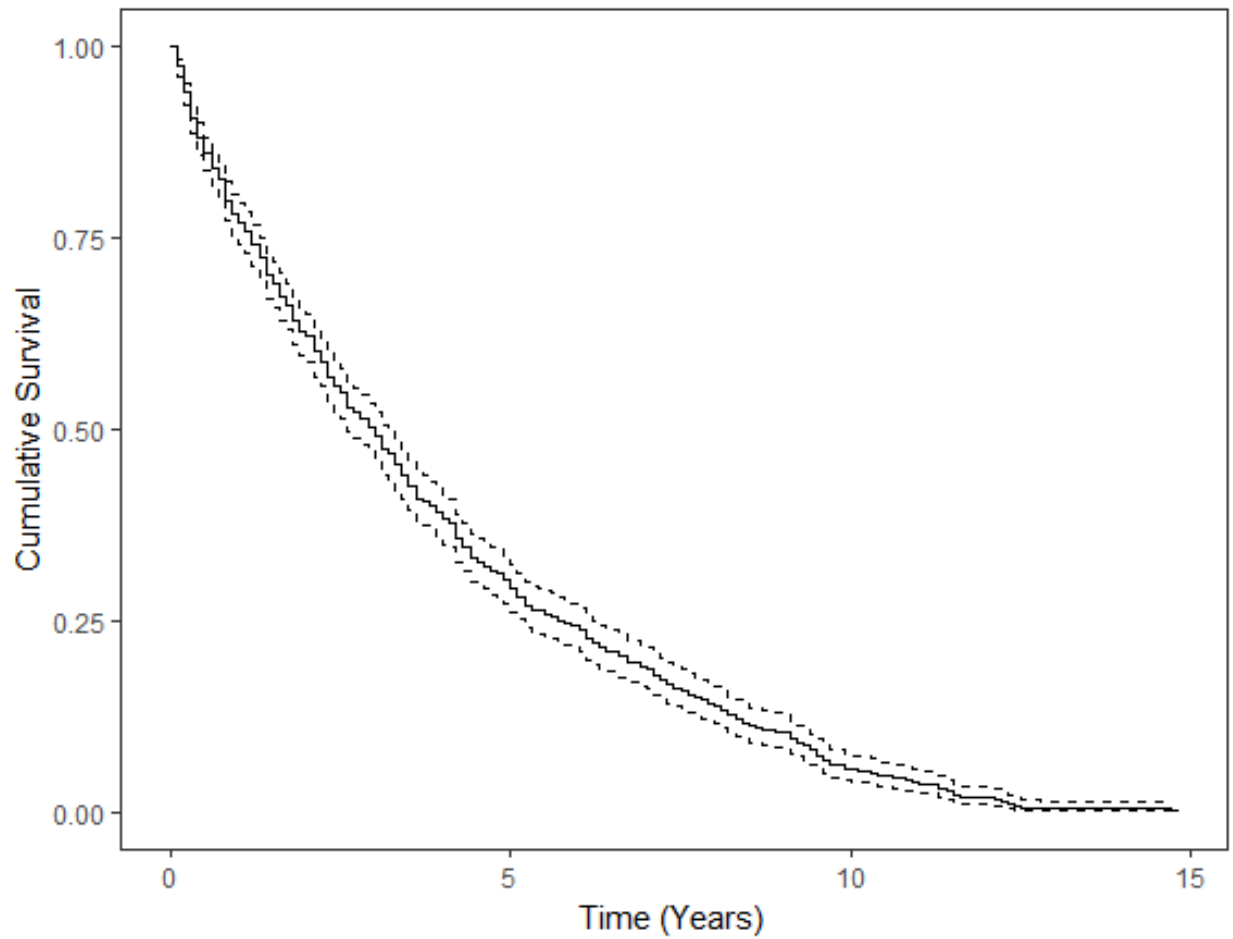


Figure 3.2. Kaplan-Meier survival estimate for Florida Scrub-Jay breeders in a marked population residing at Archbold Biological Station for all breeder cohorts from 1981 – 2016 (N = 994). The interval starts the day individuals lay or sire an egg for the first time and ends at death or right censorship, which are individuals still alive as of April 2016. Thus, the time scale represents the breeding time-span, not age in years.

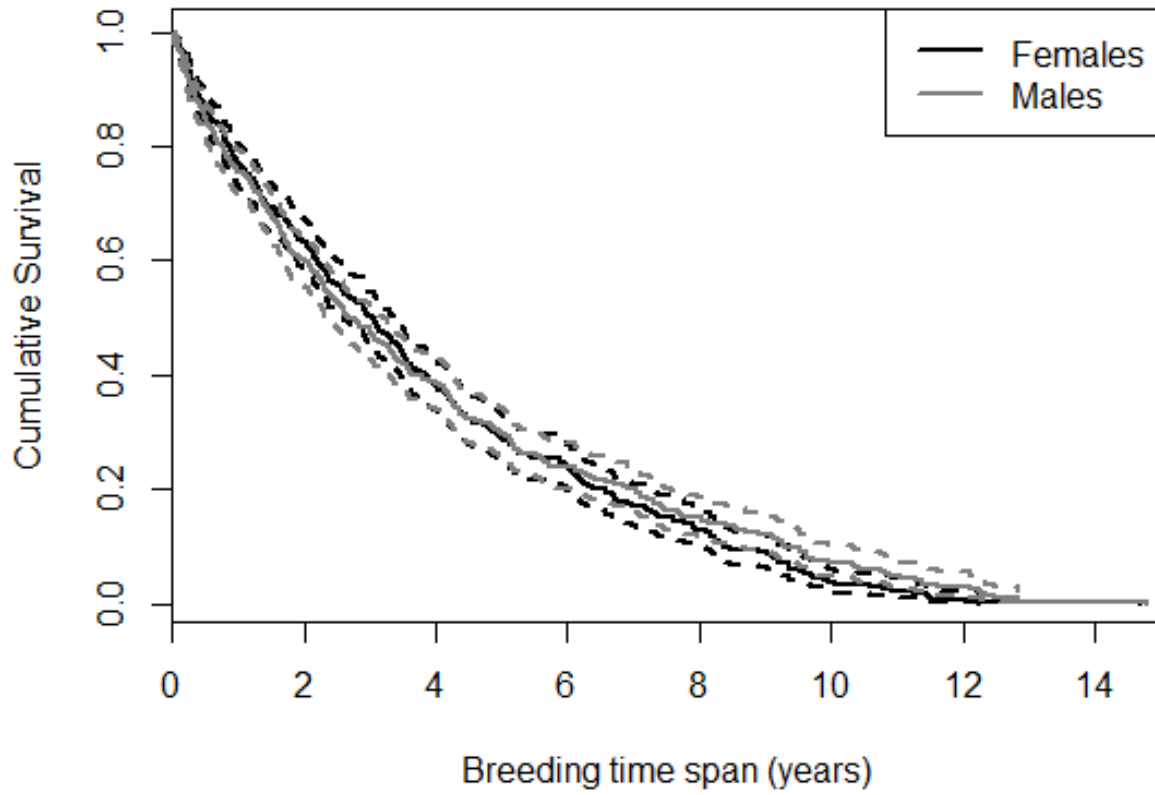


Figure 3.3. Kaplan-Meier survival estimate for male and female Florida Scrub-Jay breeders (N = 480, 478, respectively) across all years from 1981 – 2016.

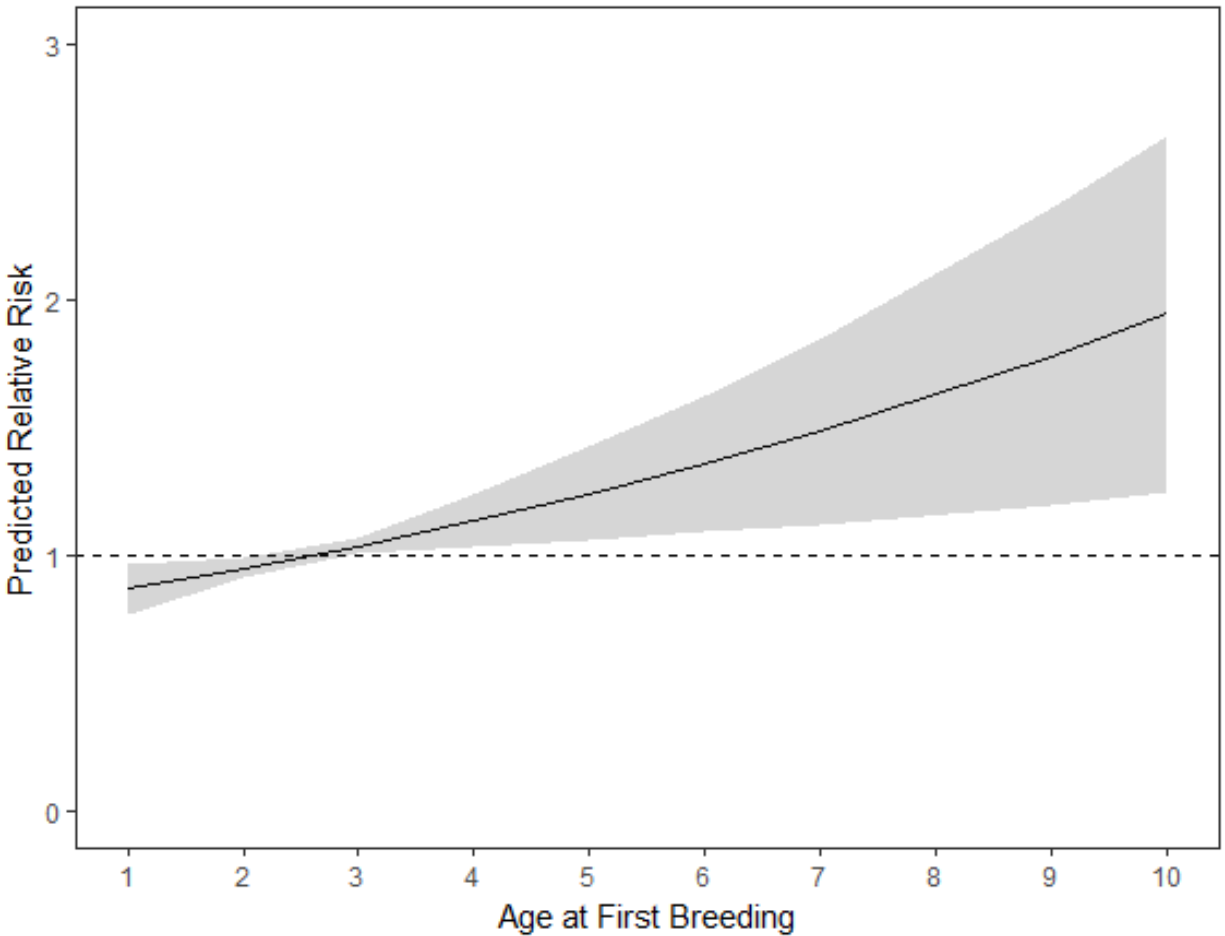


Figure 3.4. Predicted relative risk from a Cox proportional hazard model for age at first breeding for Florida Scrub-Jays. Individuals hatched on the study area are of known age, while immigrants are assigned a minimum age, which is usually age 2. Individual hazard is relative to the reference group, here it is age at first breeding and represented by the dashed line. The shaded region represents the upper and lower 95% confidence intervals.

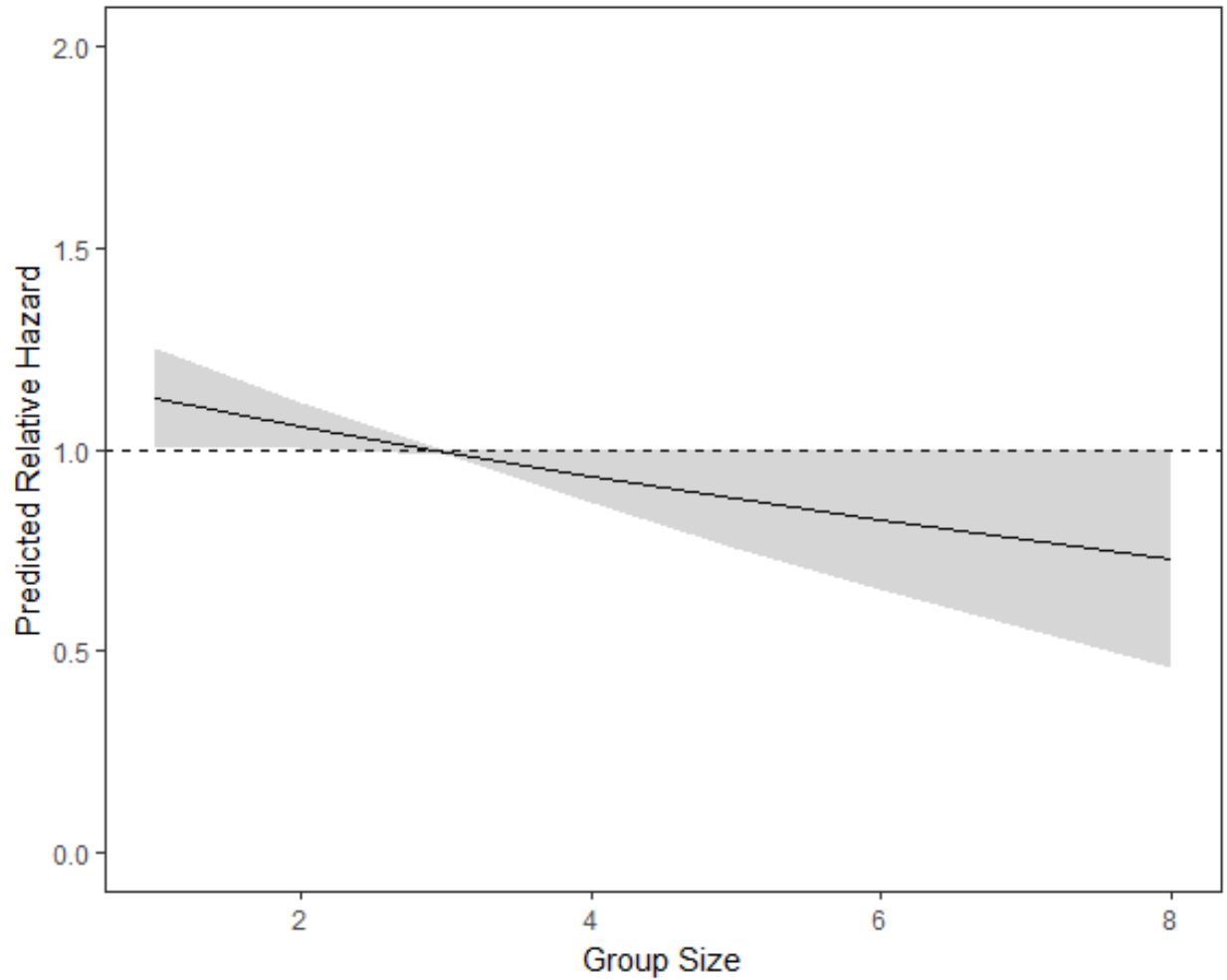


Figure 3.5. Relative risk as a function of group size across individual Florida Scrub-Jay breeding lifespans. Hazard is estimated for the mean group size where the hazard ratio is 1.0. The mean group size is where the predicted hazard line crosses the dashed line. The shaded region represents the upper and lower 95% confidence intervals.