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ECOLOGICAL CAUSES OF LIFE HISTORY VARIATION TESTED BY META-ANALYSIS, COMPARISON, AND EXPERIMENTAL APPROACHES

By

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Ecological Causes of Life History Variation

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The ecological causes of life history variation among taxa and the arrangement of such variation along geographic gradients is enigmatic despite the proximity of life history traits to fitness and implications for understanding basic and applied population ecology. One classic explanation for the arrangement of avian life histories along a ‘slow-fast’ gradient, where species at low latitudes have ‘slow’ life history traits (low fecundity and mortality) and species at high latitudes have ‘fast’ life history traits (high fecundity and mortality), is the increase in seasonality of resources with increasing latitude (Ashmole’s hypothesis). Despite broad acceptance, this hypothesis has been supported only indirectly. I tested two key predictions of this hypothesis – that most mortality occurs in winter and that most mortality is caused by starvation – using meta-analysis. Surprisingly, in many populations, the season of greatest mortality was summer, and most mortality was caused by predation. These results suggest alternative explanations for life history variation should remain under consideration despite support for Ashmole’s hypothesis.

The relationship between provisioning behavior and offspring number was long recognized to integrate key life history tradeoffs between number and quality of offspring and between current and future reproductive success. Studies of the response of parental provisioning behavior to brood size variation played a formative role in the development of life history theory. Yet, the inference of such experiments for explaining among-species differences has always been limited by lack of comparative context. I expanded predictions of alternative ecological explanations (food limitation, nest predation, adult mortality) for life history variation to an among-species context and test these predictions using a comparative-experimental design across a broad range of bird species from three continents. I found resource limitation and adult mortality risk interact to explain variation among species in responses to natural and experimental variation in brood size, with the degree of food limitation appearing to vary across a gradient of adult mortality risk. This result helps to explain the potentially conflicting results of previous studies and suggests a pluralistic approach to understanding what factors explain life history variation may be fruitful.

Understanding variation among species in mortality rates may thus be pivotal to understanding ecological causes of life history variation. To this end, I compared differences in spatiotemporal variance in survival among three temperate-breeding species with differing migratory strategy. I found that migratory behavior may be associated with reduced spatial variance in annual survival because resident species disperse less, reducing population connectivity. I also found that migratory behavior is associated with increased temporal variance in survival, counter to expectations of general theory. Given the potential importance of mortality risk in life history evolution, expanded geographic comparisons of annual and within-year patterns of variance in survival rates is likely key to understanding variation among species in life history traits.

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Chapter 1: Introduction

The expression of life history traits, or age-specific components of fecundity and mortality, determines the fitness of individuals and the growth rates of populations (Roff 2002). This deterministic relationship between life history traits, fitness, and population growth motivates a central role for life history theory in evolutionary ecology (Stearns 1992). A widely recognized yet still poorly-explained pattern in the expression of life history traits is variation among populations or species in fecundity and mortality (Stearns 1992, Ricklefs 2000, Roff 2002, Martin 2004). This pattern is perhaps best described as a 'slow-fast' gradient, along which 'slow' populations express low fecundity and low mortality, while 'fast' populations express high fecundity and mortality (Bennett and Owens 2002). Despite the near-universality of this pattern in vertebrates (Dunham and Miles 1985, Gaillard et al. 1989, Clobert et al. 1998, Rochet et al. 2000) and its consequences for evolution (e.g. Stearns 1992), population ecology (e.g. Sæther and Bakke 2000), and conservation biology (e.g. Heppell 1998), our understanding of the causes of this pattern remains poor at best.

Life history theory largely explains this broad pattern of variation among populations through tradeoffs between traits (Stearns 1989), ecological differences among populations that cause natural selection on life history traits (Roff 2002), and phylogenetic effects of shared evolutionary history on differences among species in expression of traits (Owens and Bennett 1995). Tradeoffs are invoked to explain why variation is constrained to occur along a slow-fast gradient despite persistent natural selection for increased fecundity and decreased mortality (Stearns 1989). Yet, tradeoffs do not alone explain why some species are 'fast' and some are 'slow' (Roff 2002). Ecological differences among populations in resource availability (Lack

1947) or extrinsic mortality factors (Moreau 1944, Skutch 1949, Stearns 1992) are widely invoked to explain the positioning of species along this slow-fast gradient. This line of reasoning is supported by geographic patterns in variation among species in life history traits (Jetz et al. 2008). Life history traits frequently covary strongly with latitude, suggesting that some ecological factor that also covaries with latitude is responsible (Hussell 1985). In terrestrial birds, species that occur at high latitudes display 'fast' life history traits (high fecundity and mortality) while species that occur at low latitudes display 'slow' life history traits (low fecundity and mortality), independent of shared phylogenetic history (Martin et al. 2000, Martin and Ghalambor 2001, Jetz et al. 2008). The recognition of the strength and enigmatic nature of this pattern in terrestrial birds (Moreau 1944, Lack 1947, Skutch 1949) drove the early development of general life history theory (Stearns 1992, Ricklefs 2000, Martin 2004) and remains an active area of research 60 years later.

Despite enduring research interest in explaining the ecological factors responsible for latitudinal gradients in the life history variation of birds, numerous questions remain. Several leading explanations for geographic patterns in life history variation invoke unvalidated assumptions and are supported only by relatively indirect evidence (Stearns 1992, Roff 2002). In Chapter 2, I test two generally untested and unrecognized mechanistic predictions of Ashmole's hypothesis (Ashmole 1961, 1963), a leading explanation for geographic variation in bird life histories. This hypothesis is predicated on density-dependent mortality caused by geographic variation in the seasonal dynamics of resource availability (Ricklefs 1980, Jetz et al. 2008, Ricklefs 2010). My results are contrary to two simple predictions of this hypothesis: first that most mortality should occur in seasons of low resources (i.e. winter) and second, that most mortality should be caused by starvation. Instead, a diversity of terrestrial bird species appear to commonly display greatest seasonal mortality rates in the summer, and the leading proximate cause of mortality is predation (Chapter 2). This raises key questions about the validity of this hypothesis despite general acceptance (Jetz et al. 2008, Ricklefs 2010) based on more indirect forms of support (reviewed in Chapter 2) and suggests consideration of alternative explanations, or proposal of new explanations, for geographic patterns in life history variation.

One classic context in which alternative ecological explanations for variation in the expression of life history traits have been tested is studies of the response of parental behaviors to natural or experimentally-induced variation in brood size (Nur 1984, Linden and Moller 1989, VanderWerf 1992). While many of these experiments were designed to test explanations for differences among species in life history variation, their design has been limited to single species, making generalization to an among-species context uncertain (Martin 2004). I expanded the predictions of this now-classic study design to an among-species context to allow tests for general ecological explanations for among-species variation in life history traits (Chapter 3). I then tested these predictions using a combination of comparison (29 species) and comparative experiment (9 species) from 4 study sites on 3 continents (Chapter 3). Species differed in the response of parental care, measured as provisioning rates, to natural and experimental variation in brood size, and the differences among species were explained by apparent food limitation *and* differences in adult mortality risk. My results suggest that food limitation and adult mortality risk may interact to explain the observed geographic variation in bird life history traits, which helps resolve potentially conflicting results of previous studies (e.g. Golet et al. 1998) and emphasizes that pluralist approaches may be important to ultimately understanding what ecological factors play a role in life history evolution.

Given the potential importance of adult mortality risk in explaining geographic patterns in life history variation (Chapter 3) and the role that spatiotemporal variance in mortality risk may play in population growth (Tuljapurkar 1982) and life history evolution (Roff 2002), I examined how differences among species in dispersal behavior and migratory behavior may influence spatiotemporal variance in survival rates (Chapter 4). I found that increasing dispersal among three species with differing migratory behavior (from residency to long-distance migration) was associated with increasing migratory distance and with reduced spatial variance in survival rates (Chapter 4). Yet, temporal variance in survival was not related to migratory distance as previously predicted (Greenberg 1980). Here, I have begun to address an important question raised by this dissertation that will likely be a productive target of future research: considering the potential importance of mortality rates in life history evolution, what explains geographic variation within and among species in mortality risk?

My results suggest mortality risk is important in explaining geographic variation in life histories, yet we do not know why mortality risk varies geographically. Is this variation driven by resource dynamics, predation risk, an interaction between the two, or some other ecological factor that may covary with latitude? Do differences among species in other traits, such as migratory behavior, partly explain differences in mortality risk? Do species with alternative life history strategies resolve life history tradeoffs, other than the tradeoff between number and quality of offspring I have compared among species here, differently? While I have addressed the timing and proximate causes of mortality in published studies of wild bird populations (Chapter 2) and compared how three species differ in spatiotemporal variance in survival (Chapter 4), there is a clear paucity of such information for tropical bird species, and thus understanding whether and how such patterns in mortality risk vary geographically remains an open question.

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Chapter 2: Timing and proximate causes of mortality in wild bird populations: testing Ashmole's hypothesis

Daniel C. Barton and Thomas E. Martin

Abstract

1. Fecundity in birds is widely recognized to increase with latitude across diverse phylogenetic groups and regions, yet the causes of this variation remain enigmatic.
2. Ashmole's hypothesis is one of the most broadly accepted explanations for this pattern. This hypothesis suggests that increasing seasonality leads to increasing overwinter mortality due to resource scarcity during the lean season (e.g., winter) in higher latitude climates. This mortality is then thought to yield increased per-capita resources for breeding that allow larger clutch sizes at high latitudes. Support for this hypothesis has been based on indirect tests, whereas the underlying mechanisms and assumptions remain poorly explored.
3. We used a meta-analysis of over 150 published studies to test two underlying and critical assumptions of Ashmole's hypothesis: first, that adult mortality is greatest during the season of greatest resource scarcity, and second, that most mortality is caused by starvation.
4. We found that the lean season (winter) was generally not the season of greatest mortality. Instead, spring or summer was most frequently the season of greatest mortality. Moreover, monthly survival rates were not explained by monthly productivity, again

opposing predictions from Ashmole's hypothesis. Finally, predation, rather than starvation, was the most frequent proximate cause of mortality.

5. Our results do not support the mechanistic predictions of Ashmole's hypothesis, and suggest alternative explanations of latitudinal variation in clutch size should remain under consideration. Our meta-analysis also highlights a paucity of data available on the timing and causes of mortality in many bird populations, particularly tropical bird populations, despite the clear theoretical and empirical importance of such data.

Key-words seasonal mortality, cause-specific mortality, life history, evolution, latitudinal gradient

Introduction

Explaining life history variation among species is a principle goal of evolutionary biology due to the importance of life history traits to fitness (Roff 2002) and population dynamics (Sæther & Bakke 2000). A long-recognized yet enigmatic pattern in life history variation is the increase in fecundity (clutch size) among terrestrial species birds with increasing latitude (Moreau 1944; Lack 1947; Skutch 1949). Replication of this pattern across diverse phylogenetic groups of birds on multiple continents suggests that an environmental factor that covaries with latitude is responsible (Martin 1996; Jetz, Sekercioglu & Böhning-Gaese 2008). Alternative environmental factors proposed to explain this pattern include day length (Hussell 1985), food availability (Lack 1947), nest predation risk (Skutch 1949), adult mortality risk (Law 1979; Martin 2004), and seasonality of resources (Ashmole 1961, 1963).

Ashmole's hypothesis is one of the most widely accepted explanations for latitudinal variation in clutch sizes of birds (Table 1). Ashmole's hypothesis explains clutch size variation as a function of varying seasonality in resource availability among latitudes. Under this hypothesis, population sizes are thought to be limited by mortality caused by low levels of resources during the winter season, and reproduction (clutch size) is limited by per-capita resources available during the breeding season (Ashmole 1961, 1963; Ricklefs 1980; Martin 1996; McNamara et al. 2008; Figure 1). Through this mechanism, mortality from scarce resources during the lean season (i.e. winter) is argued to regulate population size at a level substantially below the summer carrying capacity at high latitudes. The resulting increase in per-capita resources for the breeding population thus explains the latitudinal increase in clutch sizes of terrestrial birds (Figure 1).

Ashmole's hypothesis has been supported via a diversity of tests (Table 1). In particular, tests of the predicted correlation between degree of seasonality and fecundity (e.g. Ricklefs 1980; Jetz, Sekercioglu & Böhning-Gaese 2008), high seasonal variability in population sizes (e.g. Ashmole 1961) and simulation-based modeling approaches (e.g. Griebeler & Böhning-Gaese 2004; McNamara et al. 2008) are suggested to support this hypothesis of clutch size evolution (Table 1). Yet, these tests have three important shortcomings. First, tests of the predicted correlation between variation in seasonality and clutch size are indirect in that they do not test the actual mechanism of the hypothesis. Seasonality of resources as well as many other environmental factors all co-vary with latitude and thus a relationship between seasonality of resources and clutch size cannot be considered strong evidence for causation (Dunn & MacInnes 1987; Hussell 1985; Koenig 1986). Second, population sizes can vary extensively even when mortality is constant year-round if reproduction is seasonal (Fretwell 1972). Thus, population variation is not an appropriate means of testing this hypothesis. Third, simulation-based modeling approaches have accepted at least one of the assumptions of Ashmole's hypothesis (i.e. overwinter food limitation of population size) to be true *a priori* (e.g. Griebeler & Böhning-Gaese 2004; McNamara et al. 2008). While patterns predicted to result from Ashmole's hypothesis are supported, other hypotheses also can explain these patterns (Martin 1996, 2004). Ultimately, direct tests of the assumptions and mechanism of Ashmole's hypothesis are needed.

Ashmole's hypothesis makes two key assumptions regarding patterns of mortality in bird populations that have not been generally tested. First, Ashmole's hypothesis argues that mortality rates are highest during the season of lowest resource abundance (Figure 1; Ashmole 1963; Ricklefs 1980; McNamara et al. 2008). Second, Ashmole's hypothesis assumes that the primary cause of mortality is starvation due to density-dependent resource scarcity during the lean season. Despite an emerging emphasis on Ashmole's hypothesis for explaining a major worldwide pattern in life history variation (Griebeler & Böhning-Gaese 2004; Jetz, Sekercioglu & Böhning-Gaese 2008; McNamara et al. 2008; Ricklefs 2010), the underlying assumptions and mechanistic basis of this hypothesis remain largely untested. Given a diversity of alternative hypotheses, as well as the increasing acceptance of Ashmole's hypothesis (Table 1), clear tests of these assumptions are critical to advancing our understanding of the ecological basis of geographic variation in life history strategies.

We used literature data compiled from a comprehensive review and meta-analysis to test these two assumptions of Ashmole's hypothesis across a diversity of species for the first time. First, we tested whether mortality rates of bird populations were lowest in winter by reviewing bird-banding and radio-telemetry studies that estimated seasonal mortality rates of bird populations year-round. We further tested whether seasonal variation in resource productivity predicted seasonal variation in mortality rates. Second, we tested whether starvation was the primary cause of mortality in wild populations by performing a quantitative meta-analysis of studies which assigned known mortality causes to birds equipped with radio telemetry devices. Our results provide a broad characterization of the timing and sources of mortality in wild bird populations across diverse taxonomic groups.

Methods

Seasonal mortality rates of bird populations

We reviewed the literature for studies of seasonal mortality rates of bird populations from year-round mark-resight-recapture or radio-telemetry studies. We searched the literature for 'seasonal mortality birds' and 'seasonal survival birds' using the Google Scholar and ISI-Thompson Web of Knowledge databases, and manually searched years 1990-2010 of *Auk*, *Condor*, *Wilson Journal of Ornithology, Journal of Wildlife Management, Journal of Avian Biology, Journal of Field Ornithology, Ibis, Wildlife Society Bulletin,* and *Ardea*. We chose 1990 as the starting point of our manual searches because this year is near the beginning of an explosion in the number of published studies of survival using mark-recapture and radio-telemetry techniques in wildlife biology and ecology. We further supplemented our initial set of studies using forward- and backward-citations. We only included peer-reviewed studies and Master's theses or PhD dissertations in our review.

Three criteria qualified a study for admission to our review and analysis. First, studies had to report estimates of survival from at least two seasons representing an entire calendar year, and these seasons needed to represent at a minimum 'spring/summer' and 'fall/winter'. This criterion gave us our primary measure of the seasonality of survival rates – and allowed us to test whether mortality was greatest during the season of predicted low resource abundance (i.e. fall and/or winter) or not. Some studies reported survival from as few as two seasons while others reported survival rates for bi-weekly intervals for an entire year. Second, studies admitted were of natural variation in survival reported from populations in more or less natural settings. We included estimates from hunted populations when estimates of survival in the absence of hunting were also reported or the relative ranks of seasonal survival were apparently unchanged by hunting (i.e. when hunting mortality was smaller than among-season differences in mortality). Third, we admitted studies of seasonal survival that used estimates of seasonal survival developed from a technique that could reasonably assume resighting probability was at or very near 1 (such as radio-telemetry; Pollock, Winterstein & Conroy 1989), intensive searches in closed or nearly-closed populations (e.g. Arcese et al. 1992), or a mark-recapture analysis that accounted for resighting probabilities of less than 1 (Lebreton et al. 1992). This eliminated numerous band-recovery estimates of seasonal survival (e.g. Dobson 1987) because they are likely biased in several key ways, including seasonal bias in reporting probabilities, which compromise explicitly seasonal comparisons.

We combined the results of these studies into a meta-analysis to test the first assumption of Ashmole's hypothesis: that most mortality should occur in the winter. We scored each study for whether most mortality occurred in fall/winter (defined as the season of lowest resource abundance in the few tropical studies included in the analysis), a season other than winter, or whether support was equivocal (i.e. if mortality was similar year-round, or in the subset of studies of migrant populations, if migration confounded seasonal variation). To provide another more highly conservative test of Ashmole's hypothesis, we took all studies scored as equivocal and re-scored them as mortality highest in winter, because statistical power to detect differences in survival rates among seasons may often be low. Even though it is unlikely all studies with equivocal seasonality reflect highest mortality in winter, especially 'equivocal' studies reporting that migration may be the season of greatest mortality, taking this conservative approach allows examination of whether any support for Ashmole's hypothesis exists in this dataset. In the subset of studies of resident birds, we used logistic regression to test whether the probability that a study would report most mortality occurred in winter increased with latitude.

To test the predicted positive relationship between resource productivity and survival rates, we extracted monthly survival rates from studies included in this review when possible. We used survival rates in this analysis because transformation to normality to achieve the assumptions of regression was achievable with survival, but not mortality, rates. Monthly survival rates were extracted from studies by standardizing reported periodic tabular or graphical rates (using program DigitizeIt; I. Bormann, Germany 2006) to monthly rates. We tested whether monthly productivity, as measured by actual evapotranspiration (Mather 1962, 1963a, 1963b, 1963c, 1964a, 1964b, 1964c, 1965; Ricklefs 1980), predicted monthly variation in survival rates using simple linear regression of arc-sine transformed monthly survival rates on log-transformed monthly actual evapotranspiration. We excluded year-round studies of migratory populations because it was often unclear which environment these populations occupied, and thus which values of monthly actual evapotranspiration the population experienced were ambiguous.

Sources of mortality in wild bird populations

We also reviewed the literature for studies that used radio-telemetry to assign mortality causes to wild bird populations. We employed the same search strategy described above except we used the following search terms: 'known fate birds', 'mortality cause birds', and 'mortality source birds'. Some studies located during our initial search for seasonal survival rates of bird populations included known fate data and thus were included in this meta-analysis as well.

Studies were admitted to this review and analysis based on two criteria. First, we only admitted studies that assigned fates (cause-specific mortality) to telemetered birds based on standardized criteria and that reported the exact numbers of birds assigned to each specific fate. These fates were our primary measure of the different causes of mortality in each bird population. Second, we only admitted studies of wild bird populations in more or less natural settings; thus, we did not admit any introduction or re-introduction programs to our review. For each study admitted, we collected and entered into a database: species, age class(es), season(s) studied, frequency of observation, total sample size of the study, and fates assigned to different categories. Ambiguous values were treated as missing values. These data were then used in a quantitative meta-analysis.

We conducted a meta-analysis of mortalities assigned to different causes to test the prediction of Ashmole's hypothesis that the principle cause of mortality should be starvation. A preliminary analysis (a simple summed proportion across all studies in the database) suggested predation was the major source of mortality, at least when summed across studies, which led us to design a conservative test of Ashmole's hypothesis. We summed the proportion of individuals assigned to two different fate categories (predation, and all other known causes including starvation, disease, and hunter kill) within each study. We then used a random effects model (DerSimonian & Laird 1986) of the Freeman-Tukey double arcsine transformed data (Freeman & Tukey 1950) to generate a pooled across-study 'incidence rate' and 95% confidence intervals for the proportion of known mortality caused by predation. We repeated this procedure for three different categories of studies. First, and providing the most direct test of the assumptions of

Ashmole's hypothesis, were studies of adults and adult/immature pools in winter. We also repeated this procedure for studies of adults and adult/immature pools year-round in which the data were not clearly separable by season and for studies that did not fit clearly into any of the other two categories (we refer to these as 'uncategorized'). We generated within-study estimates of proportions and confidence intervals using the exact binomial method.

Our meta-analysis thus tested whether a) studies found that most individuals died from predation or causes other than predation in winter, providing our direct, but conservative, test of Ashmole's hypothesis, and b) whether studies that combined winter mortality with other seasonal mortality found that most individuals died from predation or causes other than predation, which provided a less direct test of Ashmole's hypothesis. The use of simple proportions of known or total mortality from predation (binomial estimator), rather than estimators that allow for unequal exposure to risk due to staggered entry of subjects into the population or right-censoring of data series, could introduce two biases into our results (Heisey & Fuller 1985). First, the binomial estimator may underestimate mortality caused by mortality agents if there is staggered entry of subjects into the study population. Second, if both survival rates and sample size vary seasonally, the season with the largest sample size will have an inappropriately large effect on the overall estimate of mortality rate (Heisey & Patterson 2006).

These biases should not affect our tests of Ashmole's hypothesis for two reasons. First, if we underestimate mortality caused by predation, we are providing an even more highly conservative test of the hypothesis. Second, we divided our estimates of cause-specific mortality used in the meta-analysis into season/age categories (such as winter, the key test of Ashmole's hypothesis) when possible. We took this generally inclusive approach in our meta-analysis to avoid excluding a very large proportion of studies that lacked sufficient information to calculate an estimator of cause-specific mortality other than the simple binomial estimator.

One methodological concern identified *a priori* was that radio-telemetry studies may be biased towards mis-assignment of cases of starvation as predation due to postmortem scavenging by predators (Brand, Vowles & Keith 1975). We tested whether scavenging may have biased the results of studies by testing whether studies that observed their subjects more often (daily vs. less often) were less likely to report cases of predation. We matched studies by species, age class, and season ("study category") that varied in check frequency according to their methodological descriptions. We tested whether check frequency affected proportion of mortalities assigned to predation using a mixed-effect weighted regression model with a fixed effect of check frequency nested inside a random effect of study category. We used each individual study as a sample unit with exact binomial proportion of individuals estimated to have died due to predation as the response variable, weighted by the random effect weight W_i (DerSimonian & Laird 1986). We used a t-test to assess the statistical significance of the fixed effect of interest, check frequency. Computer code used to conduct the analysis is available from DCB.

Results

Seasonal mortality of bird populations

We obtained seasonal mortality estimates using radio-telemetry for 41 populations of 19 species, and using mark-recapture for 28 populations of 26 species (Table 2; see Appendix 1 in Supporting Information). Spring and summer were the most frequently reported season of greatest mortality (lowest survival) in radio-telemetry studies (Table 2). This result did not change even when ‘equivocal’ studies were re-categorized as mortality being greatest in winter, providing a highly conservative test (Table 2).

Mark-recapture studies reported equivocal patterns of seasonality most frequently, but among studies that reported differences among seasons, spring and summer again were more frequently the season of greatest mortality than fall and winter (Table 2). Assigning greatest mortality in fall and winter to the large number of ‘equivocal’ mark-recapture studies caused fall and winter to become the season of greatest mortality (Table 2). Nonetheless, the pooled results across radio-telemetry and mark-recapture studies show that the most frequently reported season of highest mortality was during the spring or summer by a 2:1 margin, and that many studies showed no strong seasonal pattern (Table 2).

We tested whether latitude predicted the season of greatest mortality within the subset of 48 studies of resident bird populations in which hunting did not confound seasonal mortality (Appendix 1). The probability that a study reported fall or winter as the season of greatest mortality was not predicted by the difference between maximum and minimum actual evapotranspiration (logistic regression: $\beta = -\ 0.009$, $z = -0.994$, 46 df, $P = 0.32$). The probability that a study reported spring or summer as the season of greatest mortality also was not predicted by latitude (logistic regression: $\beta = 0.009$, $z = 1.105$, 46 df, $P = 0.27$). In short, latitude did not predict season of greatest mortality.

We tested the predicted positive relationship between monthly productivity and monthly survival based on monthly survival rates extracted from 40 resident bird populations. The relationship between arc-sine transformed monthly survival rates and log-transformed actual evapotranspiration varied widely among populations (Table 3). In 11 of the 40 populations examined, survival was significantly ($P < 0.10$) positively related to actual evapotranspiration as predicted by Ashmole's hypothesis. However, survival was significantly negatively related to actual evapotranspiration in 8 of the 40 populations, and was not significantly related to actual evapotranspiration in the majority (21 of 40) of studies. Thus, the positive relationship predicted by Ashmole's hypothesis was not supported among the 19 studies with significant patterns, which showed approximately equal numbers of positive (11) and negative (8) relationships between actual evapotranspiration and survival. This predicted positive relationship was also not supported across all studies regardless of whether the regression was significant, which showed approximately equal numbers of positive (17) and negative (23) relationships between actual evapotranspiration and survival. The proportion of populations showing a positive relationship between monthly actual evapotranspiration and survival did not differ between hunted (12 of 26 positive) and unhunted (5 of 14 positive) populations ($\chi^2 = 0.09$, 1 df, P = 0.76; Table 3).

Sources of mortality in wild bird populations

Predation was by far the dominant cause of mortality across the studies included in our meta-analysis. During winter, the random-effects pooled proportion of known mortality caused by predation was 0.62 (95% CI = 0.52 – 0.72; *n* = 40 populations of 20 species; Figure 2; see Appendix 2 in Supporting Information). Predation caused the largest proportion of known mortality in 23 of these 40 populations (Figure 2; Appendix 2). Among year-round studies of adult and juvenile mortality (studies that combined winter adult mortality with other seasons or age classes), the random-effects pooled proportion of known mortality caused by predation was 0.78 (95% CI = 0.73 – 0.83; *n* = 39 populations of 18 species; Figure 3; Appendix 2). Finally, for those cases that did not fit in any of the preceding categories, the random-effects pooled proportion of known mortality was 0.86 (95% CI = 0.76 – 0.94; *n* = 31 populations of 25 species;

Figure 4; Appendix 2). In 27 of these 31 populations predation caused the greatest proportion of known mortality (Figure 4; Appendix 2).

Using a highly conservative approach where unknown mortality was assigned to non-predation, the random-effects pooled proportion of all mortality was still 0.49 (95% CI = 0.39 – 0.60) during winter; 0.67 (95% CI = 0.63 – 0.71) for adults and juveniles studied year-round; and 0.82 (95% CI = 0.71 – 0.91) for studies not fitting the preceding categories.

We tested whether studies that checked status of birds less frequently than daily affected assignment of mortality to predation using data from 27 studies of 9 species (Figure 5; Appendix 2). The fixed effect of check frequency was not significant in a weighted random-effects mixed model with a random effect of species ($t_{check} = -0.49$, 16 df, $P = 0.63$). Thus, in this subset of 27 studies, check frequency was not associated with the estimated proportion of mortality due to predation.

Discussion

Ashmole's hypothesis is widely accepted as an explanation for latitudinal variation in the clutch sizes of terrestrial birds (Table 1). Our meta-analysis represents the first broad approach to testing key assumptions that form the mechanistic basis of this hypothesis (Figure 1). We could not confirm that winter is the season of greatest mortality (Table 2) or that starvation from scarce resources is the principle cause of mortality for adults in winter (Figure 2) or in any other season (Figures 3, 4), despite the vast majority of studies of seasonal mortality in birds having been conducted at latitudes greater than 30 degrees (Appendix 1). Furthermore, we did not find the predicted general positive relationship between seasonal survival rates and actual evapotranspiration, and instead found that seasonal survival rates were as often negatively correlated with actual evapotranspiration as they were positively correlated (Table 3).

Analyzing year-round radio telemetry studies and year-round mark-recapture studies, we found that the season of greatest mortality varied among species but that spring/summer was often the season of greatest mortality, rather than winter (Appendix 1; Table 2). Similarly, Bergerud (1988), in a comprehensive review of northern grouse population data, concluded that density-dependent shortage of winter food and winter mortality did not create a winter population bottleneck and did not explain breeding population sizes. We recognize that the sample of species represented in our sample of year-round radio telemetry and mark-recapture studies is not a fully representative subset of terrestrial bird diversity. Year-round radio telemetry studies of survival can only be conducted with bird species large enough to carry transmitters with large and long-lived batteries (Appendix 1). We suggest these methodological considerations resulted in our review of a large number of studies of populations in the order Galliformes (quail, grouse, turkeys) that are physically large and economically important because of hunting (Appendix 1). Likewise, year-round mark-recapture studies are generally limited to populations which are easily observed or recaptured and have known distributions year-round. These methodological issues probably resulted in the prior publication and our review of a large number of studies of Anseriformes (geese, ducks) and resident populations in the order Passeriformes (songbirds; Appendix 1). Thus, our results on the seasonality of mortality represent a narrow subset of bird diversity, and we made no attempt to control for the influence of a phylogeny given this already taxonomically-biased sample. Yet, Ashmole's hypothesis was originally proposed to generally apply to all bird species across a range of ecological conditions, including marine birds and terrestrial birds (Ashmole 1961, 1963) and has been broadly applied to explaining clutch size variation in a diversity of terrestrial bird species (Ricklefs 1980, Jetz, Sekercioglu & Böhning-Gaese 2008). Therefore we consider our results on the seasonality of mortality as generally falsifying the assumption of greatest mortality in winter across terrestrial bird species, although some bird populations did show greatest mortality in winter (Table 2; Appendix 1).

A positive relationship between seasonal survival rates and seasonal productivity is another implicit assumption of Ashmole's hypothesis (Ashmole 1961, Ricklefs 1980). Here we showed that the relationship between monthly survival rates and actual evapotranspiration, a measure of productivity, is highly variable among resident bird populations. Some populations show a positive relationship, some populations show a negative relationship, and most show no significant relationship. While this may again be the result of limited statistical power to detect such effects, even the non-significant relationships showed no hint of the positive relationship expected under Ashmole's hypothesis (Table 3). We take these results to indicate that resource abundance is not the driving factor in determining seasonal variation in survival (also see Bergerud 1988) across the diversity of high-latitude bird species represented in our meta-analysis.

This latter point was reinforced by our findings that the season of greatest mortality is not the lean fall/winter season, but most frequently summer, or alternatively, equivocal support for either. While inability to identify the season of greatest mortality (i.e. equivocal studies) may simply result from low statistical power to detect differences among seasons, the positive result of greatest mortality in the summer in numerous bird populations (Appendix 1; Table 2) is surprising and is quite contrary to Ashmole's hypothesis. Potential explanations for this pattern are many, and include increased predation intensity in summer, predation costs of reproduction, and possible carry-over effects from resource scarcity during winter. The only potential explanation consistent with a role for population size limitation by winter resources in life history evolution is possible carry-over effects from winter (i.e., Norris et al. 2004). Yet, such carry-over effects do not represent population limitation as predicted by Ashmole's hypothesis and would require an expansion and complication of the mechanistic basis of Ashmole's hypothesis. We suggest examining all three of these potential explanations will be necessary to understand why mortality is frequently greatest in the summer.

We found that starvation was clearly not the leading proximate cause of mortality in the majority of wild bird populations studied, contrary to the assumptions of Ashmole's hypothesis. We instead found that predation was the most frequently reported cause of adult mortality in winter or in studies that combined adult winter mortality data with other seasons (Appendix 2; Figures 2-4). Again, Bergerud (1988) came to the same conclusions in his analysis of northern grouse populations. While our review and meta-analysis included only the subset of bird species that can carry radio-telemetry devices and are amenable to tracking using such technology, it includes a wide body size range and a wide range of phylogenetic diversity (Appendix 2). Thus we consider our results generalizable – predation is likely the leading proximate source of mortality in free-living bird populations, as it is in the sessile eggs and nestlings of altricial birds (Martin 1995). However, it is critical to consider that we only reviewed studies that assigned proximate sources of mortality. Resource availability is theoretically proposed (McNamara & Houston 1990) and empirically demonstrated (Lima & Dill 1990; Cresswell & Whitfield 2008) to affect the predation risks accepted by birds and thus resource availability may still be the ultimate cause of much mortality in the bird populations studied. Yet, again, we note that mortality was not greatest during the lean season, so even if food is contributing to predation mortality, it is not working as predicted under Ashmole's hypothesis.

Our results suggest serious problems with the mechanistic basis of Ashmole's hypothesis, despite its broad support from more indirect methods (Table 1). The vast majority of populations included in our review and meta-analysis were temperate non-migratory species. While the majority of mortality in migrant bird populations may occur during migration (Sillett & Holmes 2002), the standing assumption for resident birds is that most mortality occurs during winter due to resource limitation (Ricklefs 1980). Yet, we found in many populations that most mortality occurs during spring or summer due to predation. Reconciling these results with current theory meant to explain life history variation and population regulation will require deeper consideration of the relationship between risk-taking and breeding, the potential role of extrinsic mortality in regulating populations of birds and its role in life history evolution, carry-over effects from conditions during one season to another, and the relationship between ultimate and proximate sources of mortality. Furthermore, future empirical research on the timing and causes of mortality in wild bird populations resident at low latitudes will provide greater insights into mechanisms of population regulation and the potential validity of Ashmole's hypothesis. We also find that our results raise important questions about how and when bird populations are regulated – understanding the relative importance of food, predation, and disease in regulating population sizes and the season(s) in which regulation occurs is of paramount importance in understanding population biology, but we still know surprisingly little about these processes in birds – particularly in the tropics.

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Table 1. Studies reporting support for Ashmole's hypothesis. 'AE' stands for actual evapotranspiration. 'Support for Ashmole's hypothesis' indicates whether results were interpreted as either positive (+) or negative support (-).

Study	Study Species	Main Result	General Method	Support for Ashmole's Hypothesis
Ashmole 1961	*Parus major* (from Gibb 1954)	High seasonal variation in population size suggested high over-winter mortality	Seasonal survey / census	+
Blondel 1985	3 *Parus* spp.	Clutch size increased with increasing seasonality of resource availability between mainland and island	Interpopulation comparison	+
Dunn & MacInnes 1985	*Branta canadensis* in N. America	Negative relationship between clutch size and latitude; unclear relationship between clutch size and productivity	Interpopulation comparison	-
Dunn et al. 2000	*Tachycineta bicolor* (nc) in N.	Positive relationship between summer productivity and clutch size after controlling for	Interpopulation comparison	+

	America	breeding density		
Evans et al. 2005	11 species in UK and New Zealand	Clutch size of introduced species reduced in less seasonal environment (New Zealand)	Compared clutch size between native and introduced range	+
Griebeler, Caprano & Böhning-Gaese 2010; Griebeler & Böhning-Gaese 2004		Models predict increased clutch size with increased seasonality of resources assuming population size limited by winter resource abundance	ecogenetic individual-based models	+
Jetz et al. 2008	5,290 bird species worldwide	Positive relationship between temperature seasonality and clutch size after controlling for other effects	Interspecific comparison	+
Koenig 1984	*Colaptes auratus* in N. America	Clutch size negatively correlated with winter AE	Interspecific comparison	+
Koenig 1986	21 N. American species of Order	Clutch size negatively correlated with winter AE	Interspecific comparison	+

	Piciformes			
Lepage & Lloyd 2004	106 S. African bird species	Clutch size increased with increasing seasonality of rainfall in arid regions	Interspecific comparison	+
McNamara et al. 2008		Model predicts increased clutch size with increasing seasonality assuming population size limited by winter resource abundance	Simulation-based approach using individual-based models	+
Møller 1984	*Hirundo rustica* and *Delichon urbica*	Clutch size not related to winter AE or ratio between summer and winter AE	Interpopulation comparison	-
Ricklefs 1980	13 breeding bird communities worldwide	Mean clutch size negatively correlated with winter AE	Compared mean clutch size among localities	+
Yom-Tov, Christie & Iglesias 1994	177 bird species in S. America	Smaller clutch sizes in S. America related to possible reduced climatic variability in temperate S. Hemisphere	Compared pattern of clutch size increase with latitude between N. America and S. America	+

Yom-Tov 1995	Bird species from 5 regions worldwide	Clutch size increased with increasing levels of competition from migrant species	Compared clutch size across regions	+
Young 1994	*Troglodytes aedon*	Clutch size negatively related to winter AE and positively to AE seasonality but not after controlling for latitude	Interpopulation comparison	+

Table 2. Season of greatest mortality and study methodology across 69 year-round studies of mortality in wild bird populations. Spring/summer was the season of greatest mortality in radio-telemetry studies ($\chi2 = 10.5$, 2 df, $P = 0.005$) but not in capture-recapture studies ($\chi2 = 2.0$, 2 df, $P = 0.37$). Spring/summer was the season of greatest mortality pooled across study methodologies ($\chi2 = 6.0$, 2 df, $P = 0.050$). Data sources are shown in Appendix 1.

Season of greatest mortality	Radio-telemetry	Capture-recapture	Pooled
Spring / summer	21	9	30
Fall / winter	9	6	15
Equivocal (no strong seasonal pattern; migration)	6	12	18
Confounded by hunting[1]	5	1	6
Total	41	28	69

[1] Not included in statistical tests – shown for comparison purposes only.

Table 3. Relationship between monthly actual evapotranspiration (AE) and monthly survival rates in 39 wild bird populations. The β and P-value are from a simple linear model of the effect of log-transformed AE on arc-sine transformed survival rates. Populations in which there was a significant effect of AE on survival rates are shown in bold. Hunted populations are denoted for comparison. Data sources are shown in Appendix 1.

Species	Study	β_{AE}	P	Hunted
Anas fulvigula	Bielefeld & Cox 2006	-0.05	0.42	Y
Colinus virginianus	Burger et al. 1995	**0.02**	**< 0.01**	Y
Colinus virginianus	Cox et al. 2004	**0.09**	**< 0.01**	Y
Colinus virginianus	Terhune et al. 2007	**-0.02**	**< 0.01**	Y
Alectoris chukar	Robinson et al. 2009	**-0.03**	**0.05**	Y
Tetrao tetrix	Angelstam 1984	-0.02	0.42	Y
Tetrao tetrix	Caizergues & Ellison 1997	0.01	0.64	Y
Bonasa bonasia	Montadert & Leonard 2003	**-0.06**	**< 0.01**	Y
Bonasa umbellus	Devers et al. 2007	**0.02**	**0.03**	Y
Bonasa umbellus	Thompson & Fritzell 1989	**0.02**	**< 0.01**	Y
Bonasa umbellus	Small et al. 1993	**0.02**	**0.21**	Y
Dendragapus canadensis	Herzog 1979	**-0.07**	**0.03**	Y
Lagopus lagopus	Smith & Willebrad 1999	0.00	0.68	Y
Centrocercus urophasianus	Sika 2006	**0.01**	**0.09**	Y
Tympanuchus pallidicinctus	Hagen et al. 2007	0.01	0.60	Y
Tympanuchus pallidicinctus	Wolfe et al. 2007	-0.01	0.79	
Tympanuchus pallidicinctus	Wolfe et al. 2007	-0.01	0.73	

Meleagris gallopavo	Palmer et al. 1993	-0.01	0.71	Y
Meleagris gallopavo	Wright et al. 1996	**-0.01**	**0.08**	Y
Meleagris gallopavo	Lehman et al. 2005	-0.01	0.80	Y
Meleagris gallopavo	Hubbard et al. 1999	-0.01	0.30	Y
Meleagris gallopavo	Kurzejeski et al. 1987	0.00	0.60	Y
Meleagris gallopavo	Nguyen et al. 2003	-0.01	0.46	Y
Meleagris gallopavo	Roberts et al. 1995	0.00	0.15	Y
Meleagris gallopavo	Spohr et al. 2004	-0.02	0.25	Y
Meleagris gallopavo	Vander Haegen et al. 1988	-0.01	0.49	Y
Meleagris gallopavo	Miller et al. 1998	**-0.05**	**< 0.01**	Y
Melegaris gallopavo	Vangilder & Kurzejeski 1995	**0.00**	**0.70**	Y
Rostrhamus sociabilis	Bennetts & Kitchen 1999	**0.11**	**< 0.01**	
Haematopus ostralegus	dit Durrell 2007	-0.04	0.17	
Dryocopus pileatus	Bull 2001	-0.02	0.12	
Petroica goodenovii	Major & Gowing 2001	**-0.30**	**0.08**	
Sitta europea	Nilsson 1982	**0.04**	**0.03**	
Parus atricapillus	Smith 1967	-0.04	0.64	
Parus atricapillus	Brittingham & Temple 1988	**0.04**	**< 0.01**	
Motacilla clara	Piper 2002	**-0.07**	**< 0.01**	
Turdus merula	Robinson et al. 2010	-0.02	0.56	
Sylvia boehmi	Schaefer et al. 2006	0.01	0.27	
Sylvia lugens	Schaefer et al. 2006	-0.13	0.17	
Melospiza melodia	Arcese et al. 1992	**0.09**	**0.01**	

Figure 1. Graphical representation of Ashmole's hypothesis. Amplitude of seasonal variation in resource availability is thought to be greater at temperate than tropical latitudes. Adult population sizes are thought to be regulated by resource availability minima that occur during the non-breeding season (i.e. winter) which are more severe in temperate regions. Adults that survive to the summer resource availability maxima are thus thought to have more resources available for reproduction in temperate regions than tropical regions. Adapted and expanded from Ricklefs (1980).

Figure 2. Forest plot of the proportion of known mortalities due to predation in populations of adults in winter (n=40; references in Appendix 2). Each entry represents a study and the exact binomial proportion of known mortalities due to predation is shown. Box size corresponds to the magnitude of the random effects weight, W_i. The random-effects pooled estimate for conservative and highly conservative tests (see Methods) is shown at bottom.

Figure 3. Forest plot of the proportion of known mortalities due to predation in populations of mixed age classes studied year-round (n=39; references in Appendix 2). Each entry represents a study and the exact binomial proportion of known mortalities due to predation is shown. Box size corresponds to the magnitude of the random effects weight, W_i. The random-effects pooled estimate for conservative and highly conservative models (see Methods) is shown at bottom.

Figure 4. Forest plot of the proportion of known mortalities due to predation in populations that were not categorized as adults in winter, fledglings, or year-round studies (n = 31; Appendix 2). Each entry represents a study and the exact binomial proportion of known mortalities due to

predation is shown. Box size corresponds to the magnitude of the random effects weight, W_i. The random-effects pooled estimate for conservative and highly conservative models (see Methods) is shown at bottom.

Figure 5. Forest plot of the proportion of known mortalities in populations studied daily (open symbols; n=10) or less frequently (closed symbols; n=17), shown by species (references in Appendix 2). Each entry represents a study and the exact binomial proportion of known mortalities due to predation is shown. Box size corresponds to the magnitude of the random effects weight, W_i. The random-effects pooled estimate for each group from a mixed model weighted by W_i is shown at bottom.

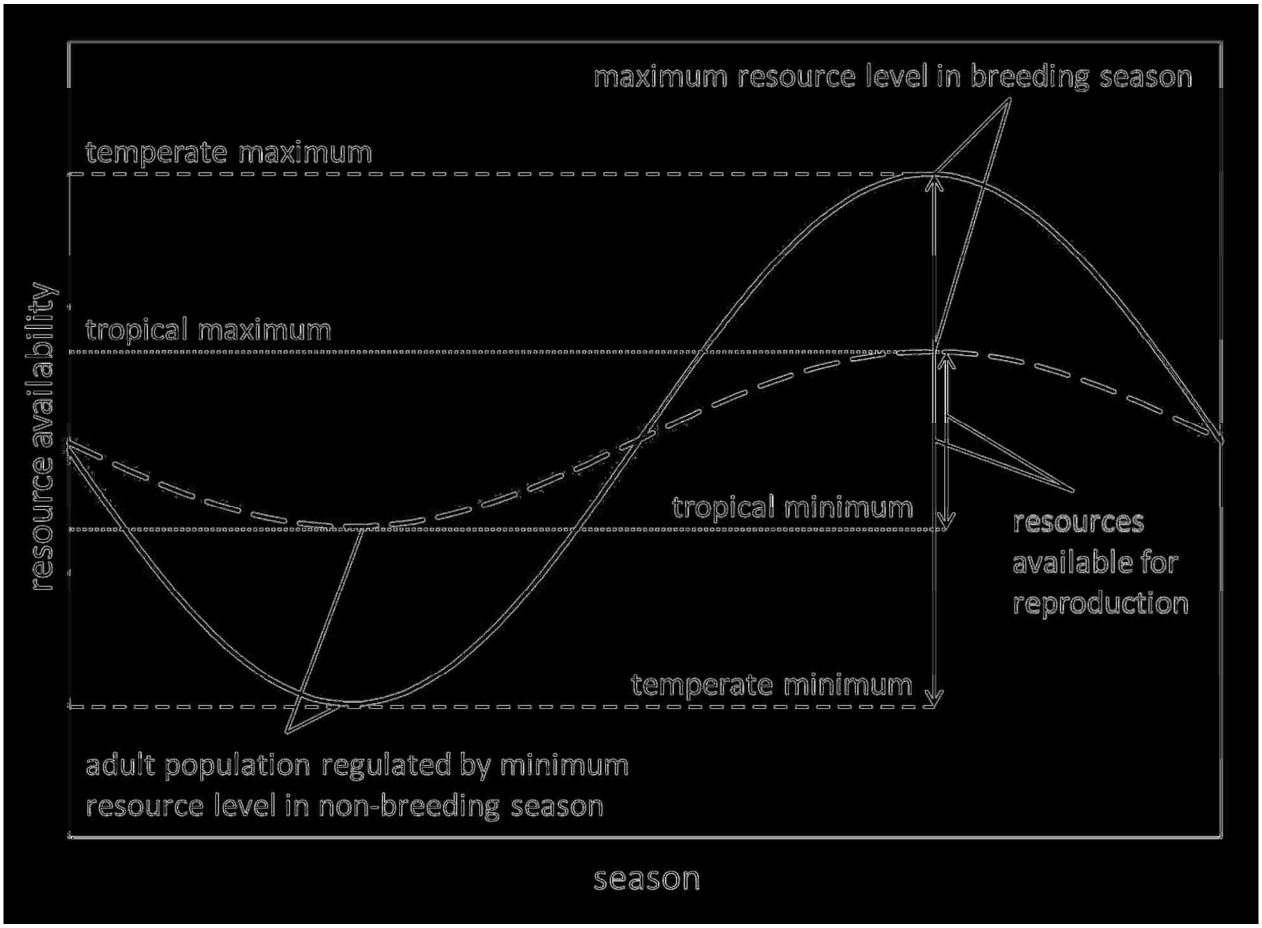
maximum resource level in breeding season
temperate maximum
tropical maximum
resource availability
tropical minimum
resources available for reproduction
temperate minimum
adult population regulated by minimum resource level in non-breeding season
season

Figure 1.

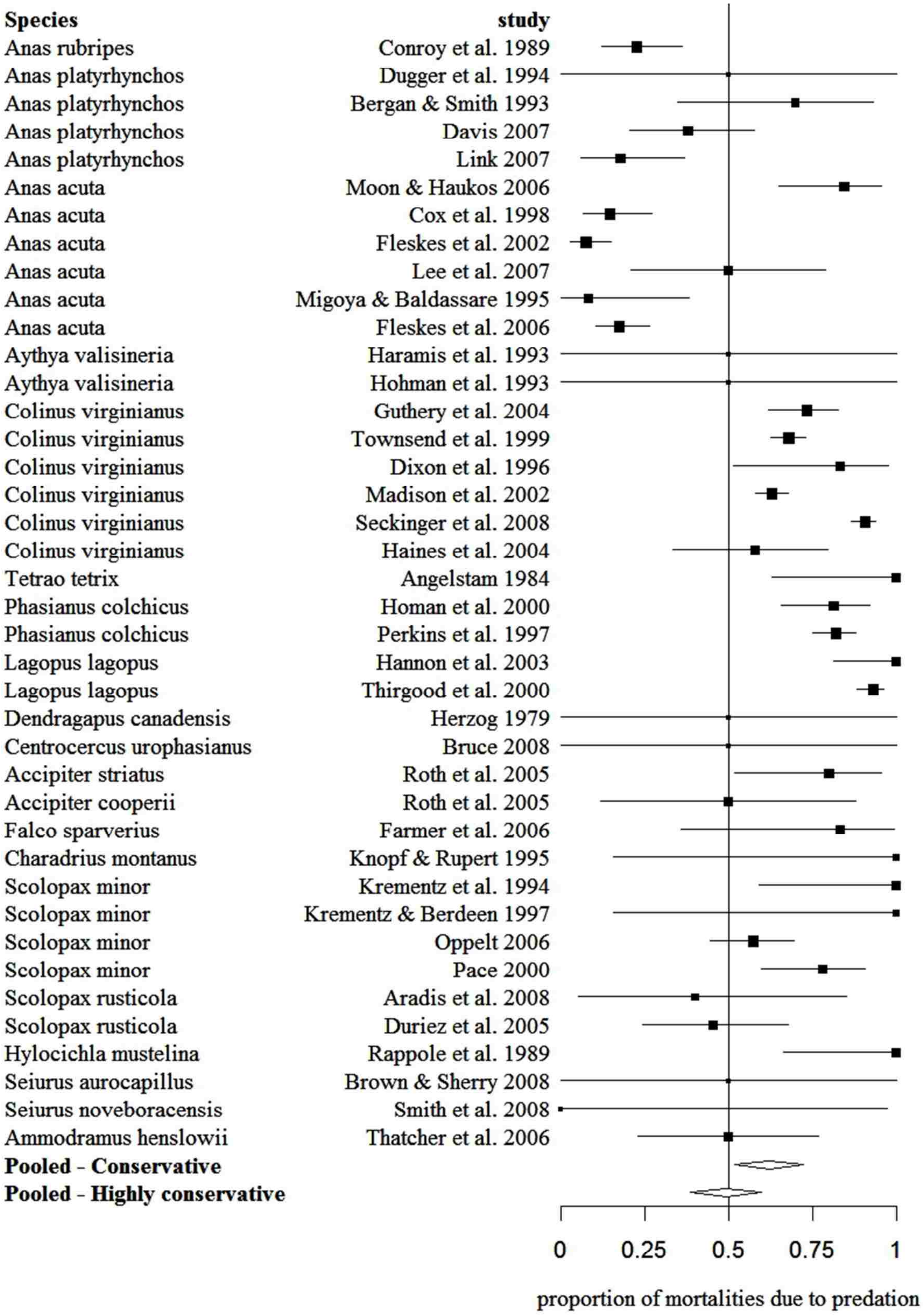
Species
study
Anas rubripes Conroy et al. 1989
Anas platyrhynchos Dugger et al. 1994
Anas platyrhynchos Bergan & Smith 1993
Anas platyrhynchos Davis 2007
Anas platyrhynchos Link 2007
Anas acuta Moon & Haukos 2006
Anas acuta Cox et al. 1998
Anas acuta Fleskes et al. 2002
Anas acuta Lee et al. 2007
Anas acuta Migoya & Baldassare 1995
Anas acuta Fleskes et al. 2006
Aythya valisineria Haramis et al. 1993
Aythya valisineria Hohman et al. 1993
Colinus virginianus Guthery et al. 2004
Colinus virginianus Townsend et al. 1999
Colinus virginianus Dixon et al. 1996
Colinus virginianus Madison et al. 2002
Colinus virginianus Seckinger et al. 2008
Colinus virginianus Haines et al. 2004
Tetrao tetrix Angelstam 1984
Phasianus colchicus Homan et al. 2000
Phasianus colchicus Perkins et al. 1997
Lagopus lagopus Hannon et al. 2003
Lagopus lagopus Thirgood et al. 2000
Dendragapus canadensis Herzog 1979
Centrocercus urophasianus Bruce 2008
Accipiter striatus Roth et al. 2005
Accipiter cooperii Roth et al. 2005
Falco sparverius Farmer et al. 2006
Charadrius montanus Knopf & Rupert 1995
Scolopax minor Krementz et al. 1994
Scolopax minor Krementz & Berdeen 1997
Scolopax minor Oppelt 2006
Scolopax minor Pace 2000
Scolopax rusticola Aradis et al. 2008
Scolopax rusticola Duriez et al. 2005
Hylocichla mustelina Rappole et al. 1989
Seiurus aurocapillus Brown & Sherry 2008
Seiurus noveboracensis Smith et al. 2008
Ammodramus henslowii Thatcher et al. 2006
Pooled - Conservative
Pooled - Highly conservative
0
0.25
0.5
0.75
1
proportion of mortalities due to predation

Figure 2.

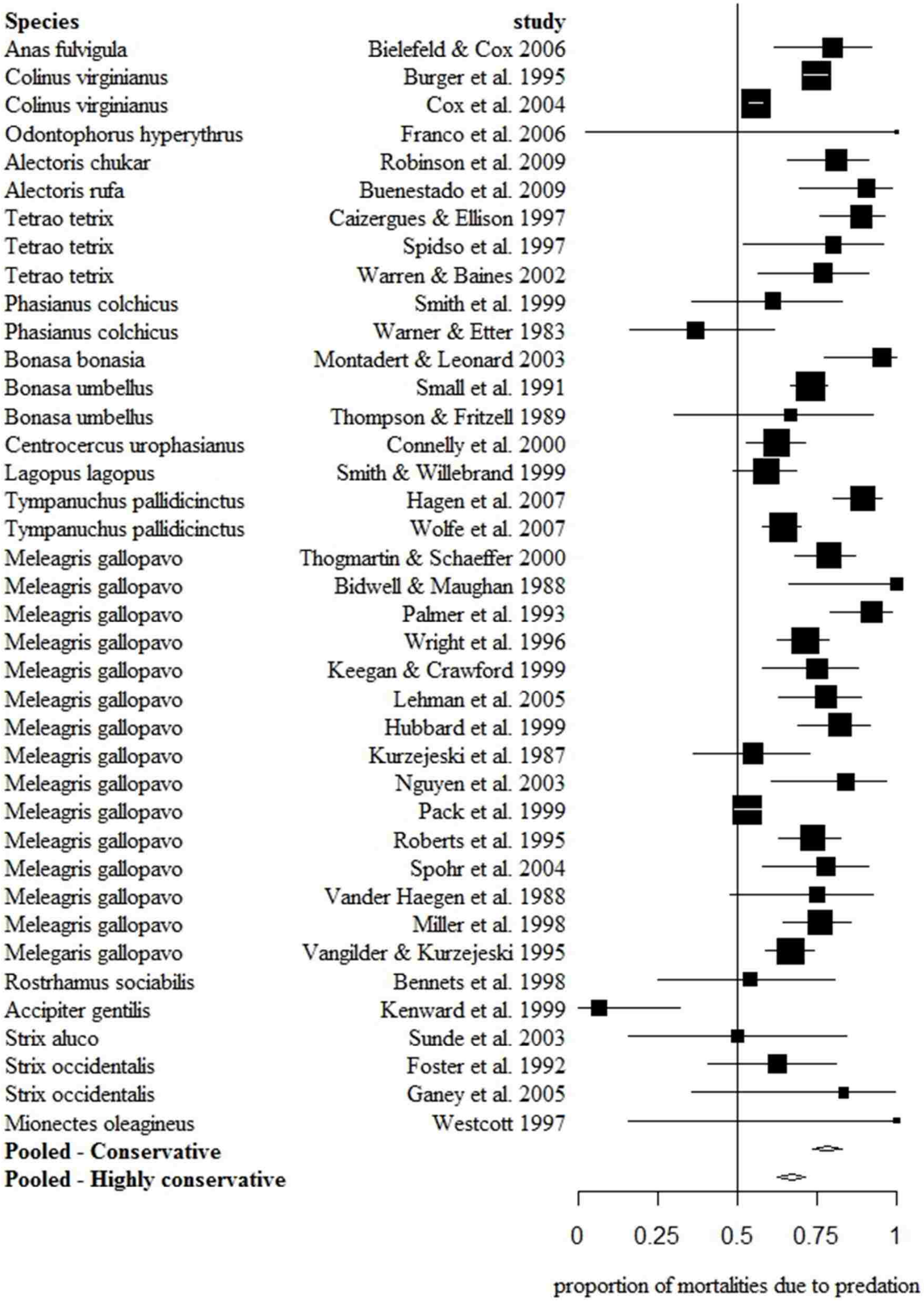
Species
study
Anas fulvigula
Bielefeld & Cox 2006
Colinus virginianus
Burger et al. 1995
Colinus virginianus
Cox et al. 2004
Odontophorus hyperythrus
Franco et al. 2006
Alectoris chukar
Robinson et al. 2009
Alectoris rufa
Buenestado et al. 2009
Tetrao tetrix
Caizergues & Ellison 1997
Tetrao tetrix
Spidso et al. 1997
Tetrao tetrix
Warren & Baines 2002
Phasianus colchicus
Smith et al. 1999
Phasianus colchicus
Warner & Etter 1983
Bonasa bonasia
Montadert & Leonard 2003
Bonasa umbellus
Small et al. 1991
Bonasa umbellus
Thompson & Fritzell 1989
Centrocercus urophasianus
Connelly et al. 2000
Lagopus lagopus
Smith & Willebrand 1999
Tympanuchus pallidicinctus
Hagen et al. 2007
Tympanuchus pallidicinctus
Wolfe et al. 2007
Meleagris gallopavo
Thogmartin & Schaeffer 2000
Meleagris gallopavo
Bidwell & Maughan 1988
Meleagris gallopavo
Palmer et al. 1993
Meleagris gallopavo
Wright et al. 1996
Meleagris gallopavo
Keegan & Crawford 1999
Meleagris gallopavo
Lehman et al. 2005
Meleagris gallopavo
Hubbard et al. 1999
Meleagris gallopavo
Kurzejeski et al. 1987
Meleagris gallopavo
Nguyen et al. 2003
Meleagris gallopavo
Pack et al. 1999
Meleagris gallopavo
Roberts et al. 1995
Meleagris gallopavo
Spohr et al. 2004
Meleagris gallopavo
Vander Haegen et al. 1988
Meleagris gallopavo
Miller et al. 1998
Melegaris gallopavo
Vangilder & Kurzejeski 1995
Rostrhamus sociabilis
Bennets et al. 1998
Accipiter gentilis
Kenward et al. 1999
Strix aluco
Sunde et al. 2003
Strix occidentalis
Foster et al. 1992
Strix occidentalis
Ganey et al. 2005
Mionectes oleagineus
Westcott 1997
Pooled - Conservative
Pooled - Highly conservative
0
0.25
0.5
0.75
1
proportion of mortalities due to predation

Figure 3.

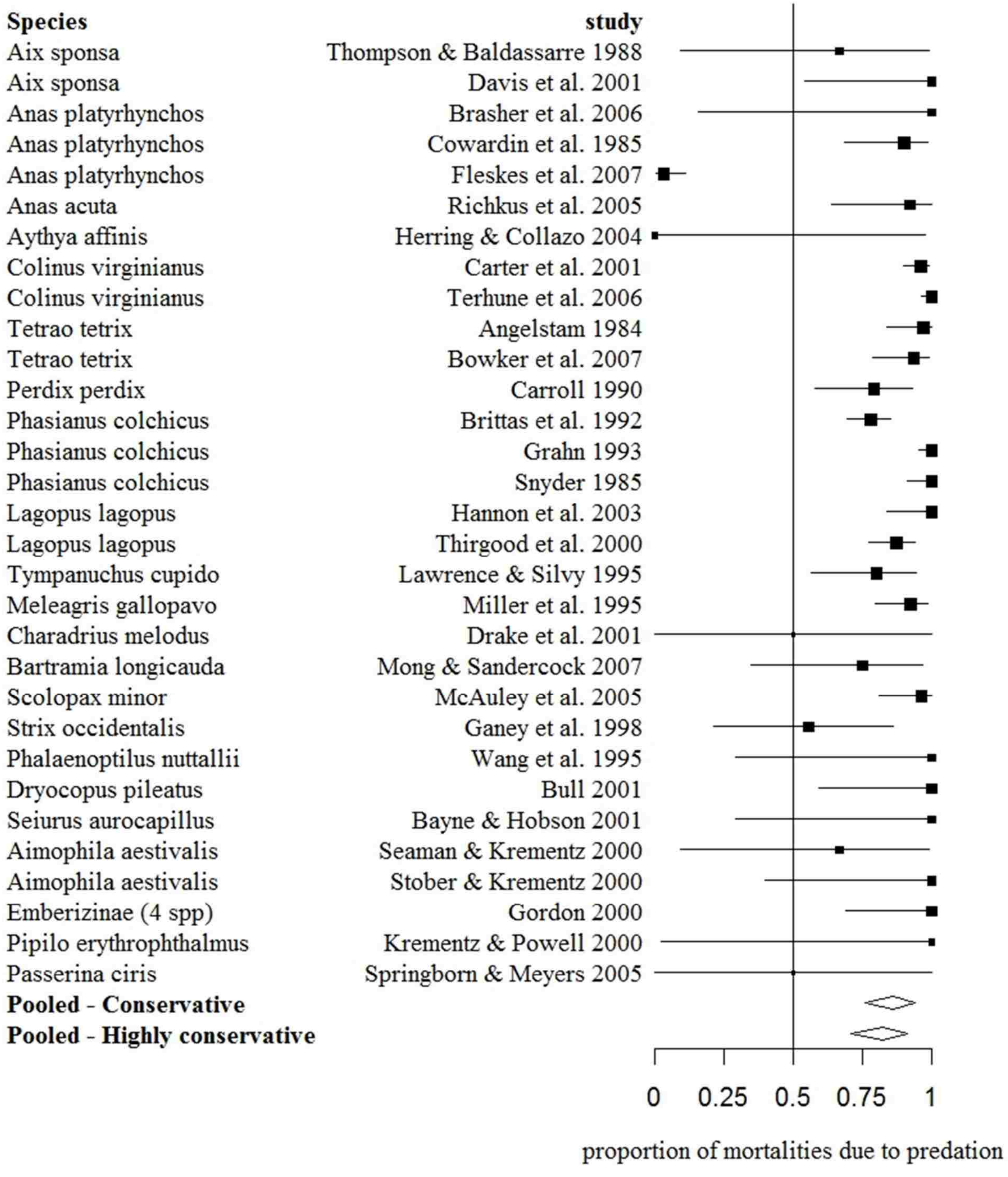
Species
study
Aix sponsa — Thompson & Baldassarre 1988
Aix sponsa — Davis et al. 2001
Anas platyrhynchos — Brasher et al. 2006
Anas platyrhynchos — Cowardin et al. 1985
Anas platyrhynchos — Fleskes et al. 2007
Anas acuta — Richkus et al. 2005
Aythya affinis — Herring & Collazo 2004
Colinus virginianus — Carter et al. 2001
Colinus virginianus — Terhune et al. 2006
Tetrao tetrix — Angelstam 1984
Tetrao tetrix — Bowker et al. 2007
Perdix perdix — Carroll 1990
Phasianus colchicus — Brittas et al. 1992
Phasianus colchicus — Grahn 1993
Phasianus colchicus — Snyder 1985
Lagopus lagopus — Hannon et al. 2003
Lagopus lagopus — Thirgood et al. 2000
Tympanuchus cupido — Lawrence & Silvy 1995
Meleagris gallopavo — Miller et al. 1995
Charadrius melodus — Drake et al. 2001
Bartramia longicauda — Mong & Sandercock 2007
Scolopax minor — McAuley et al. 2005
Strix occidentalis — Ganey et al. 1998
Phalaenoptilus nuttallii — Wang et al. 1995
Dryocopus pileatus — Bull 2001
Seiurus aurocapillus — Bayne & Hobson 2001
Aimophila aestivalis — Seaman & Krementz 2000
Aimophila aestivalis — Stober & Krementz 2000
Emberizinae (4 spp) — Gordon 2000
Pipilo erythrophthalmus — Krementz & Powell 2000
Passerina ciris — Springborn & Meyers 2005
Pooled - Conservative
Pooled - Highly conservative
0
0.25
0.5
0.75
1
proportion of mortalities due to predation

Figure 4.

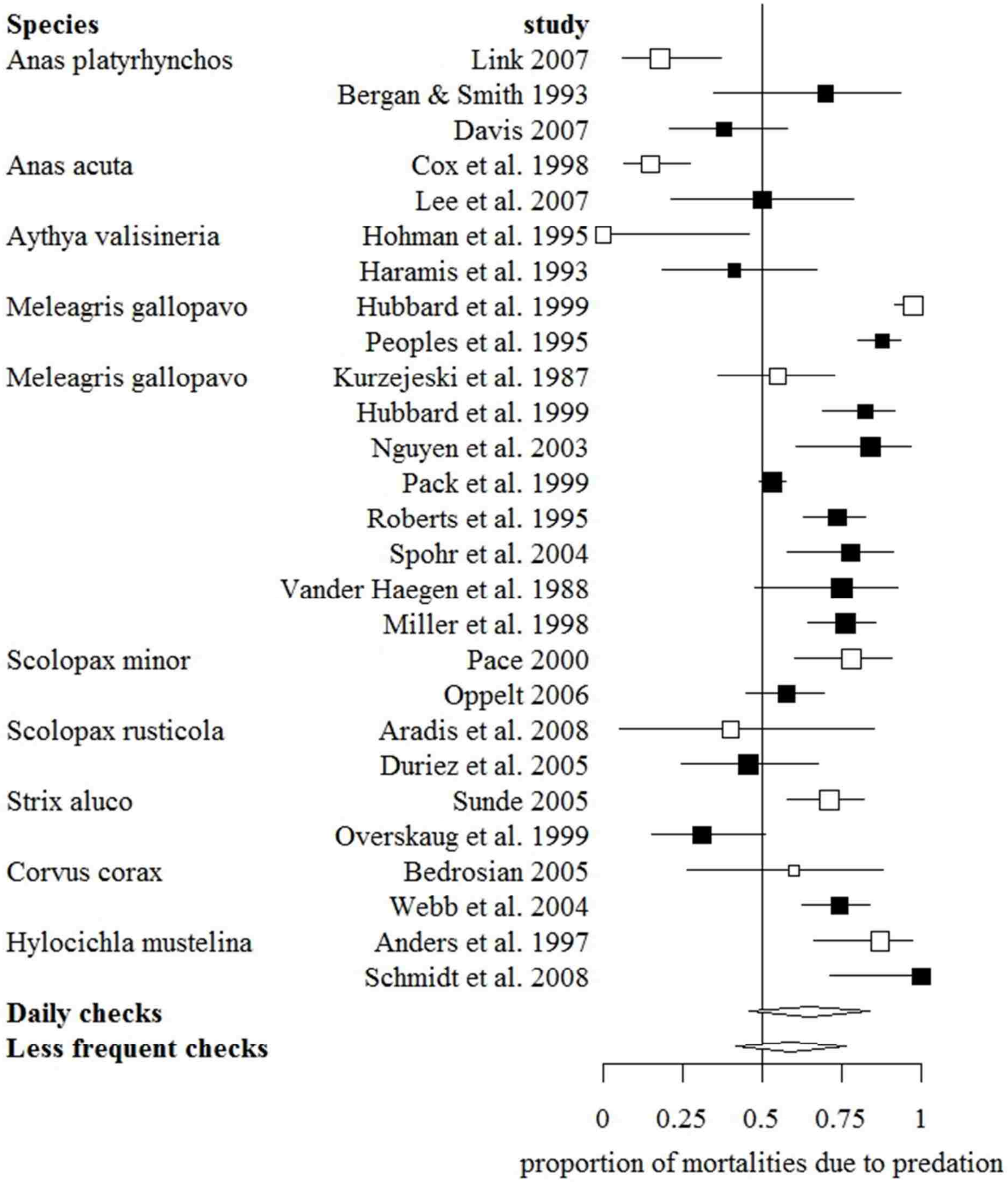
Species
study
Anas platyrhynchos
Link 2007
Bergan & Smith 1993
Davis 2007
Anas acuta
Cox et al. 1998
Lee et al. 2007
Aythya valisineria
Hohman et al. 1995
Haramis et al. 1993
Meleagris gallopavo
Hubbard et al. 1999
Peoples et al. 1995
Meleagris gallopavo
Kurzejeski et al. 1987
Hubbard et al. 1999
Nguyen et al. 2003
Pack et al. 1999
Roberts et al. 1995
Spohr et al. 2004
Vander Haegen et al. 1988
Miller et al. 1998
Scolopax minor
Pace 2000
Oppelt 2006
Scolopax rusticola
Aradis et al. 2008
Duriez et al. 2005
Strix aluco
Sunde 2005
Overskaug et al. 1999
Corvus corax
Bedrosian 2005
Webb et al. 2004
Hylocichla mustelina
Anders et al. 1997
Schmidt et al. 2008
Daily checks
Less frequent checks
0
0.25
0.5
0.75
1
proportion of mortalities due to predation

Figure 5.

Chapter 3: Causes of world-wide variation in parental provisioning behavior relative to offspring number

Daniel C. Barton, Penn Lloyd, and Thomas E. Martin

Abstract

Patterns of variation in reproductive strategies, such as the latitudinal increase in fecundity of terrestrial birds, are hypothesized to be caused by ecological factors such as resource limitation or age-specific extrinsic mortality. Numerous classic tests of such hypotheses examined the responses of parents to natural or experimental variation in offspring number. Yet, such studies often provided ambiguous tests because of their focus on single species and unnatural experimental designs that increased offspring number beyond the normal range of phenotypic variation. We redressed these issues by comparing the responses of songbird parents to unmanipulated and manipulated variation in offspring number within normal ranges. We examined among-species variation in the reaction norm between parental provisioning rate and variation in offspring number for a diversity of bird species on three continents. This reaction norm integrates critical life history tradeoffs and alternative hypotheses predict differing within- and among-species patterns of variation. First, variation in the slope of the reaction norm of per-offspring provisioning to unmanipulated variation in brood size among 29 bird species was largely explained by variation in adult mortality rate. However, the subset of species with high adult mortality appeared to adjust offspring number to parental provisioning capacity, as predicted by food limitation theory. Second, we experimentally reduced broods by approximately half in 9 bird species with divergent life histories and found that reduced broods showed increased per-nestling provisioning and reduced total provisioning, consistent with food limitation. However, the magnitude of the decrease in total provisioning rate increased with decreasing adult mortality among species, suggesting that reproductive effort is differentially adjusted to reduced brood size based on adult mortality probability. These results suggest that ecological factors thought to cause life history variation may interact and shift in importance across species and regions.

Key-words life history, evolution, latitudinal gradient, reproductive effort, provisioning behavior, parental care, food limitation, nest predation, adult mortality

Introduction

Explaining variation in parental effort and offspring number is a fundamental goal of life history theory (Cody 1966, Roff 1992, Stearns 1992). A widely-recognized yet poorly explained pattern in life history variation is the greater fecundity and parental effort of terrestrial bird species at higher latitudes (Lack 1947, Martin et al. 2000, Jetz et al. 2008). Replication of this pattern across diverse radiations of terrestrial birds and across regions suggests an environmental factor that covaries with latitude is responsible, and almost all such explanations invoke either resource limitation (Lack 1947, 1954, Ricklefs 2010) or age-specific extrinsic mortality (Williams 1966, Law 1979, Michod 1979, Martin 2004). A long-enduring context in which many of these explanations were originally proposed or tested were studies of the response of provisioning rate to natural or experimental variation in offspring number (Nur 1984, Saether 1984, Linden and Moller 1989, Golet et al. 1998, Martin 2004).

Provisioning of offspring was central to such tests because it is thought to be sensitive to food availability (Martin 1995) and extrinsic mortality (Skutch 1949, Martin et al. 2000, 2011) while encapsulating tradeoffs between offspring quality and number (Smith and Fretwell 1974) or between current and future reproduction (Williams 1966). Larger brood sizes require more provisioning to maintain offspring quality (Lack 1947, Linden and Moller 1989), but such increased effort may come at the expense of energy, physiological stress, and intrinsic mortality for parents (Sanz and Tinbergen 1999, Nilsson 2002, Bonier et al. 2011). Thus, the reaction norm of parental provisioning rate to brood size has long been thought to represent a key component of life histories and its shape has been proposed to reflect major alternative explanations for life history variation (Nur 1984, VanderWerf 1992, Conrad and Robertson 1993). Yet, past empirical tests of such explanations have provided only ambiguous support for any alternative (VanderWerf 1992, Martin 2004). We suggest this ambiguity arises for two reasons. First, past studies focused on measuring this reaction norm in single species mostly of a limited range of life history variation, which does not allow generalization to the broader observed range of life history variation (VanderWerf 1992, Conrad and Robertson 1993, Martin 2004). Second, many past studies focused on experimentally increasing brood size outside of natural ranges, which exposes parents to novel situations in which their responses are unlikely to be adaptive (Golet et al. 1998). Thus, the design of previous studies may have yielded results both difficult to interpret and generalize.

We attempted to redress these two issues and to provide a clear test of three major alternative explanations for latitudinal gradients in reproductive strategy: food limitation (Lack 1947, 1954), nest predation risk (Skutch 1949, Martin et al. 2000), and adult mortality risk (Williams 1966, Law 1979, Michod 1979, Martin 2004). We expand predictions of previous studies on single species to a comparative context to increase our ability to discriminate among alternatives and generalize our results. We compare variation among species in the slope of the reaction norm of per-nestling provisioning rate to offspring number based on unmanipulated in offspring number kept within natural limits (Fig. 1a). The slope of this reaction norm is theoretically predicted to vary among species in alternative ways under the food limitation and adult mortality hypotheses (Nur 1984). In addition, responses of provisioning rate to brood size may contrast for unmanipulated versus experimental variation. We further develop contrasting predictions for both how per-offspring provisioning rate is expected to respond to manipulated brood size under each alternative hypothesis, and for how total provisioning rate (which reflects parental effort; Nilsson 2002) is expected to respond to manipulated brood size under each alternative.

The food limitation hypothesis posits that, within and among species, parents adjust offspring number to available food resources (Lack 1954, Nur 1984, Pettifor et al. 1988) because natural selection favors the clutch size that maximizes the number of surviving offspring given available food resources (Lack 1947). Over natural variation in brood size, the food limitation hypothesis thus predicts proportionate increase of provisioning with brood size within species (i.e. reaction norm slopes of 0; Fig. 1a). When brood size is experimentally reduced, this hypothesis predicts parents will hold total provisioning rate relatively constant, because parents set provisioning effort to available food (Lack 1954, Pettifor et al. 1988). As a consequence, per-offspring provisioning rate would increase in reduced broods, which may increase offspring quality (Smith and Fretwell 1974).

The nest predation hypothesis suggests that since visually-cuing predators may be attracted to nests by parental activity, high nest predation risk constrains total provisioning rate and brood size (Skutch 1949, Martin et al. 2000, 2011). This hypothesis predicts that species with high nest predation risk should increasingly reduce per-offspring provisioning rates with increasing brood size to minimize total provisioning rate and predation risk to offspring (Eggers et al. 2005). Thus, the slope of the within-species reaction norm of per-offspring provisioning rate to natural variation in offspring number should be steeper in species higher nest predation risk (Fig. 1a). Similarly, when brood size is experimentally reduced, total provisioning rate should decrease with decreased brood size and more strongly in species at higher risk of predation.

The adult mortality hypothesis proposes species with lower adult mortality minimize costs to self during reproduction to maximize iteroparity, while species with high mortality maximize current reproductive effort (Williams 1966, Law 1979, Michod 1979, Ghalambor and Martin 2001). Over natural variation in brood size, this hypothesis predicts that species with low adult mortality risk should show steeper negative slopes (i.e., larger decreases in per-nestling provisioning effort with increasing brood size) than species with high adult mortality risk (Fig. 1a). When brood size is experimentally reduced, species with low adult mortality risk are expected to decrease total provisioning rate more than species with high adult mortality risk. These predictions reflect that longer-lived species (i.e., those with low adult mortality) should reduce effort to minimize risk to iteroparity (Williams 1966; Ghalambor and Martin 2001). Conversely, species with high adult mortality should show little change in effort because probability of future breeding is low with high adult mortality (i.e. they have little iteroparity to preserve by reducing effort). Thus, per-offspring provisioning rate is expected to increase in reduced broods of species with high adult mortality, potentially increasing offspring quality.

We tested the predictions of these alternative hypotheses using a comparative-experimental study of passerine birds. We measured and compared responses of parents to natural variation in brood size among a wide diversity of bird species representing a wide array of life history diversity at four study sites in North and South America and Africa. We further conducted experimental reductions in brood size with a subset of bird species at two study sites in North and South America.

Methods

We compared responses of parents to natural variation in brood size among 29 different bird species (Fig. 2) from Arizona (34° N), South Africa (34° S), Argentina (28° S), and Venezuela (8° N), and to experimental reductions in brood size among 9 different bird species from Arizona and Venezuela (Fig. 2). These study sites and further details of the natural history and life history traits of many of the species included in this study have also been described previously (e.g. Ghalambor and Martin 2001, Martin et al. 2006, Martin et al. 2011).

We measured parental provisioning rate (trips/hr) and per-nestling provisioning rate (trips/hr/nstl) using videotaped observations of nests (4-8 h in length) during the nestling period in Arizona (1993-2006), South Africa (2000-2004), Argentina (1997-2000), and Venezuela (2000-2008). During each year at each site, we located, monitored, and measured parental care at nests following standardized methodology (Martin and Geupel 1993, Martin et al. 2006). Offspring number was determined by direct observation of each nest, and nestling age was determined using observation of critical developmental transitions. Provisioning rates generally increase with nestling age (Lyon et al. 1987; Martin et al. 2011), and we therefore divided nestlings into 3 age groups based on major developmental transitions: before, during, or after ‘pin-break’, the emergence of flight feathers from feather sheaths. Because ‘pin-break’ represents a major developmental transition in altricial birds near completion of musculoskeletal development, we standardized our reported results to this age to allow comparisons among species with different nestling periods (Martin et al. 2011).

We experimentally manipulated brood size in 9 bird species (Fig. 2) at the Venezuela (2005-2008) and Arizona (2007-2010) study sites. To manipulate brood size, we removed approximately half the eggs in a complete clutch and replaced them with dummy eggs. We also reduced brood size by inserting a thermocouple into a single egg in a clutch as part of another study conducted at the same study sites (e.g. Martin et al. 2007). We removed dummy eggs or the egg containing the thermocouple at the time of hatching. Experimentally reduced nests were filmed every other day following hatching until failed or fledged, and were matched with a within-season control nest with the same initial clutch size when possible.

We estimated the slope of the relationship between per-offspring provisioning rate and offspring number using ANCOVA with per-offspring provisioning rate as the response variable, species and nestling age as factors, and species by nestling age and species by brood size interactions. We used parameter estimates of the species by brood size interaction as species-specific slopes of the relationship between per-offspring provisioning rate and offspring number while controlling for the effect of age. We used the t-scores of the parameter estimates of the species by brood size interaction to test whether species-specific slopes differed from 0.

We tested the effect of experimental brood size reductions on provisioning rates using two different ANOVA approaches. First, we tested whether the natural log of total provisioning rate and the natural log of per-nestling provisioning rate at 'pin break' (± 1 day) differed between within-season matched-pair treatment (reduced) and control nests. We used an ANOVA design containing the treatment by species interaction (our test of whether response varied among species), species, and a blocking variable for pair. Second, because not all reduced nests were (or could be, in the case of odd-numbered clutch sizes) reduced by exactly half, we used an ANCOVA design containing an interaction between species and a covariate for the proportionate magnitude of treatment (range: 0-0.66), species, and a blocking variable for pair. We then used this model to predict the response of each species to an average brood size reduction of 50% to standardize the magnitude of treatment for across species comparisons.

We quantified offspring quality in manipulated (reduced) and control broods by measuring nestling mass, which is an important predictor of juvenile survival in altricial birds (Nur 1984, Golet et al. 1998). We measured mass of all nestlings in a nest using a digital balance at 'pin break' age (± 1 day; see above). We tested the effect of experimental brood size reductions on nestling mass and tarsus using an ANCOVA model containing effects of treatment by species interaction, age by species interaction, species, and a within-subject error term for nest (because observations of nestlings within each nest are not independent from each other).

To determine nestling predation, we monitored nests following established protocols (Martin and Geupel 1993) to determine the number of days each nest was active and to assess success or failure. We estimated daily predation risk during the nestling period using the Mayfield method (Mayfield 1975, Johnson 1979). To determine adult mortality rates, we captured and individually marked adult birds using individual combinations of colored and numbered leg bands, and systematically recaptured and visually re-sighted marked adults throughout each study area each year. Adult survival rates were estimated using Cormack-Jolly-Seber or multistate mark-recapture models in Program MARK (Lebreton et al. 1992, White and Burnham 1999, Chapter 3). We tested for predicted correlations between estimated reaction norm slopes and responses to brood size manipulations using Pearson's correlation coefficient. We controlled for the effects of a phylogenetic hypothesis (Figure 2) on correlated evolution in the continuous characters we measured (adult and nestling mortality rate, reaction norm slope) using phylogenetic independent contrasts (Felsenstein 1985) as implemented in the PDAP Package (Midford et al. 2009) for Program Mesquite (Maddison and Maddison 2011). We used published phylogenetic hypotheses (Jønsson and Fjeldså 2006, Davis 2008) to develop our phylogenetic hypothesis (Figure 2).

Results

The relationship between per-nestling provisioning rate and natural variation in brood size varied significantly among species (Fig. 1b). Estimates of reaction norm slopes of per-offspring provisioning rate were negative for all 29 species examined and significantly less than 0 for 16 species. Slopes that did not differ from 0 could reflect low statistical power in some cases, but nevertheless, some species appear to adjust brood size proportionately to available food while others do not (Fig. 1b), lending mixed support to the food limitation hypothesis. Differences among species in reaction norm were not correlated with among-species differences in nest predation risk (Figure 3a), contrary to the prediction of the nest predation hypothesis. Differences among species in reaction norm slope were highly correlated with among-species differences in adult mortality rates (Figure 3b), supporting the prediction of the adult mortality hypothesis. Neither of these correlations was affected by the potentially confounding influence of phylogeny (Figure 2, Appendix 3).

We experimentally reduced brood size at 48 nests of 9 species that survived to ‘pin-break’ age (many more were reduced and failed due to predation) matched with 48 control nests within year and season. The natural log of total provisioning rate varied significantly among species, as did the response of the natural log of total provisioning rate to experimental reduction (Figure 4a). The three tropical (Venezuela) species showed a significant reduction in total provisioning rate in response to the brood reduction treatment while the six temperate (Arizona) species did not (Figure 4). The natural log of per-nestling provisioning rate also varied significantly among species as did the response of natural log of per-nestling provisioning rate to experimental reduction (Figure 5a). The 6 temperate species showed a significant increase in per-nestling provisioning rates in response to reductions (t-test from ANOVA, $P < 0.05$; Figure 5a) while the 3 tropical species did not (t-test from ANOVA, $P > 0.68$; Figure 5a). Reduced broods showed increased nestling mass at ‘pin break’ age in 4 of the 6 Arizona species (Figure 5b) while data were not sufficient for tests of reduced brood size on nestling mass in Venezuela species.

Magnitude of response of the natural log of total provisioning rate to brood size reduction varied from a -2.0% change (*J. hyemalis*) to a -50.5% change (*B. tristriatus*). Because the magnitude of brood size manipulation varied among treatment-control pairs from -33% to -66% and among species from -35.2% to -57.1%, we used an ANCOVA approach to predict species responses to a standardized brood size reduction of 50%. The slope of the relationship between brood size reduction magnitude and the natural log of provisioning rate varied significantly among species ($F_{\text{species X magnitude } 9,\, 39} = 6.9606$, $P < 0.001$) and was significantly different than 0 in three species (t-test from ANCOVA, $P < 0.01$) and approached significance in two species (t-test from ANCOVA, $0.05 < P < 0.10$). The predicted responses of the natural log of provisioning rate to a 50% brood size reduction varied from -1.3% (*P. chlorurs*) to -50.5% (*B. tristriatus*; Figure 4b). The predicted among-species responses to a 50% reduction from this ANCOVA approach and the estimated response of species to brood size reductions uncorrected for magnitude from ANOVA were highly correlated ($N = 9$, $r = 0.99$, $P < 0.001$).

The three tropical Venezuelan species with the lowest adult mortality, *B. tristriatus*, *P. flavipes*, and *H. leucophrys*, showed the only statistically significant (Figure 4a) and the largest (Figure 4b) reductions in total provisioning rate in response to brood size reduction. Differences among species in percentage reduction of total provisioning rate were not correlated with among-species differences in nest predation risk (N = 9, $r < 0.2$, $P > 0.5$), providing no support for the nest predation hypothesis. Differences among species in percentage reduction of total provisioning rate were highly correlated with among-species differences in adult mortality risk (Figure 4b), supporting the adult mortality hypothesis. This correlation was independent of phylogeny (Figure 2, Appendix 3).

Discussion

We found that a major prediction of food limitation theory – the apparent adjustment of brood size to parental provisioning capacity (Lack 1947, 1954) – was upheld in species with high adult mortality risk in both comparative (Figures 1b, 3b) and experimental (Figure 4) study designs. Species with high adult mortality risk apparently proportionately adjusted brood size and provisioning rate over the range of unmanipulated variation (Figure 1b; Pettifor et al. 1988). Species with high adult mortality risk also continued to provision at a high rate when brood size was experimentally reduced (i.e. were relatively unresponsive to manipulation; Figure 4) and showed increased per-nestling provisioning rate in experimentally reduced broods. Reduced broods in 4 of the 6 temperate species that showed increased per-nestling provisioning rate also showed increased nestling mass (Figure 4), suggesting benefits of increased per-offspring provisioning for offspring quality (Nur 1984; Pettifor et al. 1988).

However, species with low adult mortality risk showed alternative responses of provisioning rate to natural and experimental variation in brood size inconsistent with the predictions of the food limitation hypothesis. Responses of parents to natural and experimental variation in brood size varied across a gradient of adult mortality risk (Figures 1b, 3b). Species with high adult mortality appeared to show high parental effort across natural variation in brood size and maintained high parental effort when brood size was reduced. In contrast, species with low adult mortality show reduced per-nestling provisioning rate with increasing natural brood size and reduced total provisioning rate (and similar per-nestling provisioning rate) with experimentally reduced brood size. Surprisingly, we did not see evidence that nest predation risk affected the responses of parents to natural or experimental variation in brood size, despite the known effects of nest predation risk on mean provisioning rates in songbirds (Martin et al. 2000; Martin et al. 2011).

Food limitation may thus appear highly important in constraining the expression of life history traits in some contexts – such as within north-temperate regions, where much previous research has been conducted (Martin 2004) – but not in others, such as across regions including the tropics. Food limitation may similarly vary in importance for determining the outcome of life history microevolution (Walsh and Reznick 2008). These results may help resolve the disconnect between studies that supported food limitation as an explanation for life history variation in birds (Lack 1954, VanderWerf 1992, Jetz et al. 2008, Ricklefs 2010) and other studies that suggest food limitation is an insufficient explanation for life history variation (Owens and Bennett 1995, Ferretti et al. 2005).

Reviews of previous experimental brood size manipulation experiments have noted responses to brood size manipulation are highly variable among species (Linden and Moller

1989, VanderWerf 1992). Explanations for such wide variation in responses are likely two-fold: first, many previous studies focused on experimental increases beyond the range of natural brood size variation which expose parents to novel situations in which their responses are unlikely to be adaptive (Golet et al. 1998). Second, variation among species in responses is likely to be partly caused by differences among species in their life history traits (VanderWerf 1992). Our study confirms this idea, and we show how life history variation – expressed as adult mortality rates – may explain among-species differences in response to brood size manipulations (Figures 4, 5) and further show how such among-species differences may be used to test alternative explanations for life history variation.

We see three alternative explanations for variation among species in provisioning effort that is correlated with adult mortality rates, such as the results reported here. First, variation among species in reproductive traits may be a consequence of extrinsic adult mortality risk as suggested by classic theory that suggests low extrinsic mortality favors reduced reproductive effort to preserve iteroparity (Williams 1966, Law 1979, Michod 1979, Martin 2004). Second, seasonal resource availability dynamics may impose winter mortality and then provide high levels of food availability in the breeding season in temperate regions as predicted by Ashmole's hypothesis (Ricklefs 2010). Third, adult mortality rates may be a proximate consequence of variation in provisioning effort (Stearns 1992). The second explanation is likely insufficient because terrestrial bird species do not generally show the patterns of mortality predicted by Ashmole's hypothesis (Chapter 1). Our results suggest that the third explanation is insufficient because we found that longer-lived species adjust their reproductive effort, as measured by provisioning rate, downwards in response to brood size reductions (Figure 4). This result is not expected if variation among species in adult mortality rates is simply a consequence of reproductive effort. Thus, we suggest that variation among species in adult mortality risk may explain variation in reproductive effort as measured by provisioning behavior or clutch size as proposed by Williams (1966).

Our results suggest that adult mortality risk plays an over-arching role in determining how species resolve critical tradeoffs between current and future reproduction and between number and quality of offspring. Yet, species with high adult mortality rate may resolve the tradeoff between current and future reproduction in favor of maximizing current reproduction and thus encounter the constraints of food limitation. We suggest that food limitation shifts in importance as an interacting function of adult mortality risk across geographic regions.

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Figure legends

Figure 1. Among-species variation in reaction norms of per-offspring provisioning rate to natural variation in offspring number. **a**, Three potential reaction norms of per-offspring provisioning rate to offspring number. When the slope of this reaction norm is 0, parents increase total provisioning rate proportionally with increased offspring number, resulting in constant per-offspring provisioning. When the slope of this reaction norm is less than 0, parents increase total provisioning rate slower (less than proportional) with offspring number, thus per-offspring provisioning declines with increasing offspring number. Food limitation theory predicts slopes of 0 (e.g. line 1). The nest predation alternative predicts steeper slopes in species with higher nest predation (e.g. line 3 vs. line 2), while the adult mortality alternative predicts steeper slopes in species with lower adult mortality. **b**, Estimated reaction norms of per-nestling provisioning rate to natural variation in brood size for 29 passerine bird species from 4 study sites (N = 1644 observations). Slope varied significantly among species ($F_{\text{species X brood size } 29,\, 1529} = 9.74$, $P < 0.001$). The point estimate of all slopes is negative and for 16 is significantly different from 0 (t-test from ANCOVA, $P < 0.05$).

Figure 2. Phylogeny, standard name, geographic site, and life history traits of 29 bird species studied. Annual adult mortality rate was estimated using Cormack-Jolly-Seber models of mark-resight-recapture data collected from the study sites. Nestling predation risk was estimated for each species using the Mayfield method based on large sample sizes from each species and study site. Reaction norm slopes are the slope of the linear relationship between per-nestling provisioning rates and offspring number estimated by ANCOVA. Slopes of reaction norms significantly different from 0 (t-test from ANCOVA, $P < 0.05$) are shown in bold. Phylogeny

branches and species data are color-coded by geographic site. Branches basal to multiple geographic sites are shown in black. Names of 7 of the 9 species for which brood size was manipulated are starred, while two (*Turdus migratorious*, *Poecile montanus*) are not shown because they were only included in the experimental portion of the study. Phylogeny based on the supertrees of Jønsson and Knud (2006) and Davis (2008).

Figure 3. Among-species variation in reaction norms of per-offspring provisioning rate to natural variation in offspring number and relationship to ecological factors. **a**, Reaction norm slope and daily nest mortality were not correlated among species (n= 29, Pearson correlation, r = -0.03, P = 0.86) contrary to the nest predation hypothesis. **b,** Reaction norm slope (from Figure 1b) and annual adult mortality were highly correlated among species (n = 29, Pearson correlation, r = 0.68, P < 0.001), supporting the adult mortality hypothesis. The reported correlations were not strongly influenced by the potentially confounding effects of phylogeny (Appendix 3).

Figure 4. Among-species variation in responses of total provisioning rate to experimental brood size reductions and relationship to adult mortality risk. **a**, Species-specific total provisioning rate in control and reduced broods (by about 50%) in 9 bird species in Arizona and Venezuela. Closed symbols are control group means, and open symbols are reduction group means. Sample sizes (N = number of treatment-control pairs): *J. hyemalis* (7), *O. celata* (5), *P. chlorurus* (9), *P. montanus* (4), *T. aedon* (4), *T. migratorious* (5), *B. tristriatus* (5), *P. flavipes* (5), *H. leucophrys* (4). Each species-specific treatment-control pair is connected and labeled by color. Provisioning rate varied among species ($F_{\text{species } 8, 39} = 59.03$, P < 0.001) and response of

provisioning rate to reduction varied among species ($F_{\text{species X treatment } 9, 39} = 6.82$, $P < 0.001$). Significant reductions in provisioning rate in response to reductions were observed in 3 of 9 species (indicated by *; t-test from ANOVA, $P < 0.01$) and response approached significance in 2 of 9 species (indicated by †; t-test from ANOVA, $0.05 < P < 0.10$). **b,** Comparison of predicted percent reduction in total provisioning rate in response to a standardized 50% brood size reduction among species in relation to annual adult mortality (from ANCOVA). Percent reduction was significantly correlated with annual adult mortality rate (N = 9, Pearson correlation, r = 0.906, $P < 0.001$), supporting the adult mortality hypothesis. Significant reductions are indicated by * (t-test from ANOVA, $P < 0.01$) and † (t-test from ANOVA, $0.05 < P < 0.10$). This result was independent of phylogenetic effects (Appendix 3).

Figure 5. Among species variation in responses of per-nestling provisioning rate and offspring mass to experimental brood size reductions. **a**, Species-specific per-nestling provisioning rate in control and reduced broods (by about 50%) in 9 bird species in Arizona and Venezuela. Closed symbols are control group means, and open symbols are reduction group means. Sample sizes same as shown in Figure 4. Each species-specific treatment-control pair is connected and labeled by color. Response of per-nestling provisioning rate to reduction varied among species ($F_{\text{species X treatment } 9, 39} = 9.80$, $P < 0.001$). Significant increases in per-nestling provisioning rate in response to reductions were observed in 6 of 9 species (indicated by *; t-test from ANOVA, $P < 0.01$). **b**, Species-specific nestling mass at ‘pin break’ in control and reduced (by about 50%) broods of 6 bird species in Arizona. Symbols as in panel **a**. Sample sizes (treatment, control nests): *J. hyemalis* (7,6), *O. celata* (5,9), *P. chlorurus* (8,10), *P. montanus* (3,4), *T. aedon* (3,6), *T. migratorious* (4,4). Response of nestling mass to brood size reduction varied among species

($F_{\text{species X treatment } 6, 51} = 6.81$, $P < 0.001$). Significant increases in nestling mass were observed in 3 of 6 species (indicated by *; t-test from ANOVA, $P < 0.05$) and approached significance in 1 of 6 species (indicated by †; t-test from ANOVA, $0.05 < P < 0.10$).

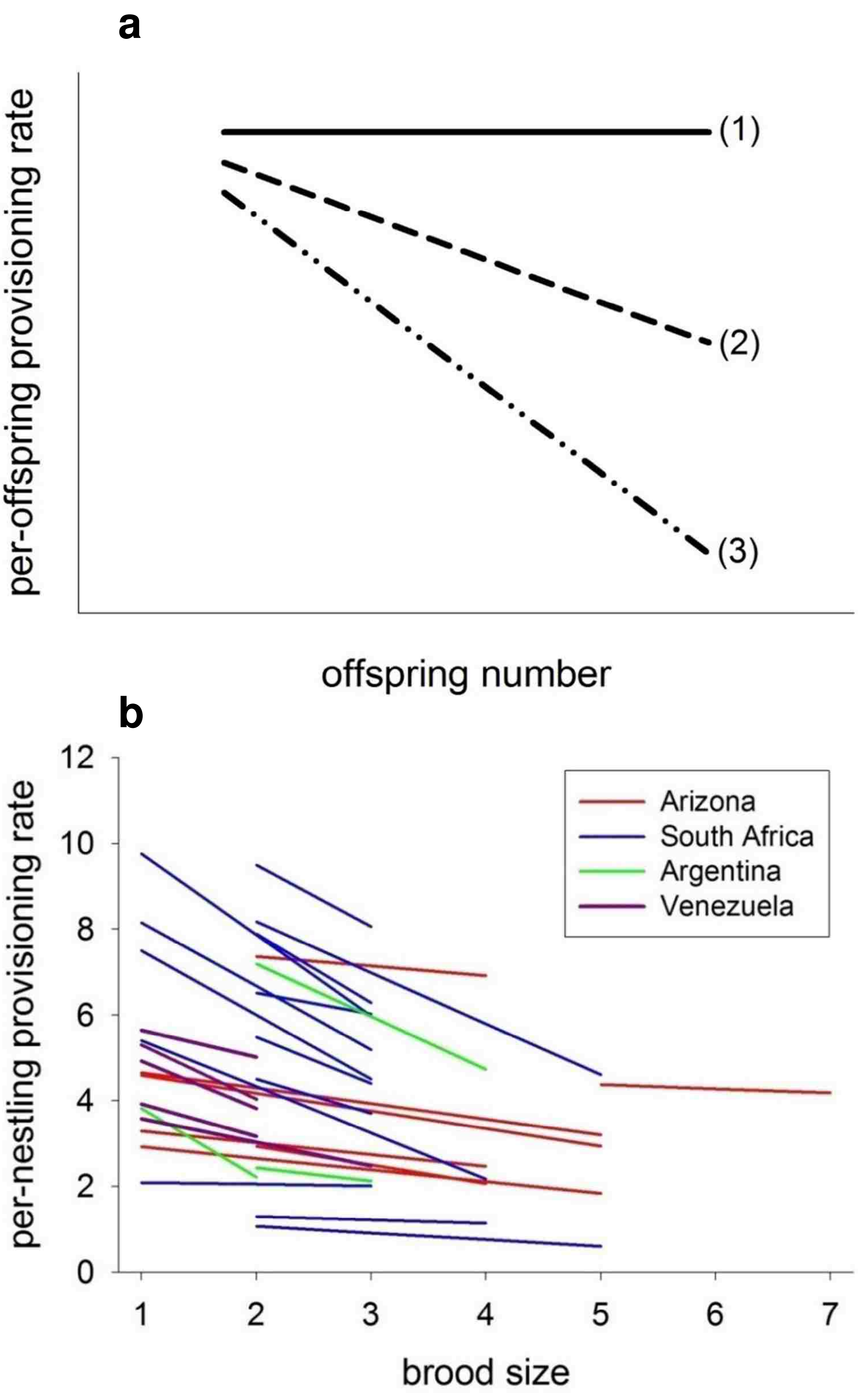
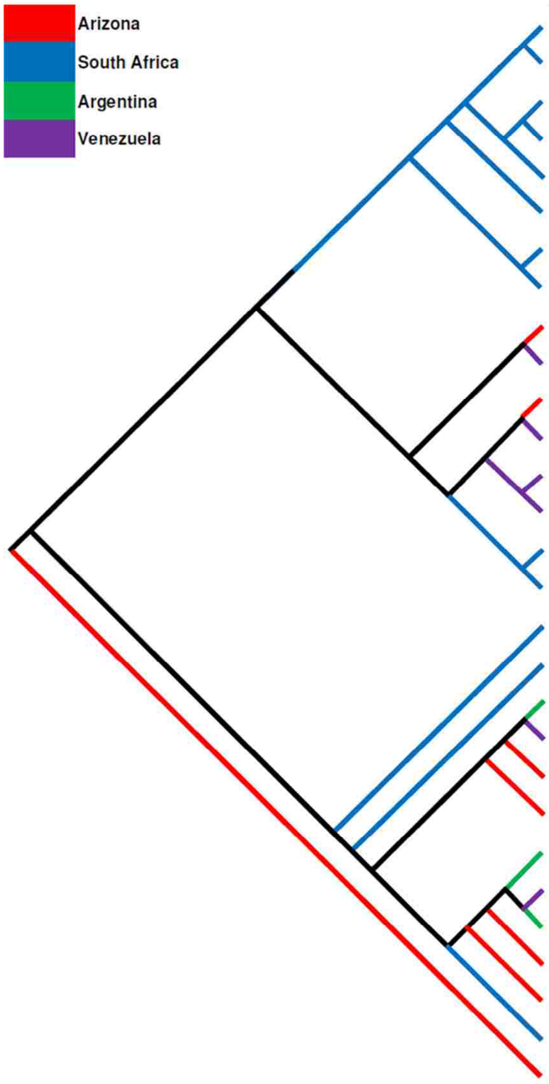

a
per-offspring provisioning rate
(1)
(2)
(3)
offspring number
b
per-nestling provisioning rate
0
2
4
6
8
10
12
1
2
3
4
5
6
7
brood size
Arizona
South Africa
Argentina
Venezuela

Figure 1.



species	**annual adult mortality rate**	**daily nest predation rate**	**reaction norm slope**
Zosterops pallidus	0.221	0.065	**-1.43**
Parisoma subcaeruleum	0.287	0.033	**-0.79**
Apalis thoracica	0.282	0.036	-0.50
Cisticola subruficapilla	0.276	0.048	**-1.08**
Prinia maculosa	0.270	0.044	**-1.19**
Pycnonotus capensis	0.255	0.059	**-1.09**
Sphenoeacus afer	0.217	0.033	-0.04
Sylvietta rufescens	0.193	0.037	**-1.89**
*Troglodytes aedon**	0.629	0.004	-0.09
*Henicorhina leucophrys**	0.147	0.037	**-1.27**
Catharus guttatus	0.449	0.048	-0.44
Catharus fuscater	0.276	0.039	**-0.75**
*Platycichla flavipes**	0.263	0.064	**-0.55**
Turdus olivater	0.365	0.048	-0.88
Cercotrichas coryphaeus	0.218	0.042	**-1.50**
Cossypha caffra	0.089	0.043	**-1.61**
Cinnyris chalybeus	0.186	0.043	**-1.48**
Serinus flaviventris	0.476	0.052	-0.16
Basileuterus bivittatus	0.169	0.031	**-1.23**
*Basileuters tristriatus**	0.157	0.072	-0.63
Cardellina rubifrons	0.513	0.039	**-0.36**
*Oreothlypis celata**	0.485	0.034	**-0.42**
Arremon flavirostris	0.167	0.037	-0.30
Buarremon brunneinucha	0.181	0.060	-1.10
Buarremon torquatus	0.100	0.033	**-1.61**
*Junco hyemalis**	0.430	0.038	-0.27
*Pipilo chlorurus**	0.440	0.040	-0.28
Emberiza capensis	0.333	0.089	-0.08
Empidonax occidentalis	0.411	0.031	-0.22

Figure 2.

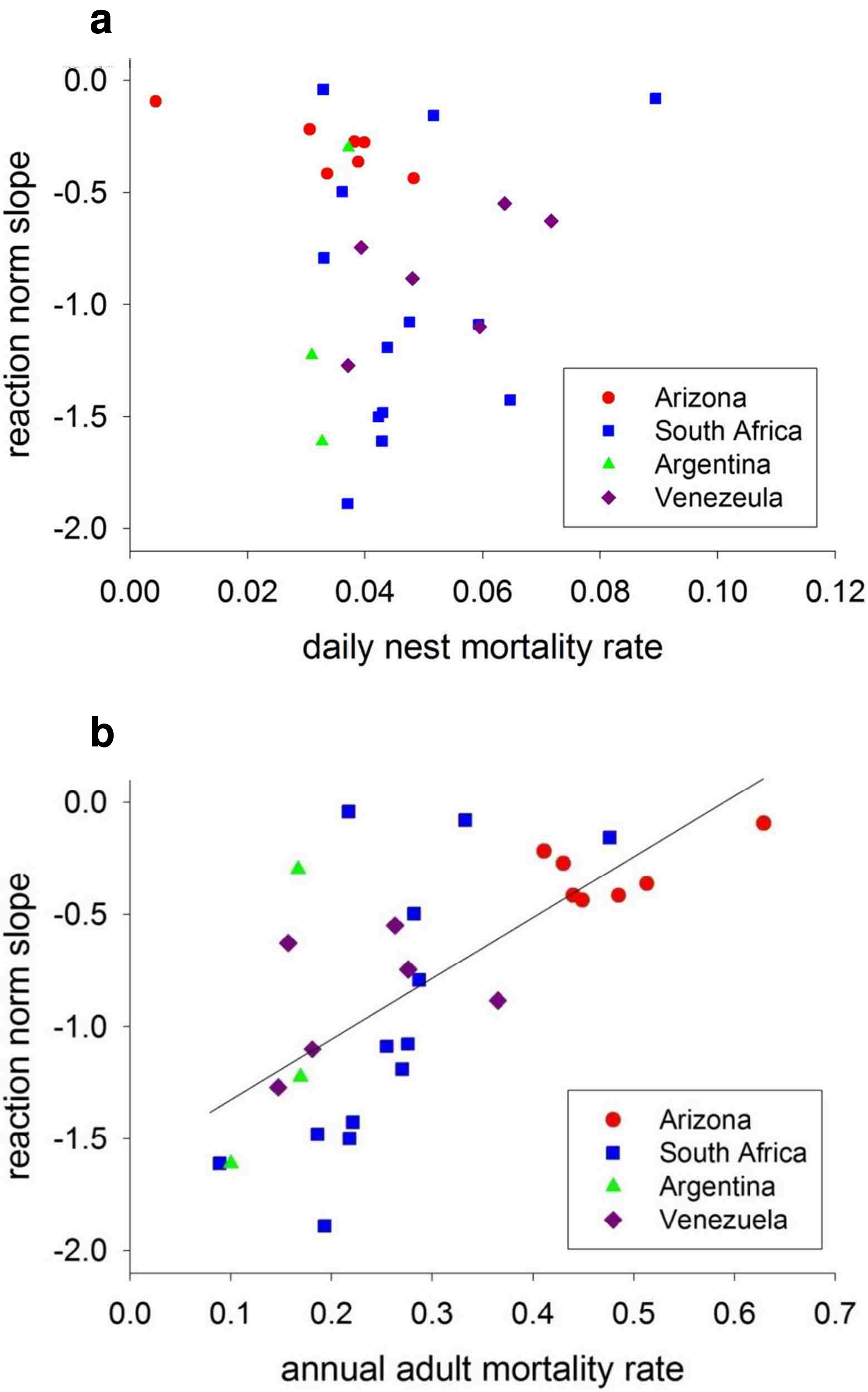

a
reaction norm slope
0.0
-0.5
-1.0
-1.5
-2.0
0.00
0.02
0.04
0.06
0.08
0.10
0.12
daily nest mortality rate
● Arizona
■ South Africa
▲ Argentina
◆ Venezeula
b
reaction norm slope
0.0
-0.5
-1.0
-1.5
-2.0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
annual adult mortality rate
● Arizona
■ South Africa
▲ Argentina
◆ Venezuela

Figure 3.

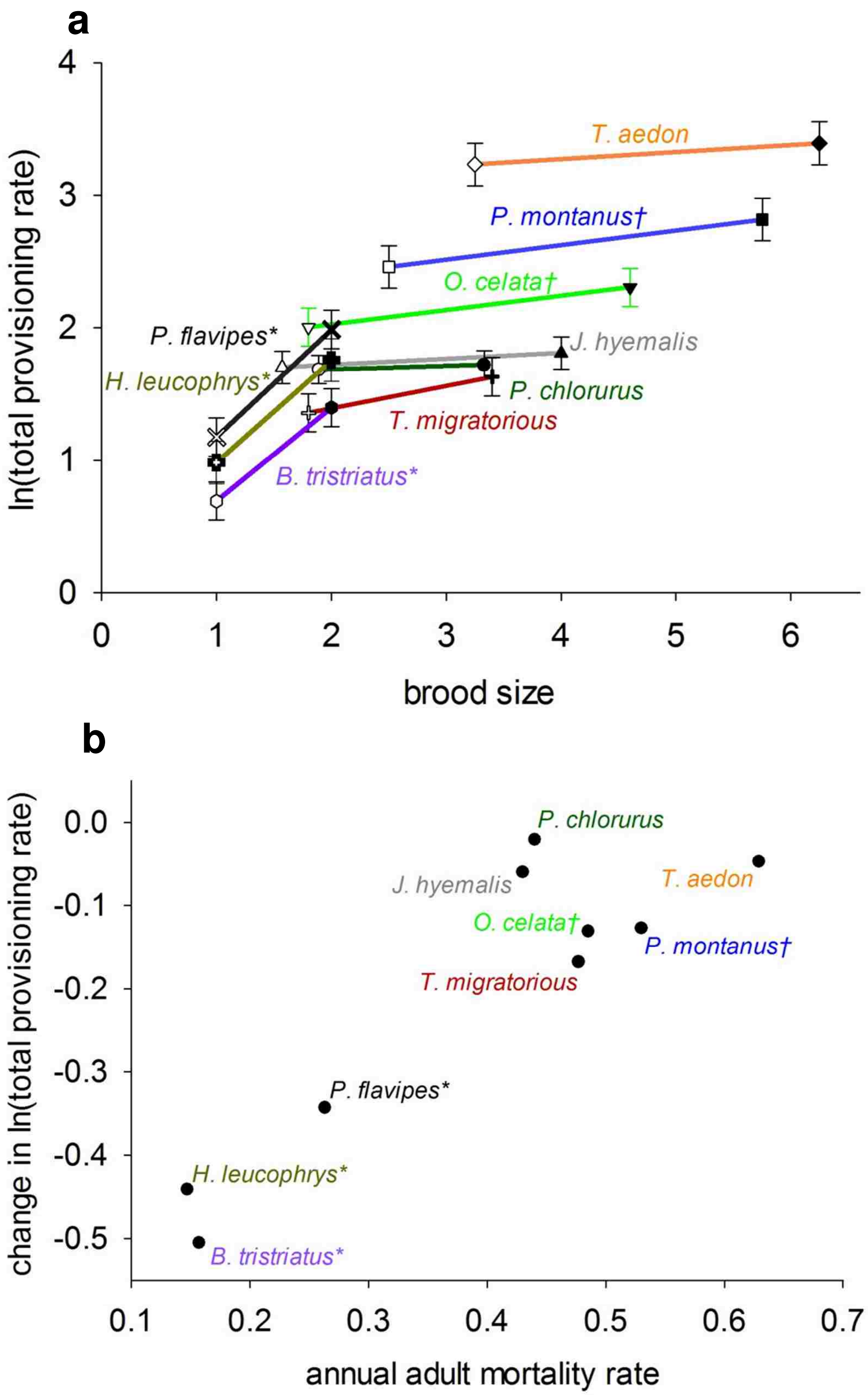

a
ln(total provisioning rate)
4
3
2
1
0
0
1
2
3
4
5
6
brood size
T. aedon
P. montanus†
O. celata†
P. flavipes*
J. hyemalis
H. leucophrys*
P. chlorurus
T. migratorious
B. tristriatus*
b
change in ln(total provisioning rate)
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
0.1
0.2
0.3
0.4
0.5
0.6
0.7
annual adult mortality rate
P. chlorurus
J. hyemalis
T. aedon
O. celata†
P. montanus†
T. migratorious
P. flavipes*
H. leucophrys*
B. tristriatus*

Figure 4.

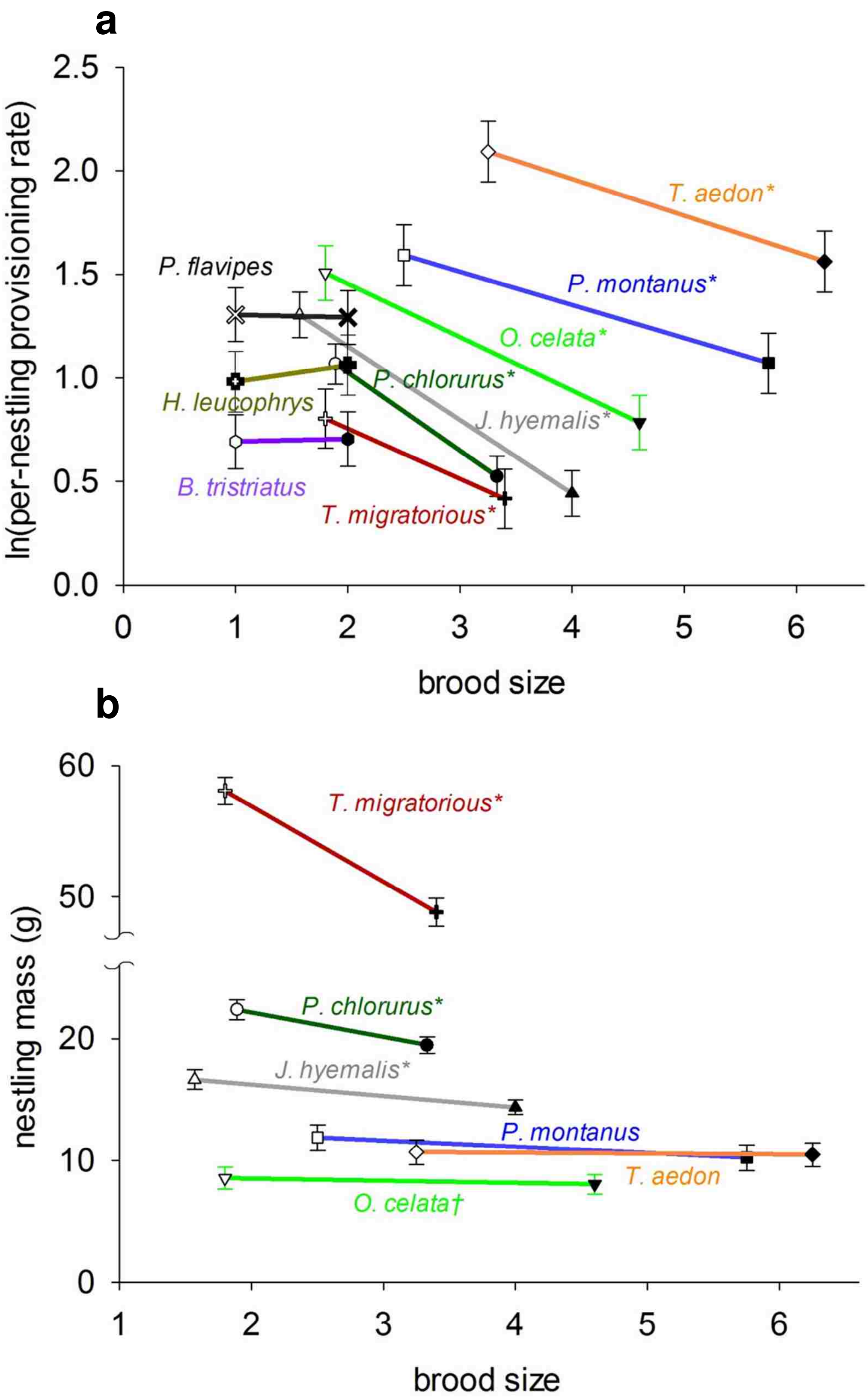

a
ln(per-nestling provisioning rate)
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
brood size
T. aedon*
P. montanus*
P. flavipes
O. celata*
P. chlorurus*
H. leucophrys
J. hyemalis*
B. tristriatus
T. migratorious*
b
nestling mass (g)
60
50
20
10
0
1
2
3
4
5
6
brood size
T. migratorious*
P. chlorurus*
J. hyemalis*
P. montanus
T. aedon
O. celata†

Figure 5.

Chapter 4: Dispersal and spatiotemporal variance in survival in three passerine bird species with differing migratory behavior

Daniel C. Barton and Thomas E. Martin

Abstract

Variation among species in dispersal movements and seasonal migration are widely predicted to hold major consequences for variation among species in population dynamics. Spatiotemporal variance in survival probability is an important determinant of population growth rate in iteroparous organisms. Spatial variance in survival is generally expected to decrease with increasing dispersal, while seasonal migration is generally predicted to decrease temporal variance in survival, yet tests of these predictions are lacking. Further, seasonal migration may increase propensity for dispersal, yet tests of this prediction are also generally lacking. Using a long-term (1993-2008) study of marked birds in Arizona and a multi-state mark-recapture modeling framework, we describe variation in breeding dispersal movements among three species of songbirds with differing migratory strategies. We further tested whether spatial variance in survival decreased with increasing dispersal movements, and whether temporal variance was lower in more migratory species, as predicted by general theory. We show that dispersal movements were greatest in a long-distance migrant, moderate in a short-distance migrant, and least in a resident songbird species. We find reduced spatial variance in survival rates in species with greater dispersal movements. We find more complex differences in temporal variation in survival rates among the three species, discuss potential explanations for such differences, and compare with a larger published dataset of 19 additional species with differing migratory strategies. Our results suggest that spatial variance in survival rates of songbirds is, as predicted by theory, partly mediated by breeding dispersal, while temporal variance in survival rates is not lower in migratory species, contrary to expectations.

Key words: dispersal, spatial variance, temporal variance, survival, migration

Introduction

Dispersal is a key biological phenomenon with diverse causes and important consequences for ecological and evolutionary processes (Clobert et al. 2001). Dispersal distances vary widely among individuals and populations (Bowler and Benton 2005) with widely recognized consequences for processes such as population dynamics (Kareiva et al. 1990, Daniels and Walters 2000) and gene flow (Bohonak 1999). Dispersal may influence the degree of spatiotemporal variance in survival rates (Pienkowski and Evans 1985) in addition to causing biased underestimates of survival rates through permanent emigration in open populations (e.g. Cilimburg et al. 2002). Survival rates and their variances are important deterministic components of population growth rates (Tuljapurkar 1982, Saether and Bakke 2000, Clark and Martin 2007) and are thus critical in the study of population ecology (Kareiva et al. 1990). Yet, the effects of differences among species in dispersal distances on spatiotemporal variance in survival rates or on bias in survival rate estimates remain generally unknown.

The degree of spatiotemporal variance in population growth rate has important consequences for long-term population growth rate (Tuljapurkar 1982) and probability of population persistence in declining populations (Morris and Doak 2002). Increased spatiotemporal variance in survival rates generally decreases long-term population growth rates and reduces probability of population persistence, particularly in iteroparous organisms (Gaillard et al. 2000, Sibly and Hone 2002). The two components of spatiotemporal variance, spatial variance and temporal variance, are thought determined by alternative mechanisms. Spatial variance in demographic parameters is expected to be low when dispersal is relatively high (effectively creating a single population) or when a high degree of environmental correlation exists across space (causing subpopulations to have similar rates; Harrison 1991). Conversely, spatial variance is expected to be high when dispersal is low or when a low degree of environmental correlation exists across space. Temporal variance in survival rates is thought to be greater in populations that experience more variable climatic conditions during an annual cycle, and in the case of birds, this is represented by species that remain resident at high latitude compared with long-distance migrants (Greenberg 1980, Mönkkönen 1992). Yet, tests of these predictions are generally lacking.

Dispersal also causes biased underestimates of survival in open populations, because permanent emigration is not separable from mortality (Lebreton et al. 1992). Increased permanent emigration from finite study areas reduces apparent survival while true survival remains unchanged and unknown (Cilimburg et al. 2002; Zimmerman et al. 2007). Extending this prediction to a comparative context, populations with reduced dispersal movements would likely show reduced differences between apparent survival at a smaller spatial scale and a larger spatial scale. Conversely, populations with greater dispersal movements would likely show larger differences between small and large spatial scale estimates (Zimmerman et al. 2007). While permanent emigration is widely recognized to create biased underestimates of survival in open populations, the degree to which variation among populations in dispersal impacts the size of this bias remains mostly unexamined (Marshall et al. 2004).

We wished to test the influence of variation in dispersal behavior on spatial and temporal variation in survival. We *a priori* selected for comparison three bird species that differed in their migratory behavior because migratory strategy is a potential predictor of among-species differences in dispersal behavior (Paradis et al. 1998). Bird species vary dramatically in their seasonal migration strategies, ranging from the longest-distance movements known in animals to resident species with limited home ranges (Alerstam 2001). Migrants generally have greater mobility than resident bird species and experience an increased probability of chance events during migration that may influence dispersal movement (Alerstam 2001). Seasonal migrant populations are therefore generally predicted to show greater dispersal movements than resident populations, although tests are rare and have somewhat confounded migration with dispersal (Paradis et al. 1998, Dawideit et al. 2009). Understanding variation among bird species in dispersal movements and whether this variation is related to migratory strategy thus also remains an open question. Nonetheless, migratory strategy was a reasonable basis of choosing species to compare dispersal movements and consequences for spatiotemporal variation in survival rates.

We conducted a 16-year mark-recapture-resight study of three passerine bird species with differing migratory strategies. We tested four predicted effects of differences among species in migratory and dispersal behavior for population dynamics and survival estimates. First, we tested our assumption, suggested by a previous study (i.e. Paradis et al. 1998), that breeding dispersal increased with migratory distance. We improved upon previous designs for testing the relationship between dispersal movements and migratory behavior (Paradis et al. 1998, Dawideit et al. 2009) by using the same methodology for comparisons across species, and by using a live encounters study of wild populations rather than a band-recovery study which may confound dispersal and migration. Second, we tested whether increased rates of breeding dispersal reduced spatial variance in survival rates. Third, we tested whether increased migratory distance reduced temporal variance in survival rates. We also compared our estimates of temporal variance in survival rates with a published dataset of temporal variance in survival rates to test whether migratory behavior predicted temporal variance in survival rates in a broader sample of species. Fourth, we tested whether variation among species in dispersal movements biased survival estimates differentially by testing whether the difference between small and large spatial scale estimates of survival increased with increasing dispersal movements.

Methods

Study Site and Species

We conducted a long-term study of marked individual birds in Coconino County, Arizona, USA from 1993-2008. Details on the location, plant community, and breeding bird community of this study site have been detailed previously (Martin 1998, 2001). We marked, recaptured, and resighted Mountain Chickadee (*Poecile gambelli*), Gray-headed Junco (*Junco hyemalis dorsalis*), and Orange-crowned Warbler (*Oreothylpis celata orestera*). Mountain Chickadee is a year-round resident or altitudinal migrant (Dixon and Gilbert 1964). Gray-headed Junco is a short-distance migrant (Nolan et al. 1995). Orange-crowned Warbler is a neotropical migrant that winters from northern to southern Mexico (Sogge et al. 2010). All three species are songbirds (Order Passeriformes) of similar body size (approximately 10-20 g) that are territorial and socially monogamous during the breeding season.

Our study area was sub-divided into five strata, each containing between two and six study plots (20 study plots total). Each stratum was a set of plots physically sub-divided from other strata by either large canyons or a ridge and secondary road. The centroids of strata varied from 0.9-10.7 km in distance from each other, and the five strata varied from 47-107 ha in area. Study plots were individual snow-melt drainages of mixed coniferous and deciduous vegetation (Martin 1998, 2001). We visited each plot to capture and mark birds from 6-10 times per season during May-July of each year. We captured birds using mist-nets and individually marked them using unique combinations of colored plastic leg bands and a single unique U.S. Fish and Wildlife Service numbered aluminum band. Mist-netting effort was kept relatively constant across space and time from 1993-2008, using constant-effort mist-netting largely following the Monitoring Avian Productivity and Survival (MAPS) protocol (DeSante et al. 1995), but also allowing shifts of net positions among years. In particular, each plot was sampled by 10-20 mist-nets, depending on plot size, for 6 hours per visit in each of the 6-10 visits per year. We also included targeted trapping of birds near nests located for other research purposes at the same study area. We concurrently conducted standardized nest-searching and monitoring at the same study area. This afforded an opportunity to resight individuals by one or more observers approximately every other day during May-July in every year.

We created individual encounter histories representing the years and strata in which individuals were encountered from our mist-netting and resighting data. While some individuals included in the study were originally marked as juveniles, our encounter histories only included data collected from the age of first breeding on, and thus our dispersal and survival estimates are limited to breeding adults. It was occasionally impossible to assign the identity of a resighted marked individual with certainty due to imperfect reading of band combinations in the field, and such observations were excluded. We split encounter histories into groups for analysis by species and sex, except for Mountain Chickadee, which could not always be sexed reliably using in-hand criteria during parts of the breeding season. Our design thus consisted of a multi-state mark-recapture model with five spatial strata and five species-sex groups (i.e. Orange-crowned Warbler males, Orange-crowned Warbler females, Gray-headed Junco males, Gray-headed Junco females, and Mountain Chickadee).

Estimating Breeding Dispersal

We used multistate mark-recapture models (White et al. 2006) to estimate annual probabilities of survival (*S*), breeding dispersal characterized as transition probability between strata (ψ), and encounter probability (p, the probability of encountering animals known to be alive and present in the study area). We were specifically interested in testing whether ψ varied among our five species-sex groups and thus developed our model set with this goal in mind. We modeled S and p as functions of strata and group, and modeled ψ as a function of group and a linear function of distance between strata. Our simplest model was thus one where S, ψ, and p were constant among strata and groups (K or number of parameters = 3), while our most general model contained interacting effects of strata and species and a within-species additive effect of sex on S and p, and interacting effects of linear distance between strata and species and a within-species additive effect of sex on ψ ($K = 42$). We were unable to evaluate temporal and spatial variance in S, ψ, and p simultaneously due to a large number of inestimable parameters in a fully time-varying model.

We used an information-theoretic approach to compare the relative support for alternative models because we were interested in comparing the explanatory value of non-nested models and specifically in comparing alternative models of ψ among groups (Burnham and Anderson 2002). Parameters, likelihoods, and a sample size- and overdispersion-corrected derivation of Akaike's Information Criteria (QAICc) were estimated for alternative models using Program MARK (White and Burnham 1999). We estimated the overdispersion parameter, $\hat{c}$ (the ratio of observed variance to predicted model variance), using the median $\hat{c}$ approach implemented in Program MARK. Because multistate models frequently exhibit likelihood functions with multiple maxima, we further used Markov-chain Monte Carlo (MCMC) estimation in Program MARK to generate posterior probability distributions of parameter estimates and evaluate whether our models had converged upon global maximum-likelihood (ML) estimates. We then used QAICc to compare relative support for alternative models in the context of our biological question of interest, whether ψ varied among species-sex groups.

Multistate mark-recapture models as implemented in Program MARK make two assumptions germane to our study. First, our analysis assumes that survival from time i to time $i+1$ does not depend upon the strata occupied by an individual in time $i+1$, and that mortality occurs before movement. Second, our analysis assumes that individuals move among strata at the same time, which in this case is between breeding seasons. We were unable to evaluate the first assumption using our design, while the second assumption appears unlikely to be violated because our marking and resighting was limited to the breeding season (May-July). Almost all movement among strata apparently occurred outside of the sampling period because observed movements among strata within a breeding season were very rare.

Dispersal and Apparent Survival Differences Between Small and Large Spatial Scales

Our design involved an open population and a finite study area, and thus permanent emigration from the entire study area was not separable from mortality (Lebreton et al. 1992). However, we were able to compare amongst groups the extent to which differential dispersal may bias estimates of survival by comparing estimated survival at a smaller spatial scale (a single stratum) with survival at a larger spatial scale (the entire study area; Marshall et al. 2004). If we define S^r as the apparent survival probability of individuals in stratum r and ψ^{rr} as the probability of an individual transitioning from stratum r to stratum r, apparent survival (ϕ) within stratum r, ϕ^r, is the product $S^r\psi^{\mathrm{rr}}$. The parameter ϕ^r thus excludes individuals that transition to another strata. In multistate models where strata are spatially based, such as ours, ϕ^r is the apparent survival at a smaller spatial scale than S^r. We will refer to this difference as $S^r - \phi^r$. We quantified the magnitude of that difference to test the degree to which dispersal may differentially bias estimates of apparent survival in species with increased dispersal. We used estimates of S and ψ from the global multistate mark-recapture (described above; $S_{sp(sex)\bullet st}$ $p_{sp(sex)\bullet strata}$ $\psi_{sp(sex)\bullet dist}$) to calculate the difference between ϕ^r and S^r because this model allowed S and ψ to vary freely among strata. We calculated $S^r - \phi^r$ for each stratum and species-sex grouping and then calculated the arithmetic mean of $S^r - \phi^r$ within each species-sex grouping for comparison.

Estimating Spatial and Temporal Variance in Survival Rates

We estimated spatial and temporal variance in annual survival rates using a Bayesian hierarchical modeling approach implemented in Program MARK version 6.1 (White et al. 2009) that separates process and sampling variance in estimates of survival rates (Gould and Nichols 1988; Lukacs et al. 2008). This modeling approach assumes that the logit-transformed survival rate of each group g in stratum i or year t is a realization of a normally distributed random variable (a 'hyperdistribution') with mean μ and standard deviation σ. We estimated the posterior probability distribution of parameters μ and σ using a Metropolis-Hastings Markov chain Monte Carlo algorithm in Program MARK. We used uninformative prior distributions for μ (Normal (0,100)) and $1/\sigma^2$ (Gamma(0.001,0.001)). We determined the number of tuning, burn-in, and posterior sampling iterations based upon inspection of preliminary chains of varying length for signs of lack of convergence to an equilibrium distribution (McCarthy 2007). We then visually examined the posterior probability distribution for signs of non-convergence and used the Gelman-Rubin statistic to quantitatively assess whether independent chains with alternative starting values converged upon similar posterior distributions (Gelman and Rubin 1992). To estimate the posterior probability distribution of the spatial variance in survival rates, we generated 25,000 samples of the posterior probability distribution after 5,000 'tuning' samples and 10,000 'burn-in' samples following inspection of multiple preliminary chains. To estimate the posterior probability distribution of temporal variance in survival rates, we generated 250,000 samples of the posterior probability distribution after 25,000 'tuning' samples and 25,000 'burn-in' samples.

We estimated spatial and temporal variance in survival separately due to the large number of inestimable parameters in a fully time-dependent multistate model. To estimate spatial variance in survival rates, we used a multi-state mark-recapture model where S and p varied among species and strata with an additive effect of sex, and where ψ varied as a function of the interaction between species-sex group and linear distance between strata. Thus, logit S of strata i (N = 5 strata) was modeled as normally distributed with mean μ_S and variance σ_S, and the distribution of logit p of strata i was modeled in the same fashion as μ_p and variance σ_p. To estimate temporal variance in survival rates, we combined all strata and used a time-dependent Cormack-Jolly-Seber model where ϕ and p varied among species with an additive effect of sex. Thus, logit ϕ and p of interval t (N = 15 intervals) were modeled as normally distributed with mean μ_ϕ or μ_p and variance σ_ϕ or σ_p. Instead of explicitly testing whether parameters vary among groups or strata (see Estimating Breeding Dispersal, above) this approach assumes that there is variance and focuses on estimating the magnitude of spatial or temporal process variance (the hyperdistribution parameter σ). We report the posterior probability distributions of μ and σ of these hyperdistributions and compare them among species-sex groups to test the prediction that spatial variance and temporal variance decrease with increasing dispersal movement and migratory distance.

Results

Breeding Dispersal

We marked 604 adult Orange-crowned Warbler (291 male, 313 female), 1066 adult Gray-headed Junco (539 male, 527 female), and 455 adult Mountain Chickadee during the course of the study, and this sample of individuals was used in all reported analyses. Multi-state mark-recapture models that included differences among species and sex in breeding dispersal probability, ψ, were strongly supported by QAICc (Table 1). Comparisons of QAICc among models showed model selection uncertainty among models including an effect of species and sex on the intercept and slope of the relationship between ψ and distance ($\psi_{\text{species•sex•distance}}$ and $\psi_{\text{species(sex)•distance}}$), a model including only an effect of species and sex on the intercept ($\psi_{\text{species(sex)+distance}}$), and a model including an effect of species but not sex on the intercept ($\psi_{\text{species+distance}}$). Median ĉ was estimated from the global model as 1.186, which suggested appropriate model fit and a lack of significant overdispersion. We graphically present model-averaged estimates from these top 4 models, which represented 98.1% of the QAICc weight (Figures 1 and 2). Estimates of the intercept of the ψ-distance function, averaged across sexes, were greatest for Orange-crowned Warbler and least for Mountain Chickadee, with Gray-headed Junco intermediate, and slopes differed among species (Figure 1). Estimates of the intercept of the ψ-distance function were greater in females than males in both Orange-crowned Warbler and Gray-headed Junco (Figure 2).

Apparent Survival Differences Between Small and Large Spatial Scales

Survival in stratum r (S^r) is greater than stratum-specific survival ignoring individuals that moved to other strata (ϕ^r) if dispersal among strata (ψ^{rx}) is greater than 0 by definition, and we estimated $\psi^{rx} > 0$ for all three species in this study (Figures 1, 2). This difference, $S^r - \phi^r$, thus varied among species-sex groups as a result of variation in ψ^{rx} among species-sex groups. Orange-crowned Warblers showed the largest values of $S^r - \phi^r$ (males: average 0.040, range

0.038-0.042; females: average 0.108, range 0.102-0.111), with Gray-headed Juncos intermediate (males: average 0.038, range 0.036-0.045; females: average 0.067, range 0.063-0.079) and Mountain Chickadees the least (average 0.023, range 0.018-0.030).

Spatiotemporal Variance in Survival Rates

Posterior probability distributions of mean (μ) and spatial process variance (σ) of strata survival rates (*S*) from our Bayesian multistate modeling approach differed by sex and species (Table 2). Mean survival rate (*S*) was greater in males than females in Orange-crowned Warbler and Gray-headed Junco, although the difference between sexes was greater in the warbler than the junco (Table 2). Mean survival rate, averaged across sexes, was relatively greatest in Orange-crowned Warbler, similar in Gray-headed Junco, and least in Mountain Chickadee (Table 2). Spatial process variance did not vary in the same order; it was relatively greatest in Mountain Chickadee, moderate in Orange-crowned Warbler, and least in Gray-headed Junco, but the magnitude of these differences was small (Table 2).

Posterior probability distributions of mean (μ) and temporal process variance (σ) of annual survival rates (ϕ) from our Cormack-Jolly-Seber modeling approach differed by sex and species (Table 3). Mean survival rate (ϕ) was greater in male than female Orange-crowned Warblers and Gray-headed Juncos (Table 3). Mean survival rate, averaged across sexes, was greatest in Orange-crowned Warbler, moderate in Gray-headed Junco, and least in Mountain Chickadee (Table 3). Temporal variance, averaged by species, was greatest in Mountain Chickadee, moderate in Orange-crowned Warbler, and least in Gray-headed Junco (Table 3). Temporal process variance was marginally greater in female than male Orange-crowned Warblers (Table 3).

Discussion

The suggestion that more highly migratory species are generally more mobile and thus may be more dispersal-prone (Paradis et al. 1998, Alerstam 2001), which served as our initial assumption for choosing species, was supported. As predicted, Orange-crowned Warbler, the most highly migratory of the three species examined, showed the greatest probability of breeding dispersal, while Mountain Chickadee, the year-round resident, showed the lowest probability of dispersal, with Gray-headed Junco intermediate (Figure 1). Females showed greater probability of breeding dispersal in both Orange-crowned Warbler and Gray-headed Junco, and indeed, differences among species in dispersal were partly driven by higher probabilities of breeding dispersal in females (Figure 2). Female-biased breeding dispersal is already widely recognized as the dominant pattern in birds (Greenwood 1980, Greenwood and Harvey 1982, Clobert et al. 2001; but see Öst et al. 2011). Given our small sample size of three species, we do not make a strong case for a causal connection between migratory behavior and dispersal, except to note that the correlation exists, and variation among species in dispersal allowed us to test the effects of interspecific variation in dispersal on spatiotemporal variance in survival.

We explored the extent to which the observed differences among species in dispersal (ψ) affected the differences between apparent survival estimates of each strata including individuals that dispersed to other strata (S^r) and strata-specific rates excluding such dispersal (ϕ^r). An increase in the difference S^r - ϕ^r with increasing ψ is unremarkable because it is expected by definition. However, the magnitude of the differences in S^r - ϕ^r is indicative of the relative degree of bias in S. We found that average S^r - ϕ^r was small in Mountain Chickadee (0.023), which showed the lowest dispersal movements (Fig. 1) while average S^r - ϕ^r was relatively large in Orange-crowned Warbler females (0.108), which showed the greatest dispersal (Figs. 1, 2).

Thus, we suggest that the difference between true survival and apparent survival may diverge quite rapidly with increasing dispersal movements, particularly in migrant species. Our strata were all > 47 ha in size, yet we still observed somewhat large S^r - ϕ^r in female Orange-crowned Warbler and Gray-headed Junco. Thus further confirms small study areas underestimate survival in migrant species that display high breeding dispersal (Cilimburg et al. 2002), and that this bias may be larger in females (Marshall et al. 2004) which generally show greater dispersal in birds (Greenwood 1980). Our results further show how the relative degree of this bias may vary among species with alternative dispersal behavior.

Variation in dispersal movement can affect the way populations respond to a dynamic environment, through the effects of dispersal on spatial variance in demographic parameters including population size, reproduction, and survival rates (Clobert et al. 2001). We found small differences among species in the spatial variance of survival rates (Table 2), which is jointly determined by dispersal movements and environmental correlation across space (Morris and Doak 2002). In interpreting our results, we make the explicit assumption that the degree of environmental correlation is very high and similar for the three species examined, which is not unreasonable as the three species were examined at the same sites in the same years in a small geographic area (<12 km at its widest point). Thus, differences observed among species in spatial variance are caused by differences in dispersal movement. In the case of the species studied here, spatial variance in survival rates decreased with increasing breeding dispersal, as predicted by general metapopulation theory (Bowler and Benton 2005). The observed differences in spatial variance of survival rates were small relative to mean survival rates. Nonetheless, such differences in the variance of demographic parameters may have large effects on population growth rates (e.g. Schorcht et al. 2009) depending upon the elasticity of the demographic parameter in question (Saether and Bakke 2000, Clark and Martin 2007).

We found fairly large temporal variation in survival rates, as well as large differences among species in temporal variation in survival rates (Table 3). Temporal process variance in demographic parameters is theoretically predicted to decrease with increasing parameter elasticity because natural selection is thought to canalize variance in traits with large effects on fitness (Pfister 1998; Gaillard et al. 2000). This prediction has been increasingly supported across a broad range of taxa including birds (Schmutz 2009), but temporal variance is also predicted to increase with increasing environmental variability (Greenberg 1980, Monkkonen 1992). Species resident at higher latitudes in temperate regions are thought to be exposed to higher degrees of environmental variability than migratory species that retreat to more equatorial latitudes during the winter, and thus the high-latitude residents may show greater temporal variation in survival rates. We found, instead, that Orange-crowned Warbler, the longest-distance migrant, showed the greatest temporal variance, with the high-latitude resident Mountain Chickadee intermediate, and Gray-headed Junco showing the least temporal variance. Temporal variance in survival rates can be caused by numerous stochastic and deterministic ecological processes, such as random weather events (Jonzen et al. 2002) or deterministic density-dependence in survival (Ekman 1984). In the case of migratory species, stochastic weather-driven processes occurring on the wintering grounds or in stopover habitat may have significant effects on demographic parameters including survival rates (Sillett et al. 2000, Sillett and Holmes 2002). Further, our study measured apparent survival, as is the case with all studies of open marked populations, and thus temporal variance in apparent survival could also reflect temporally variable long-distance dispersal not measurable by our study. We are unable to test this alternative using our dataset of three species.

We compared our results *post-hoc* with 19 previously published studies of songbird (Order Passeriformes) temporal survival variance reviewed by Schmutz (2009). We tested whether temporal variance in survival rates differed between 14 migrant and 8 resident species and found no difference (Figure 3). Thus, while migratory strategy may be predicted to play a role in determining the degree of temporal variation in survival rates, we are unable to support this prediction with either our results or by combining our results with previously published results.

We tested three predictions regarding the relationship between dispersal, migratory strategy, and population dynamics. Given the importance of dispersal behavior in numerous ecological and evolutionary processes, including population responses to anthropogenic disturbances such as climate change (Thomas et al. 2004) and fragmentation (Cushman 2006), our results suggest that population response to disturbances may depend on migratory strategy assuming that dispersal increases with migratory distance (Paradis et al. 1998, Fig. 1). Further, increasing dispersal appeared to decrease spatial variance in survival rates among species. Spatial variance in survival rates is an important component in many metapopulation models (Harrison 1991; Morris and Doak 2002), and this again suggest that intrinsic differences among populations in migratory behavior may strongly impact population biology.

We found that temporal variance in survival rates differed among species, yet was not predicted by differences among species in migratory behavior. Examining a larger dataset of temporal variance estimates of songbirds assembled by Schmutz (2009) suggested that temporal variance in apparent survival rates is not predicted by differences among populations in migratory behavior. Overall, our results thus suggest that differences among populations in dispersal behavior may be linked to migratory behavior and strongly impact key processes such as spatial variance in survival rates, yet may not be linked to temporal variance in survival rates as previously proposed. Dispersal and spatiotemporal variance in survival rates are critical elements of population dynamics, and thus consideration of a species' migratory strategy may be important in understanding and predicting population responses to natural and anthropogenic disturbances.

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Table 1. Model selection criteria for alternative multi-state mark-recapture models of the effects of species (sp), sex, and strata (st) on survival (*S*) and recapture probability (*p*) and of the effects of species, sex, and distance between strata (dist) on movement probability (ψ). Models are shown in descending order by QAICc. The 10 models with lowest QAICc are shown with the most general global model and most reduced model for comparison (in italics). The top four models, representing 98.1% of QAICc weight, are in bold.

Model			QAICc[1]	ΔQAICc[2]	Weight[3]	ℓ[4]	*K*[5]	Deviance
$S_{sp(sex)}$	**$p_{sp(sex)+st}$**	**$\psi_{sp(sex)+dist}$**	**3483.30**	**0**	**0.550**	**1**	**20**	**1883.5**
$S_{sp(sex)}$	**$p_{sp(sex)+st}$**	**$\psi_{sp(sex)\bullet dist}$**	**3484.44**	**1.134**	**0.312**	**0.567**	**22**	**1880.5**
$S_{sp(sex)}$	**$p_{sp(sex)+st}$**	**$\psi_{sp\bullet sex\bullet dist}$**	**3487.50**	**4.20**	**0.067**	**0.123**	**24**	**1879.5**
$S_{sp(sex)}$	**$p_{sp(sex)+st}$**	**$\psi_{sp+dist}$**	**3487.99**	**4.70**	**0.053**	**0.096**	**18**	**1892.2**
$S_{sp(sex)}$	$p_{sp(sex)\bullet strata}$	$\psi_{sp(sex)\bullet dist}$	3491.28	7.98	0.010	0.019	30	1870.9
$S_{sp(sex)+st}$	$p_{sp(sex)+st}$	$\psi_{sp(sex)\bullet dist}$	3491.79	8.49	0.008	0.014	26	1879.7
$S_{sp(sex)+st}$	$p_{sp(sex)\bullet strata}$	$\psi_{sp(sex)\bullet dist}$	3498.64	15.34	0	0.001	34	1870.0
$S_{sp(sex)}$	$p_{sp(sex)+st}$	$\psi_{sp\cdot dist}$	3498.80	15.50	0	0	19	1901.0
$S_{sp(sex)+st}$	$p_{sp(sex)}$	$\psi_{sp(sex)\bullet dist}$	3499.9	16.62	0	0	22	1896.0
$S_{sp(sex)}$	$p_{sp(sex)}$	$\psi_{sp(sex)+dist}$	3501.00	17.70	0	0	16	1909.3
$S_{sp(sex)\bullet st}$	*$p_{sp(sex)\bullet strata}$*	*$\psi_{sp(sex)\bullet dist}$*	*3510.86*	*27.56*	*0*	*0*	*42*	*1865.7*
$S_{.}$	*$p_{.}$*	*$\psi_{.}$*	*3585.99*	*102.69*	*0*	*0*	*3*	*2020.6*

[1] QAICc = -2*log likelihood/c-hat + 2*K* +2*K*(*k*+1)/(n-ess-*K*-1) where n-ess is effective sample size.

[2] ΔQAICc = QAICc of model – QAICc of lowest model

[3] $e^{(-1/2 * \Delta\text{QAICc of model i})}$ / $\sum(-1/2\ \Delta\text{QAICc})$

[4] Model likelihood

[5] Number of parameters

Table 2. Posterior probability distribution mean and standard deviation (SD) for annual survival (μ) and spatial process variation in annual survival (σ) for three species of birds, estimated from a hierarchical Bayes multi-state mark-recapture model. Orange-crowned Warbler (ocwa) and Gray-headed Junco (ghju) are shown split by sex and overall, while Mountain Chickadee (moch) was not separated by sex.

	μ		σ	
	mean	SD	mean	SD
ocwa	0.5667	0.0360	0.0279	0.0247
ocwa m	0.6023	0.0353	0.0278	0.0245
ocwa f	0.5302	0.0364	0.0281	0.0246
ghju	0.5556	0.0300	0.0325	0.0317
ghju m	0.5657	0.0299	0.0317	0.0316
ghju f	0.5454	0.0302	0.0329	0.0316
moch	0.5106	0.0467	0.0440	0.0402

Table 3. Posterior probability distribution mean and standard deviation (SD) for annual survival (μ) and temporal process variation in annual survival (σ) for three species of birds, estimated from a hierarchical Bayes Cormack-Jolly-Seber model. Orange-crowned Warbler (ocwa) and Gray-headed Junco (ghju) are shown split by sex and averaged, while Mountain Chickadee (moch) was not separated by sex.

	μ		σ	
	mean	SD	mean	SD
ocwa	0.5945	0.0580	0.1728	0.0535
ocwa m	0.6406	0.0553	0.1650	0.0514
ocwa f	0.5467	0.0597	0.1778	0.0551
ghju	0.5589	0.0349	0.0580	0.0444
ghju m	0.5764	0.0345	0.0575	0.0439
ghju f	0.5411	0.0352	0.0585	0.0449
moch	0.5440	0.0682	0.1399	0.1011

Figure 1. Model-averaged maximum likelihood estimates and 95% confidence intervals of the relationship between breeding dispersal probability (ψ) and distance between strata for three species of passerine bird: Orange-crowned Warbler (ocwa), Gray-headed Junco (ghju), and Mountain Chickadee (moch).

Figure 2. Model-averaged maximum likelihood estimates and 95% confidence intervals of the relationship between breeding dispersal probability (ψ) and distance between strata by sex for two species of passerine bird: Orange-crowned Warbler (ocwa, panel A), Gray-headed Junco (ghju, panel B).

Figure 3. Comparison of estimates of the temporal process coefficient of variation (CV) in annual survival rates of 22 populations of migrant and resident passerine birds. Sample size (number of studies) is shown above each box. Data from this study (Table 3) and Schmutz (2009).

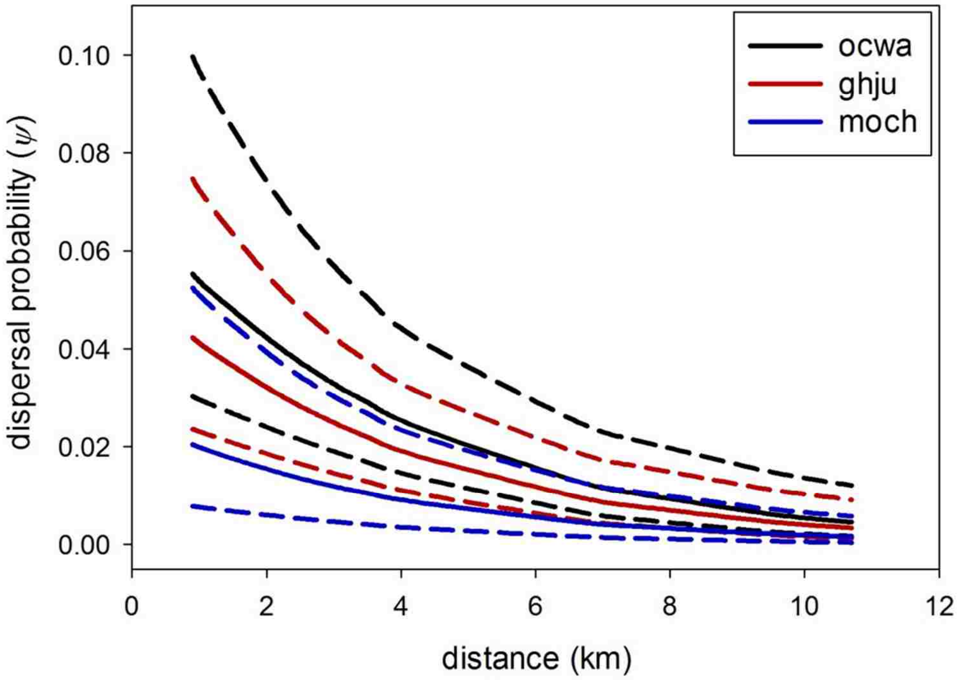
0.10
0.08
0.06
0.04
0.02
0.00
dispersal probability (ψ)
0
2
4
6
8
10
12
distance (km)
ocwa
ghju
moch

Figure 1.

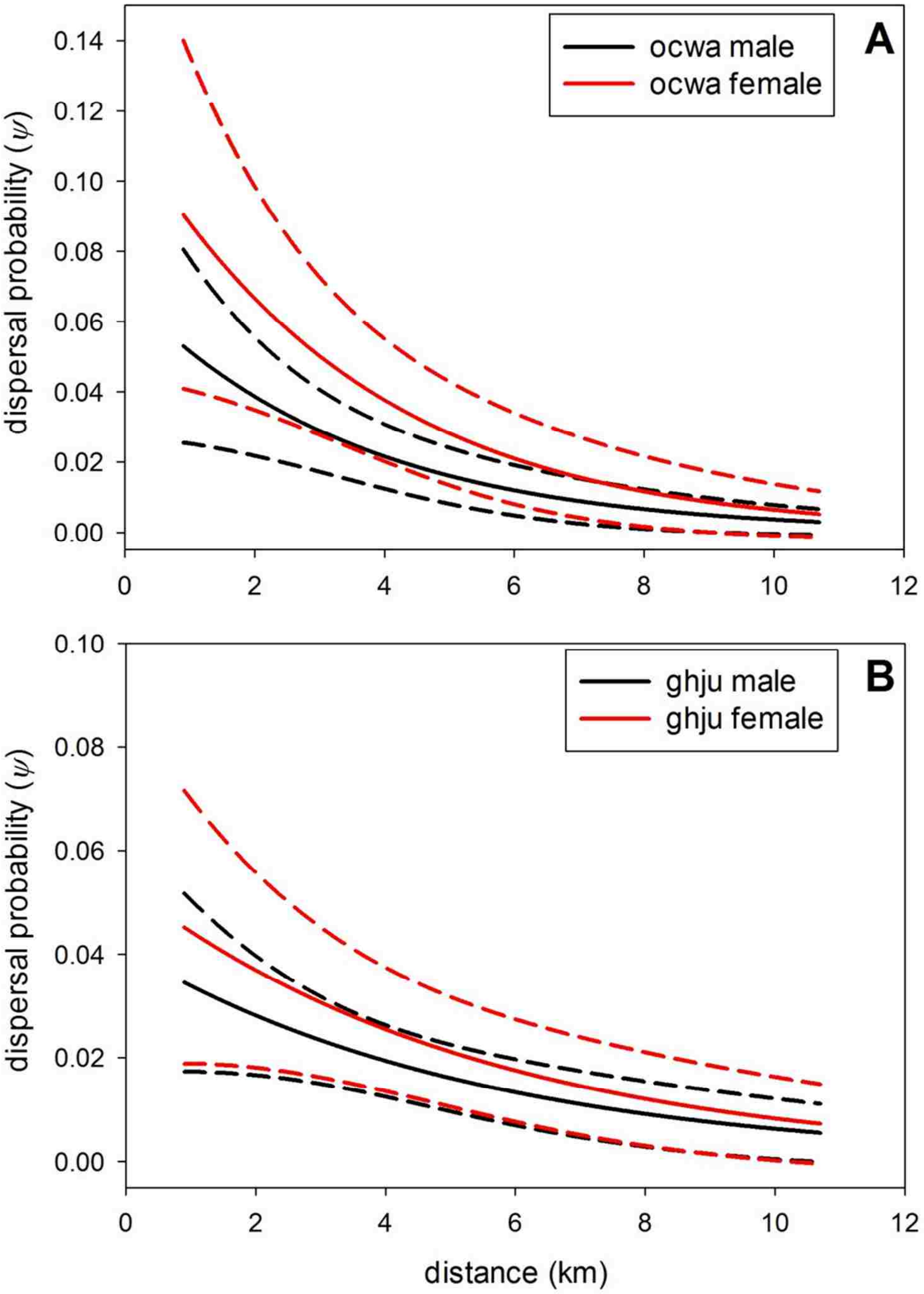
A
ocwa male
ocwa female
dispersal probability (ψ)
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0
2
4
6
8
10
12
B
ghju male
ghju female
dispersal probability (ψ)
0.10
0.08
0.06
0.04
0.02
0.00
0
2
4
6
8
10
12
distance (km)

Figure 2.

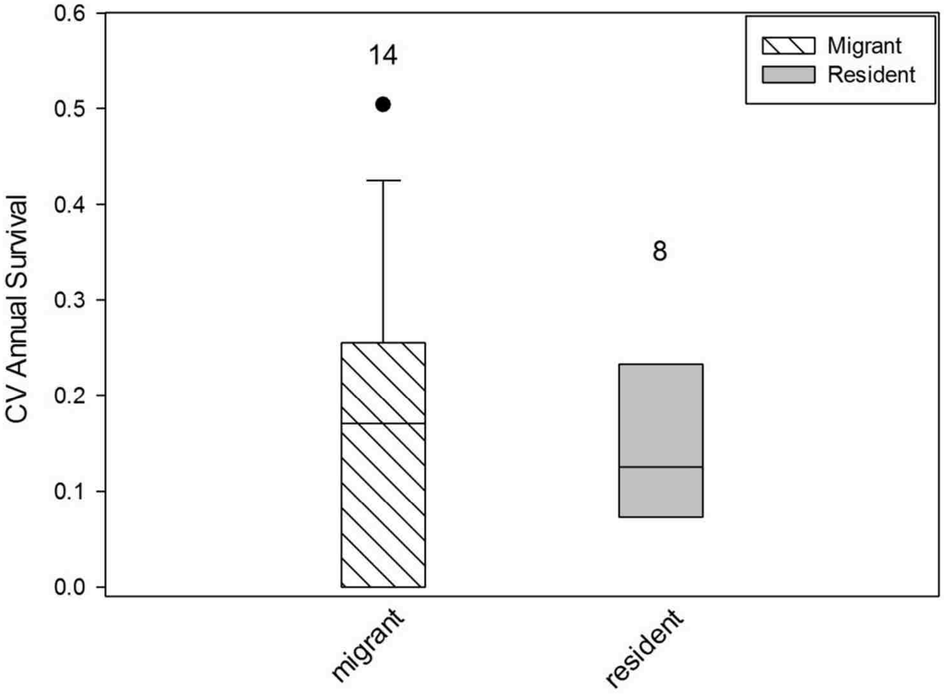
0.6
0.5
0.4
0.3
0.2
0.1
0.0
CV Annual Survival
14
8
Migrant
Resident
migrant
resident

Figure 3.

Appendix 1. Species, season of greatest mortality and data sources used in meta-analyses of seasonal mortality rates (Chapter 2, Tables 2 and 3).

species	season of greatest mortality (Table 2)	study	monthly mortality rate analysis (Table 3)	method
Tetrao tetrix	summer	Angelstam 1984	y	T
Melospiza melodia	winter	Arcese et al. 1992	y	MR
Rostrhamus sociabilis	winter	Bennetts & Kitchen 1999	y	T
Anas fulvigula	winter	Bielefeld and Cox 2006	y	T
Parus atricapillus	winter	Brittingham & Temple 1988	y	MR
Alectoris rufa	summer	Buenestado et al. 2009		T
Dryocopus pileatus	equivocal	Bull 2001	y	T
Colinus virginianus	confounded by hunting	Burger et al. 1995	y	T
Tetrao tetrix	summer	Caizergues & Ellison 1997	y	T
Protonotaria citrea	equivocal*	Calvert et al. 2010		MR
Seiurus noveboracensis	equivocal*	Calvert et al. 2010		MR

Branta hrota	summer*	Clausen et al. 2001		MR
Centrocercus urophasianus	summer	Connelly et al. 2000		T
Serinus serinus	winter	Conroy et al. 2002		MR
Colinus virginianus	confounded by hunting	Cox et al. 2004	y	T
Bonasa umbellus	confounded by hunting	Devers et al. 2007	y	T
Haematopus ostralegus	summer	dit Durrell 2007	y	MR
Parus montanus	equivocal	Ekman & Askenmo 1986		MR
Parus cristatus	equivocal	Ekman & Askenmo 1986		MR
Strix occidentalis	winter	Ganey et al. 2005		T
Chen caerulescens atlantica	equivocal*	Gauthier et al. 2001		MR
Tympanuchus pallidicinctus	summer	Hagen et al. 2007	y	T
Dendragapus canadensis franklinii	summer	Herzog 1979	y	T
Meleagris gallopavo silvestris	summer	Hubbard et al. 1999	y	T
Chen canagica	summer*	Hupp et al. 2007		T
Branta canadensis	equivocal*	Hupp et al. 2010		T

Dendroica cerulea	equivocal*	Jones et al. 2004		MR
Meleagris gallopavo intermedia	equivocal	Keegan & Crawford 1999		T
Meleagris gallopavo silvestris	summer	Kurzejeski et al. 1987	y	T
Parus montanus	equivocal	Lahti et al. 1998		MR
Meleagris gallopavo merriami	summer	Lehman et al. 2005	y	T
Anser brachyrhynchus	confounded by hunting*	Madsen et al. 2002		MR
Petroica goodenovii	summer	Major & Gowing 2001	y	MR
Meleagris gallopavo silvestris	summer	Miller et al. 1998	y	T
Bonasa bonasia	winter	Montadert & Leonard 2003	y	T
Pyrrhula murina	equivocal	Monticelli et al. 2009		MR
Centrocercus urophasianus	equivocal	Moynahan et al. 2006		T
Meleagris gallopavo silvestris	summer	Nguyen et al. 2003	y	T
Sitta europea	winter	Nilsson 1982	y	MR
Somateria spectabilis	equivocal	Oppel & Powell 2010		T
Meleagris gallopavo	confounded by	Pack et al. 1999		T

silvestris	hunting			
Meleagris gallopavo	summer	Palmer et al. 1993	y	T
Motacilla clara	summer	Piper 2002	y	MR
Anser anser	equivocal*	Pistorius et al. 2006		MR
Meleagris gallopavo silvestris	summer	Roberts et al. 1995	y	T
Alectoris chukar	winter	Robinson et al. 2009	y	T
Turdus merula	summer	Robinson et al. 2010	y	MR
Alophoixus pallidus	summer	Sankamethawee et al. 2011		MR
Sylvia boehmi	summer	Schaefer et al. 2006	y	MR
Sylvia lugens	winter	Schaefer et al. 2006	y	MR
Anser albifrons frontalis	equivocal*	Schmutz & Ely 1999		MR
Centrocercus urophasianus	summer	Sika 2006	y	T
Dendroica caerulescens	equivocal*	Sillett & Holmes 2002		MR
Lichenostomus melanops	equivocal	Smales et al. 2009		MR
Bonasa umbellus	confounded by hunting	Small et al. 1993		T
Bonasa umbellus	summer	Small et al. 1993		MR

Lagopus lagopus	winter	Smith & Willebrand 1999	y	T
Parus atricapillus	winter	Smith 1967	y	MR
Tetrao tetrix	winter	Spidso et al. 1997		T
Meleagris gallopavo silvestris	summer	Spohr et al. 2004	y	T
Strix aluco	equivocal	Sunde et al. 2003		T
Colinus virginianus	winter	Terhune et al. 2007	y	T
Bonasa umbellus	winter	Thompson & Fritzell 1989	y	T
Meleagris gallopavo silvestris	summer	Vander Haegen et al. 1988	y	T
Melegaris gallopavo	summer	Vangilder & Kurzejeski 1995	y	T
Branta bernicula nigricans	summer*	Ward et al. 1997		MR
Tympanuchus pallidicinctus	summer	Wolfe et al. 2007	y	T
Tympanuchus pallidicinctus	summer	Wolfe et al. 2007	y	T
Meleagris gallopavo	summer	Wright et al. 1996	y	T

*Migrant species excluded from some analyses (see Methods and Results).

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Appendix 2. Data sources used in meta-analysis of proximate mortality causes (Chapter 2, Figures 2-5).

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Appendix 3. Phylogenetic analyses of the relationships between ecological factors and reaction norms of feeding rate to offspring number (Chapter 3).

Figure 1. Phylogenetic independent contrasts of daily nest mortality and reaction norm slope were not significantly correlated (Pearson correlation, r = -0.085, P = 0.67).

Figure 2. Phylogenetic independent contrasts of annual adult mortality and reaction norm slope were significantly correlated (Pearson correlation, r = 0.617, P < 0.001). The line shown is the regression through the origin.

Figure 3. Phylogenetic independent contrasts of annual adult mortality and percentage change in provisioning rate in response to brood size reduction were significantly correlated (Pearson correlation, r = 0.938, P < 0.001). The line shown is the regression through the origin.

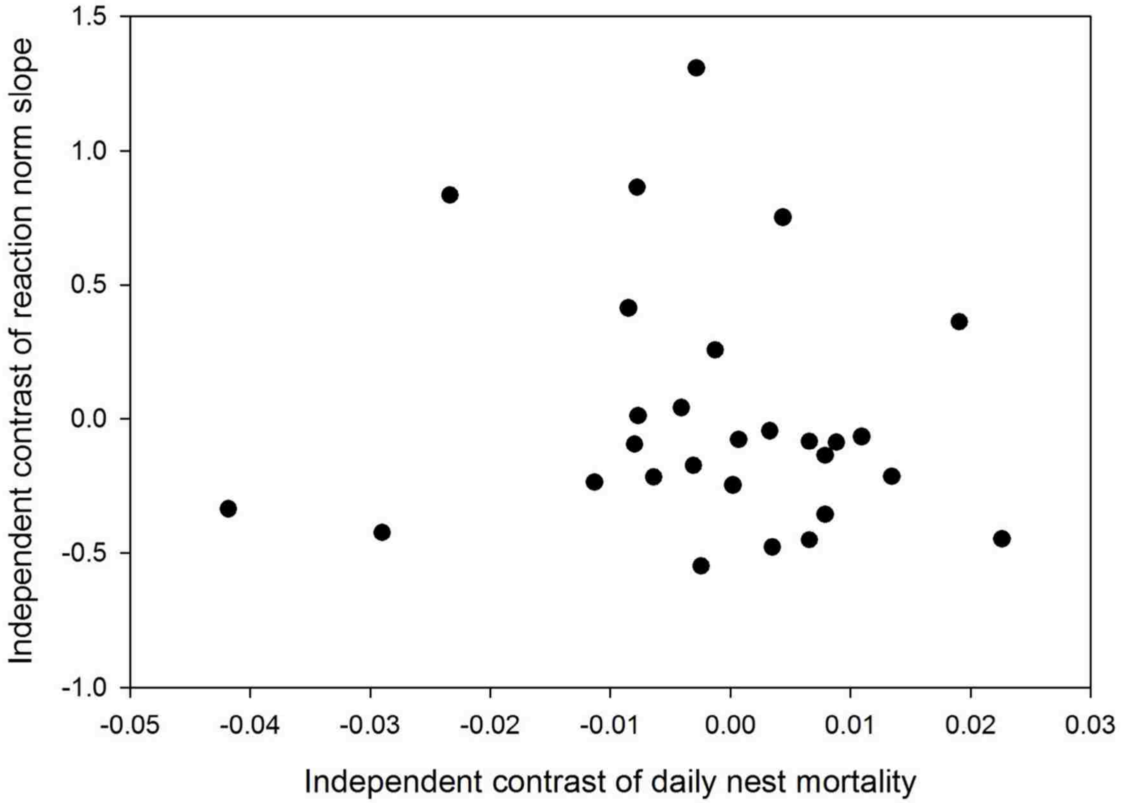
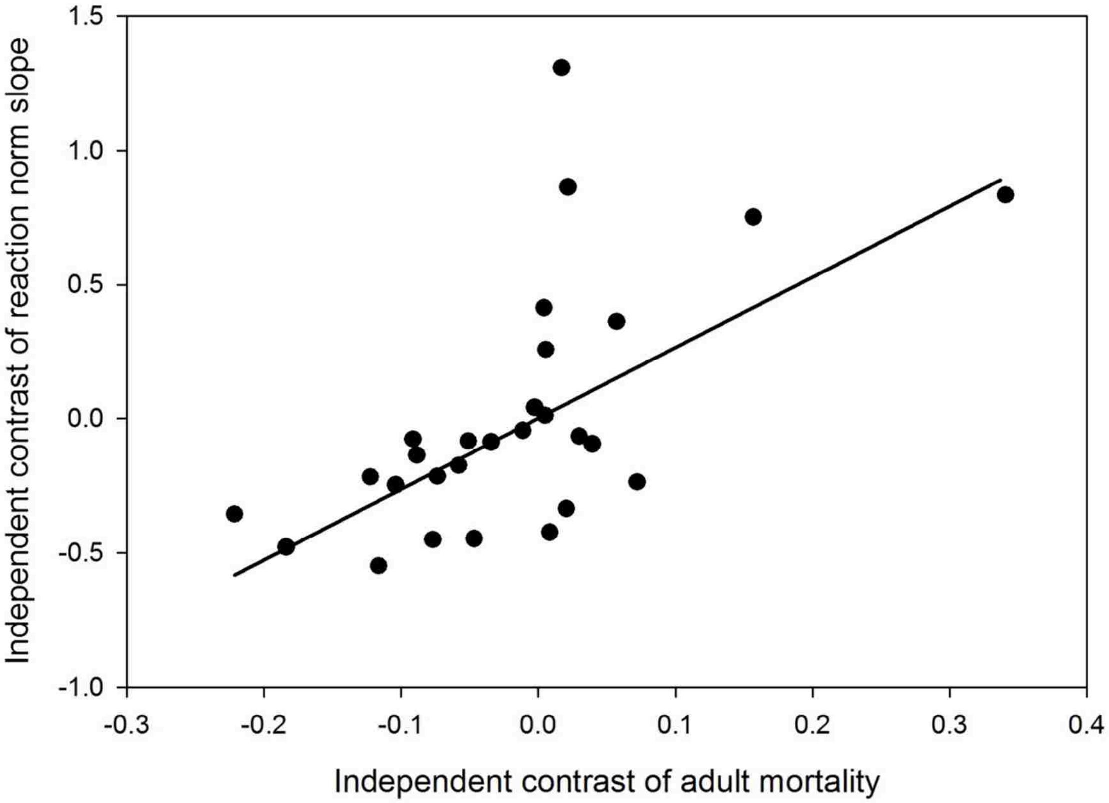
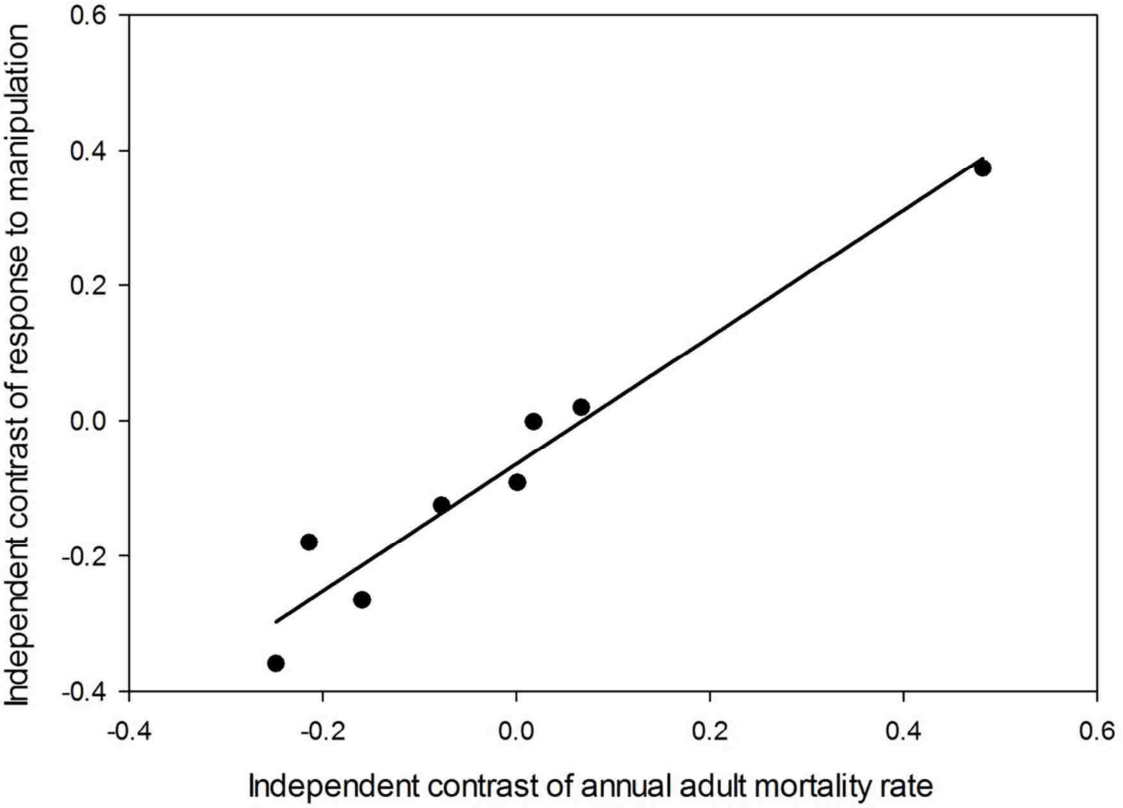

Independent contrast of reaction norm slope
1.5
1.0
0.5
0.0
-0.5
-1.0
-0.05
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
Independent contrast of daily nest mortality

Figure 1.



1.5
1.0
0.5
0.0
-0.5
-1.0
Independent contrast of reaction norm slope
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
Independent contrast of adult mortality

Figure 2.



Independent contrast of response to manipulation
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
Independent contrast of annual adult mortality rate

Figure 3.