Growing up prairie: ecological drivers of grassland songbird nestling development

by

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Abstract

Animals develop at different rates and require differing amounts of parental investment, yet the drivers of both inter- and intraspecific variation in growth are often unclear. In altricial birds, both food delivery by parents and nest predation risk are known to influence developmental strategies, but until now, it has been unclear how brood parasitism might influence host development. I studied interactions between brood parasitic Brown-headed Cowbirds (*Molothrus ater*) and three grassland-obligate songbirds at the Konza Prairie in Northeast Kansas. My three focal host species ranged in size from ~40% to 270% of cowbirds' mass: large Eastern Meadowlarks (*Sturnella magna*), medium-sized Dickcissels (*Spiza americana*), and small Grasshopper Sparrows (*Ammodramus savannarum*). We hypothesized that brood parasitism by cowbirds would influence inter- and intraspecific development variation (1) directly by exacerbating costly sibling competition and/or (2) indirectly by interacting with other environmental drivers like predation risk and food availability. Additionally, we hypothesized that (3) host species, nest-specific food provisioning rate, and spatial variation in predation risk would influence intra-specific cowbird nestling growth. I located and monitored 148 nestling-stage nests over two years, and measured the growth of 316 host nestlings' and 54 cowbird nestlings' tarsi, wings, mass, bills, and feathers every two days to quantify overall growth and the allometric scaling of structures associated with nestling competition and post-fledging mobility. Variation in host nestling development exhibited species-specific responses to cowbird parasitism; meadowlarks left the nest earlier than conspecifics in unparasitized nests, Dickcissel nestlings grew more slowly, and Grasshopper Sparrow nestlings were not directly affected by the presence of brood parasites. Brood parasitism was also associated with key drivers of nestling development including nest predation risk and provisioning rate. However, considerable variation in host growth appeared to be shaped by individual variation in parental care. Cowbird nestling mass gain and the allometric scaling of body parts associated with nestling competition varied among host species, and was associated with provisioning rate and brood size. Overall these results demonstrate that inter- and intraspecific variation in growth and development can be extremely high, even at a single site. Additionally, brood parasitism can have species- and nest-specific consequences attributable in part to individual parental behavior. These results provide insight into the relationship between a declining guild of grassland songbird host species and the native brood parasites with which they have interacted for millennia, and helps interpret host-parasite interactions in novel contexts.

Table of Contents

List of Figures

List of Tables

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Chapter 1 - Direct effects of cowbird parasitism on growth

Grassland songbird hosts respond to the direct costs of Brown-headed Cowbird (*Molothrus ater*) brood parasitism with species-specific plastic changes in growth and development

Abstract

Animals grow and develop at different rates and require differing amounts of parental investment, yet the drivers of that variation are often unclear. In altricial birds, brood parasitism presents a unique set of selective pressures potentially influencing the development of songbird hosts. I hypothesized that Brown-headed Cowbird (*Molothrus ater*) brood parasitism may exacerbate costly sibling competition which could slow nestling growth when food delivery rates are insufficient to meet demand or select for plasticity and accelerated nestling growth. If the latter, I would expect especially rapid growth of morphologies affecting competition and/or fledge age, especially in the nests of smaller host species. I studied birds at the Konza Prairie in Northeast Kansas, a site where ~50% of nests of grassland songbirds are parasitized. I located and monitored 148 nestling-stage nests of three grassland-obligate songbirds ranging in size from ~40% to 270% of cowbirds' adult mass: large Eastern Meadowlarks (*Sturnella magna*), medium-sized Dickcissels (*Spiza americana*), and small Grasshopper Sparrows (*Ammodramus savannarum*). I measured the growth of 316 nestlings' tarsi, wings, mass, bills, and feathers every two days. Host nestlings exhibited both intra- and interspecific variation in growth and development, and responded to the stressors of brood parasitism in different ways. Meadowlark growth rates and allometric scaling was unchanged but they fledged earlier from parasitized nests. Multiply-parasitized Dickcissels experienced depressed growth rates, especially in the development of eyes and feathers, yet they left the nest at the same age as unparasitized

conspecifics. The smallest hosts (Grasshopper Sparrows) prioritized the growth of their tarsi but otherwise exhibited little effect of cowbirds, suggesting that parents compensated for the presence of cowbirds through pre- or post-natal resource allocation. Songbird nestlings exhibited surprising levels of intraspecific variation in growth and development. Although a complete understanding of how parasitism influences hosts will require elucidating the ways that cowbirds affect previously-documented drivers of development, this study demonstrates that host species have evolved strategies to cope with parasitism ranging from tolerance to compensation.

Introduction

Within animal species, overall size and the relative scaling of anatomical structures vary considerably, and this variation is often driven by plastic responses to environmental conditions (McAdam et al. 2002, Rinaudo and Wang 2012). The environment experienced during the animal's development (West-Eberhard 1989, Mcmillen and Robinson 2005) can have lasting effects on their survival and performance later in life (Monaghan 2008, Taborsky 2017), for their reproductive partners (Monaghan et al. 2012), and for subsequent generations (Lummaa and Clutton-Brock 2002, Krause and Naguib 2014). While plastic responses to environmental conditions may be adaptive (Zach 1982, Nilsson and Cardmark 2001), this life history strategy may result in a mismatch between current growth and future environments (Monaghan 2008, Tschirren et al. 2009). Identifying the environmental drivers of variation in growth trajectories is critical to understanding organisms' life history, physiology (McMillen and Robinson 2005), ecological associations (Starck and Ricklefs 1998), ability to adapt to changing environments (Snell-Rood 2012), and survival (Hochachka and Smith 1991).

Birds are important models for studying life history evolution (Lindstrom 1999, Chaby

2016). They display a wide range of developmental modes associated with variation in other life-history traits (Starck and Ricklefs 1998). Altricial birds grow faster than any other vertebrates (Case 1978, Dolnik 2006) and their structure-specific growth patterns vary among species, populations, and individuals (Ricklefs and Peters 1981, Badyaev and Martin 2000, McCarty 2001). Although variation in altricial nestling growth and condition has been observed in the field (Lepcyk and Karasov 2000), the causes of this variation may be complicated (e.g. Rock et al. 2013) being affected by both genotype and environment (Schew and Ricklefs 1998).

Altricial birds require large investments in parental care (Lack 1947). Consequently, many studies have related parental care—especially provisioning—to variation in development of altricial birds (Martin 1987, Schew and Ricklefs 1998). Nestlings that receive a lot of food have higher growth rates (Soma et al. 2006) and are more likely to fledge (Schwagmeyer and Mock 2008). Thus, competition for food among nestmates can explain much of the observed variation in development. For example, fast-growing nestlings can out-compete siblings for parental attention and food (Werschkul and Jackson 1979), and/or prioritize the growth of body structures to facilitate competition at the cost of the growth of other structures, such as growing larger gapes in competitive nests (Gil et al. 2008). Nestlings also sometimes suffer sex-specific consequences of competition with individuals of the smaller sex disproportionately affected (Oddie 2000, Alonso et al. 2018).

Sibling competition, while important, is not the only driver of intra- and inter-specific variation in nestling development. A much less-commonly assessed driver is the competition between heterospecific brood-parasitic nestlings and their hosts. Brood parasites lay their eggs in the nests of other birds, freeing themselves from all parental care (Davies 2000, Feeney et al. 2013). Obligate brood parasitic nestlings are thus completely reliant on hosts, making them good

models for the study of sibling competition strategies because parasitic young gain no inclusive fitness via nestmates, and therefore can compete without cost (Lichtenstein and Dearborn 2004). While some species of brood parasites eject all host young from nests (Honza et al. 2007), the native Brown-headed Cowbird (*Molothrus ater*) of North America typically grows alongside host nestmates (Lowther 1993). Host species in the Great Plains of central North America have coexisted with cowbirds for thousands of years (Peer and Sealy 2004) and experience as much as 95% parasitism at some sites (Elliot 1978).

When cowbird and host nestlings are raised together, cowbirds beg for food more loudly and persistently than do hosts (Glassey and Forbes 2003, Pagnucco et al. 2008). This behavioral difference is most likely to affect nestling development due to asymmetries among nestmates in competitive abilities, especially for hosts nestlings that are smaller than cowbirds and thus more likely to be muscled out of the way during provisioning (Davies 2000). Although cowbirds do not always increase brood size because they often replace host eggs with their own (Sealy 1992), cowbirds reduce host nestling food intake, resulting in hosts expending more energy begging than do conspecifics in unparasitized nests (Peer et al. 2013). Brood parasitism can result in depressed growth of all host nestlings (Dearborn and Lichtenstein 2002) or only the smallest nestlings in the brood. In the latter case, parents may compensate for the presence of cowbirds by preferentially feeding their largest nestlings at the expense of the smallest (Clutton-Brock 1991). In species that exhibit sexual size dimorphism as nestlings, brood parasitism can thus result in the smaller sex being at a disadvantage (Oddie 2000, Alonso et al. 2018).

Extended opportunities for coevolution between cowbirds and their hosts means that species frequently parasitized by cowbirds may have evolved behavioral or developmental traits which help them cope with parasite-driven competition, either via fixed, population-level

responses or developmental plasticity in the presence of parasites. Such responses could manifest as parental plasticity in provisioning rates, differences in allometric scaling of certain morphologies, or plasticity in the age at which nestlings fledge. The presence of cowbirds may stimulate parents to bring more food (Kilner et al. 2004), either erasing the costs of competition or shifting costs from nestlings to their parents (Smith and Arcese 1994). Indeed, host species parasitized by various cowbird species may compensate by growing faster than unparasitized species (Remeš 2006). Similar effects of cowbirds on intraspecific variation in growth rate and developmental strategy have not previously been demonstrated, however. If parents do not compensate for parasite presence by increasing provisioning, then host nestlings may allocate energy to anatomical structures that enhance competitive ability. Prioritizing traits like leg length might allow them to stand taller than their competitors in the nest and attract more attention from provisioning parents (Oddie 2000). As energy for growth is limited, allometric patterns that facilitate competition would result in the growth of bodily structures at the expense of other body parts that, while important later in development, do not directly facilitate competition for food such as wing size and body feathers (Schew and Ricklefs 1998, Gil et al. 2008). Finally, if competition for food is intense, nestlings may fledge at an earlier age to avoid competition with cowbirds (Remeš 2006, 2010, Radersma et al. 2011). Such a strategy would be risky, however, as they could die by exposure if thermoregulatory capacity and insulative feathers are underdeveloped (Jones et al. 2017).

Grassland birds living in the eastern Flint Hills region of the Great Plains experience some of the highest rates of brood parasitism in North America (Jensen and Cully 2005, Patten et al. 2006). Cowbirds in the region are so abundant that multiple parasitism is common with some nests containing as many as nine cowbird eggs (Hatch 1983, Igl and Johnson 2007). Three

common grassland-breeding species that experience frequent parasitism are Grasshopper Sparrows (*Ammodramus savannarum*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*) (Elliot 1978). In Northeast Kansas USA, cowbirds parasitize at least twenty host species (Rivers et al. 2010) and as many as 85% of Dickcissel nests (Zimmerman 1983, Kosciuch and Sandercock 2008) providing a system in which to elucidate the effects of high parasitism pressure in a natural setting.

I assumed that cowbird nestling competition is costly to hosts because of their potential to compete with nestlings for food. Thus, in the absence of counter-adaptations by hosts, I hypothesized that nestlings would manifest the costs of cowbird competition by experiencing (1) *slower growth* overall. If this cost was mostly felt by the smallest nestlings, I expect (2) larger *within-brood variation* in growth. I hypothesized (3) that these effects would be dependent on *host size* since smaller hosts' nestlings are more likely to be outcompeted by cowbirds during provisioning. However, if host strategies have been shaped by adaptation to chronic parasitism pressures, nestlings may not grow differently at all because of (4) *parental compensation*, as parents may increase provisioning rates to accommodate the cowbird brood parasite. Alternatively, nestlings may (5) *prioritize competitive features* and allocate energy to tarsi and gapes over features like feathers. Finally, nestlings may (6) *fledge earlier* to avoid within-nest competition without otherwise adjusting their growth.

If parasitism results in (1) *slower growth*, I predicted that nestlings in parasitized nests (i) would be smaller conspecifics of the same age, and (ii) would fledge at an older age than unparasitized conspecifics. If parasitism exacerbates (2) *within-brood variation*, I predicted that, relative to unparasitized conspecifics, host nestlings in parasitized nests would (iii) exhibit higher variance in overall growth rates among siblings. If the effect of cowbirds depends on (3) *host*

size, I predicted (iv) that parasitized nestlings of smaller host species would have slower growth and/or larger within-brood variation relative to the parasitized nestlings of larger host species. If the host species have evolved strategies to counter cowbird parasitism through (4) *parental compensation,* I predicted that there would be no difference in (v) the mean body size or size of specific structures, or (vi) the fledge age. If nestlings (5) *prioritized competitive features* when parasitized, I predicted that, relative to unparasitized conspecifics, host nestlings in parasitized nests would (vii) have proportionately larger gapes and tarsi and/or (viii) smaller feathers and wings, and would (ix) leave the nest at the same age. Lastly, if hosts (6) *fledge earlier,* I expected that (x) parasitized nestlings would not grow faster or prioritize different structures yet would leave the nest at a younger age than unparasitized conspecifics.

Methods

Study site and species

I studied nestling development from April–August 2017–2018 at the Konza Prairie Biological Station (KPBS; 39.107, -96.609), a 3,487 ha site in NE Kansas owned jointly and managed by The Nature Conservancy and Kansas State University. I also worked on the adjacent Rannell's Flint Hills Prairie Preserve, a 1,175 ha prairie site owned by Kansas State University. I considered these properties as one contiguous study site, to which I refer as "Konza." The properties are managed with combinations of fire (every 1,2,3,4 or 20 years) and grazing regimes (bison, cattle, and no grazing), resulting in a dynamic vegetative landscape of perennial warm-season grasses, forbs, and shrubs (Knapp and Seastedt 1998, Owensby et al. 2008). The site receives an average of 83.5 cm rainfall annually, and monthly mean temperatures range from -3 to 27 °C (Hayden 1998). I studied birds on 16 pastures representing replicated combinations of

ungrazed, bison-grazed, and cattle-grazed areas managed in combination with annual, 2-year, or 3-year burns, selecting study areas based on previously-documented grassland bird habitat associations at the site (Powell 2008).

I assessed the effects of Brown-headed Cowbirds on nestling development in three grassland-obligate songbirds. Cowbirds are medium-sized (42–50 g) songbirds and prolific polygamous breeders, laying as many as 40 eggs a season (Fleischer et al. 1987, Holford and Roby 1993, but see Woolfenden et al. 2003). The largest host species I studied was 2-3 times larger than cowbirds; Eastern Meadowlarks (90–150 g) make large, domed nests hidden on the ground in dense prairie (Lanyon 1995). While meadowlarks at some sites experience little to no parasitism (Strausberger and Ashley 1997), in the study region, as many as 70% of nests are parasitized (Elliot 1978). Dickcissels are similar in size to cowbirds (23–29 g) and build open-cup nests approximately 0.5m off the ground in grasses and shrubs (Temple 2002). They are the most intensely parasitized of the hosts I studied, experiencing up to 95% parasitism at my study site previously (Elliot 1978). Grasshopper Sparrows were the smallest host species, being roughly a third the size of cowbirds (14-20 g). Grasshopper Sparrows create small domed ground nests well-hidden in the grass (Vickery 1996). Although they are not commonly parasitized over much of their range (Ruth 2017), in the Flint Hills of NE Kansas, as many as 48% of nests are parasitized (Rivers et al. 2010). Each of these species re-nest following nest failure and typically fledge their own young alongside cowbird parasites (Rivers et al. 2010). All three species are declining rangewide; meadowlarks have declined by as much as 89% in the last century, Dickcissel are declining by 1.2% per year, and Grasshopper Sparrows are experiencing losses as large as 4% per year in the study region (Sauer et al. 2011). Some evidence suggests that cowbird parasitism could contribute to Grasshopper Sparrow declines (Hovick and Miller 2013).

Nest searching and monitoring

Field crews located nests by observing adults feeding their nestlings and by flushing incubating females either opportunistically or while dragging a weighted 30-m rope. Each nest was marked by placing a painted rock and pin flag five meters from the nest opening, and the location recorded using a handheld GPS unit (Garmin, Olathe, KS, USA). I visited nests every 2–3 days, recording the number of host and cowbird eggs in each nest until hatching. I selected ~2/3 of nests for intensive nestling measurements, using only those for which I had high certainty of hatch date (estimate +/- 1 day). The remaining nests served as controls to assess the effects of nestling handling on nest survival. When the nest was empty, I categorized nests as "successful" if the host chicks were at or past fledge age (>6 days for sparrows and Dickcissels, >10 days for meadowlarks) and parents were seen nearby chipping or with food after the presumed fledge date. For a subset of nests, I used video footage (see below) to confirm nest success, coding them as "successful" if they fledged one or more host young and "unsuccessful" otherwise. Because only a subset of nests had cameras I used nestling age to assign nest fates at the nests without cameras, considering nests "unsuccessful" if the chicks were younger than fledge age, if the nest only fledged cowbirds, or if the nest cup was destroyed.

Nestling growth measurements

I measured nestlings in nests at which I either observed one or more nestlings hatching or they were wet at the time of my visit (day 0), or by assessing age at the first nest check after hatch based on the following criteria: dry but unable to move more than lifting their heads (day 0-1) or dry and moving around (day 1-2). In each nest for which I measured nestlings, I selected two

host nestlings and one cowbird nestling, if present. I marked the outer edge of nestling tarsi with a nontoxic Sharpie marker (Newell Brands, Hoboken, NJ, USA) to permit individual recognition prior to banding.

Every 2(-3; mean 2.2) days, I removed focal nestlings to >5 m from the nest, measured them, and returned them to the nest in <5 min. I quantified structural growth by measuring the length of each nestling's right tarsus, culmen from nares to tip, and gape at the widest point without depressing the skin. To quantify muscle growth, I measured the width of the breast muscles at the widest point and visually scored breast shape on a 4-point scale. I measured mass using a small digital scale accurate ±0.001g (AC-Pro 200, American Weigh Scales, Cumming GA, USA). To measure wing development, I digitally photographed each bird's right wing against a gridded card for subsequent analysis of flight feathers and wing bone length. I measured the length (to the nearest mm) of the ulna, the carpometacarpus, the length of first secondary and ninth primary feather, and the length of the unsheathed portion on those two feathers using Image J (Schneider et al. 2012).

I scored nestling alertness using two qualitative scales based on eye opening and activity. In 2017, I scored eye development on a three-point visual scale ranging from 0 (eyes closed) to 2 (fully open) and activity on a six-point scale ranging from 0 (does not lift head or beg) to 5 (attempts to escape). Additionally, I scored dorsal feather growth as an index of insulative capabilities on a four-point scale. In 2018, I subdivided each of these scales more finely to correspond to measurements collected in other Grasshopper Sparrow populations (Ruth 2017) and to capture more of the variation observed in the field, reclassifying 2017 scores when possible based on photographs. I describe these scales in detail in Supplementary Material. Because results based on these slightly different scales were qualitatively identical, I report only

the results based on the more precise scale, below.

I banded each nestling with a U. S. Fish and Wildlife Service numbered aluminum band a few days before fledge age (day 5–6 for sparrows and Dickcissels, day 9–11 for meadowlarks). I drew 30–100 μl of blood from the brachial vein and stored samples on ice before centrifuging within ~6 hr. I stored the red blood cells in Queen's Lysis Buffer at -20°C for up to one year prior to genetic analysis. I sexed the nestlings using CHD-P2 (5'-TCTGCATCGCTAAATCCTTT-3') and 1237L (5'-GAGAAACTGTGCAAAACAG-3') primers. I ran PCR reactions using 24 μL of DreamTaq Green PCR Master Mix (2X) and 1 μL of DNA for a 25 μL reaction. I amplified the DNA on a SimpliAmp Thermal Cycler at 94C for 2 minutes, followed by 29 cycles of 94 °C for 30 seconds, 42 °C for 45 seconds, and 72 °C for one minute, and finally extended at 72 °C for 5 minutes. I ran 4 μl of the sample through a 2% agarose gel in 1X TAE with Gel Red for 90 minutes of electrophoresis at 80V. I visualized the results with a UV transilluminator and determined the sex of each nestling individually (Kahn et al. 1998, Griffith and Orr 1999).

Modeling nest success

To model daily nest survival rate, I created species-specific candidate model sets evaluating the effect of year and/or date in the breeding season on overall nest success. To confirm that nestling measurements did not increase nest failure, I compared the daily survival rate of nests in which I measured nestlings and those subject to only brief checks every 2-3 d, limiting my dataset to only the nests that survived to hatching. I produced candidate model sets evaluating the relationships between nestling measurements (Y/N), the number of visits/days active, the species, the date, and the year. I analyzed models in R (R Core Team 2013) with the *RMark*

package (Laake 2013), which uses a maximum-likelihood approach and a logit-link function (Dinsmore et al. 2002). I interpreted the results of the top model (lowest AICc values).

Modeling growth

I reduced the dimensionality of nestling growth in species-specific "multiple factor" analyses using the *FactoMineR* package (Lê et al. 2008). I included all 14 measures of structural size, feather development, and alertness. I used the first dimension as a score of overall nestling size for each species.

To determine whether nestlings in parasitized nests *prioritized competitive features* components of development differently than those in unparasitized nests, I first calculated the residuals of each morphological trait measured on a numeric scale (i.e. excluded the Y/N activity scores) regressed against the mass of the individual at the corresponding time period. I then conducted a Principal Components Analysis (PCA) on a correlation matrix using these mass-corrected measures of development. I used the two axes that carried a combined ~50% of the explanatory power for each host species, identifying and interpreting the structures that loaded most strongly on these PCA axes as the structures that were being over- or under-prioritized relative to the individual's mass gain.

Nestling growth data are frequently fit to logistic growth curves (Brown et al. 2007). However, visual inspection of my nestling growth trajectories revealed roughly linear trajectories (Figure 1-1). Thus, I instead fit the data to linear mixed models (Bolker et al. 2009, Sofaer et al. 2013) implemented in *lme4* (Bates et al. 2014) for the three measurements of growth (overall size and the two prioritization scores) separately for each species. I assessed whether the presence and number of cowbird nestlings contributed to either overall growth of host nestlings

(*slower growth* and *parental compensation* hypotheses) or prioritization of body parts (*prioritized competitive features* hypothesis) in a two-step modeling process. I first created models that accounted for all *a priori* environmental drivers of growth other than parasitism, and then I compared top models to ones including parasitism. In the first modeling step, I created models using all interactive and additive combinations of nestling age in days (nestlings of an uncertain age were averaged, e.g. day 2-3 became 2.5), number of host nestlings, the maximum number of host eggs, and year. I controlled for repeated measures of individuals by including random effects of nest and nestling ID. I used Akaike's Information Criterion adjusted for small sample size (AICc) (Anderson and Burnham 2002) to select models $\Delta AICc < 2$ that best explained the growth of the nestlings, independent of brood parasitism.

I compared the top models identified in the previous modeling step (i.e. all models $\Delta AICc < 2$) with a second set of models that included all previous factors in additive and interactive combinations with parasitism and age*parasitism interactions to estimate the effects of parasitism while controlling for other drivers of growth and development variation. I modeled relationships between nestling growth and parasitism in three different ways: presence of cowbirds in nests as a yes/no categorical factor, the total number of cowbird nestlings in the nest, and the total number of nestlings including host and cowbird young.

I calculated the standard deviation between sibling host nestlings' size and prioritization scores (from MFA of all body parts and PCA scores of mass-corrected morphological measures) to determine whether cowbirds exacerbated inherent differences in growth between host siblings (*within-brood variation* hypothesis). Because sex sometimes affects nestling size (Alonso et al. 2018, Oddie 2000), I coded pairs of measures as "M" for nests in which I measured two male nestlings, "F" for those in which I measured only females, and "X" for nests in which I measured

one nestling of each sex. I used linear mixed models to assess the effect of year, number of host eggs, number of host nestlings, number of cowbird nestlings, total number of nestlings, parasitism Y/N, and the sex code of the measured nestlings on the size deviation scores. I interpreted the top model(s) from each candidate set (ΔAICc < 2) as the best predictors of within-nest variation in growth and structure prioritization.

I restricted my dataset to only those nests that successfully fledged young in order to evaluate the relationship between cowbird parasitism, development strategies, and fledge age (predictions ii, vi, and viii). I modeled fledge age as a function of parasitism (Y/N), year, nestling size (MFA of all body parts), and the prioritization metric (PCA scores of mass-corrected morphological measures), including nestling ID and age as random effects.

For each modeling attempt, I analyzed each species separately. I never combined related metrics (i.e. total number of nestlings and the number of host nestlings) into a single model, and included nest ID and nestling age as random effects. Because I only had sex data for the nestlings that survived the nestling period but I wanted to assess the relationships between cowbirds and host nestling in sex-dependent ways, I repeated the entire modeling process with restricted data sets containing only the sexed nestlings and included sex or nest sex score as a factor in the first modeling step. I visualized all results in the package *ggplot2* (Wickham 2016).

Results

In 2017 and 2018, I found 284 nests: 87 Eastern Meadowlark, 141 Dickcissel, and 115 Grasshopper Sparrow nests. Of these, 202 nests survived past hatching: 56 Eastern Meadowlark, 79 Dickcissel, and 67 Grasshopper Sparrow. Of those, I measured nestlings in 139 nests: 48 Eastern Meadowlark, 58 Dickcissel, and 44 Grasshopper Sparrow. I took 802 sets of

measurements on 264 host nestlings, averaging 2.7 measurement sets/nestling: 86 Eastern Meadowlark nestlings, 98 Dickcissel nestlings, and 80 Grasshopper Sparrow nestlings. Cowbirds parasitized 46.4% of the nests; 25.2% of Eastern Meadowlark nests, 36.5% of Grasshopper Sparrow nests, and 67.4% of Dickcissel nests. Of those containing measured nestlings, cowbirds parasitized 6 of 44 meadowlark nests, 35 of the 58 Dickcissel nests, and 12 of the 46 sparrow nests.

Nest success was low overall; 35.6% of all meadowlark nests, 30.5% of all Dickcissel nests, and 30.4% of all Grasshopper Sparrow nests successfully fledged at least one host nestling. The estimated daily nest survival rates were constant within seasons and between years; meadowlarks' estimated 0.932 ± 0.009 chance of daily survival resulted in an estimated nest success of 19.8% when extrapolated over the nesting period. In Dickcissels, daily nest survival was 0.914 ± 0.008, resulting in an estimated nest success of 19.8%. In sparrows, daily nest survival was 0.895 ± 0.011, resulting in an estimated nest success of 13.6%. Of the nests at which I measured nestlings, 23 of 44 meadowlark nests, 23 of 44 Dickcissel nests, and 23 of 46 sparrow nests fledged at least one host nestling. Considering only nests that survived to nestling stage, daily nest survival rates were best explained by whether or not I measured nestlings (Table S1-1). However, the beta coefficient of this relationship was positive (β=0.974 ± 0.279, Table S1-2), indicating that the nests subject to repeated disturbance were on average more successful than less-intensively studied nests.

Eastern Meadowlark growth

For the majority of meadowlark individuals, visual inspection of raw growth data revealed linear increases in body component size (e.g. mass gain, Figure 1-1) with three exceptions. Eye score

hit a maximum and stopped increasing before the end of the brooding period, gape width hit a maximum and then decreased, and the length of unsheathed feathers, which remained at 0 until midway through the brooding period and then increased roughly exponentially. Meadowlark nestlings fledged at masses ranging from 20.5 to 56.1 grams (mean=44.8±1.2 SE) and with tarsi of 20.4 to 38.4 mm (mean=34.8± 0.6 SE). Meadowlark fledge age ranged from 7 to 12 days (mean=10.3±0.1 SE) and this variation was best explained by the presence of cowbirds (Table S1-3); nestlings in parasitized nests fledging on average 1.1 days (10.4%) earlier than those in unparasitized nests (Figure 1-2). By leaving the nest one day early, a meadowlark's chance of successfully fledging increased 1.4% (based on the daily nest survival estimates).

The first dimension of the multiple factor analysis accounted for 68.8% of the variance in size of nestlings (Table S1-4). Meadowlark nestlings hatched at a larger size in 2018 but grew 7.1% more quickly in 2017 (Figure 1-3, Table S1-5). This difference in growth between years explained more variation in growth than did parasitism (ΔAICc=2.032, Table S1-6). Unparasitized meadowlarks fledged with factor scores that were, on average, 27% higher than the scores of parasitized meadowlarks when they fledged days earlier (t_{10}=2.14, P=0.06). This difference indicates that meadowlark nestlings in parasitized nests left the nest at an earlier stage in development than the unparasitized birds, in addition to leaving at an earlier age. Broods of only two nestling meadowlarks exhibited twice as much within-nest variation in nestling growth than did larger broods (Figure 1-4, Table S1-7).

The first principal component (PC1) accounted for 36.6% of the variance in prioritization (Table S1-8). Larger values of PC1 described nestlings with longer tarsi and wing feathers relative to their mass (Table 1-1). In the first modeling step, the environmental variables associated with variation in morphological prioritization were year and the number of host

nestlings (Table S1-9). When I combined the results of this first modeling step with parasitism variables, the top models included year and the total number of nestlings (of both cowbirds and hosts) (Table S1-10). Meadowlarks in nests containing the fewest (1-2) and most (5+) nestlings prioritized tarsus and feather growth relative to mass in both years compared to nestlings reared in typically-sized broods. However, the difference in PC score (0.9) represents only 6% of the range in scores observed in this dataset. The relative prioritization of tarsus and feather growth increased with age in 2017 but stayed constant through nestling development in 2018 (Figure 1-5). Within-nest variation in nestling PC1 was best explained by the year (92.1% of the weight, Table S1-11), with siblings in 2017 varying 43.6% more than siblings did in 2018 (Figure 1-6).

The second principal component (PC2) accounted for 20.8% of the variance in prioritization (Table S1-6) and positive values were associated with proportionately larger gapes and higher eye scores (Table 1-1). The environmental variables related to variation in PC2 in the first step of modeling were year and the number of host nestlings (Table S1-12). When these top models were combined with the cowbird measurements, the top model was the total number of nestlings, including cowbirds and hosts, and this model carried 60.5% of the total weight (Table S1-13). Nestlings in medium-sized (3-4 nestling) broods initially had higher gape and eye scores than did nestlings in the smallest (1-2 nestlings) and the largest broods (5+ nestlings) and this difference accounted for ~30% of the full range of variation in the data. However, the difference disappeared by day three; subsequently, nestlings in the smallest and largest broods increasingly prioritized the growth of their gapes and eyes, while nestlings in medium broods did the reverse. By the time the nestlings reached 9 days old, nestlings in the medium-sized broods had relative gape and eye scores lower than did nestlings in small and large broods; the difference between these scores represents 100% of the observed range of values (Figure 1-7). Within-nest variation

in PC2 was constant over time (Table S1-14).

Dickcissel growth

Visual inspection of raw Dickcissel growth data revealed linear increases in most body part sizes (e.g. mass, Figure 1-8), although there were a few exceptions. Eye score and gape width both which achieved a maximum on ~day 5 then ceased their trajectory. The feathers did not unsheathe until midway through the brooding period and thereafter increased close to exponentially.

Dickcissel fledge age ranged from 5.5 to 9.5 days (mean=7.4±0.1) and was best explained by nestling sex (model weight= 95.6%, Table S1-15). Dickcissel males fledged, on average, 0.6 days earlier than females (t_{50}=2.233, *P*=0.030). At the last nest check (<2 days) before projected fledge dates, Dickcissel nestlings mass varied dramatically from 7.8 to 26.8 grams (mean=15.3±0.4 SE) and their tarsi varied in length from 14.9 to 25.0 mm (mean=20.8±0.3 SE).

The first dimension of the multiple factor analysis accounted for 66.3% of the variance in growth (Table S1-16). Sex, number of host young, and year all contributed to the top models of Dickcissel size in the first round of modeling (Table S1-17). The final modeling step produced top models that included sex, year, and the number of cowbird nestlings (Table S1-18). Nestlings were larger in nests with zero or one cowbird compared to nests with two or more cowbirds, although the difference accounted for only 9% of the range of size scores (Figure 1-9). Like Meadowlarks, Dickcissel nestlings hatched with higher overall size scores in 2018 but grew 12.9% faster than did nestlings in 2017; by the end of the eight-day brooding period, nestlings in 2017 had higher size scores than did nestlings in 2018. Male Dickcissel nestlings were initially

smaller than females but grew 12.3% faster, perhaps explaining their earlier fledge age (Figure 1-10). Although the within-nest variation in nestling growth appeared to be related to the total number of nestlings, a constant model provided a similar fit to the data (constant model ΔAICc=0.635, Table S1-19).

The first principal component accounted for 34.3% of the variance in the prioritization (Table S1-20) and positive values were associated with nestlings having larger tarsi, bill, ulna, and feathers relative to mass (Table 1-1). In the first modeling step, this prioritization was best explained by sex and the number of host nestlings (Table S1-21), and this model was still the top model after including parasitism in the model set (weight=44.8%, Table S1-22). Female nestlings had slightly higher PC1 scores (i.e., relatively longer tarsi, bills, ulnas, and feathers) than did male nestlings (Figure 1-11B). In the smallest broods (1-2 host nestlings) the PC1 scores stayed constant over time, while in larger broods the scores increased with age, suggesting that these individuals increasingly invested in the growth of bones and feathers relative to mass (Figure 1-11). Within-nest variation in PC1 score was 25% higher in small broods than in larger broods, and 16.7% higher overall in 2017 than in 2018 (Figure 1-12, Table S1-23).

The second principal component accounted for 16.8% of the variance in prioritization (Table S1-20) and positive PC2 scores represented nestlings with more advanced eye development and more feather unsheathing relative to mass. The environmental factors explaining most variation in PC2 were sex and the number of host nestlings (Table S1-24). When I added the parasitism factors, the top models included sex, year, and parasitism, either represented as the number of cowbird nestlings or as a yes/no category. The next best model was simply growth over time (Table S1-25). The eyes and feathers of Dickcissels in parasitized nests were less developed relative to mass than conspecifics in unparasitized nests; this difference

encompassed 41.2% of the total range of values. The PC2 scores of male Dickcissels decreased twice as quickly as did those of females, indicating that males prioritized mass over eyes and feathers to a greater extent as they aged (Figure 1-13). Although variation in this prioritization score was twice as high in 2017 than in 2018, this variation was equally well explained by a constant model (ΔAICc=1.800, Table S1-26).

Grasshopper Sparrow growth

Like the other species, most Grasshopper Sparrow body parts grew approximately linearly (Figure 1-14). The exceptions were eye score and gape width, which peaked at ~day 4, and the length of unsheathed feathers, which remained at 0 until midway through the brooding season and then increased roughly exponentially. Grasshopper Sparrow fledge age ranged from 5 to 10 days (mean=7.6±0.1 SE) and this variation was unrelated to year, brood size, parasitism, or any size metric (Table S1-27). Mass at day 6 ranged from 8.0 to 13.7 grams (mean=11.5±0.3 SE) and tarsus length ranged from 14.5 to 20.1 mm (mean=18.2±0.3 SE).

The first dimension of the multiple factor analysis accounted for 66.1% of the variance in overall size (Table S1-28). Variation in size was best explained by the number of host nestlings (weight=66%, Table S1-29) and this was still the only factor in the top model after considering models with parasitism (Table S1-30). Grasshopper Sparrows grew 13.7% faster in small (1-2 host nestlings) or large (4+ host nestlings) broods relative to medium-sized (3 host nestlings) broods (Figure 1-15). Nests with small broods (2 host nestlings) had 122.2% higher within-nest variation in size than nests with more nestlings (Figure 1-16). However, the brood size model did not receive more support than the constant model (ΔAICc=0.434, Table S1-31).

The first principal component (PC1) accounted for 33.8% of the variance in the

prioritization (Table S1-32) and described nestlings with relatively larger ulna and flight feathers relative to mass (Table 1-1). The only environmental variable associated with variation in PC1 was the number of host nestlings (weight=66%, Table S1-33), and this single-factor model was still the top model when measures of parasitism were added to the model set (weight=65%, Table S1-34). Nestlings in large broods (4+ host nestlings) prioritized ulna and flight feather growth more than did nestlings in smaller broods (Figure 1-17). Within-nest variation in these PC1 scores was constant over time (Table S1-46).

The second principal component (PC2) accounted for 14.6% of the variance in the prioritization (Table S1-32) and described nestlings with relative larger tarsi and more developed eyes than expected based on their mass (Table 1-1). In the first modeling step, variation in PC2 was associated with the number of host eggs (weight=45.7%, Table S1-36). When parasitism factors were considered, the top model included the host number of host eggs and an additive effect of the number of cowbird eggs (ΔAICc between the top models of steps 1 and 2 was 4.334, Table S1-37). Unparasitized sparrows prioritized eye and tarsus growth more than did parasitized birds initially, but the pattern reversed as the birds grew older (Figure 1-18). PC2 scores of nestlings in small broods (1-2 nestlings), large broods (4 nestlings), and extra-large broods (5+ nestlings) stayed constant over time or slightly decreased, indicating that nestlings did not change allometry over time or decreased the energetic allocation to eyes and tarsi slightly over time. By contrast, PC2 scores of nestlings in medium broods (3 nestlings) sharply increased over time (Figure 1-19), indicating that these nestlings invested relatively more energy to eye and tarsi development as they aged. Although medium-sized broods fledged with the highest PC2 scores, the difference between medium and extra-large broods accounted for only 16.7% of the observed range of values. Within-nest variation in PC2 score was 2.5 times higher in the

smallest broods (2 nestlings) than in larger broods (Figure 1-20, Table S1-38).

Discussion

Over two years I measured the growth and development of hundreds of nestlings in nests of three species parasitized by Brown-headed Cowbirds at a site located in the epicenter of cowbird parasitism intensity (Jensen and Cully 2005). The observed parasitism rates of 24.2% of Eastern Meadowlark nests, 67.4% of Dickcissel nests, and 36.5% of Grasshopper Sparrow nests were lower than the extreme rates previously recorded at the site (Elliot 1978) but still higher than rates reported from most locations (Patten et al. 2006, Ruth 2017). I observed substantial intra- and inter-specific variation in growth, with nestlings growing to double the size of conspecifics of the same age in different nests, fledging days earlier than others, and/or differing substantially from the size of their siblings. Multiple factors were associated with intra-specific variation in development, and brood parasitism influenced host nestlings in species-specific ways.

I hypothesized that Eastern Meadowlark nestlings would be least affected by brood parasitism because they are larger than the cowbird parasites (*host size* hypothesis). Cowbirds did not directly affect the overall size of meadowlark host nestlings, but the meadowlarks did fledge earlier in parasitized nests (*earlier fledging* hypothesis). Meadowlarks in unparasitized and parasitized nests grew at similar rates, suggesting that parents could compensate for the presence of cowbirds, or that the strength of cowbird competition on hosts was small (*parental compensation* hypothesis). Meadowlark nestling growth varied substantially between years, which could be the result of variation in climate or other environmental conditions. Within-brood differences in nestling size were related to total brood size (including cowbird and host nestlings), but nestlings in the smallest broods most differed from one another. Because the

smallest broods should experience less competition than large broods, this pattern is the opposite to that predicted.

Brood size (including the host and cowbird nestlings) was related to allometry. Nestlings in the largest and smallest broods grew structures associated with mobility (tarsi and wing feathers) relatively rapidly, and increasingly prioritized the development of gapes and eyes as they aged compared to nestlings in medium-sized broods. Large broods could experience more competition than small broods, forcing nestlings to preferentially develop large gapes to solicit food, large tarsi to stand taller to monopolize provisioning events, and larger wings to leave the nests more quickly. However, this result does not explain why the smallest broods also exhibited these allometric patterns. Because parasitism does not add to the size of the brood, but rather, cowbirds replace meadowlark eggs with one of their own during laying (Sealy 1992), cowbird nestlings in this large-bodied host may not affect growth and development in unique ways, but rather, function as just another sibling competitor equivalent to conspecifics.

In contrast to the negligible consequences of cowbirds on growth and development patterns, the presence of cowbird parasites was strongly associated with fledge age. Meadowlarks fledged 10.4% earlier when cowbirds were present and fledged at smaller sizes than did nestlings in unparasitized nests. This result is consistent with meadowlarks leaving the nest earlier in development to avoid the within-nest competition from cowbird nestlings (Johnson et al. 2004). In combination, the growth and fledge age results are surprising; if parasitism does not affect growth, there are no obvious competitive costs that would select for early fledging. One alternative is that cowbirds influence adult behavior by soliciting constant provisioning via begging, or their begging may be loud enough to attract predators and increase the risk of host nestlings being eaten. In some cases, adults influence fledging decisions, enticing nestlings to

leave earlier by reducing provisioning rates or drawing the nestlings from the nests by standing outside holding food (Johnson et al. 2004, Ribic et al. 2019). I do not have data on parental behavior at the time of fledge. However, early fledging could be argued to either increase or reduce the survival of fledglings depending on the relative risks inside and outside the nest. Early fledging would allow meadowlarks to avoid potential elevated risks of nest predation in parasitized nests. However, meadowlark post-fledge survival is positively correlated to their mass at fledging (Suedkamp Wells 2007). Thus, since the meadowlarks in this study were less well developed than fledging nestlings from unparasitized nests, they would be more likely to experience reduced survival due to incomplete thermoregulatory and locomotory capacities.

Dickcissels were the most frequently parasitized of all the hosts, yet experienced none of the hypothesized responses to past parasitism (*parental compensation, prioritized competitive features,* or *earlier fledging* hypotheses). Instead, Dickcissels grew more slowly (*slower growth* hypothesis), a response to present competition. However, Dickcissels only suffered reduced growth when two or more cowbird nestlings were present; growth of hosts sharing the nest with one cowbird nestling was the same as sharing the nest with only conspecific siblings. This result suggests that parents can compensate for parasitism to a certain degree. Nestlings in parasitized nests also developed their eyes and feathers relatively more slowly. Potentially, Dickcissels experience parasitism as a developmental stressor, even in nests containing a single cowbird competitor, and this stressor affects all nestlings rather than only in the smallest members of the brood (*within-brood variation* hypothesis).

Dickcissels in parasitized nests did not differ in their allometric scaling of structures hypothesized to affect within-nest competition for food; the relative size of tarsi and bills (culmen) was similar in nestlings in parasitized and unparasitized nests, as was the within-nest

variation in those measures. Furthermore, despite cowbirds' suppression of Dickcissel growth, I found no evidence that Dickcissels in parasitized nests fledged any later than those in unparasitized nests. Consequently, Dickcissels in parasitized nests fledged at smaller sizes, suggesting that other cues trigger fledging behavior in this species.

Under the *host size* hypothesis, I expected the smallest host species, the Grasshopper Sparrow, to experience the most negative consequences of brood parasitism due to competitive asymmetries that favor parasite nestlings relative to hosts. Surprisingly, I found no evidence that parasitized sparrows experience *slower growth* or larger *within-brood variation*. Instead, sparrows appear to have adapted to the presence of cowbirds; although nestlings did not *fledge earlier,* nestlings *prioritized competitive features* and may benefit from *parental compensation.*

Within-nest variation in overall growth differed between large and small broods, but in the opposite direction to that predicted; nestlings in the smallest broods—presumably with less sibling competition—were the most dissimilar in growth rates. Sparrows in parasitized nests also had larger tarsi relative to mass, suggesting that they may prioritize the ability to stand up and compete with taller cowbird nestlings. The relatively few consequences of parasitism for this species may reflect changes in parental behavior. Adult sparrows may compensate for the presence of cowbirds by increasing pre-laying resource investment or by increasing provisioning rates. Grasshopper Sparrow nestlings may thus be spared from the costs of brood parasitism at the expense of their parents.

Overall growth was associated with the number of host young in the nest; sparrows grew the fastest in nests with the fewest and the most sparrow eggs, and slowest in the nests with the medium sized clutches. This metric does not always reflect the total number of nestlings (due to partial clutch or brood loss) but reflects one component of parental investment. The largest

clutches could be laid by high-quality parents such as experienced birds better able to provision many nestlings and thereby reduce competition. In contrast, nestlings that hatched from the smallest clutches may simply not have enough competitors to experience the cost of competition seen in the medium-sized broods. The allometric scaling of structures associated with mobility (wing bones and flight feathers) was associated with the total number of host young; nestlings in larger broods prioritized development of these structures more so than nestlings in smaller broods, potentially reflecting sibling competition, yet these birds did not leave any earlier to escape the competition as predicted. Surprisingly, none of the factors I considered was related to the 5-day range in fledge age of Grasshopper Sparrows in this study. Previous explanations for such difference in fledge age have implicated differences in growth rates or strategies, none of which were the case in our study. One possible explanation for the difference in results between studies could lie in the simultaneous high predation and parasitism pressure at the site. These two factors may drive nestlings to fledge as early as possible at Konza, which would suggest that fledge behavior responds more to site-level environmental pressures than nest microsite-level drivers in this species.

Understanding the long-term effects of cowbirds on populations is important, as cowbirds and other brood parasites have the potential to affect host population trajectories (Arcese et al. 1996, Jewell and Arcese 2008). Frequent hosts may evolve a variety of pre- and post-laying behavioral strategies to prevent or remove parasitic intruders (Yasukawa and Werner 2007, Medina and Langmore 2016), yet these host species at Konza incubate parasite eggs in approximately half of their nests. Even though these species live at the same site and fill similar niches, their responses to parasitism are not merely gradations of the same behavior but are rather species-specific responses to the stressors of parasitism. The largest and smallest hosts

(Eastern Meadowlark and Grasshopper Sparrow) exhibited different responses to the presence of cowbird nestlings; meadowlarks fledged earlier and sparrows prioritized the relative growth of competitive features like tarsi. These results suggest that plasticity in growth and development can act as strategies to mitigate the cost of cowbird competition in species adapted to cowbirds. Medium-sized Dickcissels experienced reduced growth overall in the presence of cowbirds, especially the growth of eyes and feathers, yet fledged at the same age in parasitized or unparasitized nests. This effect of cowbirds was only present in nests with more than one cowbird, suggesting that parents can compensate for a single cowbird chick in Dickcissel nests but not more. Thus, the presence of cowbirds is still an ongoing stressor for developing Dickcissels, but only when they are multiply parasitized. The presence of cowbirds explained some of the variation in host growth and development but not all, warranting further research into other hypothesized drivers of nestling growth and development variation, like pre-natal resource allocation (Slagsvold et al. 1984, Schwabl et al.1997), post-natal provisioning rates (Soma et al. 2006, Gil et al. 2008), and predation risk (Martin 1995, Monrós et al. 2002). Because brood parasitism can also affect provisioning (Kilner et al. 2004) and predation risk (Dearborn 1998), it is worth exploring the interaction between these drivers and growth and development, as this could help explain the mechanisms behind these behavioral strategies.

Nestlings' growth trajectories influence their future survival (Hochachka and Smith 1991, Starck and Ricklefs 1998) and their ability to adjust to changing environments (Moe et al. 2004). Growth rate typically varies little within species or populations (Starck and Ricklefs 1998), yet this study demonstrates that nestlings within a single population can grow to double the size of conspecifics prior to fledging. I hypothesized that this intraspecific variation was the result of competition with brood parasite nestlings and/or host species' adaptation to this competition, an

explanation that had not been previously tested. These threatened birds did respond to the presence of cowbirds through plastic changes in their growth and development, illustrating species-specific adaptive strategies that could mitigate the costs of competition with brood parasites. Understanding the relationships between life history strategies and environmental drivers like brood parasitism may require not only acknowledging the presence of intraspecific variation in growth and development, but also assessing it within populations.

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Tables

Table 1-1. Contributions of different nestling residuals to the first two dimensions of each species' Principal Components Analysis. For all identified components see Tables S1-39 through S1-41.

	Eastern Meadowlarks		Dickcissels		Grasshopper Sparrows	
measurement: mass residuals	PC1	PC2	PC1	PC2	PC1	PC2
tarsus length	0.513	0.164	0.571	0.461	0.029	0.428
bill length	0.357	0.002	0.511	0.194	0.085	0.087
gape width	0.065	0.569	-0.209	0.364	0.056	0.092
ulna length	0.408	0.027	0.641	0.219	0.610	0.000
carpometacarpus length	0.259	0.122	0.335	0.565	0.006	0.185
primary 9 length	0.742	0.000	0.813	-0.018	0.673	0.000
unsheathed primary 9 length	0.433	0.332	0.588	-0.653	0.695	0.062
secondary 1 length	0.659	0.000	0.723	0.246	0.521	0.005
unsheathed secondary 1 length	0.491	0.309	0.687	-0.613	0.692	0.073
eye score	0.000	0.612	0.318	0.560	0.000	0.660
dorsal feather score	0.201	0.304	0.673	0.044	0.316	0.072
activity score	0.262	0.057	0.628	-0.291	0.372	0.085

Figures

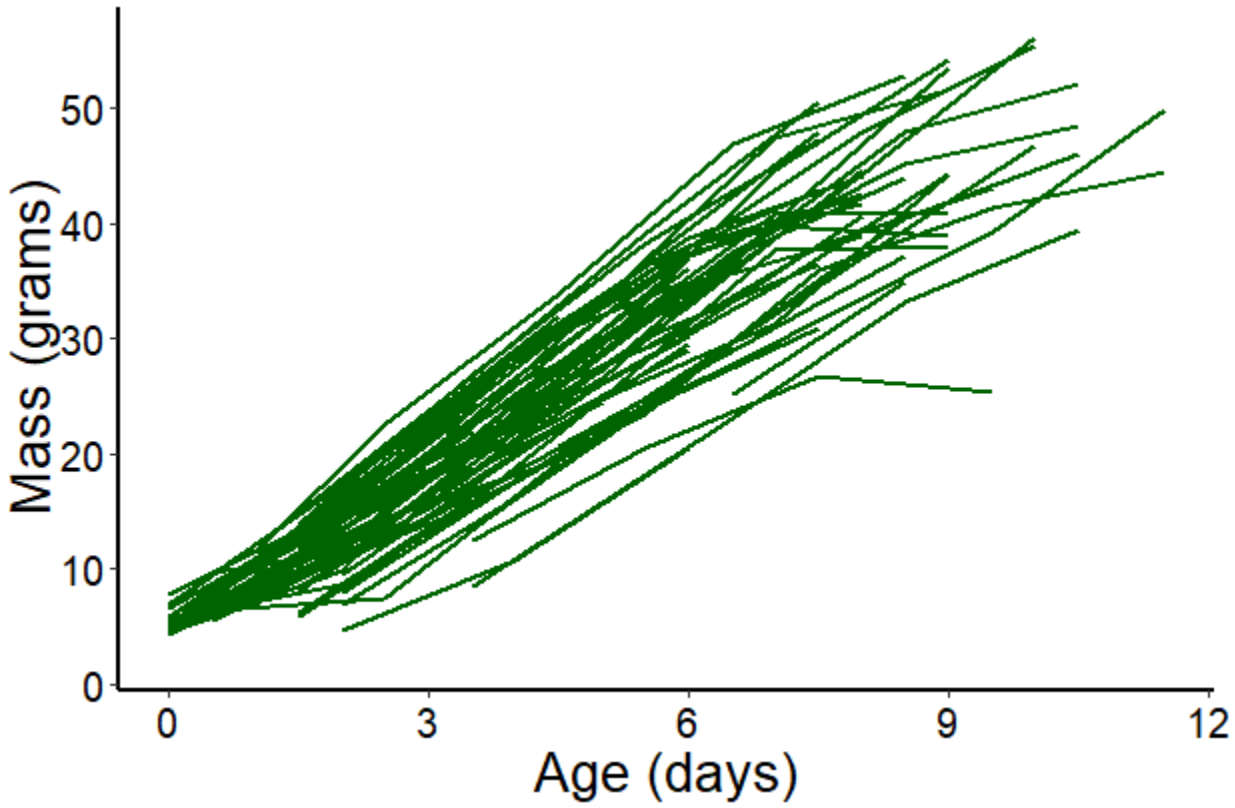

Figure 1-1. Growth of individual Eastern Meadowlarks' mass over time. Meadowlarks gained mass (in grams) in a roughly linear fashion over time (age in days). By the end of the brooding period some nestlings were twice as heavy as conspecifics. Lines connect raw measurements of a single individual.

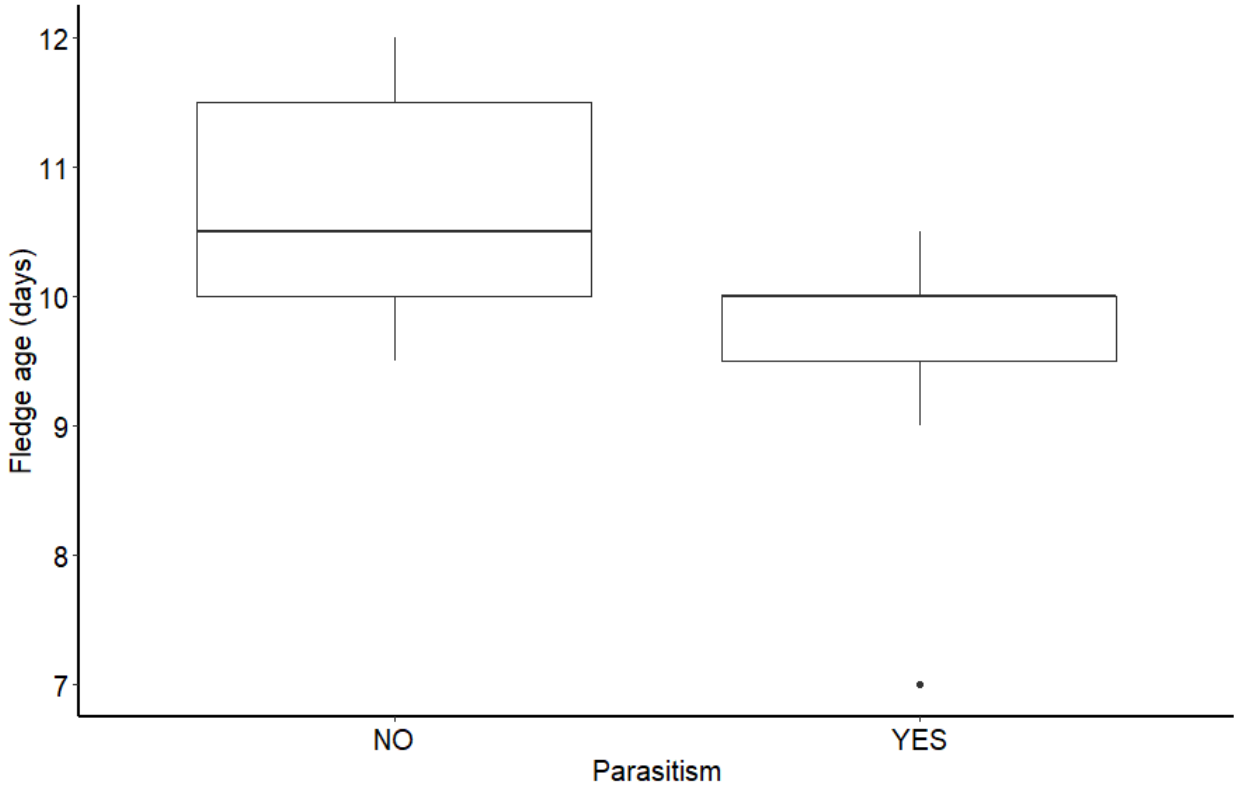

Figure 1-2. Eastern Meadowlark fledged earlier in parasitized nests. Nestlings that were raised alongside cowbirds fledged an average of 1.1 days earlier than conspecifics in unparasitized nests.

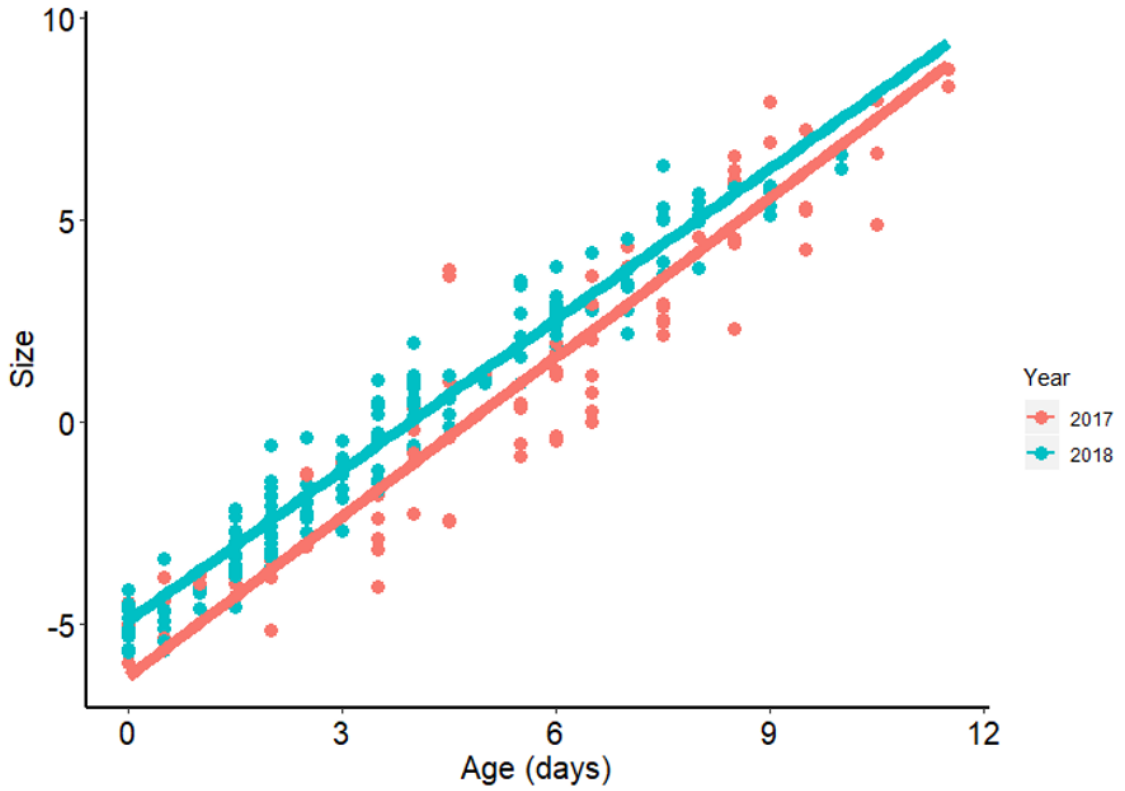

Figure 1-3. Meadowlark nestlings hatched at a larger size in 2018 (blue line) but grew 7.1% faster in 2017 (red line), eventually reaching the same size by fledge. These lines were generated with predicted values from a model that included an interaction between year and nestling age.

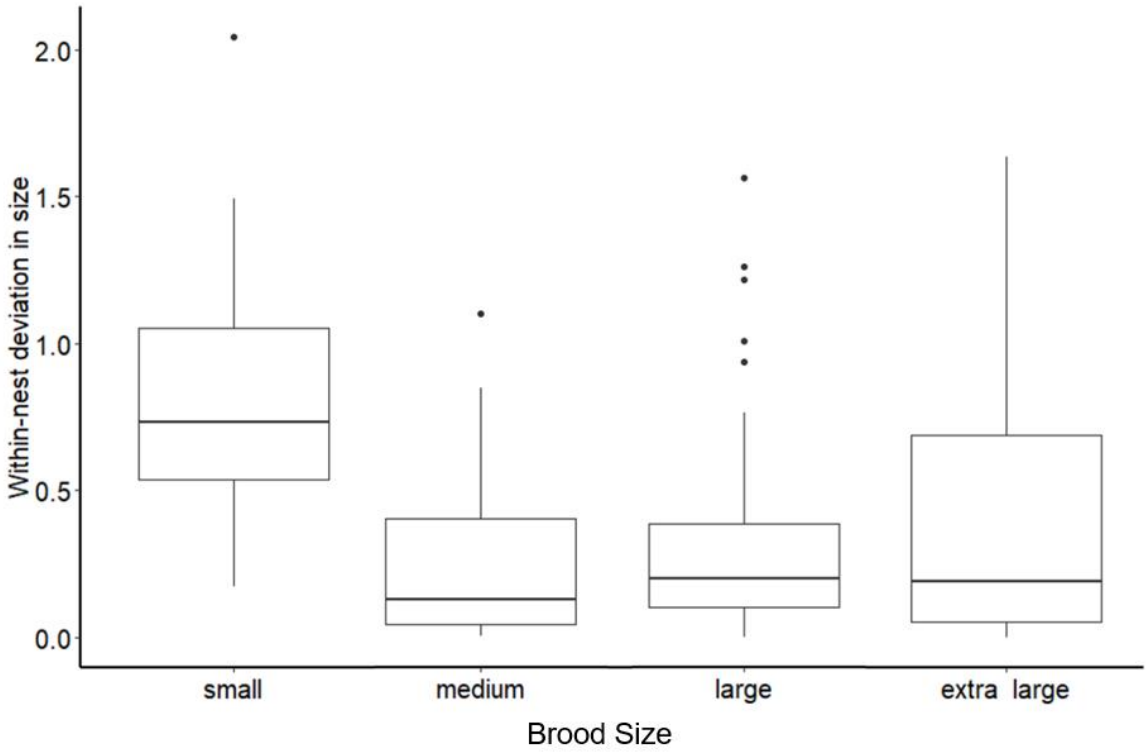

Figure 1-4. Within-nest variation in meadowlark size in broods with two nestlings ("small") was twice as high as within-nest variation in size in nests with 3 or more nestlings of either species ("medium," "large," and "extra large").

Figure 5A: 2017

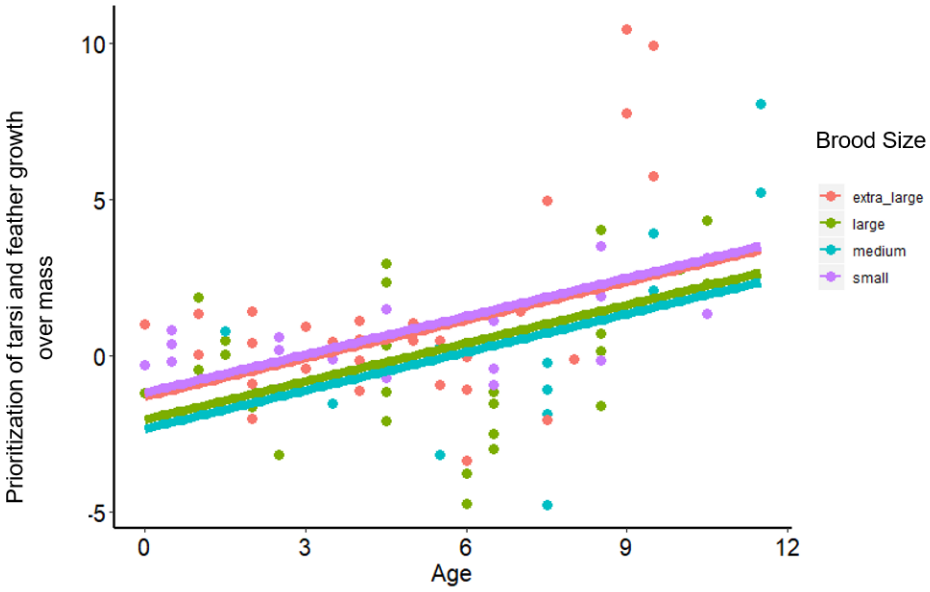

Figure 5B: 2018

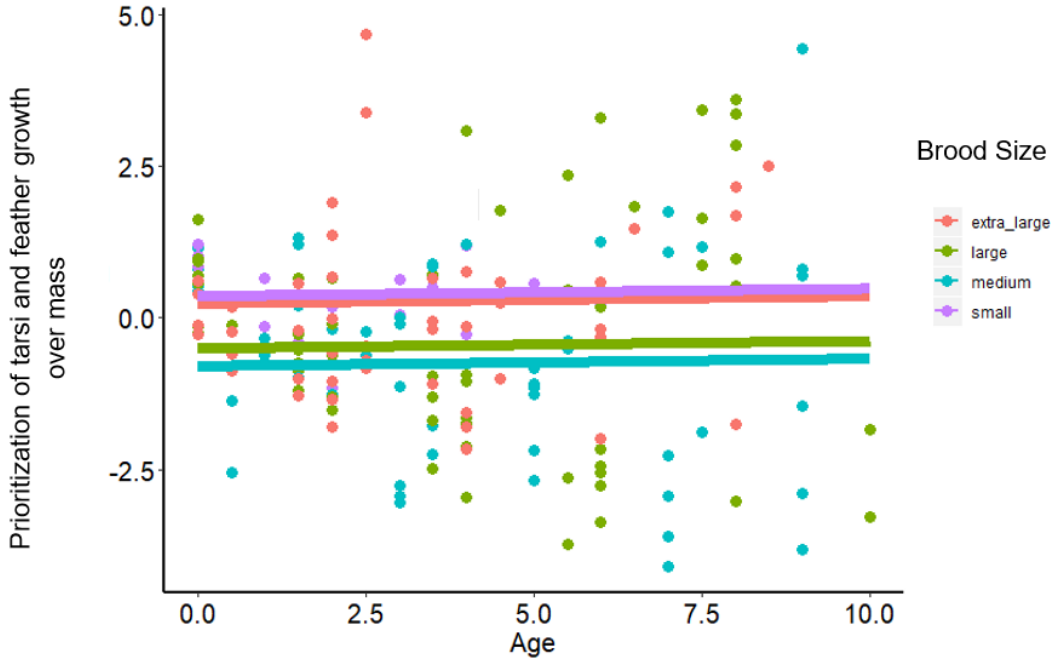

Figure 1-5. Eastern Meadowlark nestlings prioritized the growth of tarsi and feathers over mass more in the nests with the fewest nestlings (1-2 nestlings; purple lines) and the most nestlings (5+; orange lines) compared to nests of medium-sized broods (3-4; blue and green lines), although this difference accounted for little of the observed variation in this allometric pattern. These prioritization scores stayed constant as the birds aged in 2018 (B) but increased as the birds grew older in 2017 (A). These lines were generated with predicted values from a model that included an interaction between year and nestling age and an additive effect of the number of host nestlings (brood size).

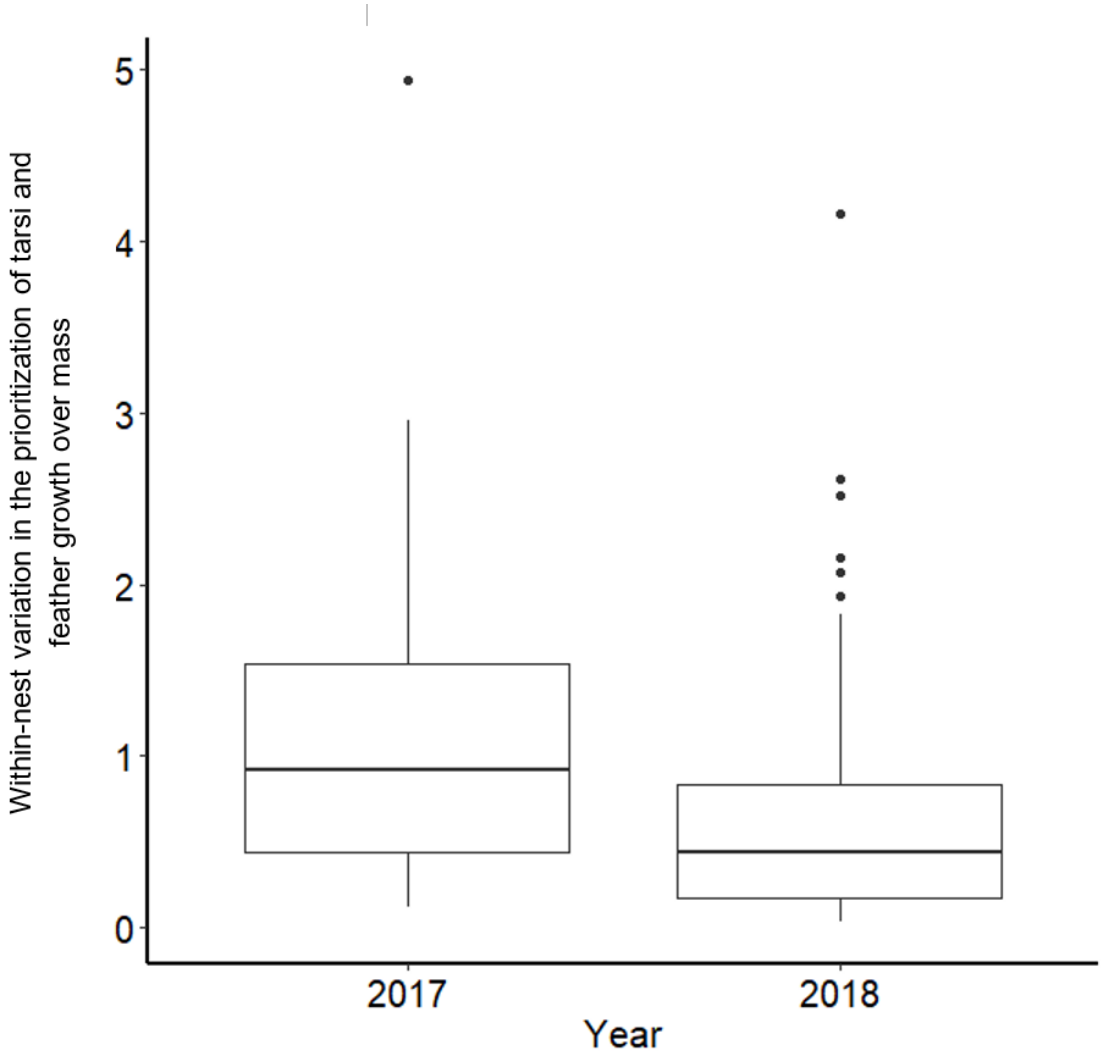

Figure 1-6. Within-nest variation in the allometric prioritization of tarsi and feather growth was 43.6% higher in 2017 than in 2018.

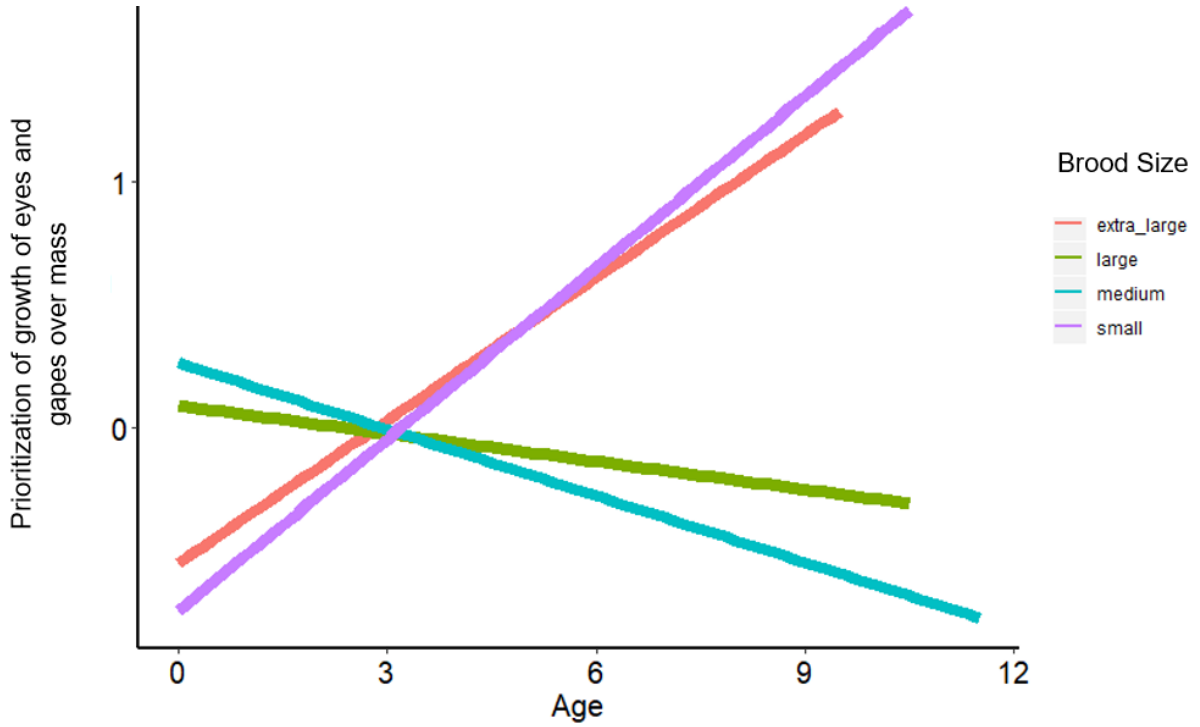

Figure 1-7. Eastern Meadowlark nestlings in the smallest (1-2; purple lines) and largest (5+ nestlings; orange lines) broods increasingly prioritized the growth of their eyes and gapes relative to nestlings in the medium-sized broods (3-4 nestlings; blue and green lines). These lines were generated with predicted values from a model that included an interaction between nestling age and the number of host nestlings (brood size).

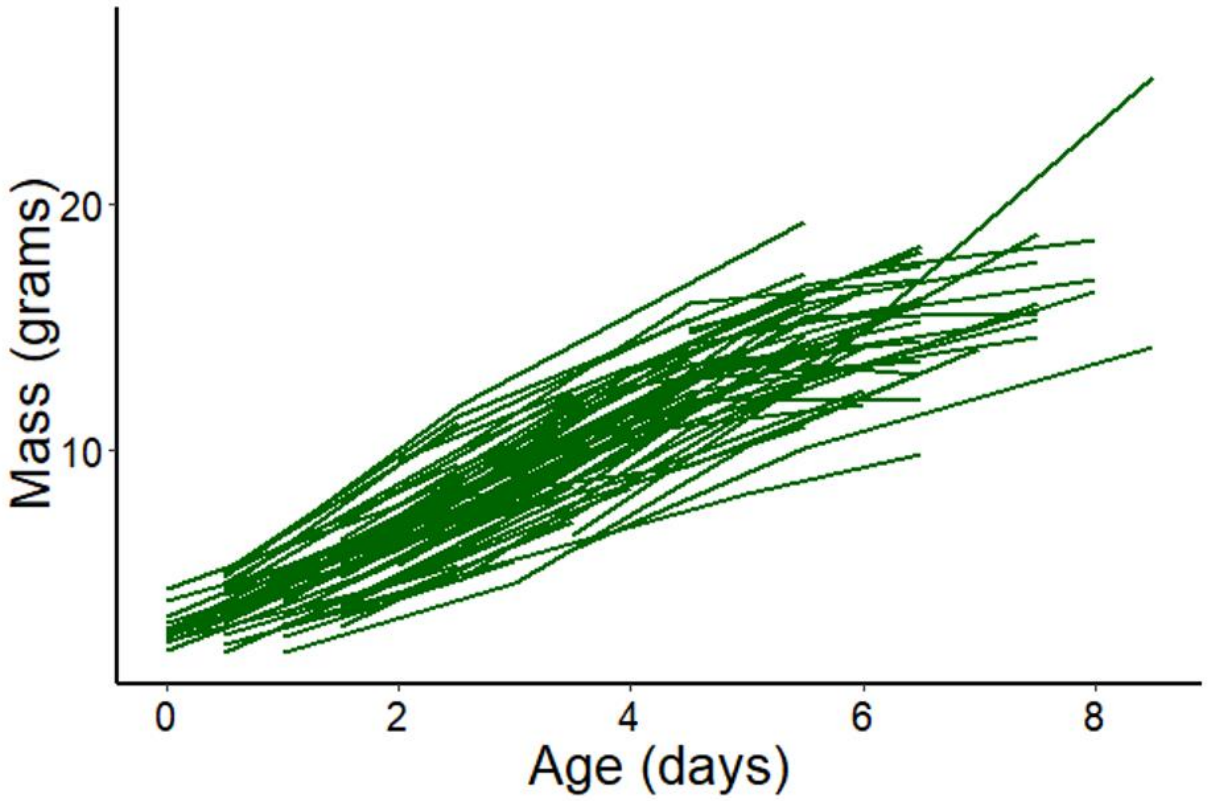

Figure 1-8. Individual Dickcissel nestlings gained mass (in grams) in a relatively linear way as they aged (in days). Lines connect the measurements of individual nestlings over time.

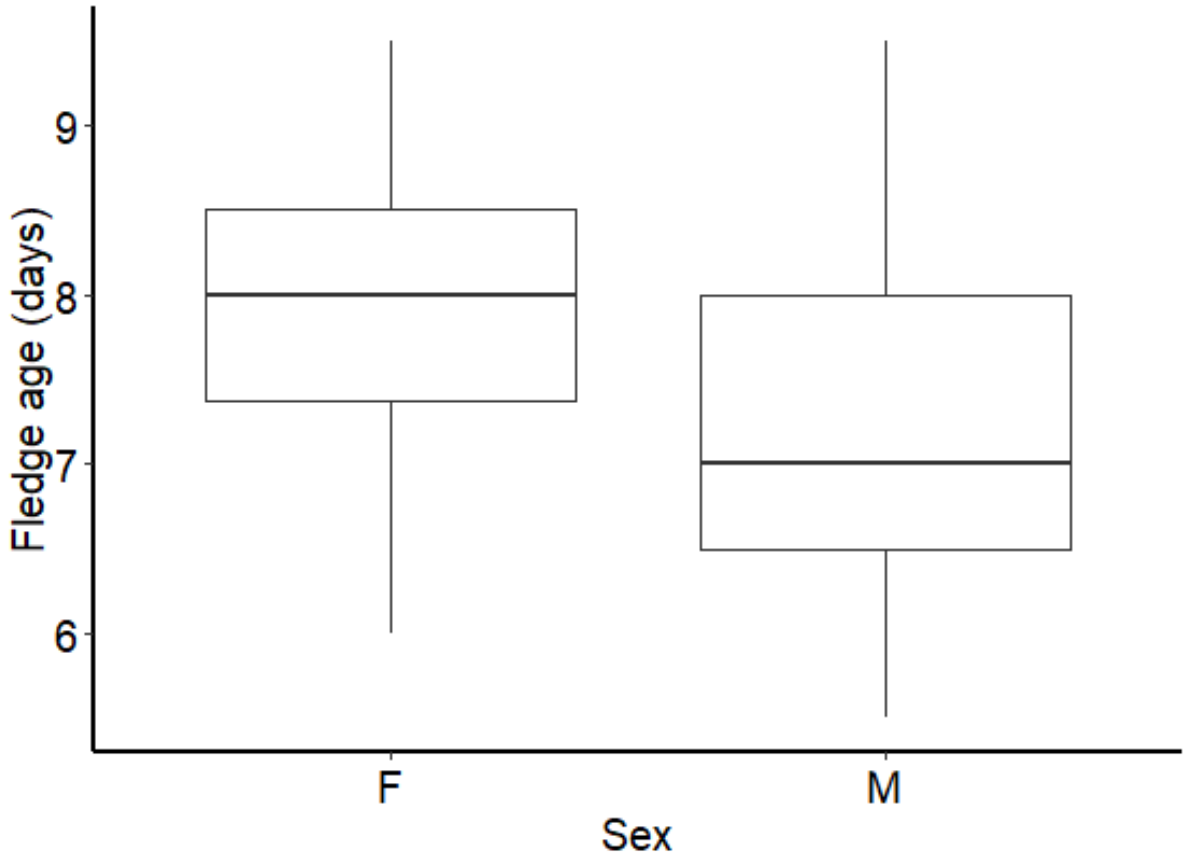

Figure 1-9. Dickcissel males fledged, on average, 0.6 days earlier than females (t_{50}=2.233, *P*=0.030).

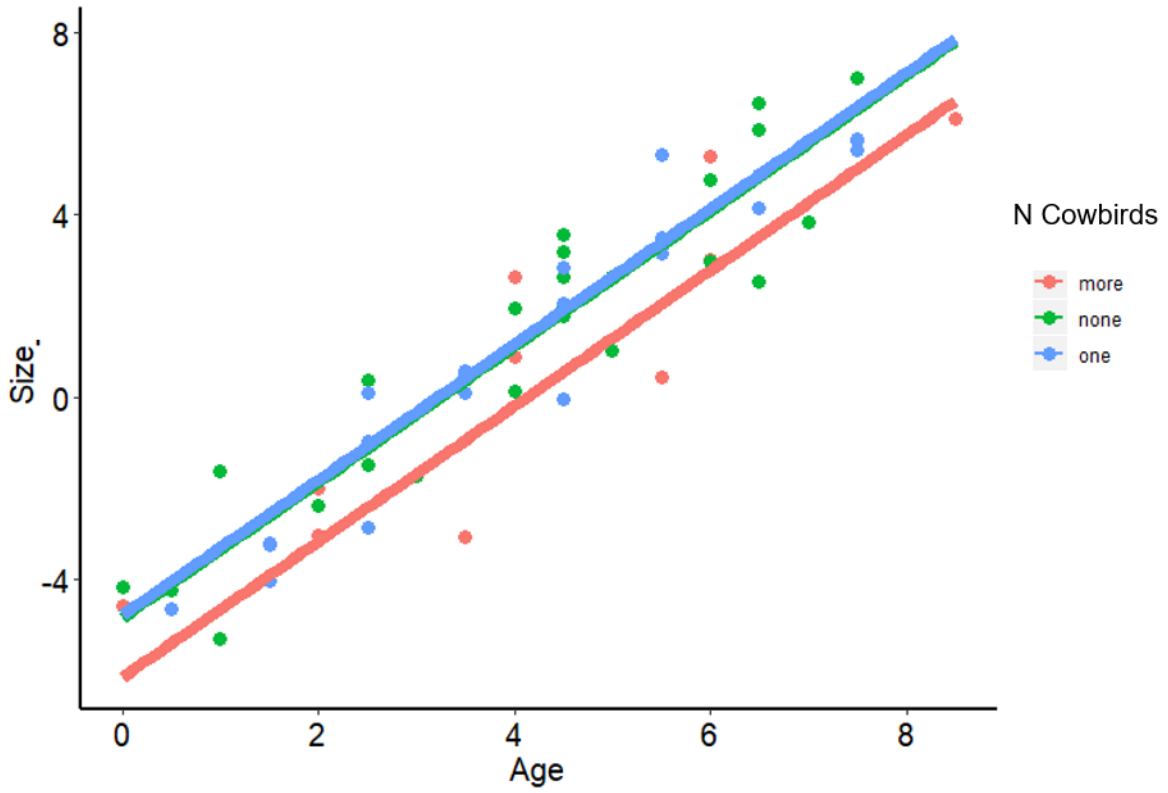

Figure 1-10. Dickcissel nestlings with zero or one cowbird brood parasite (green and blue lines) were larger than Dickcissels in nests with two or more cowbirds (orange line), although this difference accounted for only 9% of the observed range of size scores. Only female Dickcissels are graphed here. These lines were generated with predicted values from a model that included an interaction between nestling sex and age and an additive effect of the number of cowbird nestlings.

Figure 11A: Males

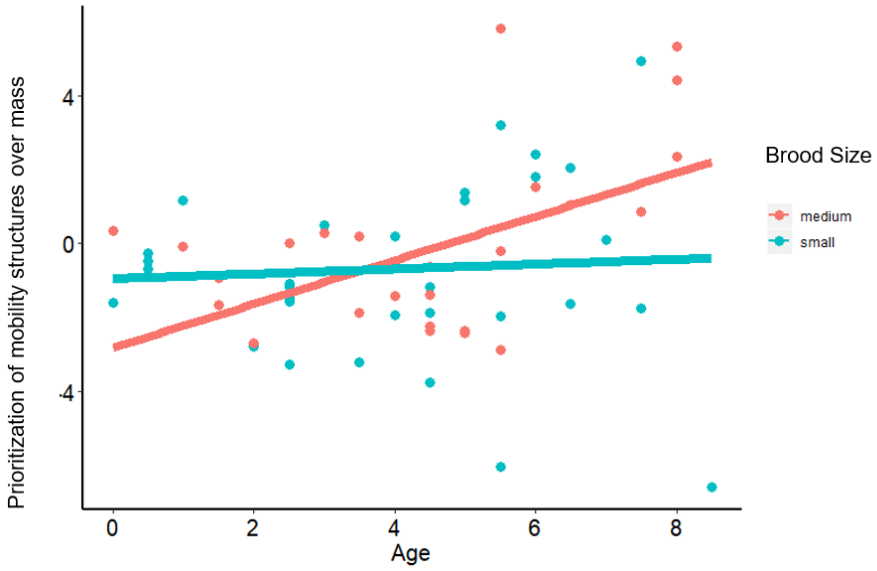

Figure 11B: Females

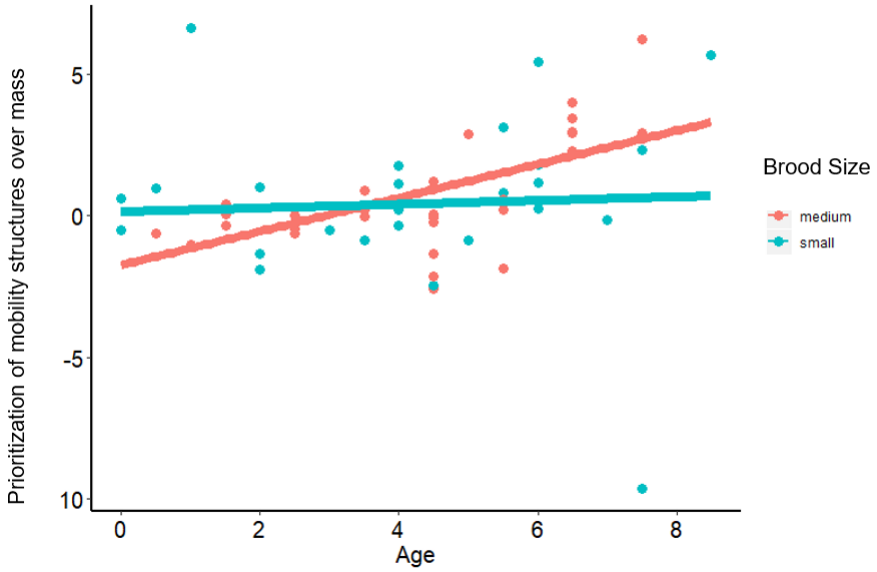

Figure 1-11. Male Dickcissels (A) grew 12.3% faster than female Dickcissel nestlings (B). Female Dickcissel nestlings prioritized the growth of their tarsi, ulna, and feathers more than male nestlings, although this difference only accounted for 6.7% of the observed variation in allometric scaling. Dickcissels in larger broods (3+ host nestlings; orange lines) increasingly prioritized the growth of their tarsi, ulna, and feathers over their mass as they aged, while Dickcissels in smaller broods (blue lines) did not. These lines were generated with predicted values from a model that included an interaction between nestling sex and age and an additive effect of the number of host nestlings (brood size).

Figure 12A.

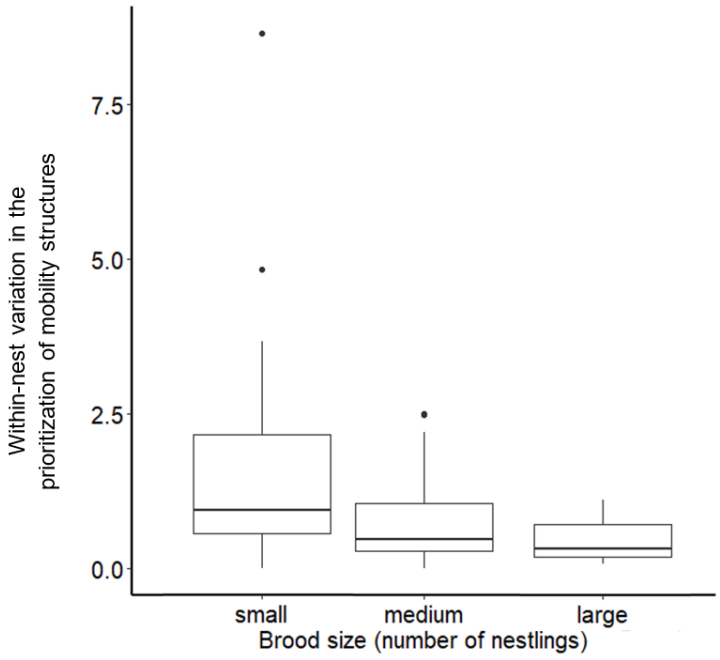

Figure 12B.

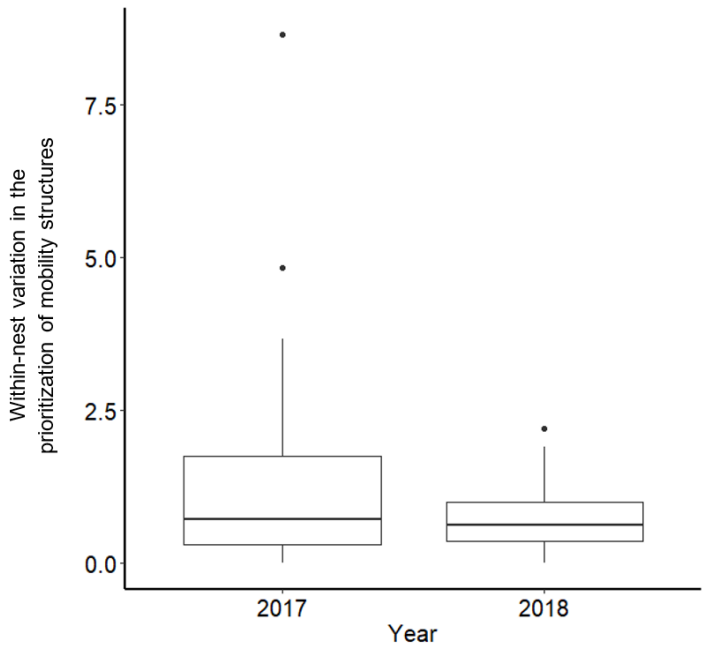

Figure 1-12. Within-nest variation in Dickcissels' prioritization of mobility structures (tarsi, ulna, and feathers) was 25% higher in small broods than in larger broods (A), and 16.7% higher in 2017 than 2018 (B).

Figure 13A

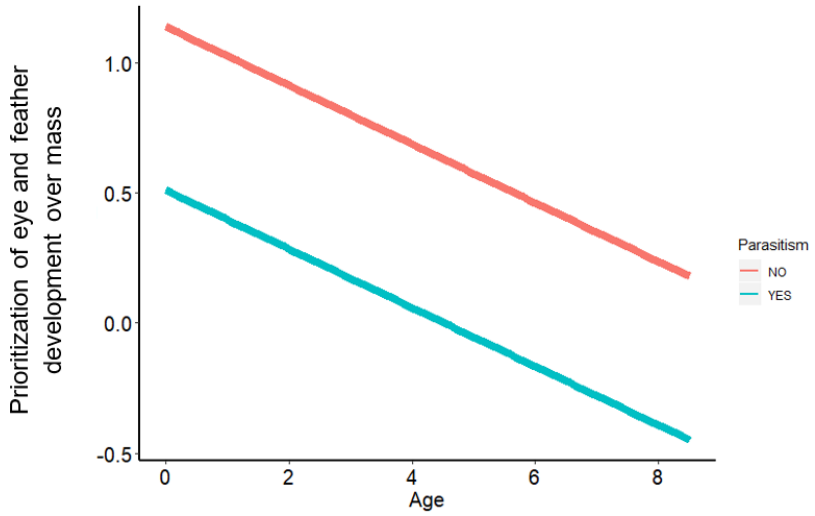

Figure 13B

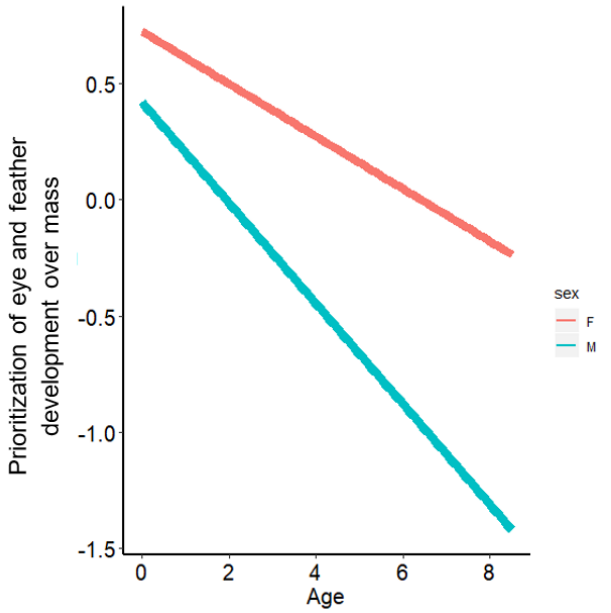

Figure 1-13. Dickcissels in (A) parasitized nests (orange line) had less developed eyes and less feather unsheathing than expected based on their mass compared to unparasitized conspecifics (blue line). (B) Females (orange line) prioritized eyes and feather unsheathing more than males (blue line) over time. These lines were generated with predicted values from a model that included an interaction between nestling sex and age and an additive effect of parasitism (Y/N).

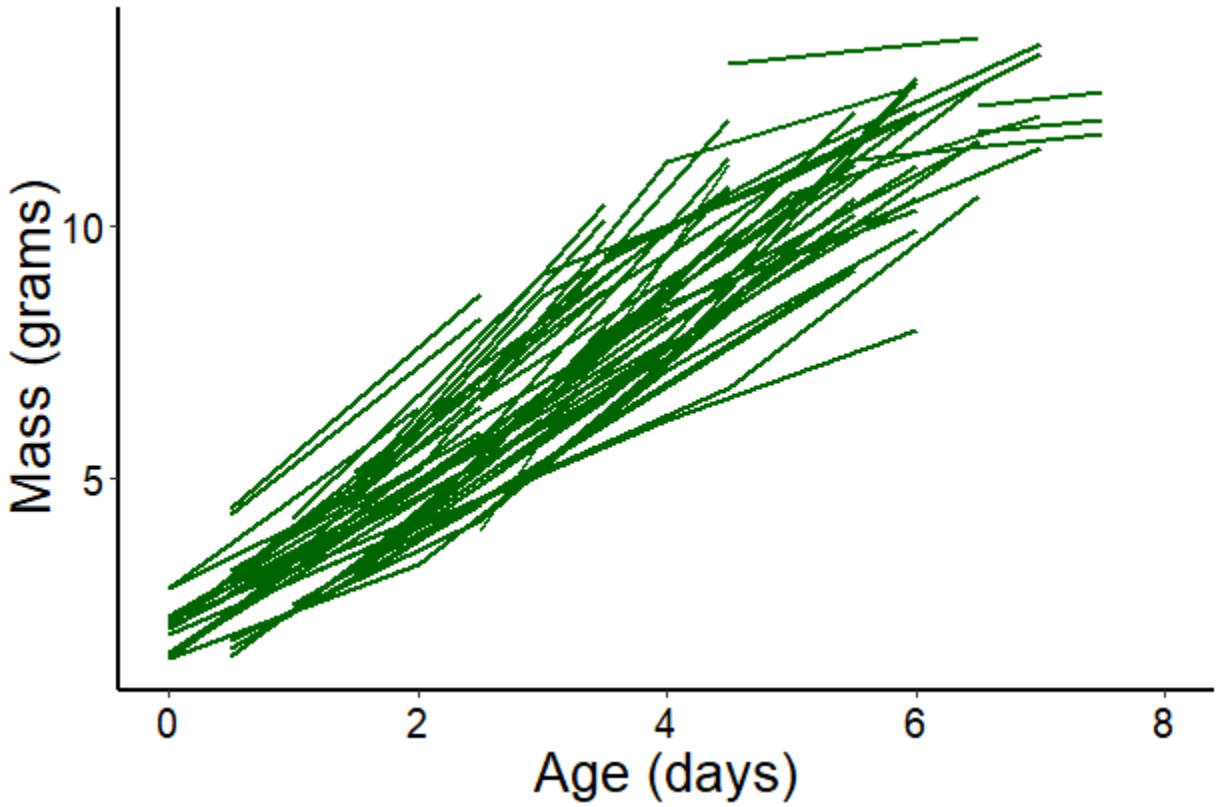

Figure 1-14. Individual Grasshopper Sparrow nestlings gained mass (in grams) in a relatively linear fashion over time (age in days). Lines connect the measurements of individual nestlings over time.

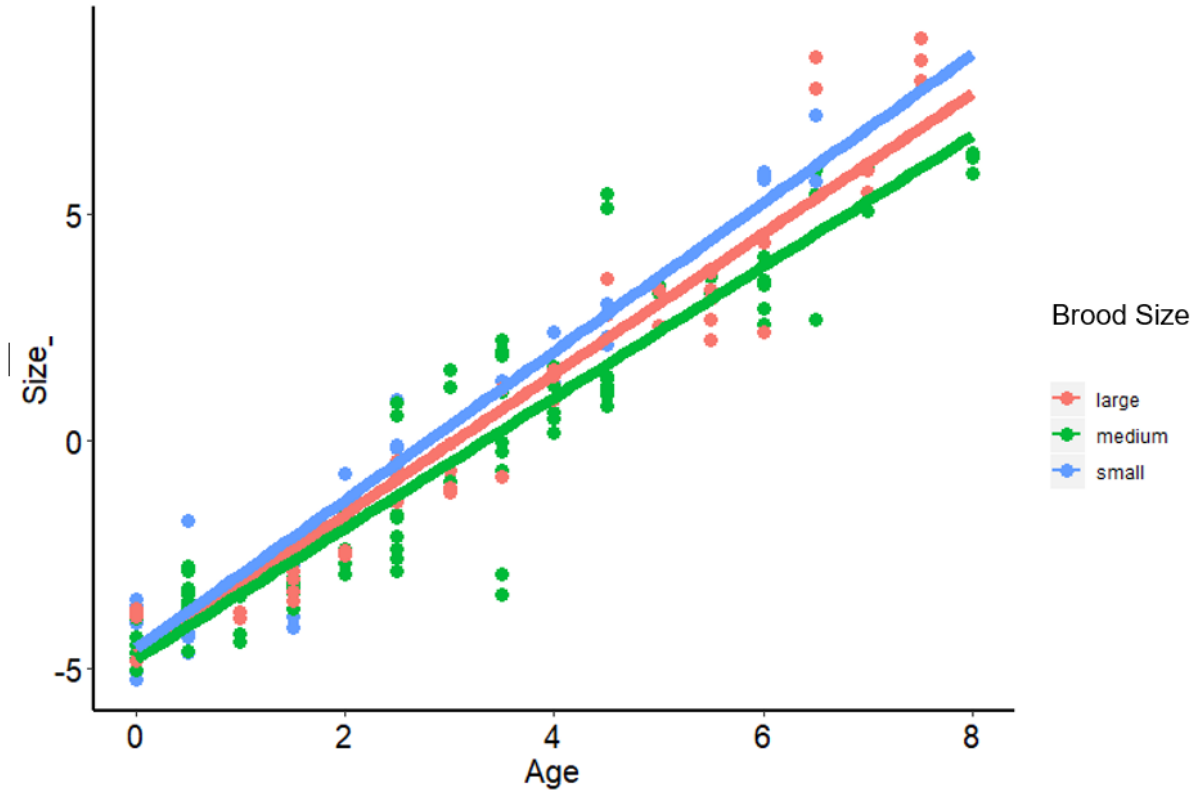

Figure 1-15. Grasshopper Sparrows in the smallest (1-2 host nestlings; blue line) and largest (4+ host nestlings; orange line) broods grew 13.7% faster than sparrows in the medium sized (3 host nestling; green line) broods. These lines were generated with predicted values from a model that included an interaction between nestling age and the number of host nestlings (brood size).

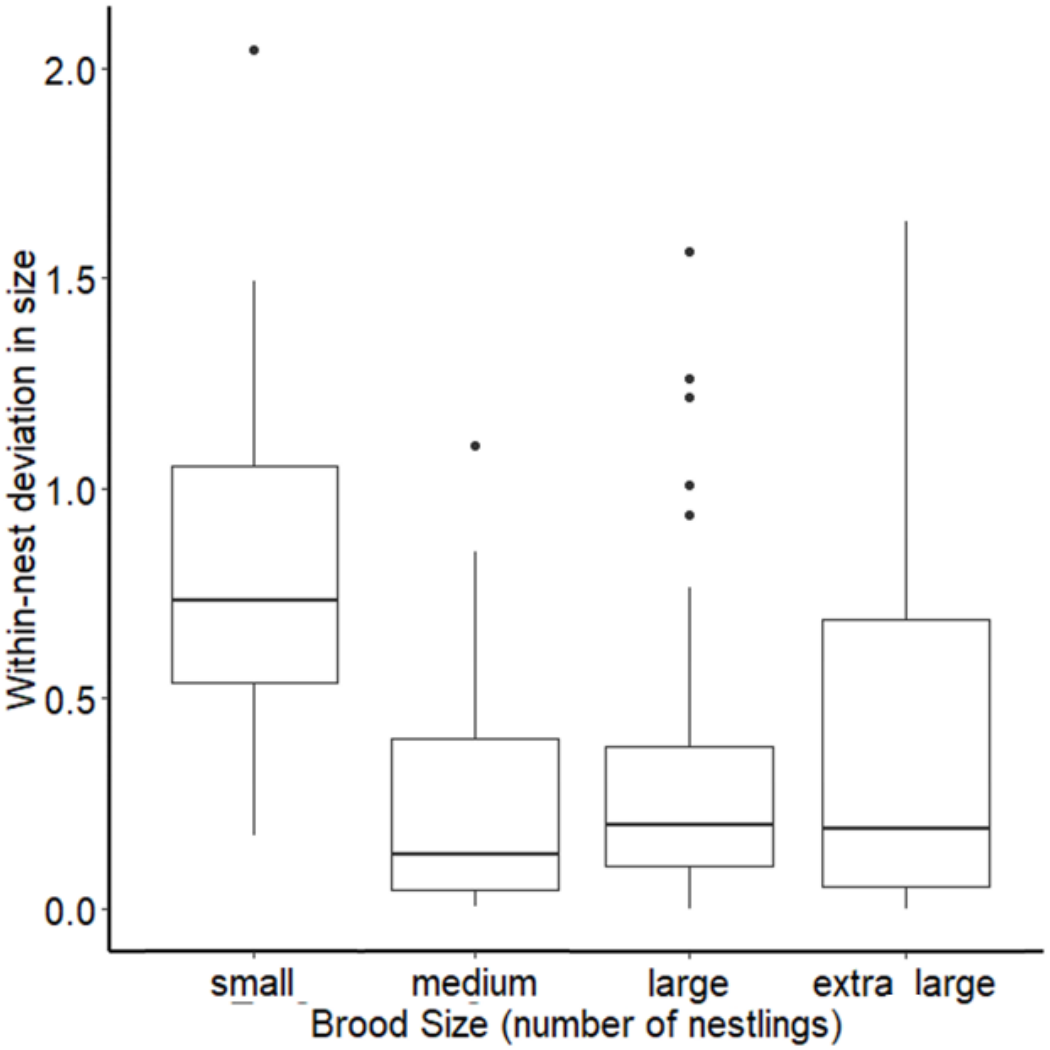

Figure 1-16. Nests with only two sparrow nestlings ("small" brood) had 122.2% higher within-nest variation in size compared to nests with more sparrow nestlings ("medium," "large," and "extra large" broods).

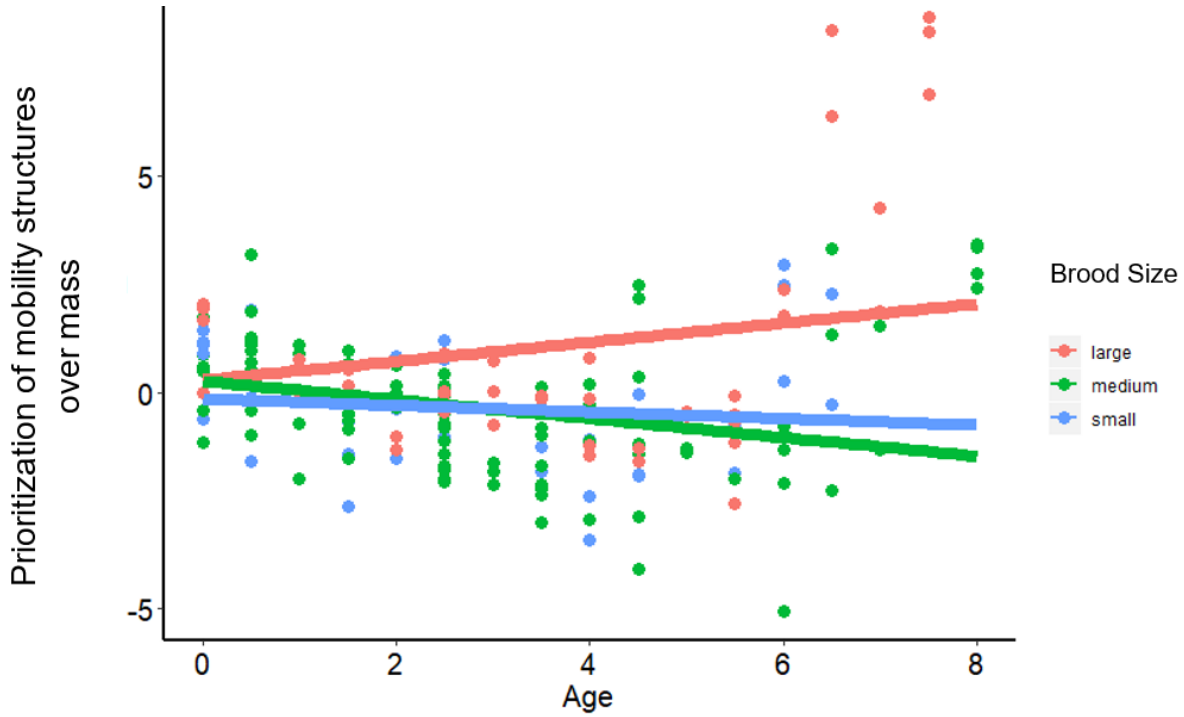

Figure 1-17. Grasshopper Sparrows in large broods (4+ host nestlings; orange line) prioritized mobility structure (ulna and flight feather) growth more than nestlings in smaller broods (blue and green lines), although this only accounted to 28.7% of the variation in observed allometric scaling. These lines were generated with predicted values from a model that included an interaction between nestling age and the number of host nestlings (brood size).

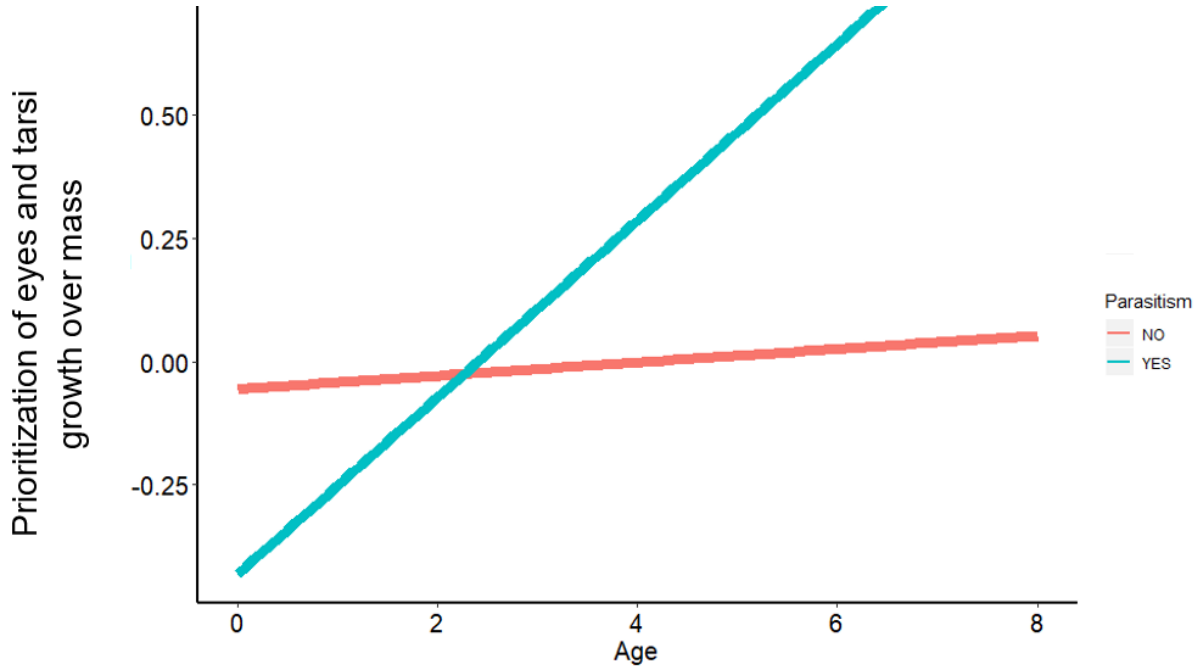

Figure 1-18. Parasitized sparrow nestlings (blue line) prioritized the growth of their eyes and tarsi relative as they aged relative to unparasitized sparrows (orange line). These lines were generated with predicted values from a model that included an interaction between nestling age and the number of host eggs and an additive effect of parasitism (Y/N).

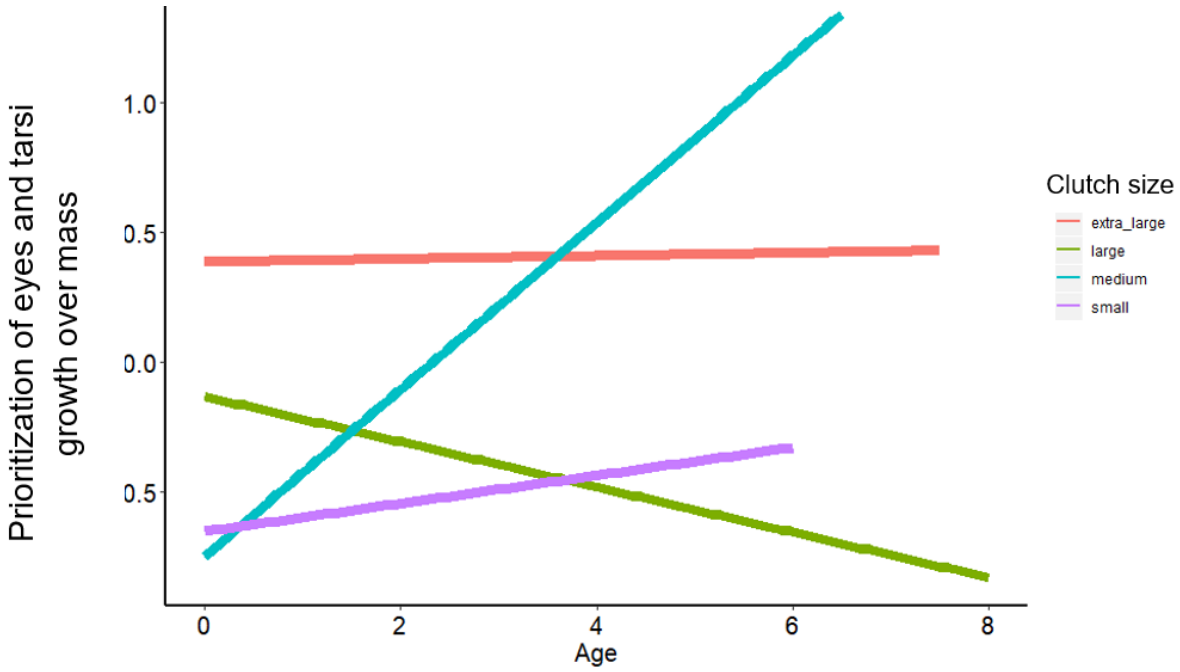

Figure 1-19. Sparrow nestlings in medium-sized broods (3 nestlings; orange line) increasing prioritized the growth of eyes and tarsi over mass as they aged, but nestlings in smaller and larger broods did not. These lines were generated with predicted values from a model that included an interaction between nestling age and the number of host eggs and an additive effect of parasitism (Y/N).

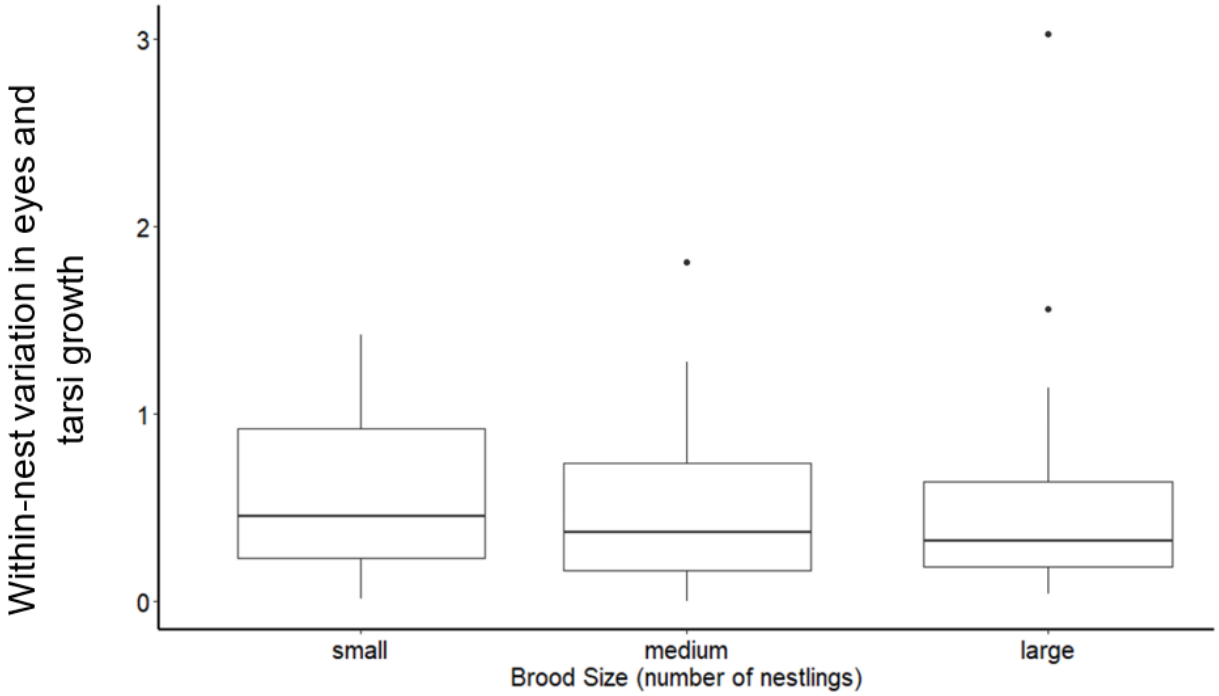

Figure 1-20. Within-nest variation in the prioritization of eye and tarsi growth was 2.5 times higher in the smallest broods compared to the larger broods of Grasshopper Sparrows.

Chapter 2 - Indirect effects of cowbirds on growth

Brown-headed Cowbird (*Molothrus ater*) nestlings do not affect host nestling growth and development through indirect effects on provisioning rate or predation risk

Abstract

Wild animals must cope with environmental stressors and can do so by altering their growth rates and the amount of energy that they allocate to the development of different body parts. While we understand the relationships between individual drivers and variation in growth and development, it is not always clear how animals manage to respond to multiple conflicting drivers simultaneously. I quantified the growth of grassland songbird nestlings in nests with and without Brown-headed Cowbird (*Molothrus ater*) brood parasites to test hypotheses regarding the consequences of cowbird parasitism for nestling development—both directly, as a result of nestling competition for food, and indirectly, by interacting with predation risk and provisioning rates at the nest. Over two summers, I measured 264 host nestlings from three species—Eastern Meadowlarks (*Sturnella magna*), Dickcissels (*Spiza americana*), and Grasshopper Sparrows (*Ammodramus savannarum*). The hosts experienced high parasitism (~48% overall) and high predation (~80%) rates, and exhibited substantial variation in growth rates, such that some nestlings fledged weighing twice as much as conspecifics of the same age. Using nest cameras, I documented >3400 parental provisioning visits during >1,000 hours of nest camera footage. Adult sparrows with more cowbirds in the nest increased their *per capita* provisioning rate, but this increase was not related to variation in sparrow development. The number of cowbirds in the nest did not influence the provisioning rates of the large meadowlarks or the medium-sized Dickcissels, nor the predation risk of any species. Parasitized meadowlarks prioritized mass gain

over the growth of wings or tarsi, perhaps in response to competition with cowbirds, and left the nests days earlier than did unparasitized conspecifics. Parasitized Dickcissels prioritized mass gain over the growth of their tarsus but fledged at the same age. Development of Grasshopper Sparrows did not vary among parasitized and unparasitized nests, perhaps because parents compensate for the presence of cowbirds by increasing provisioning rates. These results illustrate three different ways that host species accommodate parasite nestlings and suggest that other environmental drivers such as predation risk may exert stronger selection on nestling growth in this system. Developing birds respond to multiple conflicting environmental stressors by variation in allometric scaling, ultimately exhibiting substantial intraspecific variation in growth and development as a response to environmental drivers at the nest microsite level.

Introduction

Animals face a variety of environmental stressors, such as restrictions in food availability (Krause et al. 2017), inclement weather, or the risk of predation (Martin and Briskie 2009). They can respond to these stressors in different ways, like changing behavior to avoid or mitigate a stressor (Dmitriew 2011) or changing their phenotype to prioritize different traits (Welberg and Seckl 2001). The ability to adjust to environmental conditions is particularly advantageous during early offspring growth and development, as plasticity in growth rates and the development of bodily structures can allow individuals to adjust to their natal environment (Schew and Ricklefs 1998, Maestripieri 2011), increasing their likelihood of current and future survival (Mousseau and Fox 1998, Snell-Rood 2012). Connecting the variation in environmental drivers to variation in growth and development provides an opportunity to not only identify the

stressors currently affecting a population, but also to assess individuals' abilities to cope with those stressors (Sheriff and Love 2013).

Birds have long been used to understand the relationships between the environment and life history (Lindstrom 1999, Chaby 2016). Growth rates vary dramatically between different groups of birds (Starck and Ricklefs 1998), making them exceptional models with which to study the effects of environmental drivers on development. Variation in food availability, predation risk, and competition with conspecific and heterospecific nestmates affects development among families, species, and even individuals (Badyaev and Martin 2000, McCarty 2001). However, these drivers do not exist in isolation; developing birds may experience predation and competition for food simultaneously, yet little is known about the combined and interactive effects of these and other drivers of developmental strategies. To understand how animals may respond to both a direct environmental stressor and its influence on other drivers of growth and development variation, I assessed the direct relationships between competition with heterospecific brood parasites and songbird nestling growth and development, and the indirect effects of parasitism on growth through interactions with food availability and predation risk.

Birds' growth and development is directly affected by food availability; developing birds faced with food restriction may suffer lower body condition (Schoech 1996), slower growth rates (Talloen et al. 2008), and lower survival (Mock et al. 2009). Since altricial birds receive all their food from adults (Kilner and Johnstone 1997, Wright and Leonard 2007), parental decisions can influence nestling development (Deeming 2002) and survival (Hõrak 2003). Nestlings compete for parental attention, soliciting care by begging (Wright and Leonard 2002). Nestlings can adjust to high-competition environments by growing faster to compete with their siblings (Werschkul and Jackson 1979) or prioritizing the components of growth that enhance

competitive abilities such as longer legs that allow them to reach higher to solicit food (Oddie 2000) or larger gapes (Gil et al. 2008). As birds' variation in growth and development may be primarily driven by competition for food, we hypothesized that *provisioning rate* would influence growth rates and/or the allometric scaling in favor of competitive body features, especially in nests with more competitive offspring (Pap and Márkus 2003) or limited access to food.

In addition to competition for food, variation in bird growth and development can also be a product of variation in predation risk (Martin and Briskie 2009). Nest predation is the primary driver of breeding failure in birds (Martin 1995). Because traveling to the nest may attract visual predators (Martin et al. 2000), parents can choose to minimize risk by reducing provisioning rates (Ghalambor et al. 2013) thereby slowing nestling growth (Talloen et al. 2009). Alternatively, predation risk may shift the way that nestlings allocate energy to anatomical structures, favoring the growth of the body parts such as wings that increase their ability to escape (Coslovsky and Richner 2011). Therefore, we hypothesized that *predation risk* may also influence nestling growth rates or the allometric scaling of body parts related to escape ability.

Heterospecific brood parasitism presents a useful system in which to address questions about the effects of direct competition and interactions with other external drivers on nestling growth and development. Obligate brood parasites lay their eggs in other species' nests, forcing host parents to care for their developing offspring (Rothstein 1990, Davies 2000). This care is costly to parents and young (Rothstein and Robinson 1998, Peer and Sealy 2004). Some host species have evolved strategies to prevent parasitism, such as choosing and defending safe nest sites (Trnka et al. 2012) or abandoning parasitized nests and starting over (Guigueno and Sealy 2011). Other species raise the parasites with their own offspring, often with direct consequences

for the offspring's growth and development; nestlings are sometimes outcompeted for food, suffer decreased growth rates and increased mortality (Davies et al. 1998, Tanaka and Ueda 2005) or adjust their allometry to prioritize the growth of competitive features like gapes. Yet despite the clear cost of direct *nestling competition* with brood parasites, few studies have found evidence for effects of this hypothesized driver of variation in nestling growth and development (Weatherhead 1989, Kozlovic 1998), suggesting that the direct consequences of brood parasitism be complicated by the indirect interactions between brood parasitism and other environmental drivers of growth and development.

The presence of brood parasites can directly affect the provisioning behavior of adult birds, thereby interacting with the hypothesized *provisioning rate* driver of growth and development variation. Host siblings should reduce their begging when satiated because of kin selection (Mock and Parker 1998); brood parasites, free of this constraint, often beg louder and more frequently than do host young (Holen et al. 2001, Glassey and Forbes 2003). When parasite nestlings are present, parents may increase provisioning rates (Kilner et al. 2004) and exhibit an increase in biparental care (Grayson et al. 2013). Increased parental care may benefit host young as well, especially if parents preferentially feed their own young over the parasites (Grim and Honza 1997). Thus, paradoxically, host nestlings grow as fast or faster in parasitized nests than unparasitized nests due to increased adult provisioning, shifting costs from nestling to parents.

Brood parasitism can also increase *predation risk* at the nests. Parasites can directly increase predation risk when their loud and frequent begging draws predators to the nest (Dearborn 1998, Haskell 2002, McDonald et al. 2009). Furthermore, parasites commonly act as nest predators (Benson et al. 2010, Rodewald and Kearns 2011), removing and eating host eggs (Scott et al. 1992, Granfors et al. 2001) and killing nestlings (Stake and Cavanagh 2001, Igl

2003). As predation by brood parasitic species may be more consequential for nest success than nestling competition (Whitehead et al. 2000), it stands to reason that the indirect effects of parasitism on predation risk could be more influential than competition on host development.

I determined the relationships between provisioning risk, predation risk, direct competition with brood parasites, and nestling development in hosts of the Brown-headed Cowbird (*Molothrus ater*), a generalist brood parasite native to central North America (Lowther 1993). As the host study species—Eastern Meadowlarks (*Sturnella magna*), Dickcissels (*Spiza americana*), and Grasshopper Sparrows (*Ammodramus savannarum*)—are species of conservation concern, understanding the ways their nestlings respond to environmental stressors may be particularly informative (Peterjohn and Sauer 1999, Faaborg 2002, Sauer et al. 2011). In the Flint Hills of NE Kansas, USA, these species experience particularly high rates of brood parasitism (Igl and Johnson 2007) and nest predation, making this an ideal location at which to understand the interactions of these drivers.

I hypothesized that cowbird parasitism would affect host nestling growth and development indirectly by affecting (1) *provisioning rate* or (2) *predation risk*, or directly by increasing (3) *nestling competition*. If the presence of cowbird nestlings interacted with the (1) *provisioning rate* I expected nests with cowbirds would (i) receive higher *per capita* provisioning rates (visits/hour/nestling) and consequently have nestlings with (ii) higher masses and/or (iii) reduced prioritization of competitive body parts (tarsi) compared to host nestlings in nests with no cowbird parasites. If the presence of cowbird nestlings interacted with the (2) *predation risk*, I expected nests with cowbirds would (iv) suffer higher predation rates than nests without cowbirds and/or (v) be located in areas of higher predation risk than nests with cowbirds, resulting in host nestlings which (vi) prioritize the growth of mobility-enhancing structures

(wings) more than nestlings in nests without any cowbirds. Finally, if the presence of cowbirds increases (3) *nestling competition* I expected that (vii) host nestlings would gain mass more slowly and/or (viii) prioritize the growth of competitive body parts (tarsi) more than conspecifics without cowbird parasites. I expected these direct effects to be (ix) dependent on the size of the hosts, with the hosts smaller than the cowbirds experiencing the largest effects of competition. I measured the growth of parasitized and non-parasitized nestlings of three host species and tested predictions of these hypotheses (Figure 2-1) using species-specific multilevel structural equation models.

Methods

I studied the effect of cowbirds on the growth of host species at two tallgrass prairie sites in Northeast Kansas, United States. Konza Prairie Biological Station (KPBS; 39.107, -96.609) is a 3,487 ha experimental landscape owned by the Nature Conservancy and managed by Kansas State University. Konza is divided into replicated experimental watersheds managed with different combinations of fire frequencies (every 1, 2, 3, 4, or 20 years) and grazing regimes (bison, cattle, or no large herbivores) (Knapp and Seastedt 1998). I worked on sixteen units at Konza that support large numbers of the focal host species (Powell and Busby 2013). I also worked on the adjacent Rannell's Preserve, a 1,175 ha tallgrass prairie site owned by Kansas State University. Rannell's Preserve is managed with higher cattle stocking densities and burned every year (Owensby et al. 2008). Hereafter I referred to both sites as "Konza."

Brown-headed Cowbirds (*Molothrus ater*) are medium-sized (42–50 g) passerines (Kilner 2003) and generalist brood parasites (Lowther 1993) of over 220 host species (Friedmann and Kiff 1985, Ortega 1998). At Konza, cowbirds parasitize at least 20 species

(Rivers et al. 2010) at species-specific parasitism rates as high as 85% (Zimmerman 1983). It has been speculated that this species can regulate host population growth (Jewell and Arcese 2008), so understanding the impact of cowbirds may be important for both evolutionary studies and conservation efforts.

Eastern Meadowlarks (*Sturnella magna*) are large (90–150 g) grassland-obligate passerines from north-central North America (Lanyon 1995). They build large domed nests on the ground in tallgrass prairies, raising one or two broods over the course of a summer (Lanyon 1995). Meadowlarks are much larger than cowbirds and thought to be a poor host (Strausberger and Ashley 1997) yet raise cowbirds in as many as 70% of nests (Elliot 1978). Meadowlarks experience lower predation rates than the other study species, with nest success rates as high as 30% (Klug and Jackrel 2010). This success may be due to the concealment of nests or because their nestlings quickly grow to sizes too large for common, small-mouthed nest predators to consume (Davison and Bollinger 2000). Meadowlark populations have declined rapidly over the last half-century and are of international conservation concern (North American Bird Conservation Initiative 2016).

Dickcissels (*Spiza americana*) are grassland and shrubland passerines approximately the same size as their cowbird parasites (23–29g) (Temple 2002). They build open-cup nests suspended in vegetation, approximately one meter or less off the ground (Temple 2002). Dickcissels are frequently parasitized at Konza and across their range, with parasitism frequencies as high as 95% (Elliot 1978). High parasitism may be due to their conspicuous nests and blue eggs (Yahner and DeLong 1992). Dickcissels also experience high predation rates, with nest success as low as 14% (Patterson and Best 1996); their populations are declining by as much as 1.2% per year (Sauer et al. 2011).

Grasshopper Sparrows (*Ammodramus savannarum*) are small (14–20g) grassland-obligate passerines (Vickery 1996). They build small domed grass nests on the ground (Vickery 1996). Although Grasshopper Sparrows are not commonly parasitized across most of their range (Ruth 2017), they are typically parasitized more frequently than are meadowlarks (Patten et al. 2006), with parasitism rates as high as 50% in this region (Rivers et al. 2010). Grasshopper Sparrows are experiencing range-wide declines (Sauer et al. 2011), some of which may be related to cowbird parasitism (Hovick and Miller 2013).

Finding nests and measuring nestlings

Field crews located nests by incidentally flushing birds while walking through the prairie, by following adult birds carrying food, and by systematically dragging a 30-m rope across the prairie to flush incubating and brooding females. The nest location was recorded with a handheld GPS unit (Garmin, Olathe, KS, USA) and its position marked by placing a painted rock and a pin-flag five meters from the nest opening. Crews returned every 2–3 days until the eggs hatched, noting the number of cowbird and host eggs in the nest. Once the nestlings hatched, I selected ~60% of nests for intensive nestling measurements and placed nest cameras (see below) at a subset of those nests. I monitored all nests until the nestlings fledged, died, or disappeared. If the nestlings disappeared before the average species-specific fledge age for the site (6 days old for Dickcissels and Grasshopper Sparrows, 10 days old for meadowlarks with hatch day counted as "0") I assumed that they had been depredated, recording instances of partial and complete nest predation. I coded the nestlings as having successfully fledged if they disappeared after the average fledge age, the nest cup was not destroyed, and parents were seen nearby with food. If

the nestlings survived to 5 days old for Dickcissels and Grasshopper Sparrows or 9 days old for meadowlarks, I banded them with a U.S. Fish and Wildlife Service numbered, aluminum band.

I performed intensive nestling measurements at ~60% of the nestling-stage nests. At each nest I selected two host offspring, attempting to not bias the sample by picking nestlings with any particular attribute. I marked the legs of the nestlings with non-toxic permanent marker (Newell Brands, Hoboken, NJ, USA) for individual recognition (Weatherhead 1989). I measured the length of the nestling's right tarsus using calipers. I placed a gridded notecard underneath the nestling's right wing and took a digital image. I weighed each nestling using a small digital scale accurate ±0.001g and returned the nestlings to the nests. I used ImageJ (Schneider et al. 2012) to calculate the length of the ulna bone, the carpometacarpus, the outermost primary feather shaft (P9), the outermost secondary feather shaft (S1), and the unsheathed portion of those feathers from digital photos.

Measuring provisioning and predation risk

I monitored nests using small security cameras (950 nm, Model ENC-100, EZ Spy Cam, Los Angeles, CA) mounted on a tent stake and camouflaged using locally-collected plants and camo-patterned duct tape. I placed the camera approximately 5-10 cm from the nest cup and attached it to a 100 ft siamese coaxial cable, which I buried underground using small garden knives and trowels to disturb the vegetation as little as possible. The cable connected to two 12-volt batteries (Power-Sonic PS-1270-F2, 12V 7Ah Sealed Lead Acid Battery, Power-Sonic, San Diego, CA, USA) and a small DVR (NY-P0122 Portable Mini DVR SecuMate SD Slot AV Recorder, SecuPlus, Gravenpolder, Netherlands) placed inside a waterproof container at least 20m from the nest cup. I recorded 24-hour footage on 16GB SD cards and stored the videos on

external hard drives. In 2017 I watched videos using VLC media player (VideoLAN), recording the identity of the nest visitor and any events that occurred at the nest throughout the entire nesting period from camera set-up to nest completion. In 2018 I used the program DeepMeerkat (Weinstein 2018) to extract the still frames in which motion occurred and quantified activity at the nest from the extracted frames. I identified the predators to species whenever possible, consulting taxonomic experts when identification was ambiguous. I calculated N visits/hour by summing all probable provisioning events when the nestlings were 4 days old, and divided that number by the N hours of footage/nest on that day. I then divided the N visits/hour by the number of nestlings to calculate a *per capita* provisioning rate as a measure of visits/nestling/hour.

Using the R (R Core Team 2013) package *RMark* (Laake 2013) I modeled nest success as a function of combinations of the following factors: year, species, and time of year using maximum-likelihood and a logit-link approach (Dinsmore et al. 2002). I compared candidate models against a constant model based on AICc scores. I interpreted the results of the top model and checked the effect of nest cameras by comparing the top model against the same set of factors with the addition of camera status (yes or no).

I measured predation directly by recording disappearance of nestlings prior to fledging. In addition, I wanted to quantify the perceived risk of predation that the birds would be experiencing when allocating resources to clutches and broods, so I estimated the density of depredated nests (including partially and completely depredated nests) at a given nest microsite using kernel density estimators. Using arcMap (ESRI, Redlands, CA, USA) I mapped the location of all nests that experienced partial or complete brood loss due to predation. I used the kernel density estimator to generate maps for each year with the density of depredated nests in

nests/hectare. I overlaid the location of all nests onto each map and extracted the density at each point, generating a value for perceived predation risk in depredated nests/hectare.

Analyses

I created species-specific multilevel longitudinal structural equation models to estimate the relationships between provisioning rate, parasitism, predation risk, and their interactions on nestling growth and development; multilevel because we took measurements of environmental drivers at the nest level and measurements of growth at the individual nestling level, and longitudinal because we measured growth over time. For each measure of nestling growth (see below) I created a species-specific model including the effect of the number of cowbird nestlings on predation risk and brood size, and the effect of the number of cowbird nestlings, predation risk, and brood size on nestling growth. Because I did not have provisioning data for all nestlings, I created a second set of models that, in addition to the previously assessed pathways, also included the effect of the number of cowbird nestlings and brood size on provisioning rate, and the effect of provisioning rate on nestling growth. I ran these models on a restricted dataset that only included the nests for which we had provisioning data. I ran all models with the random effect of NestID to account for the multilevel structure and the random effect of NestlingID to account for the repeated measures of individual nestlings. I included the interactive effect of age with all of the drivers to determine how growth and development change over time, and ran all the models using the packages *nlme* (Pinheiro et al. 2019), *lme4* (Bates et al. 2015), and *piecewiseSEM* (Lefcheck 2016).

To examine the effects of direct and indirect effects of cowbirds on the overall size of nestlings, I modeled mass gain over time, using each of the measurements instead of an overall

change over time metric in order to include nestlings measured only once. To determine what influenced the allometry of competitive structures, I divided tarsus length by mass and quantified the effect of the hypothesized drivers on this mass-corrected tarsus value. To determine what influenced the allometry of mobility-enhancing structures, I scaled the length of the wing bone and feather measurements to overall body size by dividing each measurement by nestling mass. I conducted a correlation matrix principal components analysis on mass-corrected wing measurements that resulted in two axes of variation that described >60% of the variance. I used these two PC scores as response variables in the models.

In addition to structural equation models, I examined the relationships between rates of mass gain, allometry (change in mass-corrected tarsus or PCA wing values over time), the number of cowbirds in the nest, and the *per capita* provisioning rate on nestling fledge age and the success of the nest. I modeled these relationships using linear mixed models to account for the random effect of NestID. I graphed all results in *ggplot2* (Wickham 2016).

Results

In 2017 and 2018, I found 284 nests (87 Eastern Meadowlark, 141 Dickcissel, and 115 Grasshopper Sparrow), of which 202 survived to the nestling stage. Nest parasitism varied among species; 25.2% of meadowlark nests, 65.5% of Dickcissel nests, and 34.1% of sparrow nests contained at least one cowbird egg. Many nests were parasitized with multiple eggs; eight of the 20 (40%) parasitized meadowlark nests contained more than one cowbird egg (max: 4 eggs), 53 of the 89 (60%) parasitized Dickcissel nests were multiply parasitized (max: 5 eggs), and 24 of the 40 (60%) parasitized sparrow nests were multiply parasitized (max: 5 eggs). Across all nests found, meadowlark nests contained an average of 1.5 cowbird eggs, Dickcissel nests

contained 2.0 cowbird eggs, and sparrow nests contained 1.8 cowbird eggs. The total number of nestlings in the nest (hosts and cowbird combined) was positively related to the number of cowbirds that hatched in the nest across all host species ($F_{3, 336}$=32.5, P<0.001); the total number of nestlings increased with the number of cowbird nestlings (Figure 2-2A). However, the total number of nestlings was not related to the number of cowbird eggs that were laid in the nest ($F_{5,334}$=1.7, P=0.136); increasing numbers of cowbird eggs did not increase the number of nestlings that eventually hatched (Figure 2-2B). Nest success was not affected by the number of cowbird nestlings (t_{195}=-0.4, P=0.676) or cowbird eggs (t_{268}=0.9, P=0.344).

I measured 86 nestlings in 48 meadowlark nests, 98 nestlings in 58 Dickcissel nests, and 80 nestlings in 44 sparrow nests 802 times total, averaging 2.7 measurements per nestling (range:1-5). Nest visits did not negatively affect survival rates; nests at which I took time series of nestling measurements were more likely to survive than those that I left as controls (Chapter 1). I video-recorded parental behavior at 61 nests (27 meadowlark nests, 21 Dickcissel nests, and 18 sparrow nests), recording 6,237 hours total. Nests with cameras were less likely to be depredated than nests without cameras (Table S2-1). Limiting the provisioning analysis to day 4 restricted the sample size to 43 nests: 21 meadowlark nests (4 parasitized), 14 Dickcissel nests (9 parasitized), and 8 sparrow nests (2 parasitized). I analyzed 1,255 meadowlark provisioning visits over 480 recorded hours, 1,355 Dickcissel provisioning visits over 342 hours, and 804 sparrow visits over 201 hours. Across all species, nests with more nestlings of any species (larger brood sizes) received more provisioning visits per hour, such that nests with five nestlings were visited twice as often as nests with only two nestlings (t_{41}=3.2, P=0.003, Figure 2-3A). After correcting visits/hour metric for the number of nestlings, nests with more nestlings (larger brood sizes) received fewer *per capita* provisioning visits (visits/nestling/hour), such that nests with

five nestlings received ~30% fewer provisioning visits than nests with two nestlings (t_{41}=2.7, *P*=0.010, Figure 2-3B).

By day 2 some individuals were already double the mass of conspecifics, despite hatching at similar masses (Figure 2-4). This resulted in substantial variation by the end of the brood period; for instance, meadowlarks at day 10 weighed as little as 22 grams or as much as 55 grams (Figure 2-5). As tarsus length and mass were correlated, tarsus lengths were similarly variable, with some individuals as much as 40% larger than their conspecifics by fledge age (Figure 2-6).

Meadowlark mass gain over time was positively related to predation risk; nestlings in areas with more depredated nests nearby gained mass more quickly than nestlings in safer nests (overall SEM: Fisher's C_6=21.38, *P*=0.002; pathway: β=0.1, *P*=0.002 Figure 2-7A). When I included provisioning behavior, however, mass gain was most related to provisioning rate; meadowlark nestlings that received more *per capita* food visits gained mass at a slower rate than meadowlark nestlings that received fewer visits (overall SEM: Fisher's C_8=14.92, *P*=0.061; pathway: β=-0.2, *P*=0.002, Figure 2-7B). Dickcissel growth data was unrelated to environmental variation (Fisher's C_4=27.92, *P*<0.001, Figure 2-7C). However, when I restricted the dataset to just nests with provisioning data, provisioning rate was associated with mass gain; Dickcissels at nests with higher *per capita* day-4 provisioning rates increased mass more quickly (β=0.5, *P*=0.015, Figure 2-7D), such that Dickcissel nestlings that received 1.25 visits/nestling/hour on day 4 were on average 4.5 grams (40%) heavier at fledge age (day 6-7) than conspecifics which received 0.5 fewer provisioning visits/nestling/hour (Figure 2-8). The number of cowbirds in the nest was not related to provisioning rate directly, but brood size increased with increasing number of cowbird nestlings (β=0.9, *P*=0.000, Figure 2-7D) and brood size was negatively

related to provisioning rate (β= -0.6, *P*=0.034, Figure 2-7D); nests with more nestlings of either species received fewer food visits/nestling/hour such that nests with two nestlings received double the average number of visits *per capita* per hour than nests with six nestlings (Figure 2-9). The number of cowbird nestlings was also associated with elevated predation risk (β= 0.632, P<0.001, Figure 2-7D), but again, predation risk was not related to Dickcissel mass gain. It is important to note, however, that this reduced model did not fit the data well (Fisher's C_8=7.49, *P*=0.485). Sparrow nestlings in small broods gained mass faster than nestlings in large broods (overall SEM: Fisher's C_6=10.74, *P*=0.097; pathway: β=-0.2, *P*=0.011, Figure 2-7E), such that by day 6 sparrows in the largest broods (5+ nestlings) were ~15% lighter than the sparrows in the smallest broods (1-2 nestlings) (Figure 2-10). However, brood size was unrelated to the number of cowbird nestlings. The restricted model included positive relationships between the number of cowbird nestlings (β=0.4, *P*=0.034, Figure 2-7F), predation risk (β=0.8, *P*=0.000, Figure 2-7F), and, most notably, the provisioning rate (β=0.4, *P*=0.031, Figure 2-7F). Nests with a single cowbird parasite received, on average, two times as many provisioning visits per nestling per hour as nests with no cowbirds or nests with two cowbirds (Figure 2-11). Despite these relationships, sparrow mass gain was not related to provisioning rate, the number of cowbirds, or the predation risk. Like the Dickcissel reduced provisioning model, the sparrow model did not fit the data well, likely due to my having only three parasitized sparrow nests with provisioning data (Fisher's C_{10}=13.56, *P*=0.194).

Mass-corrected tarsus lengths steadily declined as the birds aged but some birds hatched with values almost twice that of conspecifics (Figure 2-12). Meadowlarks in nests with cowbird nestlings prioritized mass gain over tarsus gain as they aged (overall SEM: Fisher's C_6=21.38, *P*=0.002; pathway: β=-0.2, *P*=0.025, Figure 2-13A), ultimately resulting in nestlings with 25%

smaller mass-corrected tarsi by fledge (Figure 2-14), although this pattern was not present in the restricted dataset analysis (overall SEM: Fisher's C_8=14.92, *P*=0.061; Figure 2-13B). Meadowlark tarsus prioritization was also related to predation risk; nestlings in riskier nests differed in their allometry, favoring mass gain over tarsus growth (full dataset: β=-0.2, *P*=0.020, Figure 2-13A; restricted dataset: β=-0.34, *P*=0.019, Figure 2-13B). Meadowlark nestlings in risky nests (>0.4 depredated nests/ha) had smaller mass-corrected tarsi by day 9, but this difference only accounted for ~15% of the total variation in observed mass-corrected tarsus scores, and nestlings in safer nests (<0.4 depredated nests/ha) reached the same mass-corrected tarsus length three days later (Figure 2-15). The allometry of Dickcissel tarsus growth was not directly related to the number of cowbird nestlings in the nest, although it was related to brood size (which was correlated with number of cowbird nestlings); Dickcissels in larger broods initially had higher mass-corrected tarsus scores, but prioritized the growth of their mass more than Dickcissels in smaller broods (overall SEM: Fisher's C_4=27.92, *P*<0.001; pathway: β=-0.4, *P*=0.022, Figure 2-13C) so that by day 4 the nestlings all had similar allometric patterns (Figure 2-16). The model including provisioning rate did not fit the data well (Fisher's C_8=7.49, *P*=0.485, Figure 2-13D) but did reveal interesting patterns for further study. Increased brood size was negatively related to *per capita* provisioning rates (β=-0.6, *P*=0.034, Figure 2-13D) but not to tarsus prioritization, which was instead positively related to predation risk. Dickcissels in high-risk nests (>0.2 depredated nests/ha) prioritized their tarsus growth more than Dickcissels in less-risky areas (β=0.4, *P*=0.032, Figure 2-13D) but variation in predation risk resulted in little difference between mass-corrected tarsus lengths (Figure 2-17). The allometry of sparrow tarsus growth was also positively related to predation risk (overall SEM: Fisher's C_6=10.74, *P*=0.097; pathway: β=0.3, *P*=0.003, Figure 2-13E); sparrows in nests in higher-risk areas (>0.4 depredated

nests/ha) hatched with 20% mass-corrected tarsi than did sparrows in low risk areas (<0.4 depredated nests/ha) and favored the relative growth of their tarsus throughout their development (Figure 2-18). The number of cowbirds in the nest was not related to sparrow tarsus prioritization in either the full (Figure 2-13E) or restricted model (Fisher's C_{10}=13.56, *P*=0.194; Figure 2-13F).

To test whether birds shifted allocation to favor the growth of their wings, I calculated the ratio of each pair of feather and wing bone measurements to mass and combined them using a principal component analysis, generating two major axes of variation which accounted for 93.61% of the variation combined (Figure S2-1). The first axis (PC1) primarily explained the prioritization of overall wing growth relative to mass, with larger values indicating larger mass-corrected feather and bone lengths. This wing size principal component was the only metric that did not change directionally over a birds' age (Figure 2-19). Meadowlark nestlings' allometric scaling shifted in favor of mass gain over wing growth as they aged (overall SEM: Fisher's C_6=21.38, *P*=0.002; pathway: β=-0.256, P=0.017, Figure 2-20A), but only in nests with cowbirds (Figure 2-21). Meadowlark nestlings also prioritized mass growth over wing growth in nests with higher predation risk (β=-0.3, *P*=0.039, Figure 2-20A). However, this pattern was no evident in the reduced data set (Fisher's C_8=14.92, *P*=0.061, Figure 2-20B). Prioritization of the wing growth was not related to the number of cowbirds in the nests for Dickcissels (Fisher's C_4=27.92, *P*<0.001; Figures 2-20C-D). Dickcissel wing allometry was instead related to provisioning rate (β=-1.5, *P*=0.006), although the overall model did not fit the data well (overall SEM: Fisher's C_8=7.49, *P*=0.485, Figure 2-20D). By day 6, nestlings receiving more than 1.08 provisioning visits per nestling per hour had mass-corrected wing sizes half that of nestlings receiving fewer than 1.08 provisioning visits/nestling/hour (Figure 2-22). Sparrows in nests with low predation risk (<0.4 depredated nests/ha) hatched with mass-corrected wings as much as four

times as large as sparrows in areas of high predation risk (>0.4 depredated nests/ha, Figure 2-23). Instead of increasing their relative wing sizes over time to match the nestlings in low-risk nests, nestlings in the high-predation-risk nests prioritized mass gain more than wing size growth relative to conspecifics in low-risk nests (overall SEM: Fisher's C_6=10.74, *P*=0.097; pathway: β=-0.3, *P*=0.024, Figure 2-20E). All of the drivers were related to sparrow wing prioritization in the restricted data set, but there was poor model fit overall and low sample size (i.e. 3 parasitized nests, overall SEM: Fisher's C_{10}=13.56, *P*=0.194); sparrows prioritized wing growth in nests with higher *per capita* provisioning rates (β=1.4, *P*=0.009, Figure 2-20E), more nestlings in the brood (β=4.4, *P*=0.003, Figure 2-20E), and nests with higher predation risk (β=5.3, *P*=0.020, Figure 2-20E). Sparrows reduced wing prioritization (shifted toward allometric patterns of higher mass relative to wing growth) in nests with more cowbirds (β=-4.4, *P*=0.036, Figure 2-20E).

The second axis of the wing principal components analysis (PC2) primarily described differences in feathers vs. wing bone length (Table S2-2, Figure 2-24). None of the hypothesized drivers explained variation in meadowlark feather growth prioritization in either the full model (overall SEM: Fisher's C_6=21.38, *P*=0.002; Figure 2-25A) or the model restricted to the nests with provisioning data (overall SEM: Fisher's C_8=14.92, *P*=0.061; Figure 2-25B). Dickcissels in riskier nests prioritized mass gain over the growth of their feathers (overall SEM: Fisher's C_4=27.92, *P*<0.001; pathway: β=-0.2, *P*=0.026, Figure 2-25C). However, by fledge age (day 6-7), nestlings had very similar mass-corrected feather scores regardless of predation risk near the nest (Figure 2-26). This relationship between predation risk and Dickcissel mass-corrected feather scores was only present in the full model analysis, not the restricted model with provisioning (overall SEM: Fisher's C_8=7.49, *P*=0.485; Figure 2-25D). The relationship between predation and mass-corrected feather scores was more pronounced in the sparrow nestlings; the

sparrows in nests in areas of high predation risk favored mass gain over the growth of their feathers (overall SEM: Fisher's C_6=10.74, *P*=0.097; pathway: β=-0.5, *P*=0.000, Figure 2-25E) so that by fledge age (6-7 days), the difference between the PC2 scores for the sparrow nestlings in the high-risk (>0.4 depredated nests/ha) and low risk (<0.4 depredated nests/ha) nests accounted for almost a third of the total observed variation in PC2 scores (Figure 2-27). The model restricted to nests having provisioning data was a poor fit for the data (Fisher's C_{10}=13.56, *P*=0.194) but suggested that sparrow feather prioritization was instead related to brood size (β=-2.0, *P*=0.048, Figure 2-25F); large sparrow broods (4+ nestlings) had longer relative feather lengths early in development, but sparrows in smaller broods (<4 nestlings) increased their prioritization of feather growth over time so that by fledge age (day 6-7) the sparrows all had similar mass-corrected feather scores (Figure 2-28).

Fledge age varied among species; meadowlarks left the nest at 10.5±1.5 days (range: 7-12 days), Dickcissels at 7.3±1.2 days (range: 5.5-9.5 days), and sparrows at 7.2±1.3 days (range: 5-10 days). Variation in fledge age was not related to predation risk in any species (meadowlark: t_{124}=-0.2, *P*=0.820; Dickcissel: t_{30}=-0.8, *P*=0.411; sparrow: t_{21}=-0.4, *P*=0.659), nor to mass gain (meadowlark: t_{122}=0.4, *P*=0.352; Dickcissel t_{30}=0.3, *P*=0.760; sparrow t_{21}=0.2, *P*=0.824), relative wing growth (meadowlark: t_{122}=-0.5, *P*=0.634; Dickcissel: t_{30}=-1.0, *P*=0.297; sparrow; t_{21}=-0.3, *P*=0.800), or relative tarsus growth (meadowlark: t_{122}=1.3, *P*=0.199; Dickcissel t_{30}=0.4, *P*=0.695; sparrow t_{21}=0.3, *P*=0.794). Meadowlark nestlings that left the nest early (before day 9) had higher mass-corrected feather scores compared to meadowlarks that fledged later (t_{122}=3.047, *P*=0.003). By the time those late-fledging birds left the nest their allometry had converged on those of nestlings that fledged before day 9 (Figure 2-29). Feather length allometry was not related to fledge age in Dickcissels (t_{146}=-1.505, *P*=0.135) or sparrows (t_{67}=-0.770, *P*=0.444).

In all species, provisioning rate was negatively correlated with the fledge age; nestlings that receive more provisioning visits/nestling/hour left the nest at younger ages than nestlings receiving fewer provisioning visits (t_{49}=-2.2, *P*=0.031, Figure 2-30); increasing provisioning rates by 1 visit/nestling/hour resulted in a ~2 day decline in average fledge age. For meadowlarks, fledge age was also strongly related to the number of cowbirds in the nest; as the number of cowbirds increases the fledge age decreased; parasitized meadowlarks fledged 3.5 days (30%) earlier, on average, than non-parasitized conspecifics (t_{21}=-3.5, *P*=0.002, Figure 2-31). Parasitized meadowlarks' mass at fledge day (~day 7) was not statistically different from the mass of unparasitized conspecifics at the same age, suggesting that the parasitized birds did not grow faster but simply left the nest earlier than did unparasitized meadowlarks ($F_{2,266}$=1.388, *P*=0.251). Parasitism was not related to the fledge age of Dickcissels (t_{30}=0.5, *P*=0.607) or sparrows (t_{21}=0.3, *P*=0.755).

Nest fate was not associated with mass-corrected feather growth (meadowlark: z_{86}=-0.1, *P*=0.956; Dickcissel: z_{95}=0.1, *P*=0.907; sparrow: z_{175}=0.2, *P*=0.877), the mass-corrected tarsus growth (meadowlark: z_{86}=0.6, *P*=0.577; Dickcissel: z_{95}=-0.1, *P*=0.947; sparrow: z_{175}=0.1, *P*=0.911), or the number of cowbird nestlings (meadowlark: z_{86}=0.1, *P*=0.939; Dickcissel: z_{54}=-0.4, *P*=0.726; sparrow: z_{175}=-0.4, *P*=0.723). Meadowlarks that were depredated before they left the nest had higher mass-corrected wing sizes more before their death (z_{86}=2.2, *P*=0.027, Figure 2-32), but the wing growth of successful and depredated Dickcissels (z_{221}=1.4, *P*=0.155) or sparrows (z_{172}=-1.3, *P*=0.191) did not differ. Successful sparrows gained mass slower than the sparrow nestlings that were ultimately depredated (sparrow z_{80}=-1.8, *P*=0.074), although the depredated birds were never more than 10% heavier than successful conspecifics (Figure 2-33). Mass gain did not differ between depredated and successful meadowlarks (z_{86}=-0.1, *P*=0.936) or

Dickcissels (z_{95}=0.1, *P*=0.913). Finally, the nests which ultimately were depredated before they fledged had received ~50% fewer provisioning visits per nestling per hour on day 4 for both Dickcissels (z_{55}=-2.7, *P*=0.007, Figure 2-34A) and sparrows (z_{33}=-1.8, *P*=0.075, Figure 2-34B) but not meadowlarks (z_{86}=-0.9, *P*=0.348).

Discussion

I related the growth of host nestlings to the presence of cowbird brood parasites and the interactions between cowbird presence, provisioning rate, and predation risk in order to understand the ways nestling growth and development patterns respond to multiple contrasting environmental stressors. Despite a large sampling effort I found little evidence that the presence of cowbirds affects nestling development directly through competition, or indirectly by mediating the effects of other environmental drivers. Rather, intraspecific growth and development variation was more frequently related to provisioning rate and predation risk alone.

Host nestlings at this site varied dramatically in their growth rates and development strategies, as previously observed (Chapter 1). The host species were parasitized at different rates; Dickcissel nests were almost twice as likely to be parasitized as Grasshopper Sparrow nests, and ~2.6x more likely to be parasitized as Eastern Meadowlark nests. The majority (60%) of Dickcissel and sparrow nests, if parasitized, contained more than one cowbird egg; this rate was lower (40%) for meadowlarks, but still higher than has been reported for the species (Strausberger and Ashley 1997). The number of cowbird eggs did not increase the total number of nestlings in the nest, consistent with cowbirds ejecting a host egg and replacing it with one of their own (Sealy 1992). However, the number of cowbirds was higher in larger brood sizes, perhaps because low-quality females with smaller clutches abandoned parasitized clutches before

hatch. The nest success rates in this study were some of the lowest ever recorded for these species (although see Patterson and Best 1996), yet brood parasitism did not affect nest success.

I hypothesized that the presence of begging cowbird nestlings would increase the *per capita provisioning rate*, ultimately benefiting the host nestlings and allowing them to gain mass faster or reduce the amount of energy they spent prioritizing competitive structures like long tarsi. Parents visited nests with larger broods more often, but this did not translate to more visits per nestling per hour, indicating that the birds can adjust their provisioning behavior to accommodate more nestlings (Pap and Markus 2003), but not enough to prevent increased competition in the largest broods (Mock and Forbes 1995). The presence of cowbirds was unrelated to the *per capita* provisioning rates of Eastern Meadowlarks. Because meadowlarks are as much as three times larger than cowbirds, their nestlings may not experience increased competition for food from cowbirds, so they may not adjust their provisioning behavior in the presence of cowbirds. The number of cowbirds in Dickcissel nests was positively associated with brood size, a surprising result given my assumption that cowbirds always remove a host egg during laying. Nestlings in larger broods experienced lower *per capita* provisioning rates; therefore, cowbirds may influence provisioning behavior in Dickcissel nests, but their influence is comparable to the addition of another host nestling. The presence of cowbirds nestlings in Grasshopper Sparrow nests did increase *per capita* provisioning rates. However, this increase in provisioning was not related to higher mass gain or prioritization of competitive structures, as predicted, but rather increased investment in the overall growth of wings relative to mass. However, the provisioning data for sparrow was limited to three parasitized nests and six unparasitized nests so these results must be treated as preliminary. Given this caveat, however, cowbirds appear to have the largest impact on host provisioning behavior in the smallest host

species but their effect on provisioning rate did not influence nestling growth in any host species, suggesting that this indirect effect of brood parasitism is not a primary driver of differences among nestlings in mass gain or in allometric scaling.

I hypothesized that loud begging calls of cowbirds would increase the *predation risk* at the nest with consequences for host nestling allocation to the growth of mobility-enhancing structures like wings. The number of cowbirds was not related to the predation risk (number of depredated nests/ha) at meadowlark nests. However, nests with cowbirds were located in areas of higher predation risk for Dickcissels and sparrows, but this relationship was not linked to any change in growth and development of hosts. The presence of one or more cowbirds in the nest did not increase the predation risk, suggesting this indirect effect of parasitism is not a primary driver of variation in allometry of mobility-related morphology.

The addition of the provisioning data and the predation risk data to prior analyses of the direct effects of cowbirds on host nestling development provided more nuanced insight into *nestling competition* between cowbirds and hosts. Neither variation in meadowlarks' overall growth nor prioritization of tarsus or feathers was related to the presence of cowbirds in prior (Chapter 1) or current analyses. Instead, cowbird competition influenced meadowlark mass gain. Parasitized meadowlarks' allometric patterns were skewed in favor of mass over tarsi or wings. Increasing mass may allow meadowlarks to outcompete cowbirds in scramble competition (Mock and Parker 1997). Parasitized meadowlarks fledged the nest days earlier than unparasitized conspecifics. Thus, although Eastern Meadowlarks are as much as three times the size of their cowbird parasites, they appear to still experience direct cowbird competition.

Dickcissels' overall growth was depressed in the presence of cowbirds (Chapter 1), so I expected that direct cowbird competition would result in slower mass gain, but this was not the

case. Instead, Dickcissels growing in large broods (including cowbirds) had shorter mass-corrected tarsi, the opposite pattern observed in other host species (Rock et al. 2013). Perhaps as with meadowlarks, increased mass may help the Dickcissels compete with their nest mates. Despite altered development, Dickcissels in parasitized nests left the nest at the same time as conspecifics raised without cowbirds. Altogether, these results suggest that parasitized Dickcissels suffered reduced overall growth, but the parents' ability to increase provisioning meant that host nestlings fledged at the same time as unparasitized conspecifics and experienced similar nest success.

Grasshopper Sparrows are a third the size of cowbirds, so I expected them to experience the most dramatic consequences of brood parasitism. However, the number of cowbirds did not directly relate to any metric of sparrow growth and development. Sparrows in large broods gained more mass than sparrows in smaller broods at the expense of feather development, but this relationship was not related to the number of cowbird nestlings. Sparrow nestlings in parasitized and unparasitized nests differed little in overall growth or in allometry (Chapter 1). Cowbirds presence was not related to the risk of predation at the nest site, and nests with cowbird parasites did not experience lower predation rates. Sparrows may be able to compensate for the presence of cowbirds by provisioning as much as twice as frequently when cowbirds are present (Kilner et al. 2004).

Brood parasitism is costly enough to developing host nestlings and provisioning parents (Peer et al. 2005) to drive the evolution of anti-parasitism strategies (Avilés et al. 2006). Rather than ejecting parasite eggs or abandoning parasitized nests, many grassland-nestling host species raise cowbirds alongside their own, and seemingly do so with little consequence for the growth of their own offspring (Chapter 1). Within host species, however, nestlings vary dramatically in

growth rates and developmental patterns. I hypothesized that this variation was related to parasitism not directly, but through the interactions between cowbird parasitism and other factors affecting nestling development. While parasitism may affect provisioning behavior in the smallest hosts, I saw no relationship between parasitism and provisioning behavior in the larger species, and no relationship between predation risk and parasitism, implying that, despite cowbird competition and their ability to alter feeding rates and predation risk in other systems, they do not influence host development in the system I studied. Within the native range of the cowbird, these host species have evolved species-specific strategies to accommodate high rates of parasitism without suffering increased nest failures and, potentially, without increasing costly parental provisioning behavior. In all the nests, they gained mass very quickly and fledged very early relative to conspecifics in other regions. As cowbirds expand their range (Ortega 1998), new host species' nest success and population trajectories may well depend on their ability to adjust their growth and development strategies through the allometric patterns favoring mass gain, changes in provisioning behavior, and reduced fledge ages.

Instead of finding evidence of indirect effects of cowbirds on host development, I found that host intraspecific growth and development variation was associated with natural variation in predation risk and provisioning rate. This result is particularly noteworthy, as all of these nests are located in a small (<35 km^2) geographic region; previous reports of intraspecific variation in growth rate show evidence of patterns between locations (Sofaer et al. 2018) or between experimentally manipulated nests (Coslovsky and Richner 2011), rather than at a single location with natural variation in predation risk and provisioning rate.

The *provisioning rate* hypothesis led me to predict that nestlings would gain mass more quickly in nests with higher provisioning rates, a pattern that we observed in Dickcissel nests.

However, the opposite was true for meadowlarks, who gained mass more slowly in nests with more parental visits. This may be the result of the quality of the food rather than quantity, as birds visiting more frequently may be forced to spend less time searching for nutritious food (Grieco 2002). Further work on the effects of provisioning rate should include an analysis not only of the number of nest visits but also the quality of the food fed to each individual nestling.

I did not hypothesize that provisioning rate would influence nest fate, yet I observed a relationship between provisioning rate and realized predation rates; Dickcissels and sparrows in nests with lower provisioning rates were more likely to be depredated. While the mechanism underlying this pattern is not clear, it is possible that it was the result of changes in parental behavior, as parents who are aware of nearby predators reduce provisioning rates to protect the nestlings without success (Dmitriew 2011, Bonnington et al. 2013). Alternatively, the correlation may indicate that low-quality parents were unable to bring as much food to the nest and also unable to adequately protect their nestlings from predators; this seems unlikely, as we have no footage of any parent ever successfully protecting nestling from predators at the nest. Finally, this relationship could have resulted from food-starved nestlings begging more loudly and attracting predators (McDonald et al. 2009), a possibility given that the top predator of these species was the Yellow-bellied Racer, a snake that hunts nestlings using auditory cues (Sutton 1960).

The expectation of the *predation risk* hypothesis was that nestlings in nests located in high-risk areas would shift their allometric patterns in favor of mobility-enhancing structures like wings to quickly escape nest predators. The hosts at this site suffer predation rates as high as 85% (Chapter 1), so it is possible that these birds are prioritizing predator avoidance over competition with cowbirds. However, the most at-risk host nestlings did not prioritize the growth

of their wings, but Dickcissel and sparrow nestlings did prioritize the growth of their tarsi over mass gain. As both species fledge before they are flight-capable, well-developed tarsi may help them avoid predators after they leave the nest (Smith 1963). All three host species prioritized the growth of their mass in high-risk areas—meadowlarks prioritized the growth of their mass over their tarsus and Dickcissels and sparrows prioritized the growth of their mass over their feathers. Early investment in mass may prepare birds for predation-induced food shortages post-fledging (McNamara and Buchanan 2005), favor escape performance (Higginson et al. 2012), and/or protect nestlings from small predators (Thompson et al. 1999). Indeed, one Grasshopper Sparrow nest was attacked by a Yellow-bellied Racer (*Coluber constrictor*) but the nestlings were able to avoid predation because they were too large to fit in the snake's mouth. Increasing mass gain reduces fledge age in some open-cup nesters, allowing them to escape risky nests more quickly (Cheng and Martin 2012), and/or protects them from exposure death if they leave the nest early, yet mass gain was not related to the fledge age at other grassland sites (Ribic et al. 2018). All three host species left the nest at young ages compared to other populations (i.e., average Dickcissel fledge age of 9 days in Illinois; Harmeson 1974), so fledge age may reflect differences in predation risk among sites rather than at the nest level. These grassland host nestlings do not prioritize wing growth in nests with high predation risk but do prioritize their tarsi and mass, potentially to avoid predators both within the nest and after fledging.

Much of the variation in grassland bird growth and development strategies I observed was related to the risk of nearby predators, suggesting that the high predation rates at this site may be forcing nestlings to adjust their development strategies to promote survival from predators rather than competition with nestlings or cowbirds. However, in this study, some variation was attributable to adult behavioral decisions (provisioning rate) and strategies to

mitigate the costs of brood parasitism. Even at a site like Konza where birds experience some of the highest brood parasitism and predation rates recorded, these birds have maintained enough variation in development and parental care to respond to multiple stressors simultaneously. These results indicate that inter- and intraspecific variation in songbird development is shaped by complicated interactions of environmental conditions at regional, local, and nest microsite levels. To understand how animals adjust to stressful and changing environments, we need to assess these individual-level consequences and follow their ramifications throughout an organisms' lifetime.

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Figures

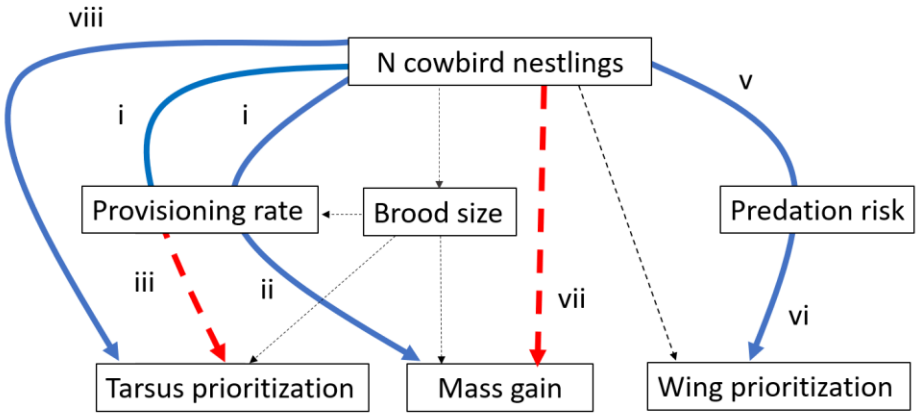

Figure 2-1. Hypothesis/Prediction structure. I hypothesized that nestling mass-corrected tarsus length (tarsus prioritization), mass-corrected wing size (wing prioritization), and mass gain would be affected by provisioning rate, cowbird parasitism, and predation risk. The predicted direction of these relationships is indicated by the color of the line; blue solid lines indicate a predicted positive relationship and red dashed lines indicate a predicted negative relationship. Numerals indicate the prediction (see Introduction for more details).

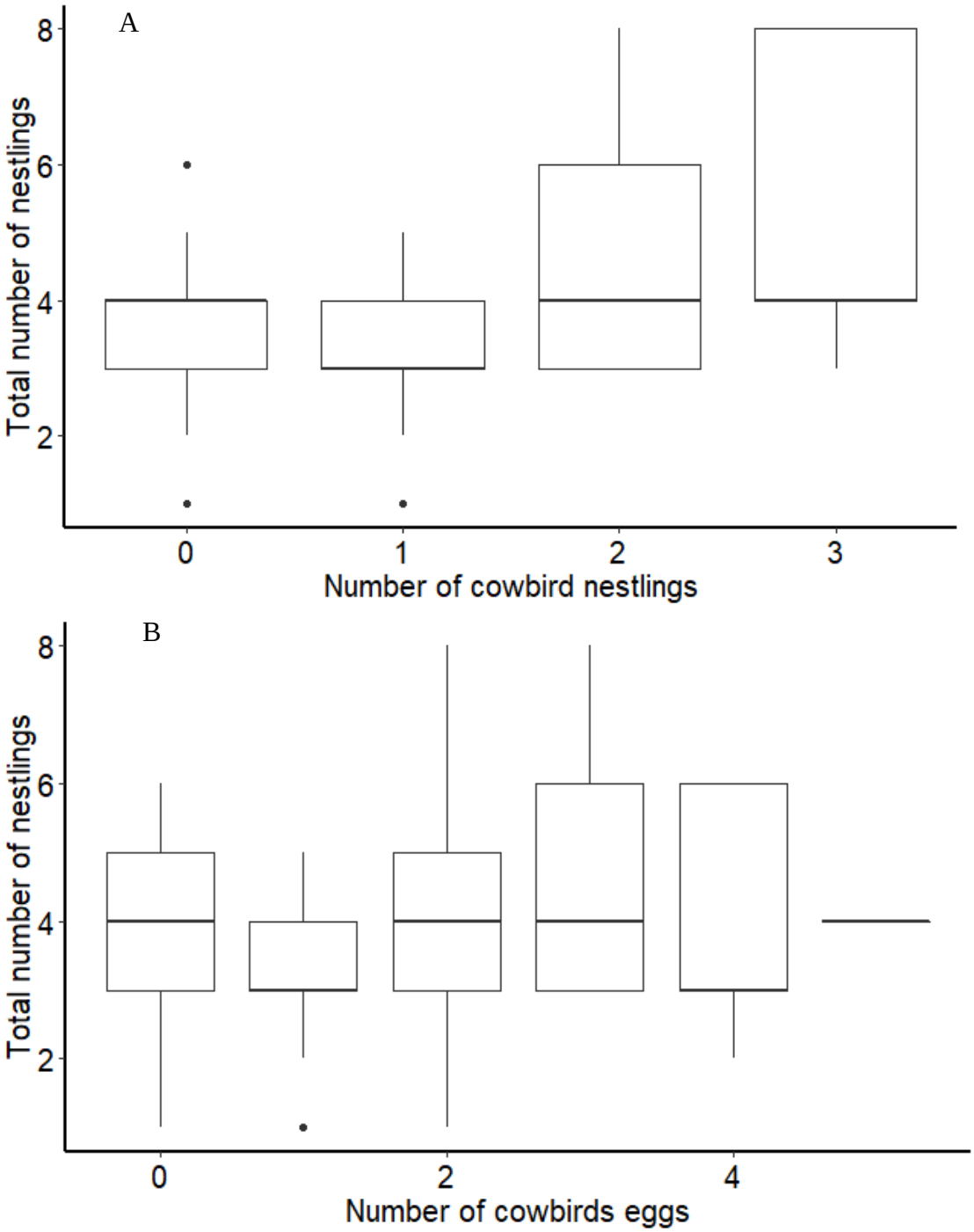

Figure 2-2. Nests with more (A) cowbird nestlings had more nestlings total ($F_{3, 336}$=32.5, *P*=0.000), but nests with more (B) cowbird eggs did not have more nestlings total ($F_{5,334}$=1.7, *P*=0.136).

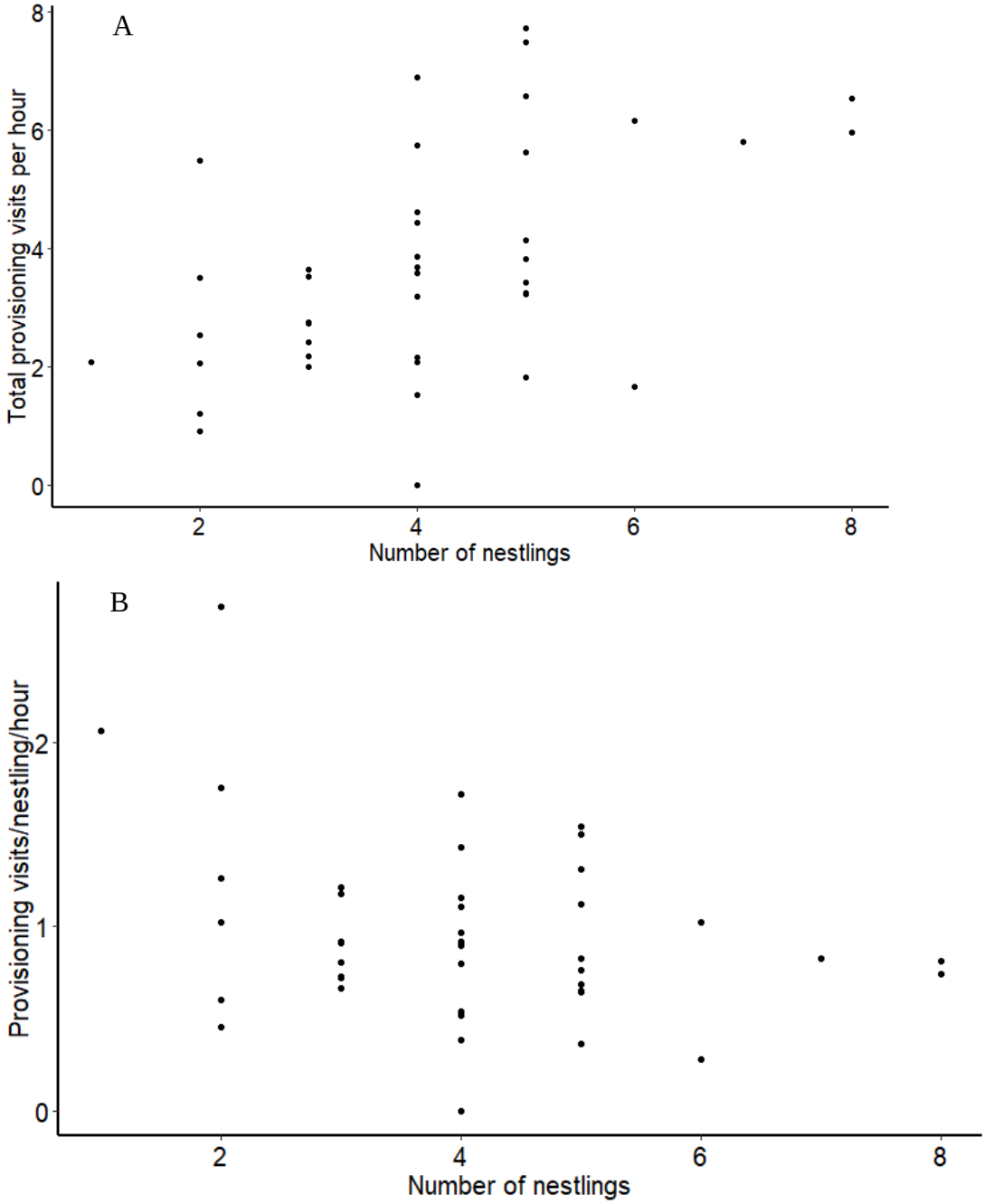

Figure 2-3. Nests with more nestlings of either species (hosts and cowbirds) received (A) more provisioning visits per hour (t_{41}=3.2, *P*=0.003) but (B) fewer provisioning visits per nestling per hour (t_{41}=2.7, *P*=0.010).

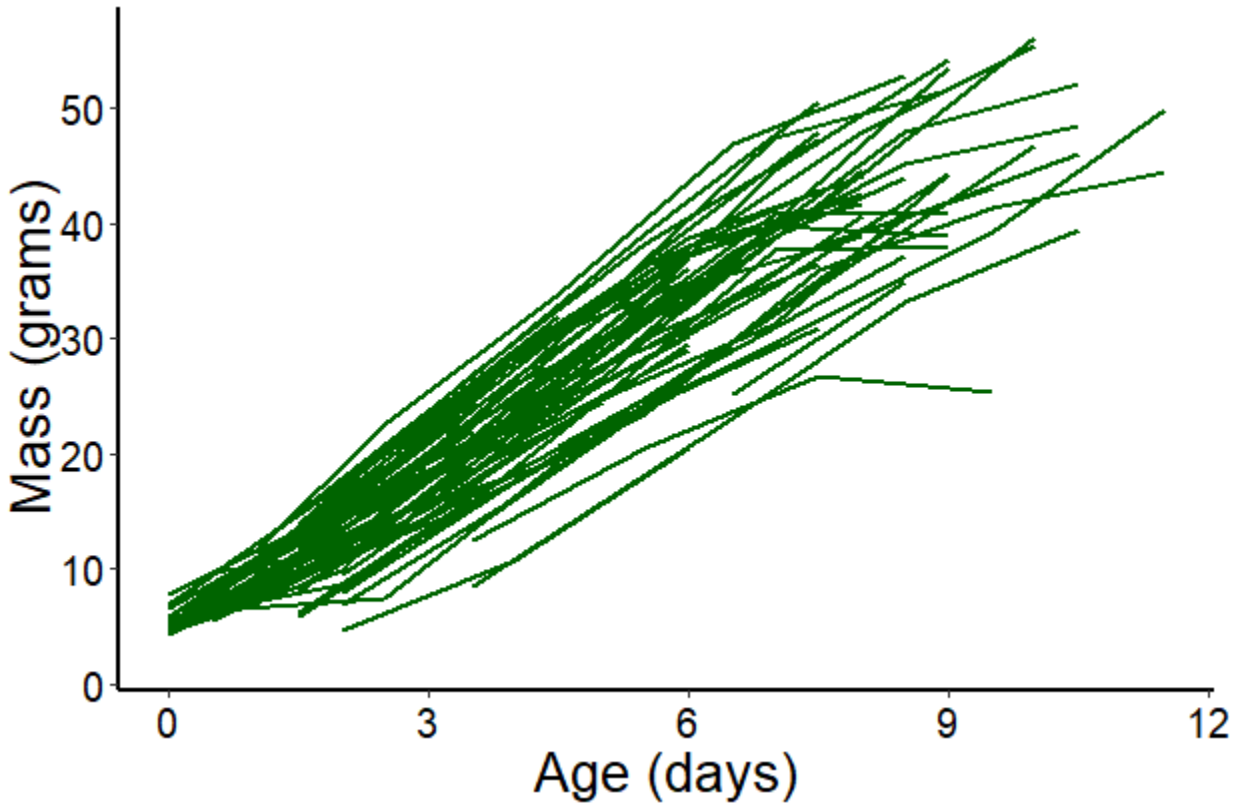

Figure 2-4. Growth trajectories showing the mass (grams) gain of individual meadowlarks nestlings as they age (in days). Each line represents a single individual.

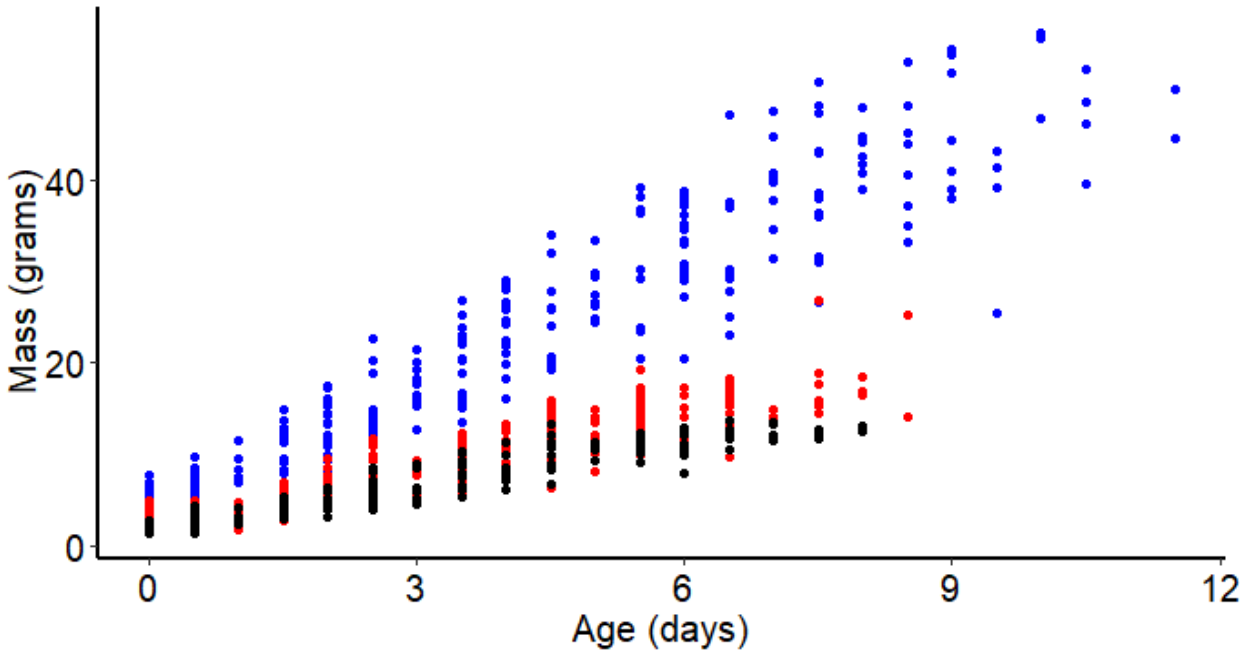

Figure 2-5. Host mass measurements (in grams) over time (in days from hatch day=0). Blue dots represent Eastern Meadowlark nestlings, red dots represent Dickcissel nestlings, and black dots represent Grasshopper Sparrow nestlings.

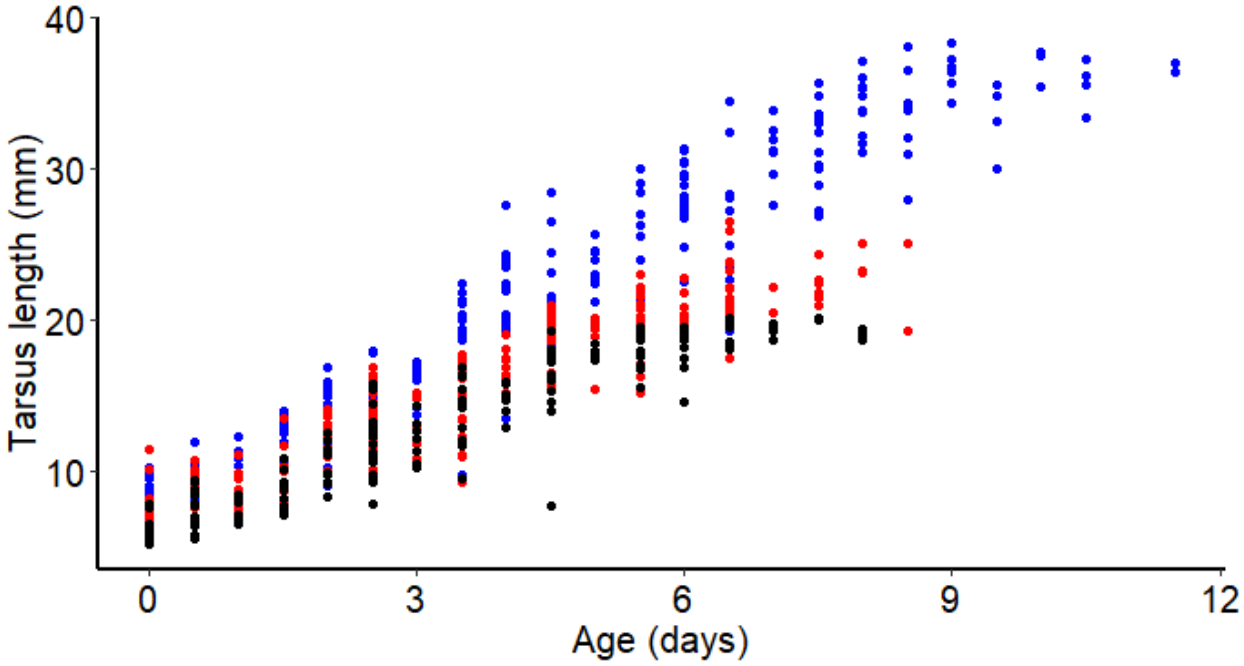

Figure 2-6. Host tarsus measurements (in mm) over time (in days from hatch day=0). Blue dots represent Eastern Meadowlark nestlings, red dots represent Dickcissel nestlings, and black dots represent Grasshopper Sparrow nestlings.

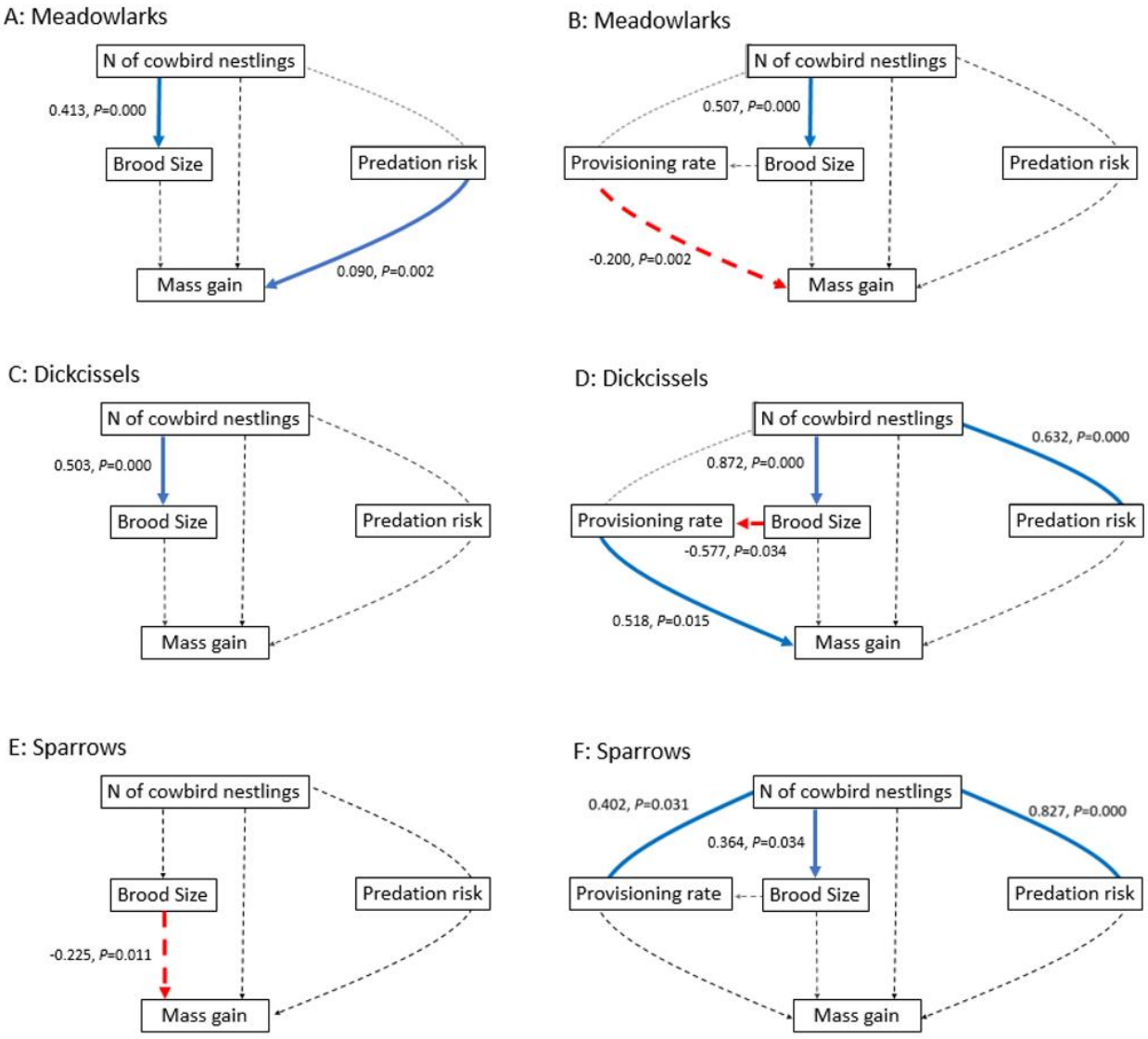

Figure 2-7. Combined results of species-specific structural equations modeling variation in nestling mass gain. Blue solid lines indicate positive (β>0) relationships (P<0.05), red dashed lines indicate negative (β<0) relationships, and gray dashed lines indicated pathways included in the model but not related. Each relationship is labelled with the standardized β value and *P* value. The panels portray the A) full model for Eastern Meadowlarks (Fisher's C_6=21.38, *P*=0.002), B) reduced model for Eastern Meadowlarks (Fisher's C8=14.92, P=0.061), C) full model for Dickcissels (Fisher's C4=27.92, P<0.001), D) reduced model for Dickcissels (Fisher's C8=7.49, P=0.485), E) full model for Grasshopper Sparrows (Fisher's C6=10.74, P=0.097), and F) reduced model for Grasshopper Sparrows (Fisher's C10=13.56, P=0.194).

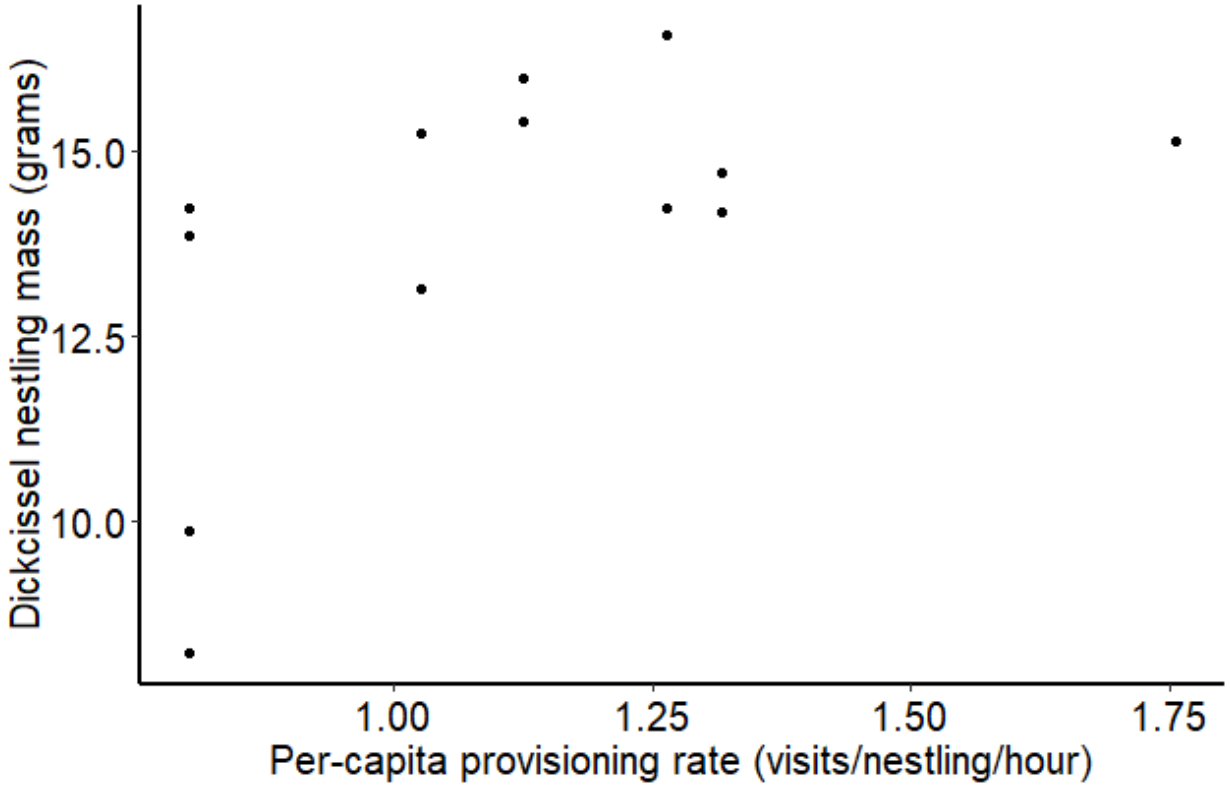

Figure 2-8. Dickcissel nestlings at nests with higher *per capita* provisioning rates (visits/nestling/hour) gained mass faster than conspecifics at nests with lower *per capita* provisioning rates (β=0.5, *P*=0.015).

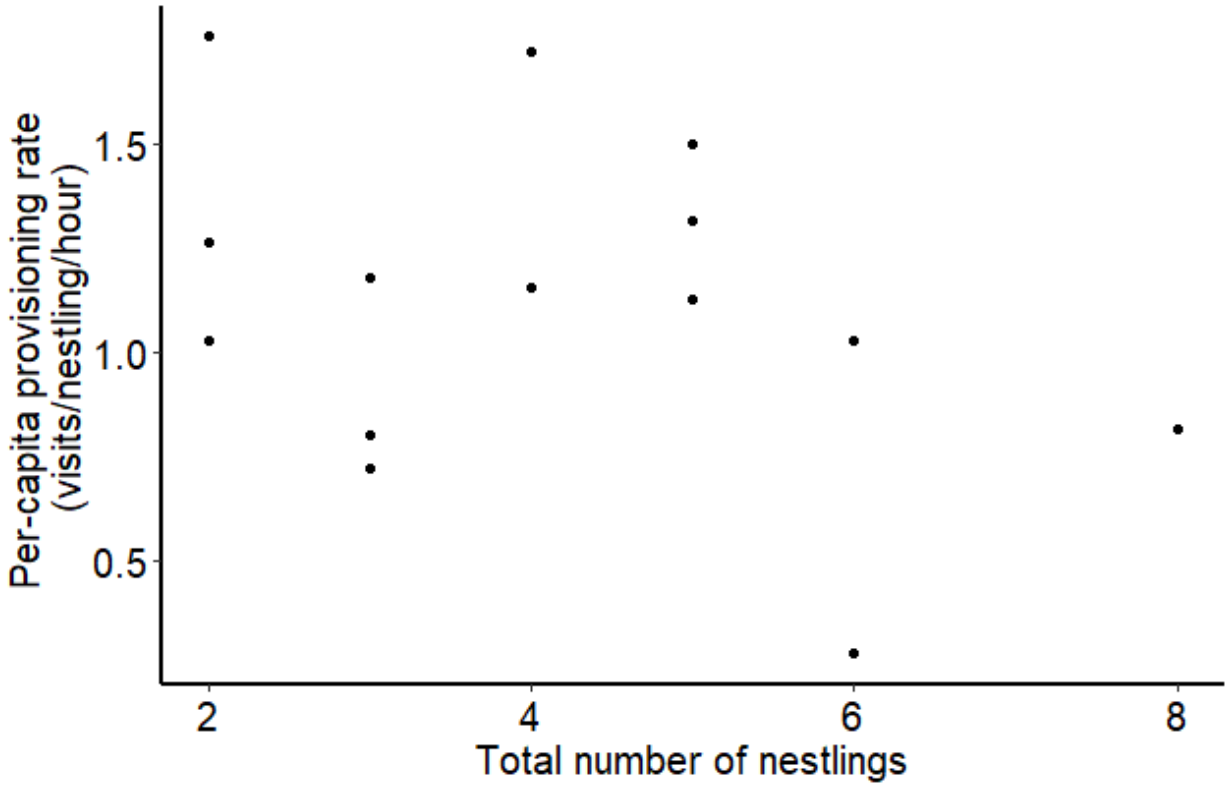

Figure 2-9. Dickcissel nestlings in nests with more nestlings (either cowbirds or conspecifics) received fewer provisioning visits per nestling per hour (β= -0.6, *P*=0.034).

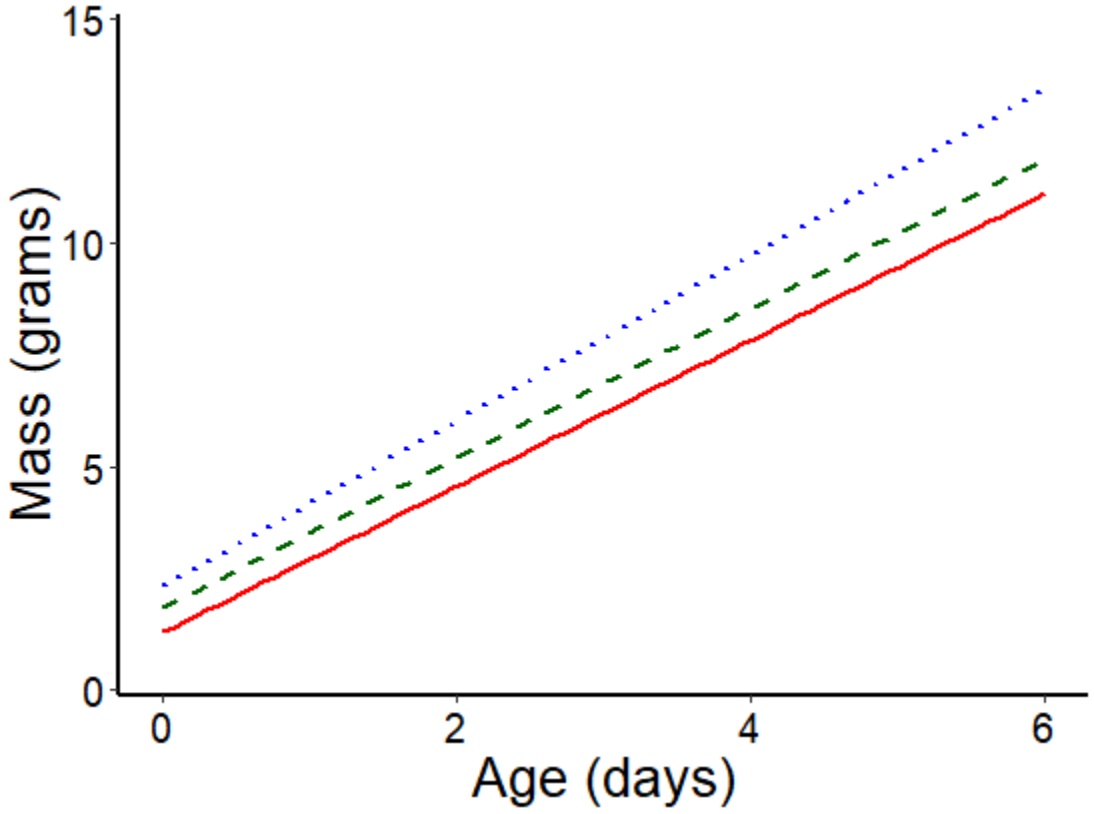

Figure 2-10. Sparrow nestlings in smaller broods (1-2 nestlings, blue dotted line) gained mass faster than nestlings in medium broods (3-4 nestlings, dashed green line) and larger broods (5+ nestlings, red solid line) (β=-0.2, *P*=0.011). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on mass gain (see Figure 2-7E).

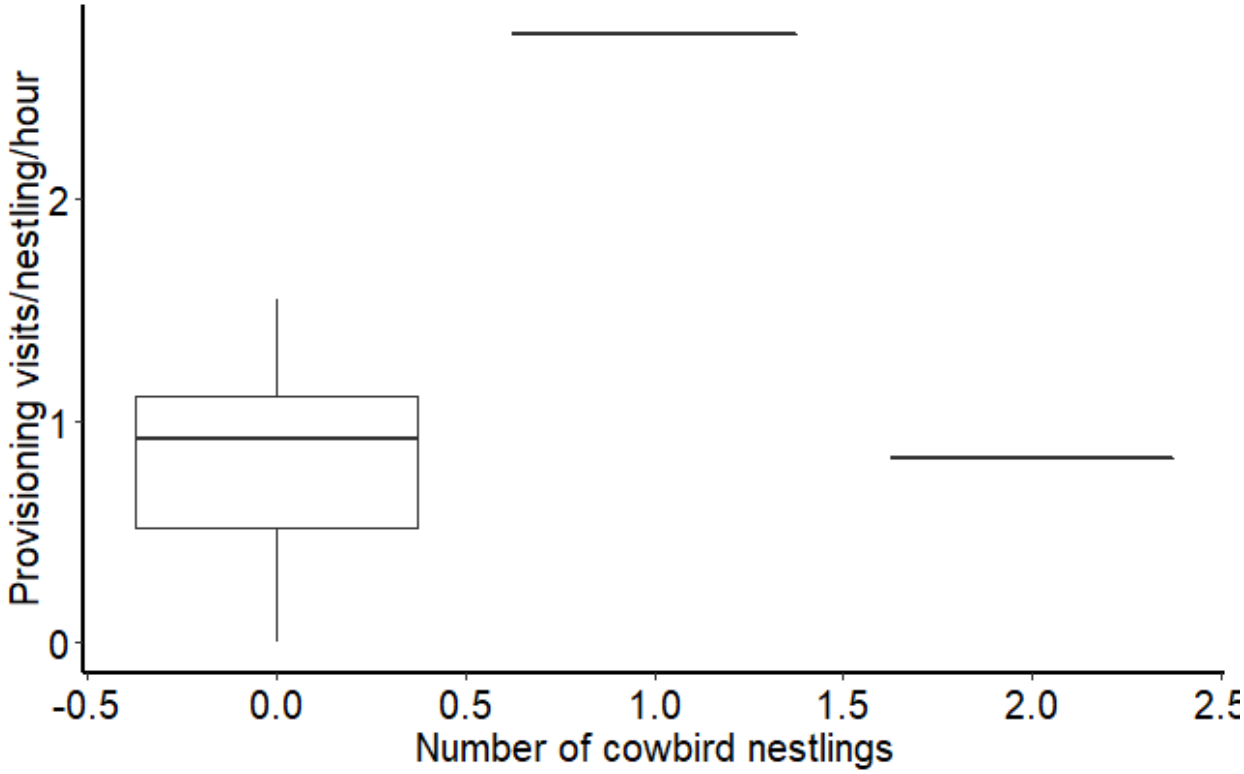

Figure 2-11. Sparrow nestlings in nests with one cowbird received more provisioning visits/nestling/hour than sparrow nestlings in nests with no cowbirds or two cowbirds, although note that I only have provisioning data for three parasitized sparrow nests (β=0.4, *P*=0.031).

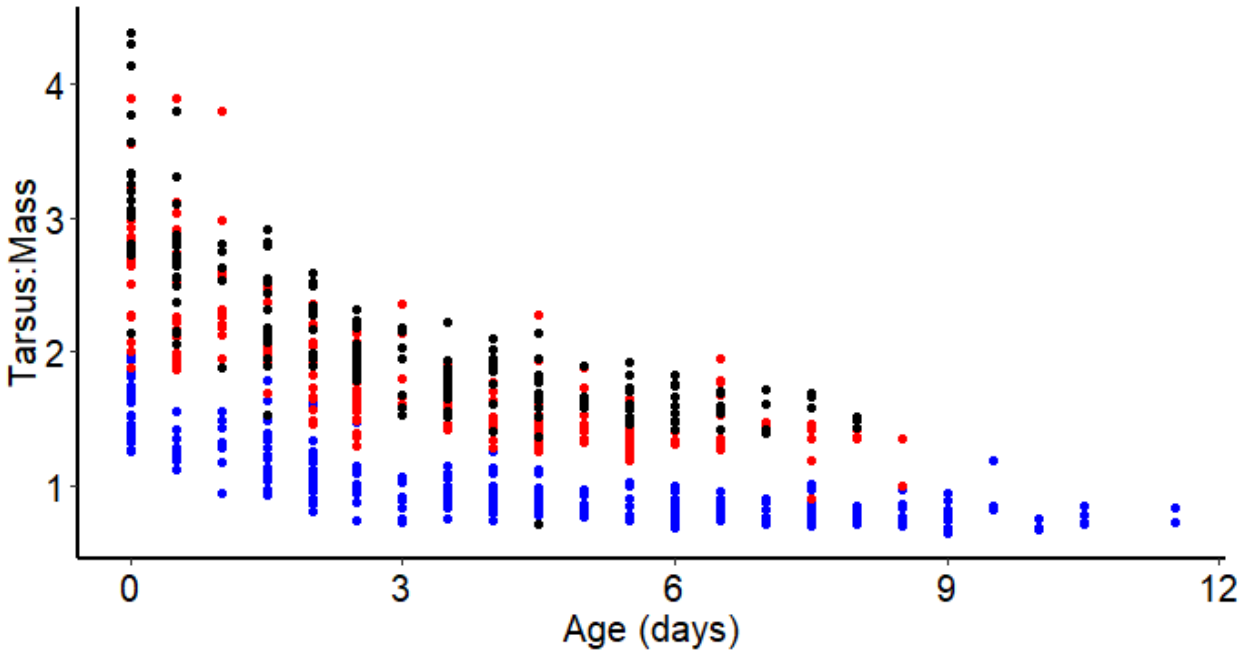

Figure 2-12. Host mass-corrected tarsus values over time (in days from hatch day=0). Blue dots represent Eastern Meadowlark nestlings, red dots represent Dickcissel nestlings, and black dots represent Grasshopper Sparrow nestlings.

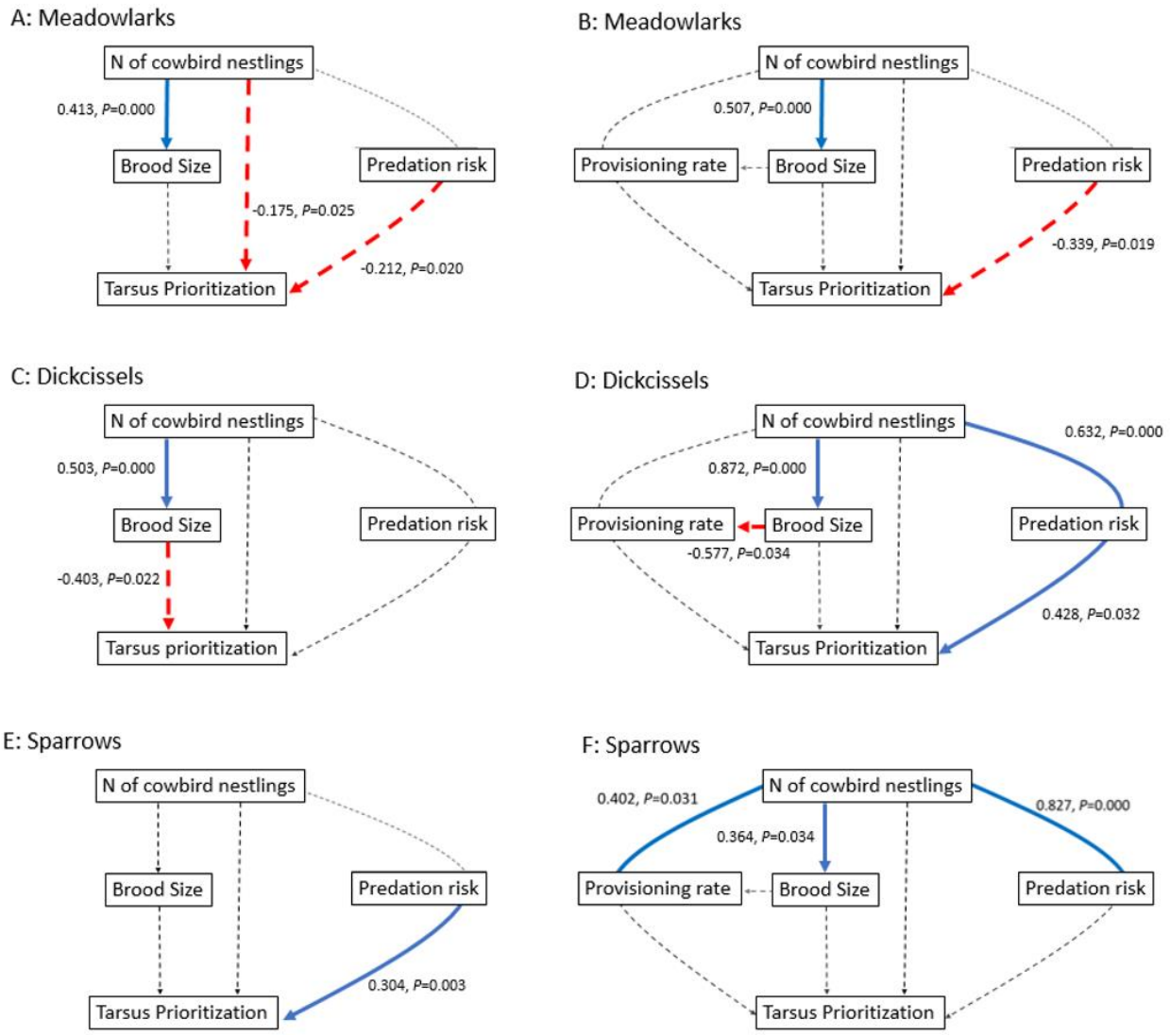

Figure 2-13. Combined results of species-specific structural equations modeling variation in mass-corrected tarsus lengths (tarsus prioritization). Blue solid lines indicate positive (β>0) relationships (P<0.05), red dashed lines indicate negative (β<0) relationships, and gray dashed lines indicated pathways included in the model but not related. Each relationship is labelled with the standardized β value and *P* value. The panels portray the A) full model for Eastern Meadowlarks (Fisher's C_6=21.38, *P*=0.002), B) reduced model for Eastern Meadowlarks (Fisher's C8=14.92, P=0.061), C) full model for Dickcissels (Fisher's C4=27.92, P<0.001), D) reduced model for Dickcissels (Fisher's C8=7.49, P=0.485), E) full model for Grasshopper Sparrows (Fisher's C6=10.74, P=0.097), and F) reduced model for Grasshopper Sparrows (Fisher's C10=13.56, P=0.194).

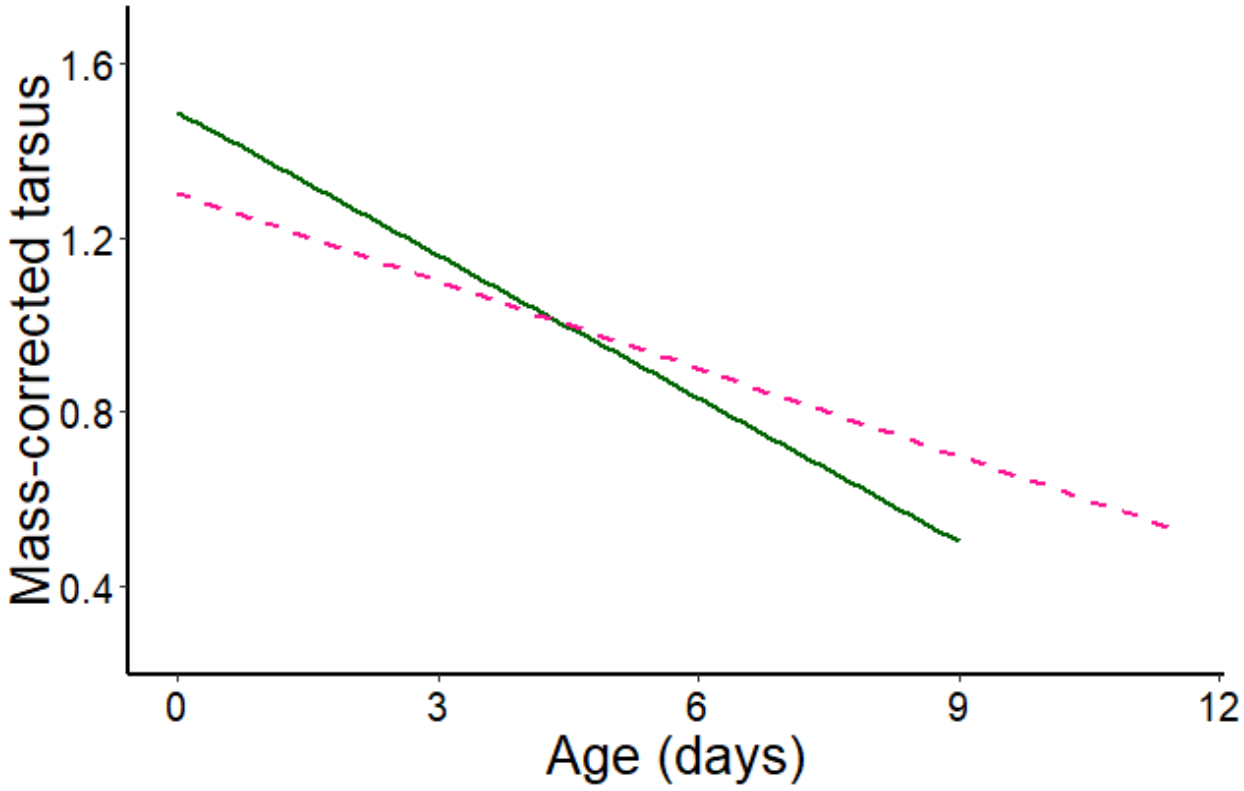

Figure 2-14. Parasitized meadowlarks (green solid line) prioritized mass gain over tarsus gain as they aged relative to unparasitized conspecifics (pink dashed line) (β=-0.2, *P*=0.025). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on change in mass-corrected tarsus lengths over time (see Figure 2-13A).

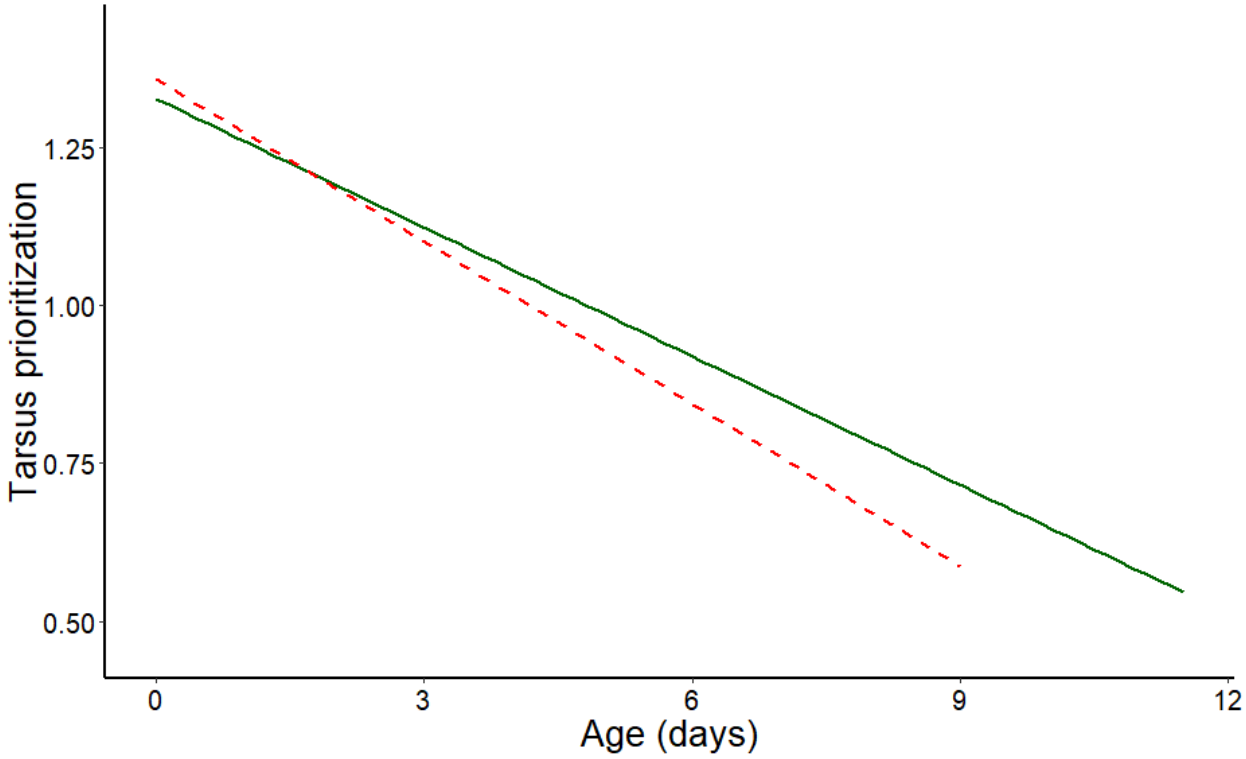

Figure 2-15. Meadowlarks in nests with higher risk (>0.4 depredated nests/ha) prioritized mass gain over tarsus growth as they aged relative to meadowlarks in nests with lower predation risk (<0.4 depredated nests/ha) (β=-0.2, *P*=0.020). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected tarsus lengths over time (see Figure 2-13A).

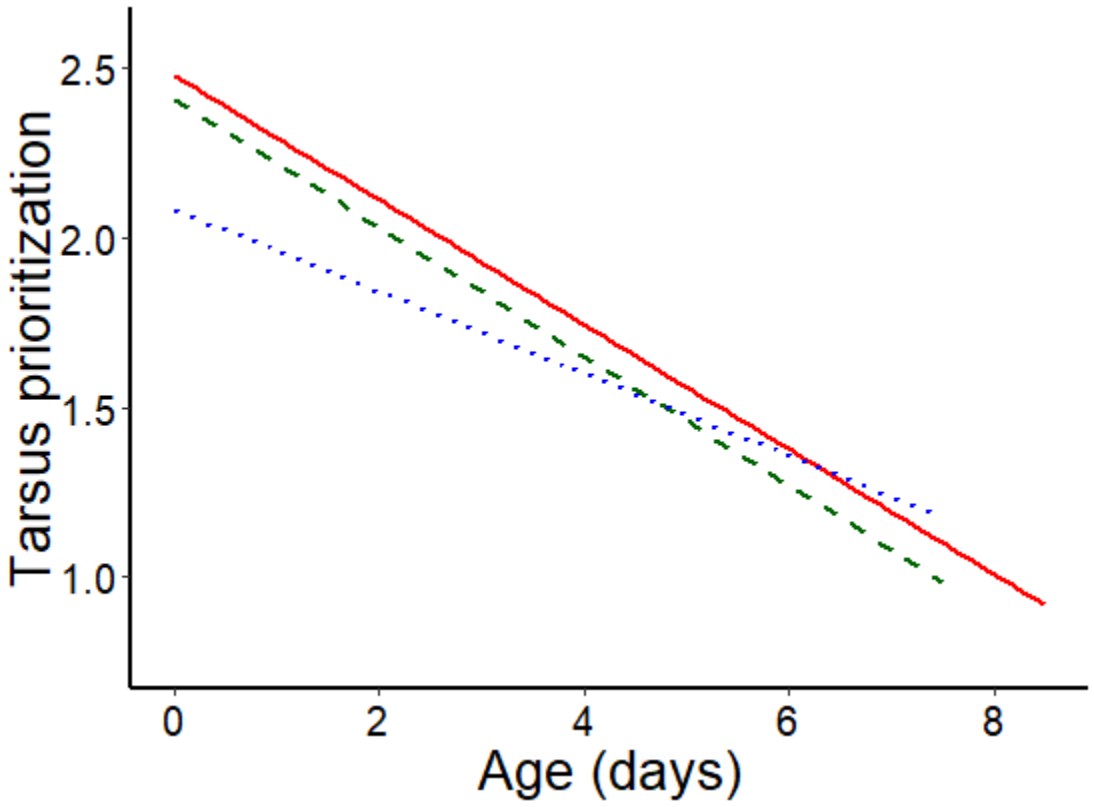

Figure 2-16. Dickcissels in large broods of cowbirds and conspecifics (4+ nestlings, red solid line) and medium broods (3 nestlings, green dashed line) prioritized the growth of their mass more than their tarsi relative to Dickcissels in smaller broods (1-2 nestlings, blue dotted line) (β=-0.4, *P*=0.022). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected tarsus lengths over time (see Figure 2-13C).

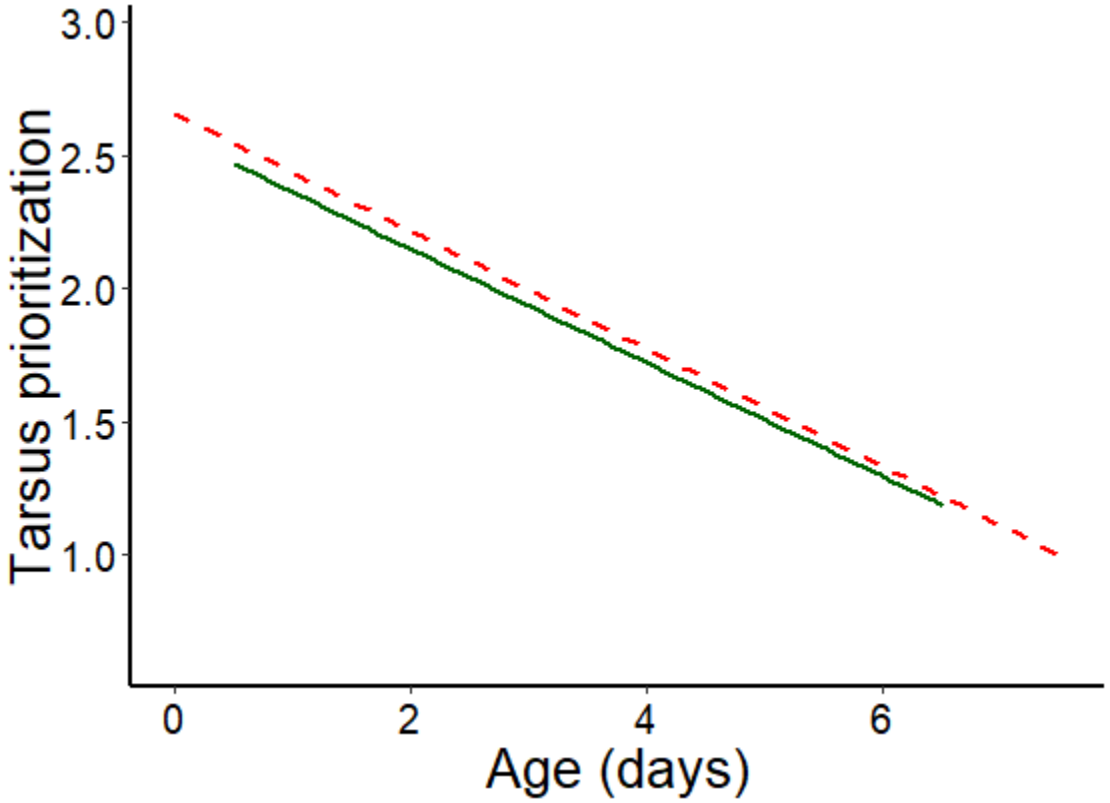

Figure 2-17. Dickcissels in nests with higher predation risk (>0.4 depredated nests/ha, red dashed line) prioritized the growth of their tarsus more than Dickcissels in less risky areas (<0.4 depredated nests/ha, green solid line) (β=0.4, *P*=0.032). Lines are predicted values based on the reduced structural equation modelling the effect of environmental drivers on the change in mass-corrected tarsus lengths over time (see Figure 2-13D).

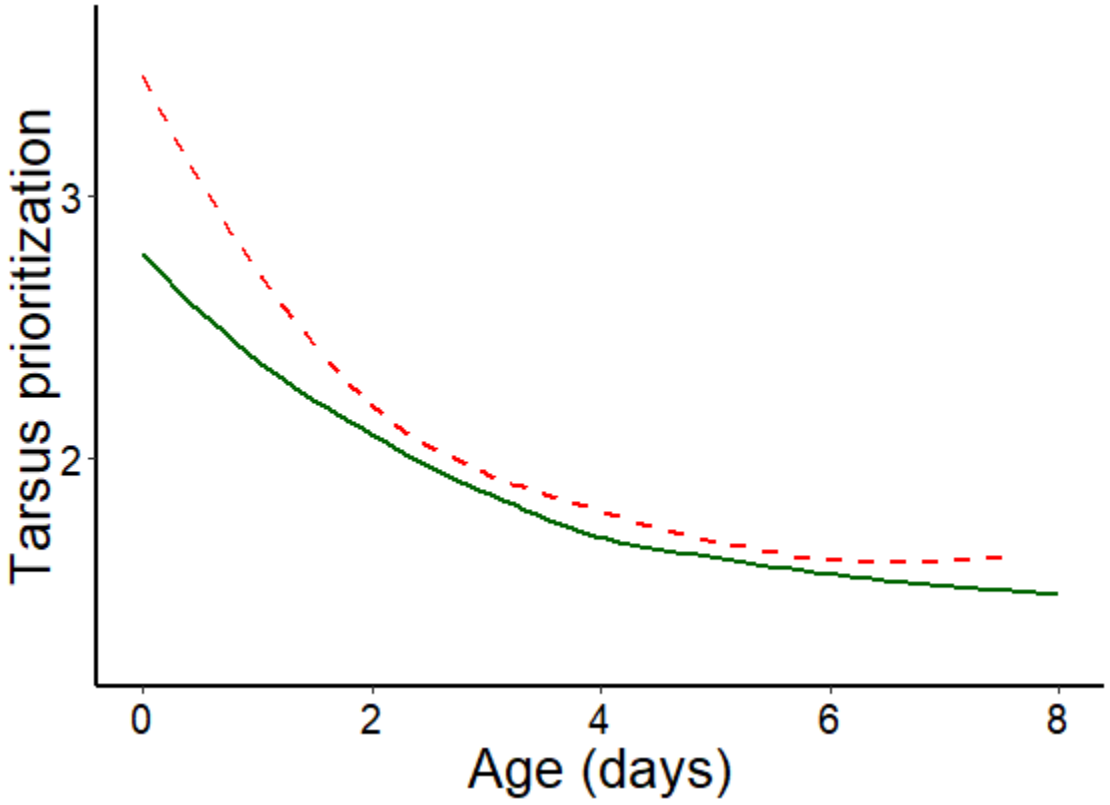

Figure 2-18. Sparrows in nests with higher predation risk (>0.4 depredated nests/ha, red dashed curve) prioritized the growth of their tarsus more than sparrows in less risky areas (<0.4 depredated nests/ha, green solid curve) (β=0.3, *P*=0.003). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected tarsus lengths over time (see Figure 2-13E).

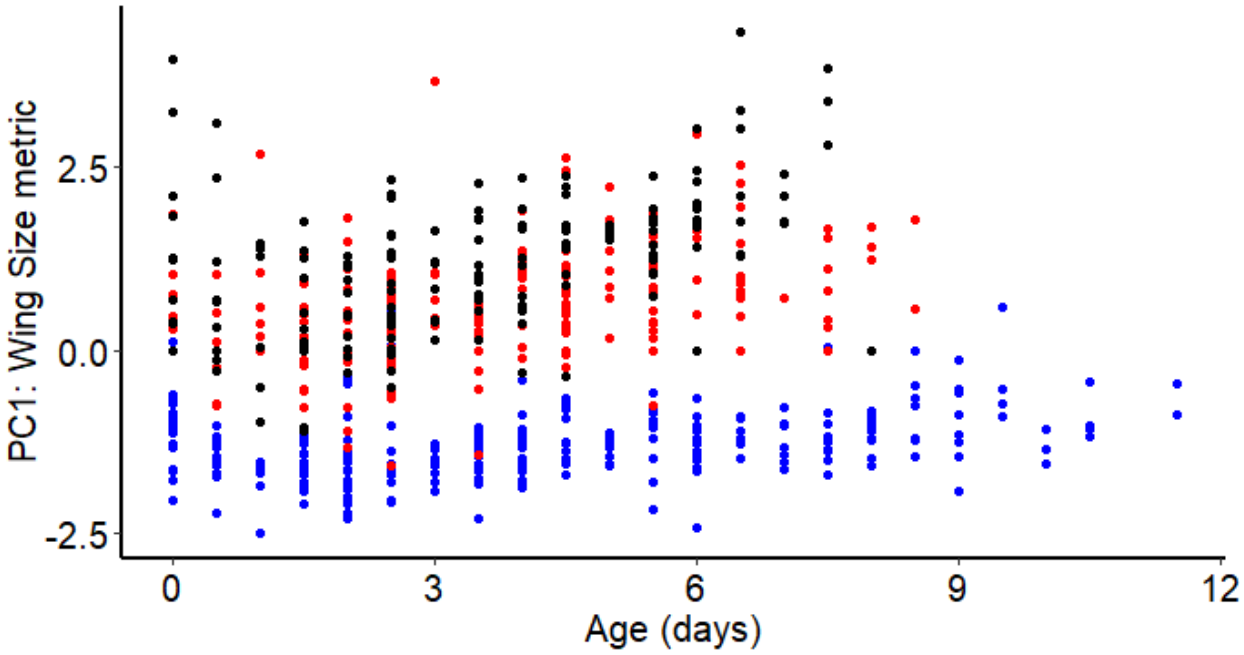

Figure 2-19. Host Wing Principal Component 1 scores over time (in days from hatch day=0). Principal component 1 represents the mass-corrected wing scores, with larger numbers indicating significantly larger wing composite scores than expected based on the nestling's mass. Blue dots represent Eastern Meadowlark nestlings, red dots represent Dickcissel nestlings, and black dots represent Grasshopper Sparrow nestlings.

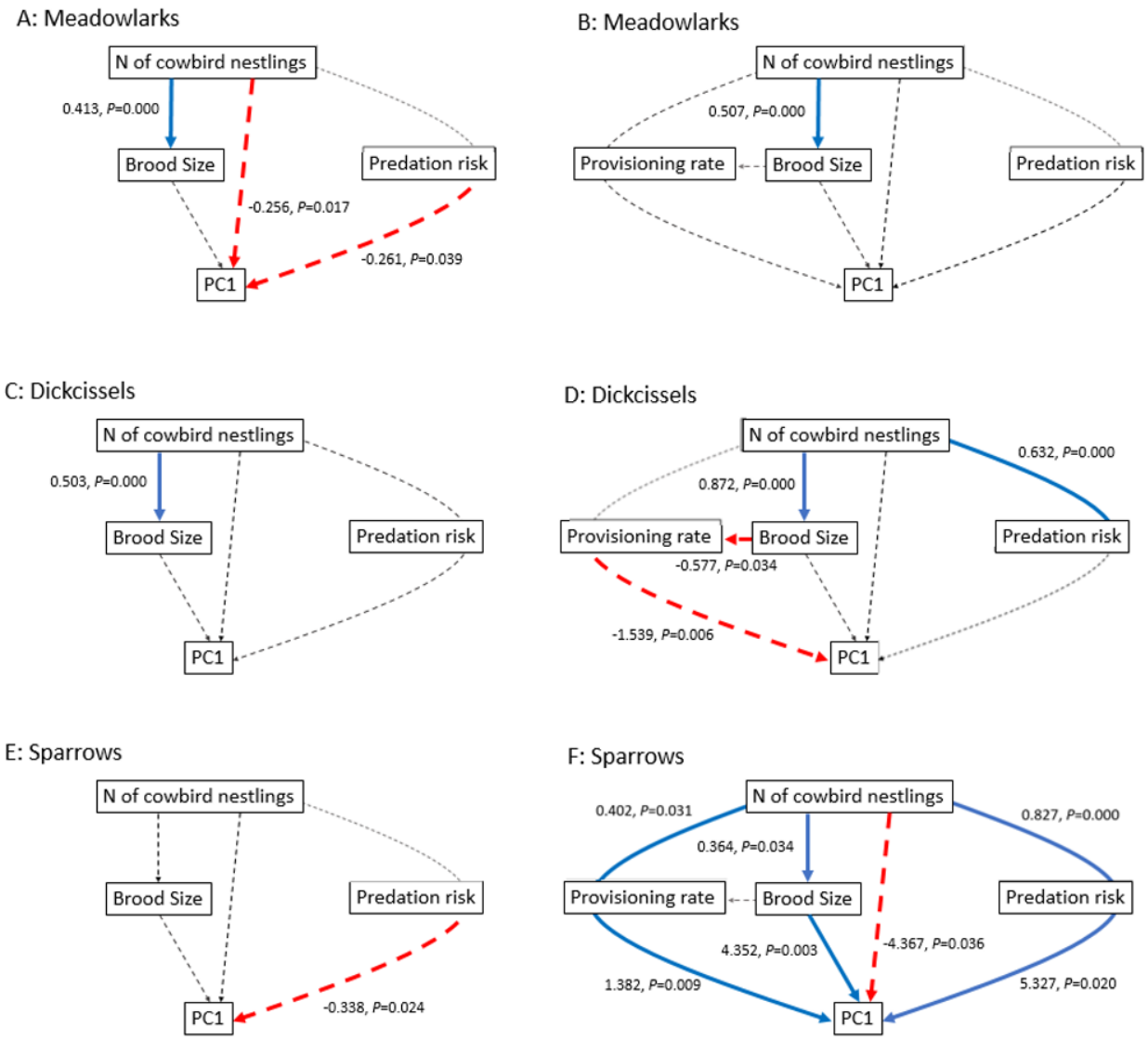

Figure 2-20. Combined results of species-specific structural equations modeling variation in principal component one, mass-corrected wing size. Blue solid lines indicate positive (β>0) relationships (P<0.05), red dashed lines indicate negative (β<0) relationships, and gray dashed lines indicated pathways included in the model but not related. Each relationship is labelled with the standardized β value and *P* value. The panels portray the A) full model for Eastern Meadowlarks (Fisher's C_6=21.38, *P*=0.002), B) reduced model for Eastern Meadowlarks (Fisher's C8=14.92, P=0.061), C) full model for Dickcissels (Fisher's C4=27.92, P<0.001), D) reduced model for Dickcissels (Fisher's C8=7.49, P=0.485), E) full model for Grasshopper Sparrows (Fisher's C6=10.74, P=0.097), and F) reduced model for Grasshopper Sparrows (Fisher's C10=13.56, P=0.194).

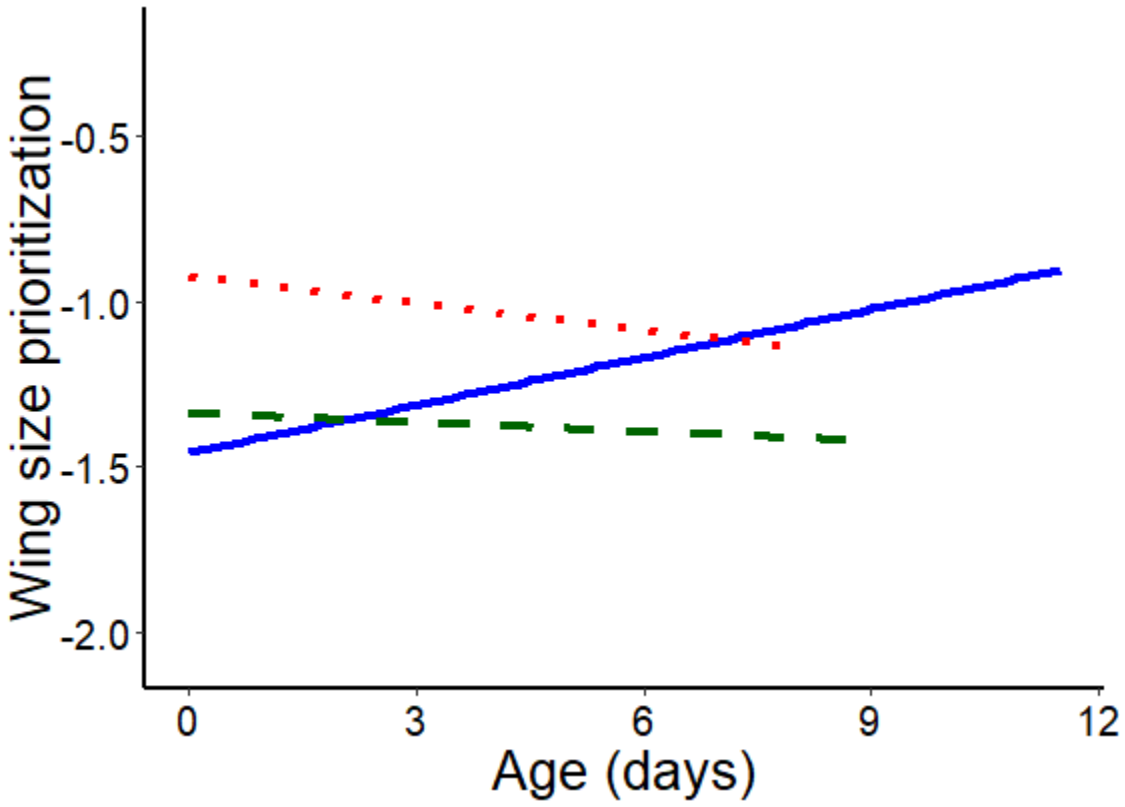

Figure 2-21. Meadowlark nestlings in nests with one (green dashed line) or two (red dotted line) cowbirds prioritized their mass growth over their wing growth as they aged, but non-parasitized conspecifics (blue solid line) prioritized wing growth instead (β=-0.256, *P*=0.017). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected wing scores over time (see Figure 2-20A).

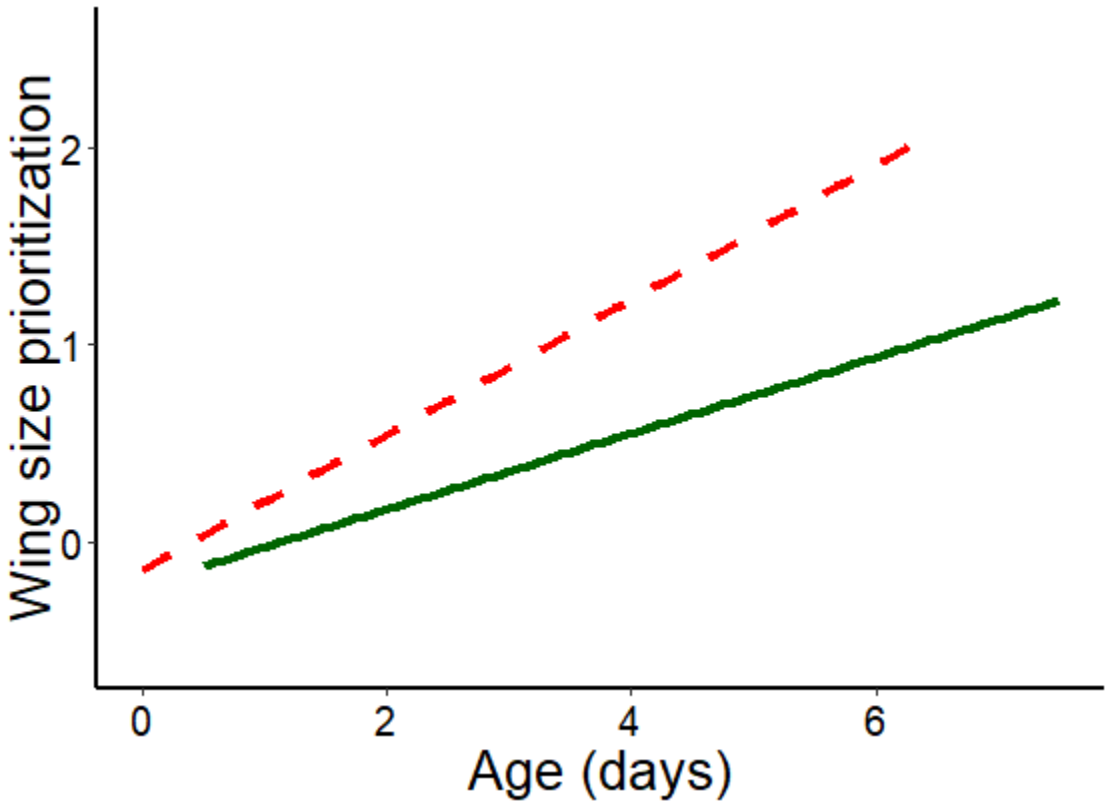

Figure 2-22. Dickcissel nestlings receiving more provisioning visits/nestling/hour (>1.08, green solid line) prioritized wing size less than nestlings receiving fewer provisioning visits/nestlings/hour (<1.08, red dashed line) (β=-1.5, *P*=0.006). Lines are predicted values based on the reduced structural equation modelling the effect of environmental drivers on the change in mass-corrected wing scores over time (see Figure 2-20D).

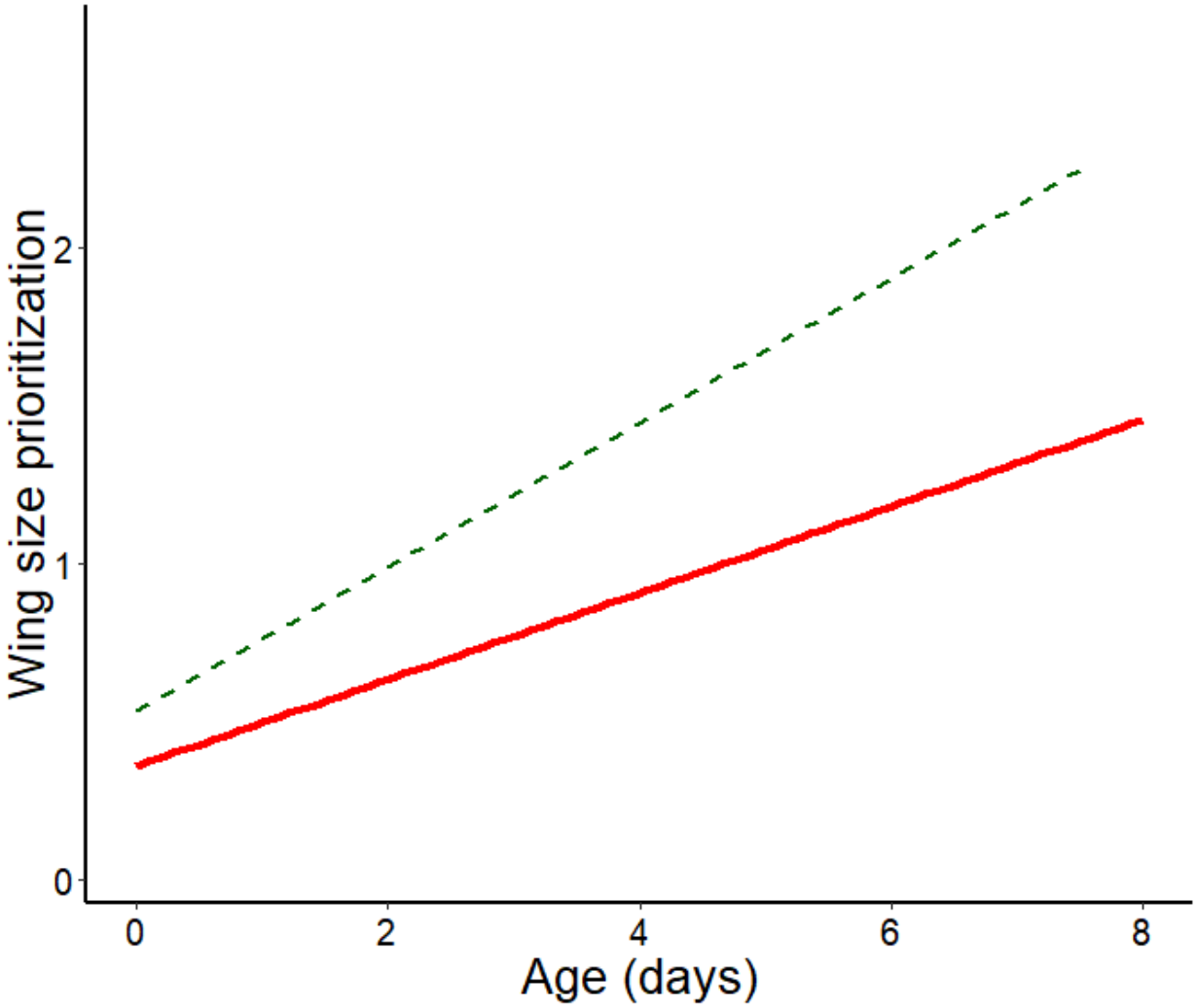

Figure 2-23. Sparrow nestlings in nests with lower predation risk (<0.4 depredated nests/ha, green dashed line) prioritized wing size growth more than conspecifics in higher-risk nests (>0.4 depredated nests/ha, red solid line) (β=-0.3, *P*=0.024). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected wing scores over time (see Figure 2-20E).

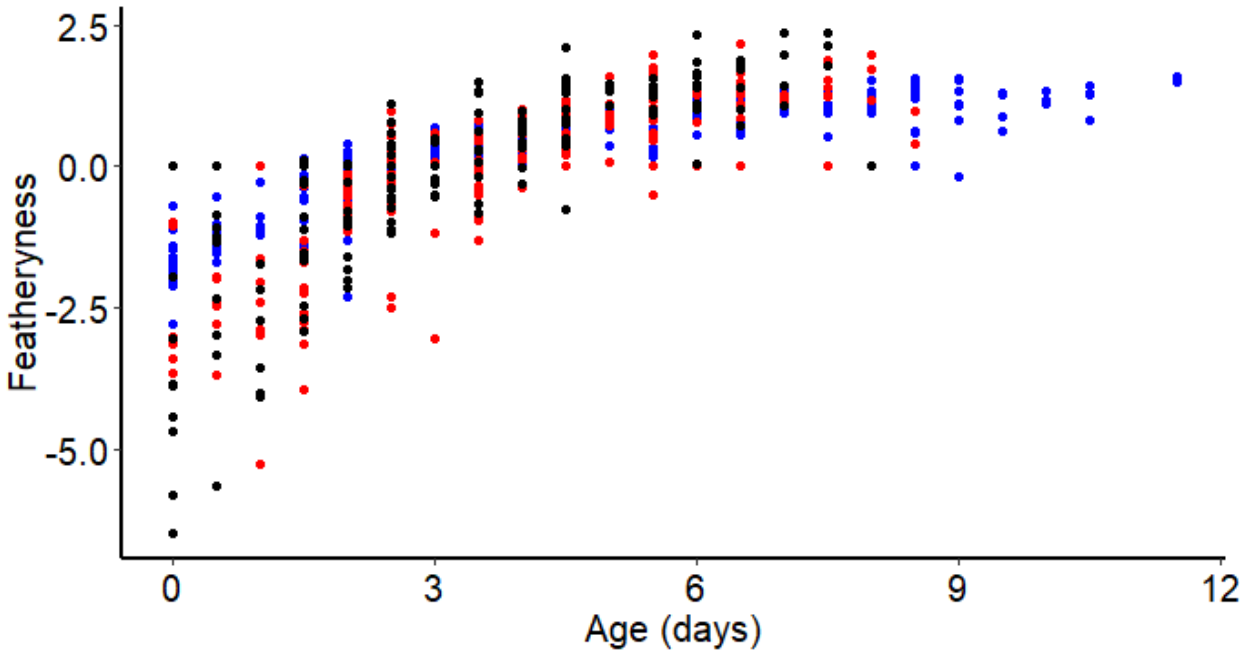

Figure 2-24. Host Wing Principal Component 2 scores over time (in days from hatch day=0). Principal component 2 represents higher mass-corrected feather development. Large numbers indicate that nestlings have higher mass-corrected feather lengths, potentially indicating prioritization of feather development over mass gain.

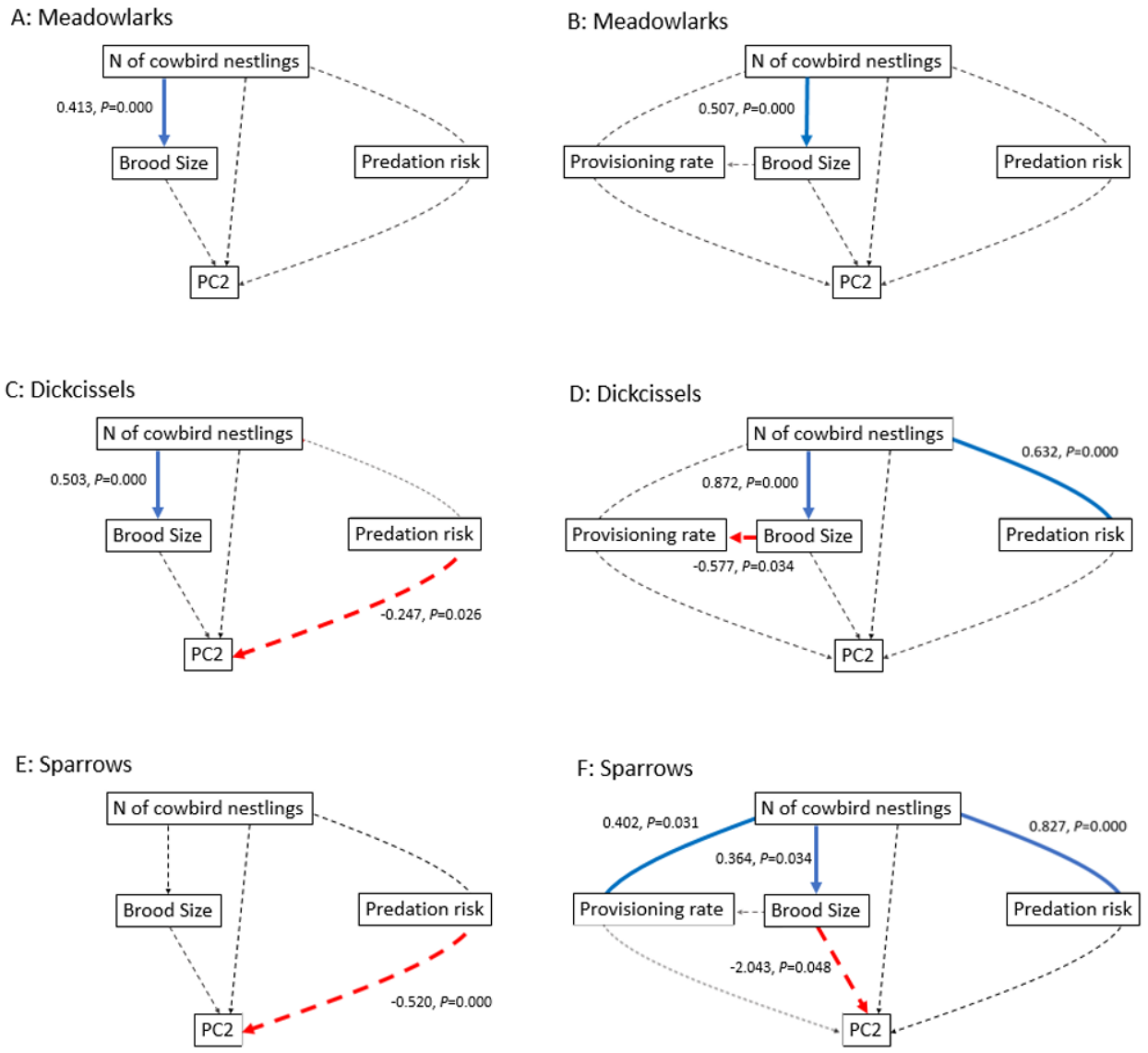

Figure 2-25. Combined results of species-specific structural equations modelling variation in mass-corrected feather lengths (PC2) over time. Blue solid lines indicate positive (β>0) relationships (P<0.05), red dashed lines indicate negative (β<0) relationships, and gray dashed lines indicated pathways included in the model but not related. Each relationship is labelled with the standardized β value and *P* value. The panels portray the A) full model for Eastern Meadowlarks (Fisher's C_6=21.38, *P*=0.002), B) reduced model for Eastern Meadowlarks (Fisher's C8=14.92, P=0.061), C) full model for Dickcissels (Fisher's C4=27.92, P<0.001), D) reduced model for Dickcissels (Fisher's C8=7.49, P=0.485), E) full model for Grasshopper Sparrows (Fisher's C6=10.74, P=0.097), and F) reduced model for Grasshopper Sparrows (Fisher's C10=13.56, P=0.194).

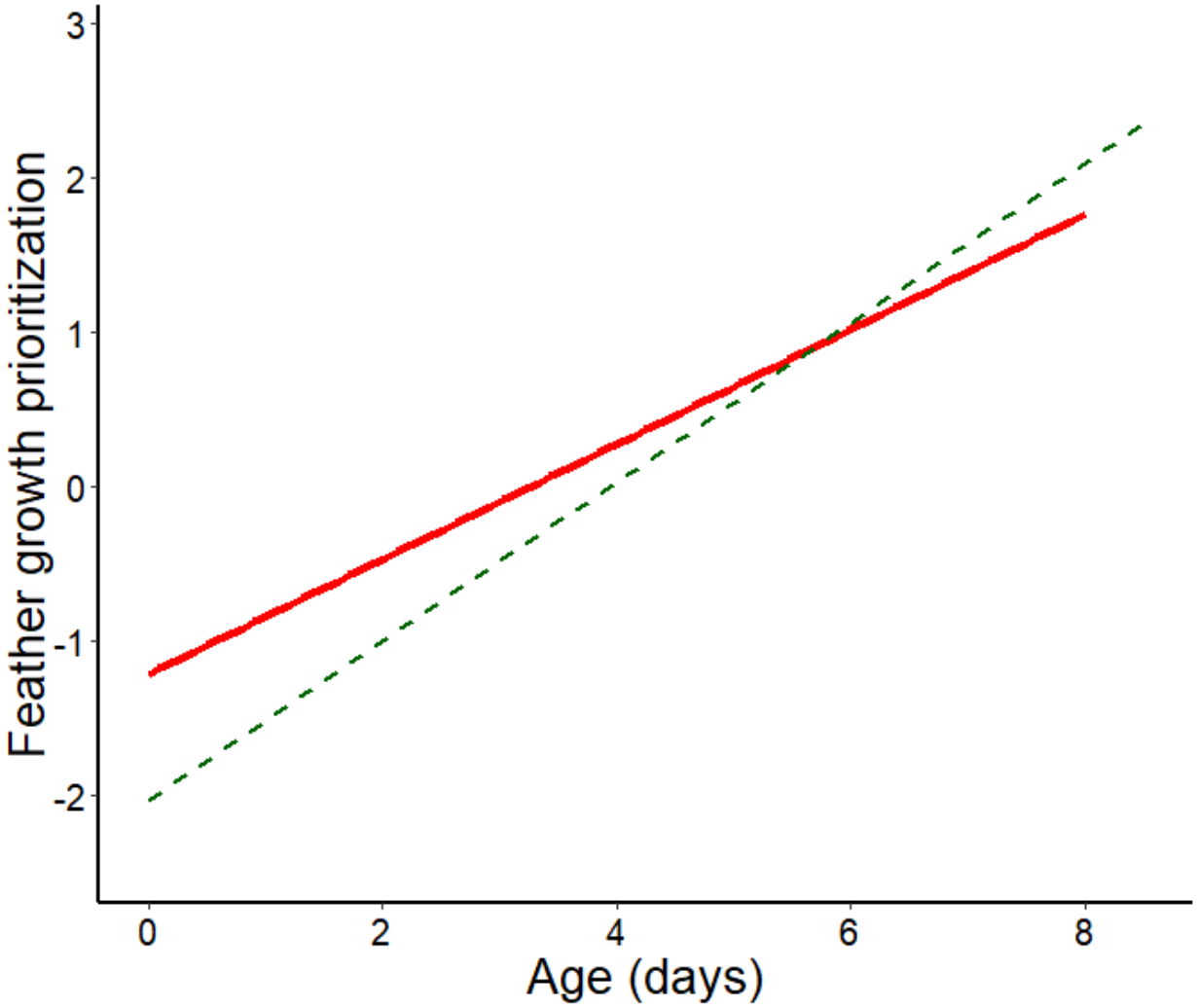

Figure 2-26. Dickcissel nestlings in nests with lower predation risk (<0.4 depredated nests/ha, green dashed line) prioritized their feather growth more over time than Dickcissel nestlings in nests with higher risk (>0.4 depredated nests/ha, red solid line) (β=-0.2, *P*=0.026). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected feather scores over time (see Figure 2-25C).

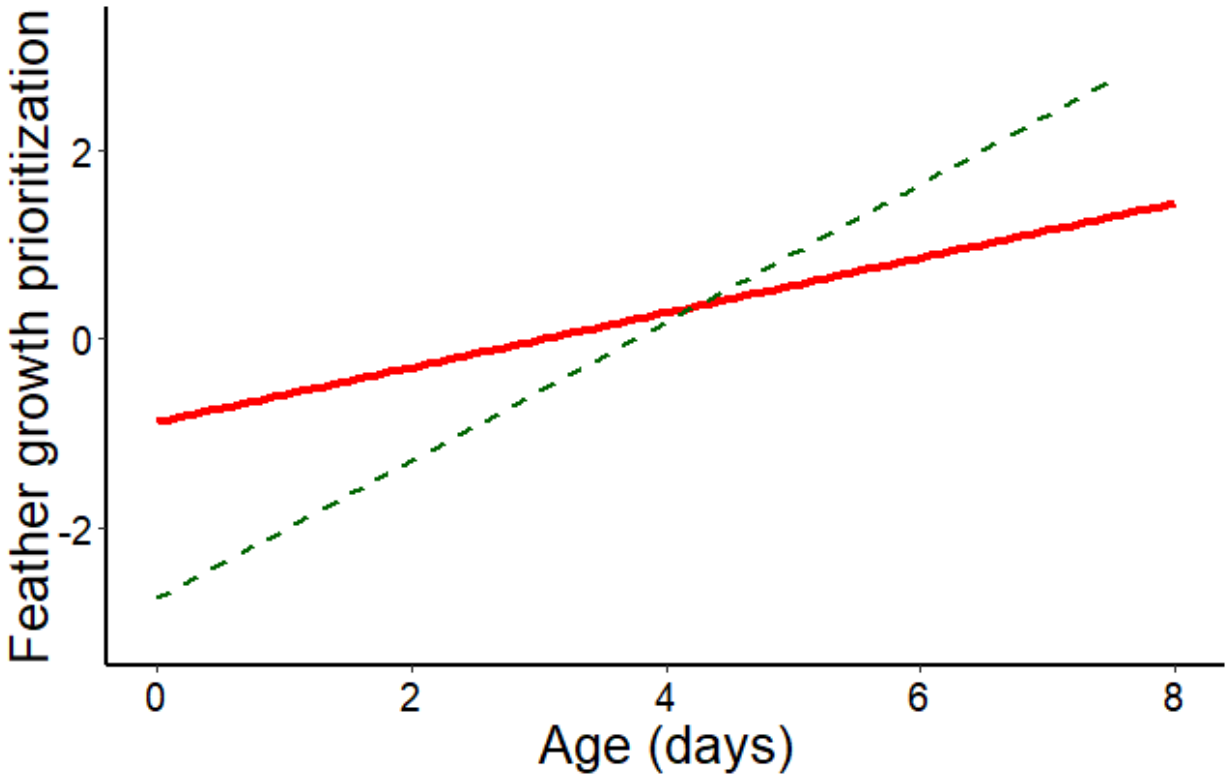

Figure 2-27. Sparrow nestlings in nests with lower predation risk (<0.4 depredated nests/ha, green dashed line) prioritized their feather growth more than conspecifics in nests with higher risk (>0.4 depredated nests/ha, red solid line) (β=-0.5, *P*=0.000). Lines are predicted values based on the full structural equation modelling the effect of environmental drivers on the change in mass-corrected feather scores over time (see Figure 2-25E).

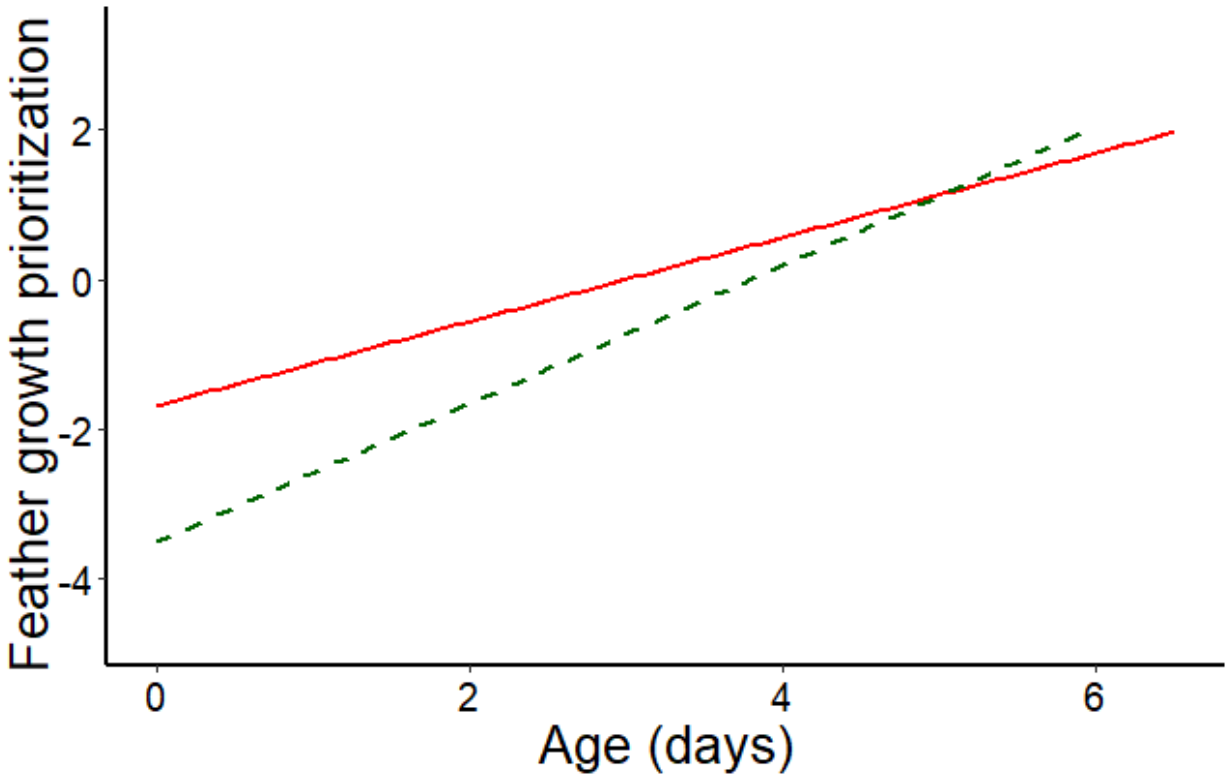

Figure 2-28. Sparrow nestlings in smaller broods (<4 nestlings, red solid line) prioritized feather growth as they aged relative to sparrow nestlings in large broods (4+ nestlings, green dashed line) (β=-2.0, *P*=0.048). Lines are predicted values based on the reduced structural equation modelling the effect of environmental drivers on the change in mass-corrected feather scores over time (see Figure 2-25F).

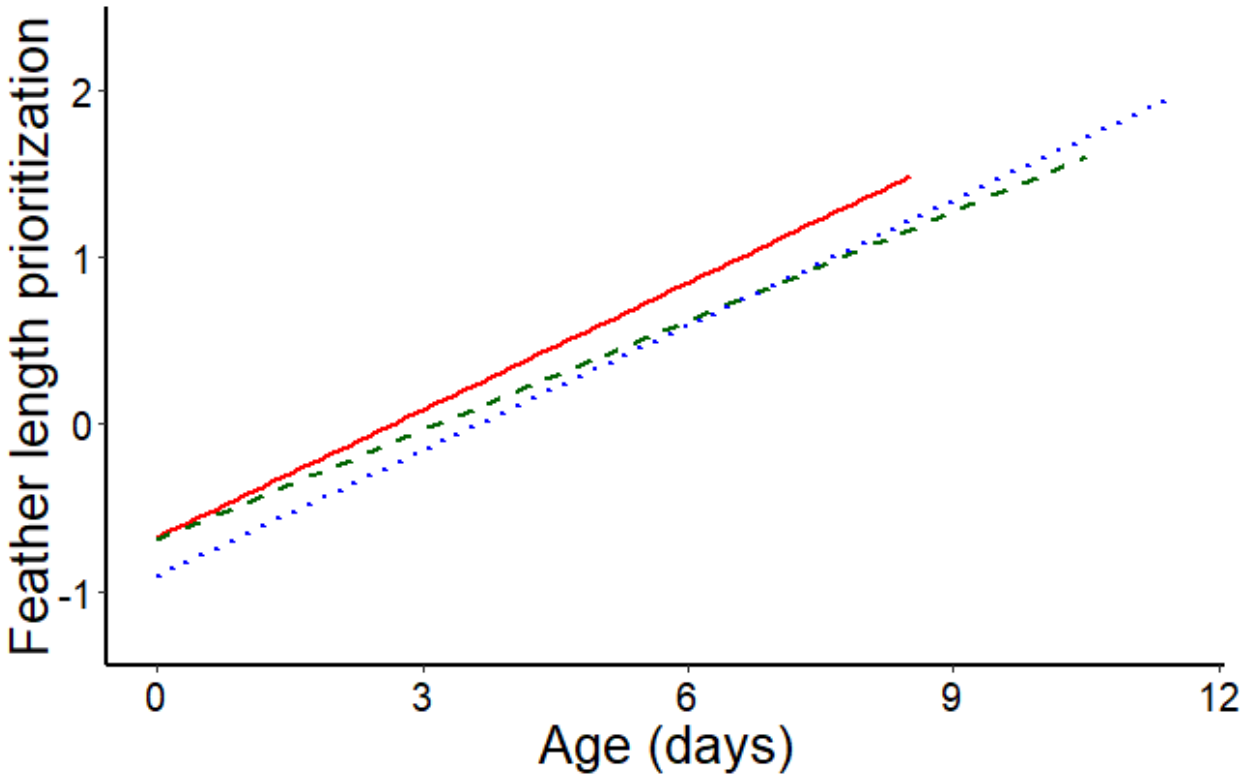

Figure 2-29. Meadowlark nestlings that fledged before day 9 (red solid line) prioritized their feather growth more than meadowlarks that took longer to fledge (blue dotted and green dashed lines) (t_{122}=3.047, *P*=0.003). Lines are predicted values based on linear mixed models relating fledge age to growth metrics.

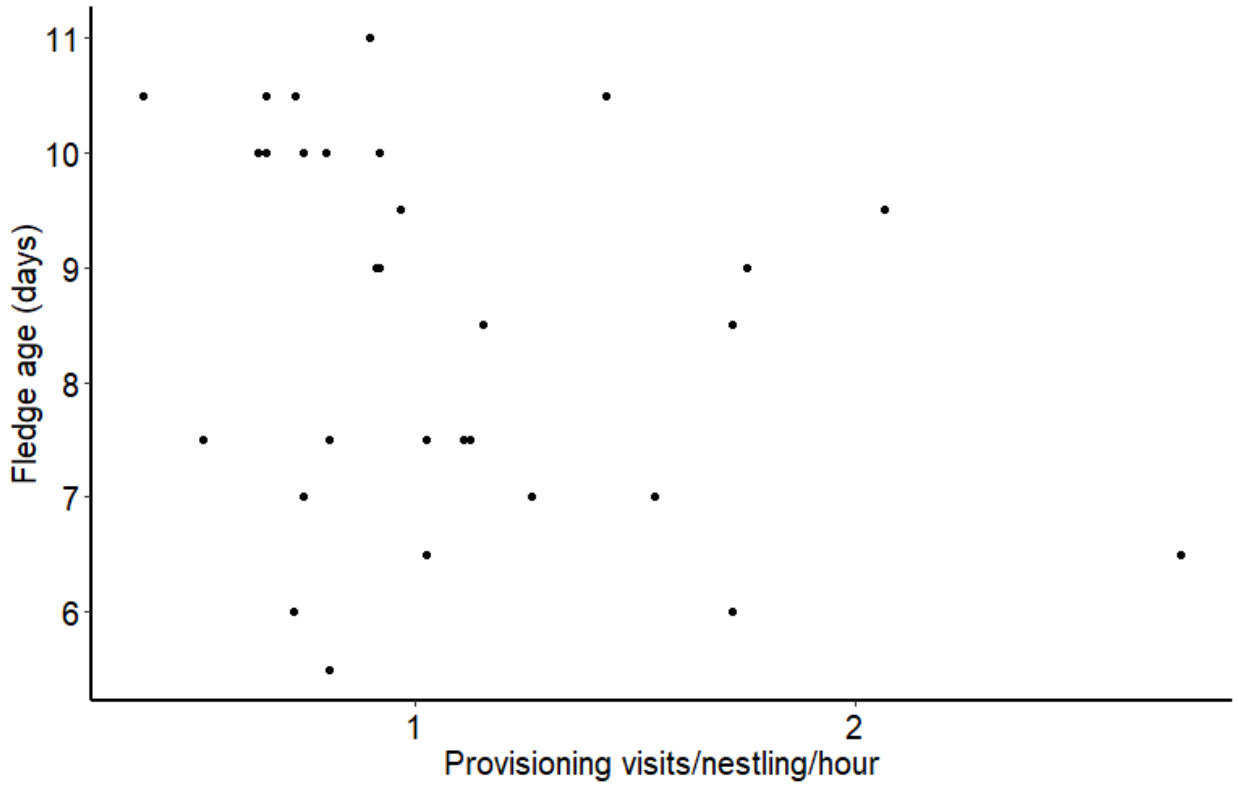

Figure 2-30. As provisioning visits per nestling per hour increase, the fledge age of nestlings (in days) decreases across all species (t_{49}=-2.2, *P*=0.031).

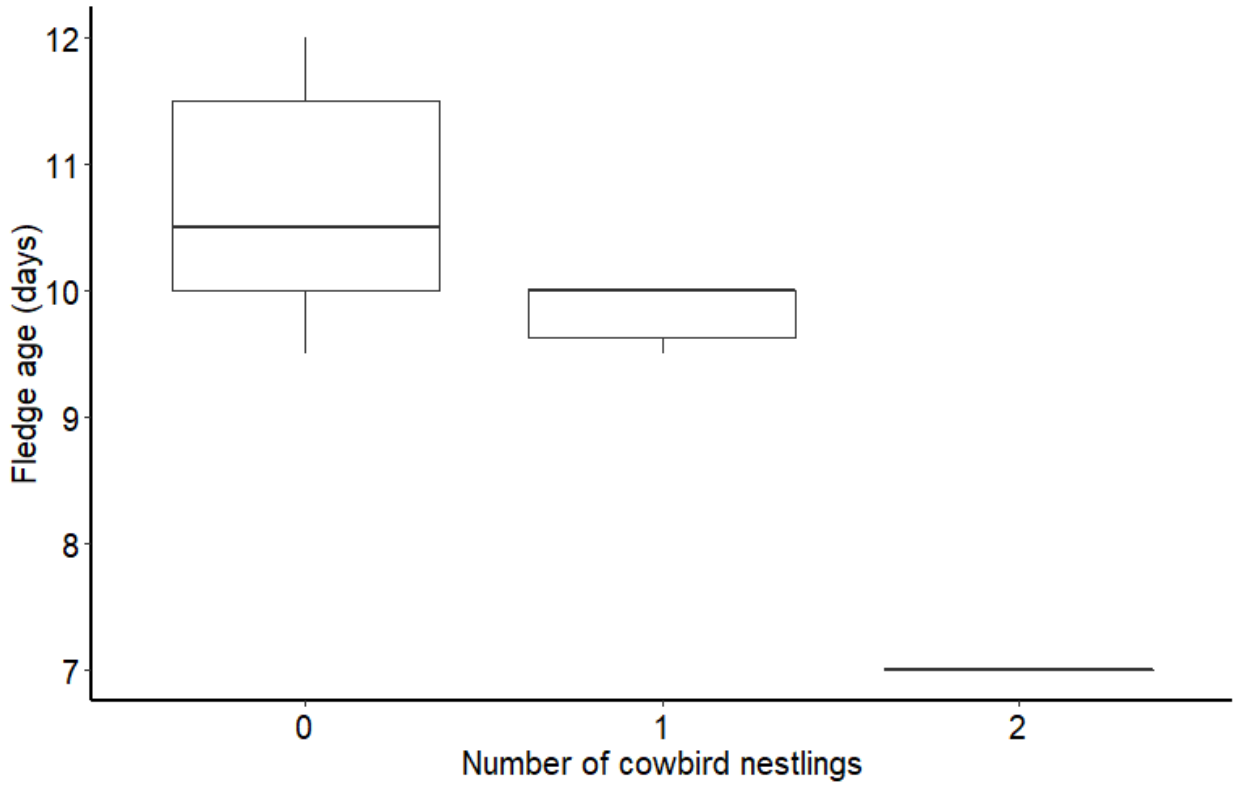

Figure 2-31. Parasitized meadowlarks fledged 30% earlier on average than non-parasitized conspecifics (t_{21}=-3.5, *P*=0.002).

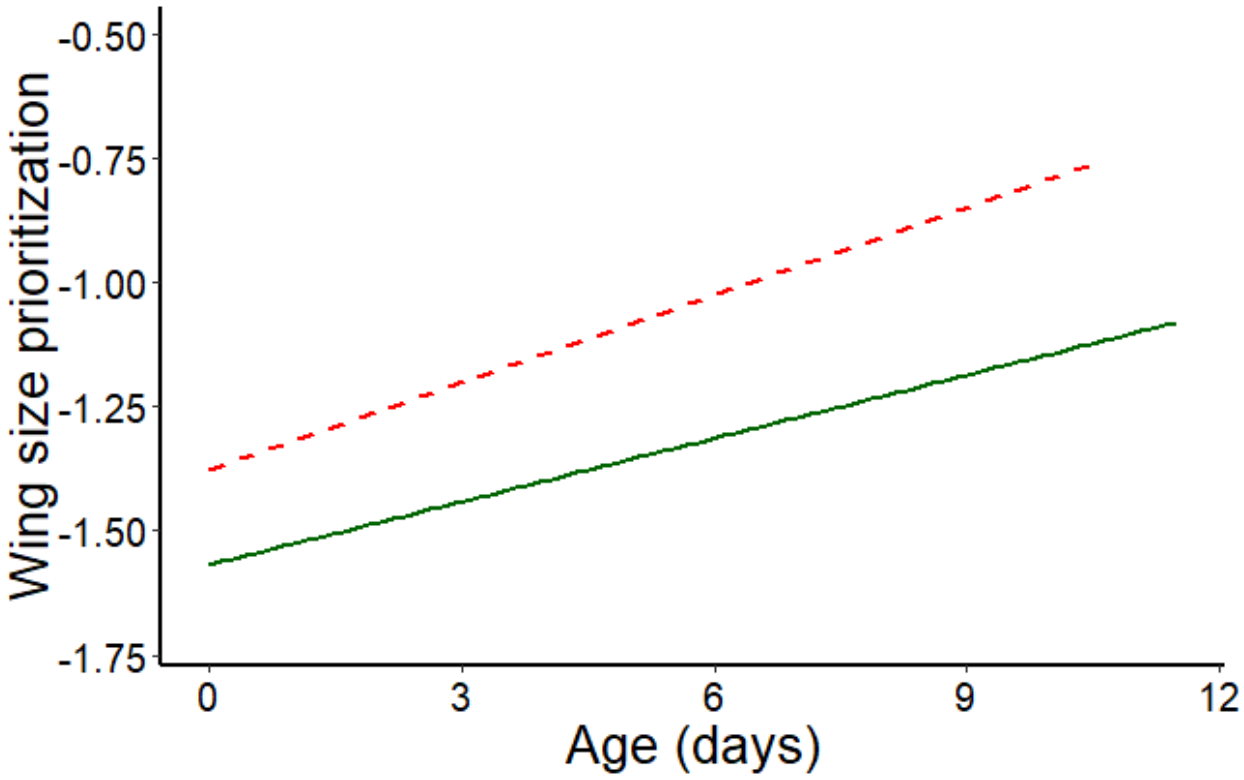

Figure 2-32. Meadowlark nestlings that were depredated before they left the nest (red dashed line) had higher mass-corrected wing scores than conspecifics that were ultimately successful (green solid line) (z_{86}=2.2, *P*=0.027). Lines are predicted values based on linear mixed models relating nest fate to growth metrics.

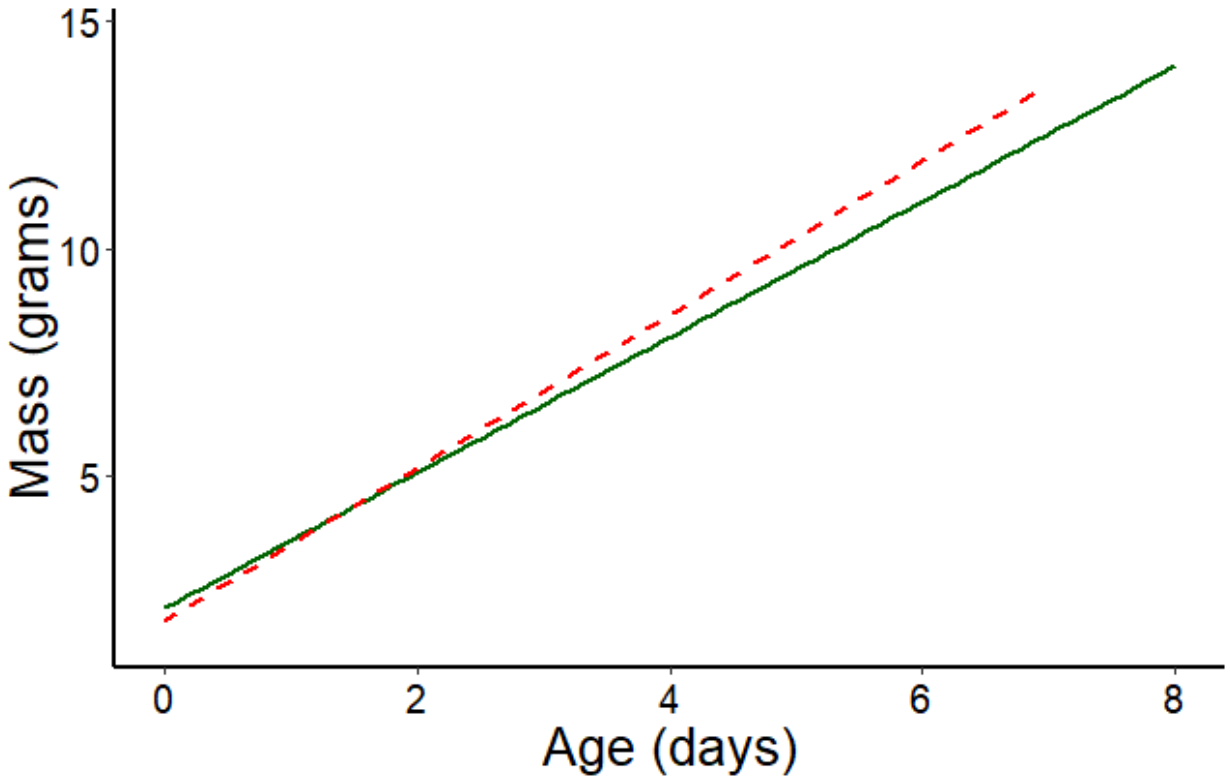

Figure 2-33. Sparrow nestlings that were depredated before they left the nest (red dashed line) had gained mass more quickly than the sparrow nestlings that were ultimately successful (green solid line) (z_{80}=-1.8, *P*=0.074). Lines are predicted values based on linear mixed models relating nest fate to growth metrics.

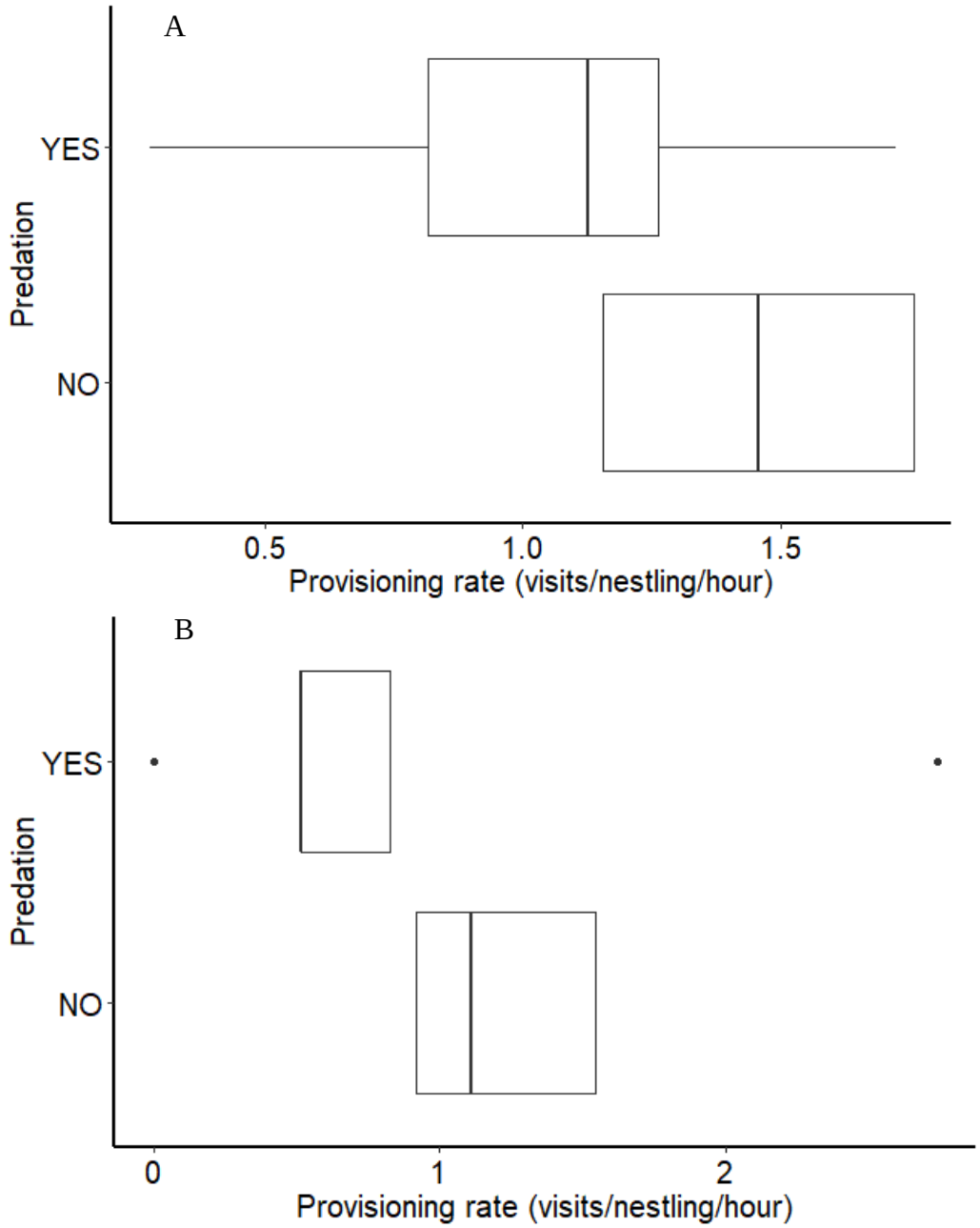

Figure 2-34. (A) Dickcissel and (B) sparrow nests that were ultimately depredated had received fewer provisioning visits per nestling per hour on day 4 (Dickcissel: z_{55}=-2.7, *P*=0.007; sparrow: z_{33}=-1.8, *P*=0.075).

Chapter 3 - Effect of host species on cowbird growth

Nestling competition affects the growth and development of parasitic Brown-headed Cowbird (*Molothrus ater*) nestlings, but does not influence laying decisions of female cowbirds

Abstract

Animal offspring grow at different rates and the relative sizes of different structures change as they develop. Variation in growth has implications for fitness and population dynamics. Differences in growth can result from both genetic variation and plastic responses to the natal environment, but disentangling these drivers is challenging. A tractable approach to isolating the role of natal environment on development is by studying generalist avian brood parasites. These species lay their eggs in the nests of other species, exposing offspring to substantial variation in natal environment due to differences in host species' nesting biology. I determined the effect of environmental drivers on the growth and relative development of legs and wings of the parasitic Brown-headed Cowbird (*Molothrus ater*) in the nests of three grassland songbird species. I used nest cameras to quantify provisioning rates at a subset of those nests. Using multilevel structural equation models, I elucidated the relationships between host species, brood size, provisioning rate, predation risk, and cowbird development. Cowbird growth varied substantially among individuals, with some nestlings weighing twice that of conspecifics by their 8th day of life. They grew most quickly in nests of the smallest host species where cowbirds likely outcompeted host nestlings for food. Cowbirds' legs grew relatively faster in nests with higher *per capita* provisioning rates. Variation in predation risk was unrelated to cowbird growth, despite predation risk influencing growth of host nestlings. These results show that intraspecific variation in development can be the result of individual plastic responses to

local environmental variation, especially food availability and sibling competition, but hosts and parasites respond to drivers at different scales.

Introduction

Animal growth rates and development strategies vary dramatically among species and individuals (Badyaev and Martin 2000, McCarty 2001) and have long-lasting effects on survival and fecundity of the developing individual (Mousseau and Fox 1998), its reproductive partners (Monaghan et al. 2012), and their offspring (Lummaa and Clutton-Brock 2002). Although developmental differences are partially attributable to genetic variation (Westeberhard 1989, McCarty 2001), environmental factors often explain a substantial portion of the variation in growth (Hoffmann and Merilä 1999). Separating phenotypic plasticity from genetic variation can be complicated, especially when individuals experience very similar environmental conditions (Schew and Ricklefs 1998, Snell-Rood 2012). However, identifying these environmental drivers of variation in growth and their consequences is important in the study of life history and conservation (Sheriff and Love 2013).

Many studies of the evolution of life history strategies have focused on birds (Lindstrom 1999, Chaby 2016). Bird species grow at very different rates, vary in their allometric scaling, and/or fledge (leave the nest) at different stages (Gil et al. 2008). Environmental drivers such as food availability, sibling competition, and predation risk affect bird growth and development, but studying the nature of these drivers and their interactions can be difficult. While these environmental drivers may differ substantially among different bird species, a single species inhabits more similar environments, perhaps explaining why intraspecific variation in growth rate is rarely observed in passerine birds (Starck et al. 1995). Brood parasites, however, lay their

eggs in host nests rather than raising their own young themselves (Davies 2000). A generalist brood parasite species may parasitize hundreds of species (Friedmann and Kiff 1985) and individual females potentially lay eggs in nests of several species. Thus, their offspring must cope with substantial variation in environmental conditions resulting from diverse host species' nesting ecology, and consequently the parasites' growth rates vary by host species (Remeš 2010), providing a system in which to identify the effects of environmental variation on growth and development. Previous research on parasite growth variation compared growth rates for host species using a single average value of cowbird growth per host species (Remeš 2010); by focusing on variation in parasite growth and development both among hosts and among nests of the same hosts, this study uses brood parasites as a model to examine the relationship between growth and not only host-species-level differences, but also other fine-scale measurements of environmental variation.

I tested hypotheses explaining the effects of environmental drivers and their interactions on nestling growth in Brown-headed Cowbirds (*Molothrus ater*). Cowbirds are generalist brood parasites native to the Great Plains of North America (Lowther 1996). Across their range, cowbirds parasitize more than 220 species (Friedmann and Kiff 1985). Cowbird growth varies dramatically among nests of different host species with fledging masses ranging from 14.8 to 28.2 grams (Remeš 2010). Because cowbirds experience both a broad range of natal environments and exhibit variation in development, they provide an ideal system in which to study development strategies.

Cowbirds and other altricial nestlings are completely dependent on parental care for days to weeks after they hatch (Kilner and Johnstone 1997, Wright and Leonard 2002). Nestling growth rate and survival is typically higher with increasing food quantity and quality. Therefore,

I hypothesized that variation in the *per capita provisioning rate* will be related to variation in growth and development (Soma et al. 2006). If provisioning rates fall below the threshold needed for nestling development (Morandini and Ferrer 2015), within-nest competition for resources can be fierce, slowing growth (Naguib et al. 2006). Brood parasitic nestlings are exceptional competitors, begging for food more loudly and frequently than do host nestlings (Dearborn and Lichtenstein 2002), extending their bodies higher than their nestmates to access food, and accelerating the development of their gapes which provides a visual cue to parents that induces feeding (Davies et al. 1998, Tanaka and Ueda 2005).

The total number of nestlings in a brood can influence nestling competition, parental care, growth rates, and nest success; thus, I hypothesized that *brood size* will affect cowbird development as well. Parents often visit nests with larger broods more frequently, but this may not necessarily increase the *per capita* provisioning rate (Rivers et al. 2014). The evidence for relationships between brood size and cowbird growth is mixed. In some cases, cowbirds raised in large broods do not gain mass as quickly as cowbirds in nests with fewer nestlings (Hatch 1983). However, cowbirds in large broods sometimes receive more food than cowbirds in small broods (Kilner et al. 2004), resulting in no difference in growth between cowbirds in nests of species of varying mean brood size (Remeš 2010). The consequences of brood size are likely dependent on the parents' capacity to increase feeding rates to meet demand which likely varies by host species and environmental context (Hegner and Wingfield 1987).

Host size influences cowbird growth rates (Remeš 2010) as it does in other brood parasites (Kleven et al. 1999). Cowbirds raised in nests of small hosts typically suffer from low provisioning rates, while cowbirds in the nests of large hosts face high nestling competition (Kilner 2003). These results, however, are based on estimates of average cowbird growth rates

and provisioning rates/host species. Within nest of host-species, considerable variation in other environmental factors like predation risk or *per capita* provisioning rate exist. Host size may ultimately influence cowbird nestling survival with cowbirds raised in intermediate-sized host nests more successful than cowbirds raised by smaller or large (>80g) hosts (Lorenzana and Sealy 2001). I hypothesized that *host size* would influence cowbird growth and development, with cowbirds growing the most quickly in the nests of hosts with smaller-bodied nestlings.

A fourth hypothesized driver of cowbird nestling development variation is nest *predation risk.* Predation is the primary cause of breeding failure in birds (Martin 1995) and consequently, a key driver of avian life history traits (Martin and Briskie 2009). Songbirds parasitized by cowbirds experience predation rates ranging from 10% (Best 1978) to 90% (Jensen and Cully 2005). The fear of potential predation can influence development; under high predation risk, nestling grow faster and fledge earlier (Monrós et al. 2002), or they prioritize the growth of wings, increasing their mobility and escape potential (Coslovsky and Richner 2011). Parents make decisions to minimize the risk of predators following them to the nest and/or to minimize their own predation risk; these decisions may produce alternative nestling growth patterns. Scared parents reduce provisioning to avoid attracting predators (Martin et al. 2000, Ghalambor et al. 2013), resulting in reduced offspring growth rates (Naef-Daenzer and Keller 1999) and prolonged brooding periods (Martin and Briskie 2009). Furthermore, parents' perception of risk may be mediated by the presence of cowbirds themselves via two potential mechanisms: (a) cowbird adults are common nest predators eating eggs and killing nestlings (Scott et al. 1992, Rodewald and Kearns 2011); and (b) nestling cowbirds' loud begging may reveal nest locations, thereby increasing predation risk (Haskell 2002).

I tested the *provisioning rate*, *brood size*, *host size*, and *predation risk* hypotheses in a population of Brown-headed Cowbirds breeding in the northern Flint Hills region of central USA. Parasitism rates are exceptionally high in this region, affecting 90% of nests in some species (Hatch 1983, Jensen and Cully 2005). I quantified the growth of cowbird nestlings in three common cowbird host species in the region (Elliot 1978): Eastern Meadowlarks (*Sturnella magna*), Dickcissels (*Spiza americana*), and Grasshopper Sparrows (*Ammodramus savannarum*) (Ortega 1998, Rivers et al. 2010). These species exhibit inter- and intra-specific variation in brood sizes, provisioning rates, and predation rates (Chapter 2).

I predicted that if cowbird growth and development is primarily affected by *provisioning rate*, then (i) cowbirds would have a higher mass in nests where parents provision more frequently (calculated as provisioning visits per nestling per hour) than in nests where parents provision less frequently, regardless of host species size (Figure 3-1). If growth and development is most affected by *brood size*, I predicted that (ii) cowbirds would experience adverse effects of competition in large broods because the *per capita* provisioning rate would be lower, resulting in lower cowbird masses. I predicted that cowbirds prioritize growth of competitive structures (i.e. legs that enable them to raise their bodies during begging) in (iii) larger broods or in nests with (iv) fewer provisioning visits per nestling. Additionally, I explored the indirect mechanisms linking brood size and cowbird development by testing for relationships between brood size and both provisioning rates and predation. If growth rates are primarily driven by differences in *host size*, I predicted that in nests of smaller relative to large host species (v) cowbirds would grow faster because they can better outcompete the smaller host nestlings, independent of provisioning rates. Finally, if growth rates are driven by differences in *predation risk*, I predicted that (vi) cowbirds would be smaller when raised in areas of high predator risk due to decreased

provisioning, or (vii) cowbirds in high-risk nests would prioritize the growth of structures that increase mobility (wing bones and feathers) to enable earlier fledging. I tested these predictions with structural equation models (Figure 3-1).

Methods

I studied cowbirds over two seasons (2017 and 2018) at the Konza Prairie Biological Station and Rannell's Preserve, adjacent tallgrass prairie sites in Northeast Kansas, USA. The Konza Prairie Biological Station (KPBS; 39.107, -96.609) is an experimental prairie site with high prairie heterogeneity due to replicated variation in fire treatments (every 1, 2, 3, 4, or 20 years) and grazing regimes (no grazers, cattle, and bison; Knapp and Seastedt 1998). I studied birds on sixteen of these units, focusing on pastures burned every 1, 2, or 3 years and grazed by no grazers, cattle, or bison. The Rannell's Preserve is managed with higher stocking rates of cattle and annual fire typical of rangeland management in the region (Owensby et al. 2008). This range of management regimes represent those with the highest densities of grassland-obligate songbirds at the site (Powell and Busby 2013). I will hereafter refer to both sites as "Konza."

Cowbirds are medium-sized (42–50 gram) songbirds native to the Great Plains of North America (Lowther 1993, Kilner 2003). Although they parasitize hundreds of species inhabiting a range of vegetation types including deciduous forests (Friedmann and Kiff 1985, Ortega 1998), they prefer grassland habitats (Rothstein 1994). They are the second-most common passerine breeding at Konza (Rivers et al. 2010), where they parasitize at least twenty species (Rivers et al. 2010). Previous research demonstrated that the majority of parasitized nests at the site contained at least two cowbird eggs (Rivers et al. 2010a), with some nests containing as many as nine (Hatch 1983).

I quantified the growth and development of cowbird nestlings in nests of the three most common grassland-obligate songbirds, all of which share a long history of living alongside cowbirds in the tallgrass prairies of the Great Plains. These species span a range of sizes; Eastern Meadowlarks are the largest, growing to as much as three times the size of cowbirds (90–150 g), Dickcissels are medium-sized (23–29g), and Grasshopper Sparrows are the smallest, maturing at about a third the size of cowbirds (14–20g) (Lanyon 1995, Vickery 1996, Temple 2002). Over their range, meadowlarks are parasitized infrequently (Friedmann 1963, Patten et al. 2006), yet at Konza, 25–70% of meadowlark nests contain cowbird eggs (Elliot 1978, Chapter 1). Dickcissels are the most frequently parasitized host species at the site with parasitism rates as high as 95% (Elliot 1978). Grasshopper Sparrows are parasitized at intermediate rates, with up to 50% of nests containing cowbird eggs in this region (Elliot 1978, Rivers et al. 2010). Nest success is highest in meadowlarks at ~30% (Elliot 1978), lower in Dickcissels with as few as 14% of nests surviving (Patterson and Best 1996), and Grasshopper Sparrow success ranges geographically from below 10% at Konza to 50% at other sites (Vickery et al. 1992).

Nest monitoring and nestling measurements

From April–August 2017–2018 field crews located nests by flushing incubating and brooding parents off nests opportunistically while walking or by systematically dragging a weighted rope through the prairie, and by observing the behavior of provisioning parents. Nests were marked by placing a painted rock and a pin flag five meters from the nest opening and the location was recorded with a handheld GPS unit (Garmin, Olathe, KS, USA). Crews returned to nests every other day to record the number of host and cowbird eggs. When eggs hatched, I returned every other day to measure nestlings, considering the day nestlings hatched as day 0. If

nestlings disappeared before their earliest known fledge age (day 6 for Dickcissels and Grasshopper Sparrows, day 10 for meadowlarks) I assumed they had been depredated. I considered nestlings to have successfully fledged if they disappeared at or after fledge age, if the nest cup was intact, and if parents were seen nearby with food. I banded each nestling a day before fledge (day 5 for Dickcissels, Grasshopper Sparrows, and cowbirds in those nests, and day 9 for meadowlarks and cowbirds in those nests) with a U.S. Fish and Wildlife Service band. I extracted 30–100 μl of blood from the brachial vein, centrifuged the samples, and stored the red blood cells in Queen's Lysis Buffer at -20°C until I could extract DNA for genetic sexing.

Predictions of the *predation risk* hypothesis rely not on the actual depredation of nests but rather the fear of predation that parents experience, so I estimated predation risk as the density of depredated nests in nests/ha. I plotted the locations of depredated nests of all species in GIS (ESRI, Redlands, CA, USA) and using a kernel density estimator to generate values of depredated nests/ha for each location. I extracted values from the kernel density estimator at the location of every nest creating a predation risk value expressed as number of depredated nests/ha in the local area. I will refer to this as "predation risk" to differential it from the realized predation events, which I will call "predation rate."

I took nestling measurements at approximately two-thirds of the nestling-stage nests each year. I selected a single cowbird nestling to measure at each nest, attempting to not bias the sample by picking a nestling with any particular attribute. I distinguished cowbird nestlings from sparrow and Dickcissel nestlings by their white (rather than yellow) gapes (Rothstein 1977). I distinguished cowbirds from meadowlark nestlings based on the cowbirds' smaller size and higher propensity to beg (Dearborn 1999). I measured the tarsus length using calipers and mass using a small digital scale accurate to ±0.001g. I took a photo of each nestling's right wing

against a gridded notecard. I measured the length of the ulna, carpometacarpal, ninth (outermost) primary feather, first secondary feather, and the unsheathed portions of those feathers from photos using Image J (Schneider et al. 2012).

I mounted miniaturized nest cameras at 27 parasitized nests (Winder et al. 2016). I selected nests that had reached nesting stage, as incubating adults abandon nests more frequently (Renfrew and Ribic 2003). Each camera set-up consisted of an infrared bullet camera (950 nm, Model ENC-100, EZ Spy Cam, Los Angeles, CA) connected underground by a co-axial cable to a small DVR (NY-P0122 Portable Mini DVR SecuMate SD Slot AV Recorder, SecuPlus, Gravenpolder, Netherlands) powered by two sealed, 12V lead acid batteries. The cameras recorded footage twenty-four hours a day. Due to differences in nest failure timing and the day on which recording began, nests varied in the nestling age for which I had footage. Thus, I selected the nestling age (day 4) for which I had footage from the maximum (15) number of nests containing cowbirds. In 2017 I watched raw footage at speeds varying from 0.25-4x speed using VLC media player (VideoLAN Organization). In 2018 I used the program DeepMeerkat (Weinstein 2018) to extract the still frames in which motion occurred and quantified activity at the nest from the extracted frames.

I recorded the identity of each visitor to the nest (parent, predator, field technician), the duration of stay and activity at the nest. I could not always see which nestling was being fed because the parents' backs often blocked the view; therefore, I calculated *per capita* provisioning rate as the number of parental visits with food per nestling per hour. I identified predators responsible for partial predation events, when some but not all nestlings were depredated, and full predation events when possible.

I sexed the nestlings using CHD-P2 (5'-TCTGCATCGCTAAATCCTTT-3') and 1237L (5'-GAGAAACTGTGCAAAACAG-3') primers. I ran PCR reactions using 24 µL of DreamTaq Green PCR Master Mix (2X) and 1 µL of DNA for a 25 µL reaction. I amplified the DNA on a SimpliAmp Thermal Cycler at 94C for 2 minutes, followed by 29 cycles of 94C for 30 seconds, 42C for 45 seconds, and 72C for one minute, and finally extended at 72C for 5 minutes. I ran 4 µl of the sample through a 2% agarose gel in 1X TAE with Gel Red for 90 minutes of electrophoresis at 80V. I visualized the results with a UV transilluminator and determined the sex of each nestling individually (Kahn et al. 1998, Griffith and Orr 1999).

Analyses

The nestlings grew roughly linearly (Figure 3-2), contrary to most studies of nestling growth which fit the data to a logistic curve (Brown et al. 2007). To determine which environmental factors most strongly affected growth of cowbird nestlings, I constructed linear mixed models in a structural equation model framework. I created a series of linear mixed models relating host species, brood size (total number of nestlings of both species), and predation risk (depredated nests/ha), and interactions between these factors to a single metric of cowbird growth (see below). I included an interaction with age for every variable to account for growth of the nestlings over time. I included nestling ID as a random effect to account for repeated measures of individuals. I used z-scores to scale all continuous variables so I could compare the effect sizes directly. For the subset of nests for which I had provisioning data, I constructed a separate set of structural equation models which included an additional effect of provisioning rate. I constructed models in the R (R Core Team 2013) packages *nlme* (Pinheiro et al. 2019), *lme4* (Bates et al. 2015), and *piecewiseSEM* (Lefcheck 2016).

Because nestling mass increased roughly linearly (Figure 3-2), I used mass as a proxy for overall size. To determine whether cowbirds prioritized the growth of tarsi relative to overall size, I divided tarsus by mass and used these mass-corrected tarsus measurements as the dependent variable in a separate set of analyses. Similarly, to determine whether cowbirds prioritized the growth of wings relative to overall size, I divided the length of the ulna, carpometacarpus, 9th primary, and 1st secondary by the nestlings' mass. I constructed a correlation matrix principal components analysis to create a reduced set of independent axes describing mass-corrected wing morphology. I used the second principal component as response variables in a third set of analyses, as the first component did not change over time. I calculated hatching and fledging success of cowbird eggs (eggs hatched or fledged/total N cowbird eggs encountered) separately for each host species' nest. I compared predation risk, cowbird fledging success, fledge age, and size at fledge among host species using Analysis of Variance (ANOVA).

Results

Over the two years of the study, I found 284 hosts nests (87 meadowlark, 141 Dickcissel, and 115 sparrow nests), 46.4% of which contained at least one cowbird egg. The three species' average clutch sizes (host and cowbird eggs) were very similar to each other, but each species displayed large intraspecific variation; meadowlark nests contained 4.2 eggs (range:1-8 eggs), Dickcissel nests contained 4.1 eggs (range:1-9), and sparrow nests contained 4.0 eggs (range 1-6 eggs). Similarly, the nests that survived to the hatching stage had similar average brood sizes (host and cowbird nestlings) and large intraspecific ranges; meadowlark nests contained 3.6

nestlings (range:1-6 nestlings), Dickcissel nests contained 3.2 nestlings (range:1-5 nestlings), and sparrow nests contained 3.5 nestlings (range: 1-5 nestlings).

Parasitism rates varied considerably among hosts; 25.2% of Eastern Meadowlark nests (N=87), 65.5% of Dickcissel nests (N=141), and 36.5% of Grasshopper Sparrow nests (N=115) contained at least one cowbird egg or nestling. If parasitized, host nests often contained more than one cowbird egg; on average, meadowlark nests contained 1.5 cowbird eggs (range: 1-4 eggs), Dickcissel nests contained 2.0 cowbird eggs (range: 1-5 eggs), and sparrow nests contained 1.8 cowbird eggs (range:1-5 eggs). Cowbird eggs were most likely to hatch in sparrow nests (48%) followed by Dickcissel (39%), and meadowlark (35%) nests. Over this study, 39 cowbirds fledged from 26 Dickcissel nests (23% of eggs laid), 19 fledged from 10 sparrow nests (21% of eggs laid), and 6 fledged from 5 meadowlark nests (24% of eggs laid; Table 3-1).

I measured 54 cowbird nestlings during their development; five in meadowlark nests, 35 in Dickcissel nests, and 13 in Grasshopper Sparrow nests. Repeated nestling measurements did not increase predation risk at the nests (Chapter 1), nor did the presence of nest cameras (Chapter 2). Meadowlarks at four parasitized nests made 289 provisioning visits during 101 hours of video footage, Dickcissels at nine parasitized nests made 823 provisioning events during 157 hours of footage, and sparrows at three parasitized nests made 278 provisioning events during 49 hours of footage.

Mass gain varied among individuals (Figure 3-2); at eight days old, the largest cowbirds were 39.6% larger than same-age conspecifics (mean=28.0 grams, range=19.6-32.4g). The structural equation models (Figure 3-3A) revealed that brood size (including cowbirds and host nestlings) differed among host species in the studied nests; Dickcissels raised on average one more nestling than did meadowlarks, and three more nestlings than did Grasshopper Sparrows

(Figure 3-4). Predation risk also varied among hosts; Dickcissels placed their nests in relatively safe areas (0.39 depredated nests/ha +/- 0.03 nests/ha), followed by meadowlarks (0.41 depredated nests/ha +/- 0.06 nests/ha), and Grasshopper Sparrows (0.50 depredated nests/ha +/- 0.04 nests/ha) (Figure 3-5). However, mass gain was unrelated to variation in brood size and predation risk, and overall the model did not fit the data well (Fisher's C_6=1.936, *P*=0.926; Figure 3-3A).

In analyses restricted to only those nests for which I had provisioning data, brood size was associated with lower *per capita* provisioning rates; the smallest broods, with only 1-2 nestlings, received an average of 1.38 visits/nestling/hour, while the largest broods, with 6-8 nestlings, received 0.78 visits/nestling/hour (β=-0.4, *P*=0.000, Figure 3-3B). Provisioning rate varied among species ($F_{2, 37}$=14.7, *P*=0.000, Figure 3-6), with Eastern Meadowlarks making the fewest visits/nestling/hour (mean=0.78 visits/nestling/hour), followed by Dickcissels (mean=1.14 visits/nestling/hour), and Grasshopper Sparrows provisioning most frequently (mean=1.26 visits/nestling/hour). Remarkably, however, variation in brood size and provisioning rate was not related to variation in cowbird mass gain (SEM: Fisher's C_6=7.82, *P*=0.252, Figure 3-3B). The only factor consistently associated with variation in cowbird mass gain was host species; on average, cowbirds gained 3.32 grams/day in meadowlark nests, 3.38 grams/day in Dickcissel nests, and 3.60 grams/day in sparrow nests.

Cowbird nestlings' tarsi grew linearly over the brooding period and also exhibited considerable inter-individual variation; by day 5, some nestlings had tarsi 30% longer than conspecifics (Figure 3-7). I calculated mass-corrected tarsus values to determine whether the cowbirds prioritized tarsus growth over mass gain (Figure 3-8). Structural equation models using the complete set of nests revealed no associations between mass-corrected tarsus measurements

and either host species, brood size, or predation risk, although these models were not a good fit for the data (Fisher's C_6=1.936, *P*=0.926; Figure 3-9A). However, when accounting for the negative relationship between brood size and provisioning rate, the reduced dataset (using only nests for which I had provisioning data) model revealed that mass-corrected tarsus length was positively related to *per capita* provisioning rate (SEM: Fisher's C_6=7.82, *P*=0.252; pathway: β=0.6, *P*=0.047, Figure 3-9B). Mass-corrected tarsus measurements also varied by host species; cowbirds' mass-corrected tarsus values declined by 0.16 mm/gram/day in meadowlark and Dickcissel nests and by 0.18 mm/gram/day in sparrow nests as the birds aged.

A principal component analysis produced two main axes of variation which together accounted for 96.5% of the total variation in size-corrected wing measurements (Figure S3-1). The first axis of variation primarily described the overall wing size relative to mass (mass-corrected wing size) (Table S3-1). This mass-corrected wing size component (PC1) remained fairly constant (Figure 3-10) indicated that wings grew isometrically with other aspects of body size. Consequently, I constructed structural equation models using PC2, which represented a trade-off between feather growth and wing bone growth (Table S3-1). Larger PC2 values were associated with longer mass-corrected wing lengths, while smaller values were associated with mass-corrected feather lengths. This metric declined over time as birds began to grow their feathers (Figure 3-11). Individual variation in PC2 was not related to variation in any of the proposed drivers or their interactions in the structural equation models using the complete set of nests (Fisher's C_6=1.936, *P*=0.926; Figure 3-12A) or the reduced dataset (Fisher's C_6=7.82, *P*=0.252; Figure 3-12B).

While some evidence suggests that cowbirds' sexual dimorphism appears in early development (Tonra et al. 2008), I found no evidence that development differed between male

and female cowbirds (data not shown). However, the detected sex ratio appeared to differ among host species; meadowlarks and Dickcissels had roughly equal proportions of male and female cowbirds, but the four cowbirds sexed from Grasshopper Sparrow nests were all female. Even accounting for species-specific differences in nest predation risk by including host species as a random effect in linear mixed models, nests in areas of lower predation risk (fewer depredated nests/ha) were more likely to raise female cowbirds than male cowbirds (Figure 3-13, $z_{36}=2.4$, $P=0.017$).

Cowbird fledge age varied among host species; cowbirds in meadowlark nests fledged on average 1-2 days later (meadowlark nest mean: 9.8 days, range: 9.5-10.0 days) than cowbirds in Dickcissel nests (mean: 8.4 days, range:7-10 days) or Grasshopper Sparrow nests (mean: 8.0 days, range: 6.5-9.5 days) ($F_{2,83}=20.9$, $P<0.001$, Figure 3-14).

Discussion

Over two summers I studied the growth of cowbird nestlings in nests of three grassland host species. Cowbird parasitism was frequent at the site, with approximately 50% of nests containing cowbird eggs and ~40% of those eggs surviving to hatch. The mass of cowbirds at the site varied as much as 40% by day 6. The mean mass of cowbirds on day 8 (28.0g) was almost as high as the largest 8-day-old cowbirds found at other sites (Kilpatrick 2002). Despite sharing the same site (often in very close proximity) and consequently, many environmental conditions such as weather and food availability, variation in cowbirds' mass at day ~8 represented 80% of the maximum variation among all hosts over cowbirds' whole range (Remeš 2008). Tarsus size varied by as much as 30% by day 5, and the extent to which they prioritized the growth of mass relative to tarsi varied by as much as 20%.

The expectation of the *provisioning rate* hypothesis was that increased *per capita* provisioning rate would be positively related to the overall size of nestlings, as nestlings would have more energy to grow if they received more food. However, I found no direct relationship between *per capita* provisioning rate and nestling mass gain. I predicted that increased competition driven by lower *per capita* provisioning rates would lead to tarsus-biased allometry, but instead observed the opposite; cowbirds' mass-corrected tarsi lengths increased in nests with higher provisioning rates. A possible explanation for this result is that skeletal growth may be more restricted by food availability than is mass gain (Talloen et al. 2009). Consequently, when food is restricted tarsus growth may slow relative to mass gain. The cowbirds receiving more food may therefore have been able to increase their relative tarsus growth due to a release from food limitation.

Under the *brood size* hypothesis, I expected that nestlings in larger broods would have to compete more for food, resulting in a negative relationship between brood size and mass-corrected tarsus growth. Brood size was indeed related to provisioning rate; nestlings in the smallest broods received more provisioning visits per nestling per hour, potentially reducing the competition between the nestlings. However, these high provisioning rates were related to an increase in mass-corrected tarsus lengths over time rather than a decrease as initially predicted.

Per the *host size* hypothesis, I expected that cowbirds would experience lower competition in the nests of smaller hosts, resulting in increased mass gain and decreased mass-corrected tarsus growth. I found evidence for both predictions; cowbirds in the nests of the small Grasshopper Sparrows gained mass more quickly and exhibited a faster decline in mass-corrected tarsus values compared to cowbirds growing in Dickcissel and meadowlark nests. However, despite size differences between the Dickcissels and meadowlark hosts, cowbirds

gained mass at similar rates in the nests of these species. These results suggest that, while host size is an important driver of variation in brood parasite growth, the difference is measurable only when the cowbirds are larger than their hosts.

If female cowbird nestlings were smaller and less competitive than males at this site (Weatherhead 1989), female cowbirds may survive better in less competitive nests, resulting in a higher percentage of females relative to males in sparrow nests. The sample size for sex comparisons was very limited because I only collected blood samples from nestlings surviving to fledge age, so I cannot make strong conclusions about the sex ratios. However, it is interesting to note that the sex ratios in the two larger host nests were even, while all the cowbirds sexed in the sparrow nests were female as predicted. I did not detect any variation in growth between the sexes, suggesting that skewed sex ratios, if they exist, may not be related to size-based competition.

The expectation of the *predation risk* hypothesis was that cowbirds would prioritize the growth of mobility-enhancing structures such as wings when they were growing in high-predation areas and/or experience reduced overall growth if fearful host parents were visiting the nest less frequently. The density of nearby predators (predation risk), actual nest predation rate, *per capita* provisioning rate, and the relative growth of feathers to wing bones varied, but none of these measurements were related to each other. This result stands in contrast to nestling cavity-nesting birds whose wing growth increased when the perceived predation risk was experimentally increased (Coslovsky and Richner 2011). This discrepancy could be the result of differences in fledge stage, as cowbirds leave the nest before their wings are fully developed, and therefore may rely less on wings to escape predators. The host species in this system prioritize mass gain in high-risk nests rather than wing growth, a strategy that could be useful if the birds

reach a size large enough to deter nest predators with a small gape (Chapter 2). It is particularly surprising, then, that the cowbirds in the nests of these same hosts do not show a similar response to predation risk. This suggests that the ability of the hosts to respond to predation risk was not mediated by differences in post-natal parental care, as the cowbirds in the nest would also experience these responses, but instead, may result from pre-natal allocation in response to perceived predation. Female cowbirds may not respond to predation risk over the same spatial scales as the host parents pre-laying, possibly because cowbirds do not occupy small territories. Despite being raised at a site with particularly high predation rates and in nests with hosts able to respond to perceived predation risk, cowbird growth and development variation is not related to local variation in predation risk.

Cowbirds choose the nests they parasitize; their choice of hosts could therefore be the result of selection for efficient growth or enhanced success (Louder et al. 2014). Cowbirds at this site gained more mass than did cowbirds at other sites, suggesting that mid-continental grassland birds are better hosts for developing cowbirds than hosts in other ecosystems, perhaps due to high insect densities (Yanahan and Taylor 2014). Yet even within this guild, cowbirds did not parasitize the hosts at equal rates; cowbirds laid eggs in Dickcissel nests twice as frequently as in sparrow nests (65.5%), and almost four times as frequently as in meadowlark nests (24.2%), and Dickcissels had the most cowbird eggs/nest on average. Although cowbirds at other sites grew the best in intermediate-sized host nests (Kilner 2003), cowbirds eggs in Dickcissel nests at the site were not more likely to hatch than eggs in sparrow or meadowlark nests, and cowbird nestlings in Dickcissel nests did not grow any faster than did cowbirds in sparrow or meadowlark nests. Dickcissels did not have a higher *per capita* provisioning rate, although they did nest in areas with lower densities of depredated nests. However, while Dickcissel nests were more

successful than sparrows, they were less successful than meadowlarks' in this study (Chapter 1). The net effect of species-level differences in parasitism and stage-specific success resulted in a remarkably similar percentage of cowbird eggs fledging from the nests of each host species, ranging only from 21% in sparrow nests to 24% in meadowlark nests. Taken altogether, these results suggest that female cowbirds' host choice is not influenced by differences in the growth, development, or fledge success of cowbirds in different hosts' nests as previously hypothesized (Aviles et al. 2006). Instead, the preference for Dickcissel nests may be a result of nest availability. Humans find Dickcissels' open-cup nests more easily than the domed nests of meadowlarks and sparrows, and the same may be true for cowbird females (Burhans 1997). Additionally, if Dickcissel nests are more abundant, cowbirds may spend more time searching for Dickcissel-type nests than other species' nests.

Offspring growth and development patterns vary widely (Dmitriew 2011), greatly impacting survival (Starck and Ricklefs 1998) and future fecundity (Mauck et al. 2004), but it is often hard to separate the effects of genetic variation from the effects of plastic responses to different environments (Schew and Ricklefs 1998). Generalist brood parasites provide a unique opportunity to explore the role of environmental plasticity in growth and development. This study demonstrates that intraspecific variation in development can be the result of individual responses to environmental variation, especially food availability and sibling competition, but that hosts and parasites respond to drivers at different scales. These plastic responses may play a critical role in shaping past host-parasite evolutionary relationships and could influence species' abilities to adapt to future environmental change (Arendt and Wilson 1997, Moe et al. 2004). Understanding the scale and the degree to which environmental variation can influence inter- and intraspecific variation in development may become a critical part of species management; these

results indicate that we cannot expect environmental change to affect populations and individuals in uniform ways, even if those individuals are environments as similar as the same nest. Accounting for intraspecific variation in development in natural systems, focusing on individual responses to environmental drivers, and, ultimately, following this variation through birds' lifetimes will be required to assess the true impact of growth and development on fitness, population growth, and evolutionary trajectories.

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Tables

Table 3-1. Number of cowbird eggs per nest, the % that hatch and fledge per egg laid, and the total number of cowbirds that fledge in each of the host nests across Konza.

	GRSP	EAME	DICK
N eggs/nest	0.68	0.37	1.36
% hatch	0.48	0.35	0.39
% fledge	0.21	0.24	0.23
total N fledge	19	6	39

Figures

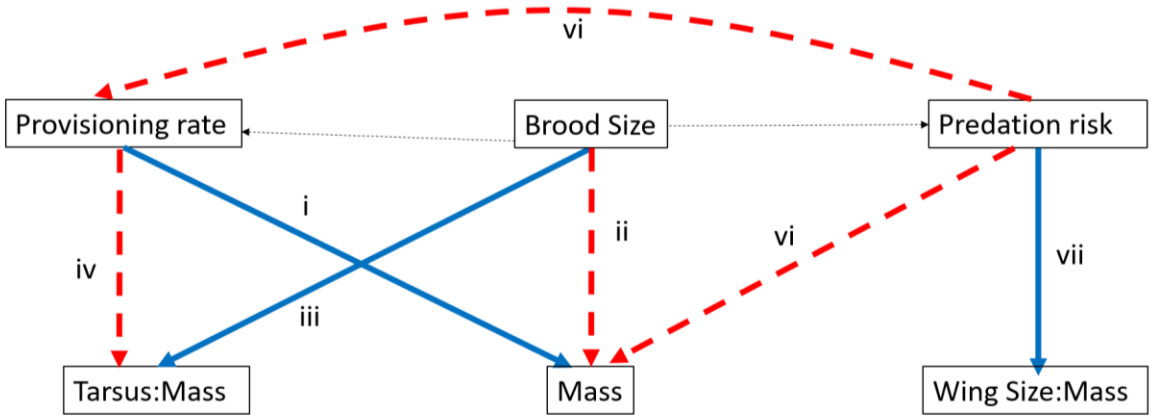

Figure 3-1. Hypothesis/Prediction structure. I hypothesized that cowbird mass-corrected tarsus, mass-corrected wing size, and mass measurements would be affected by provisioning rate, brood size, host species size, and predation risk. The predicted direction of these relationships is indicated by the color of the line; blue solid lines indicate a predicted positive relationship and red dashed lines indicate a predicted negative relationship. Numerals indicate the prediction (see Introduction for more details).

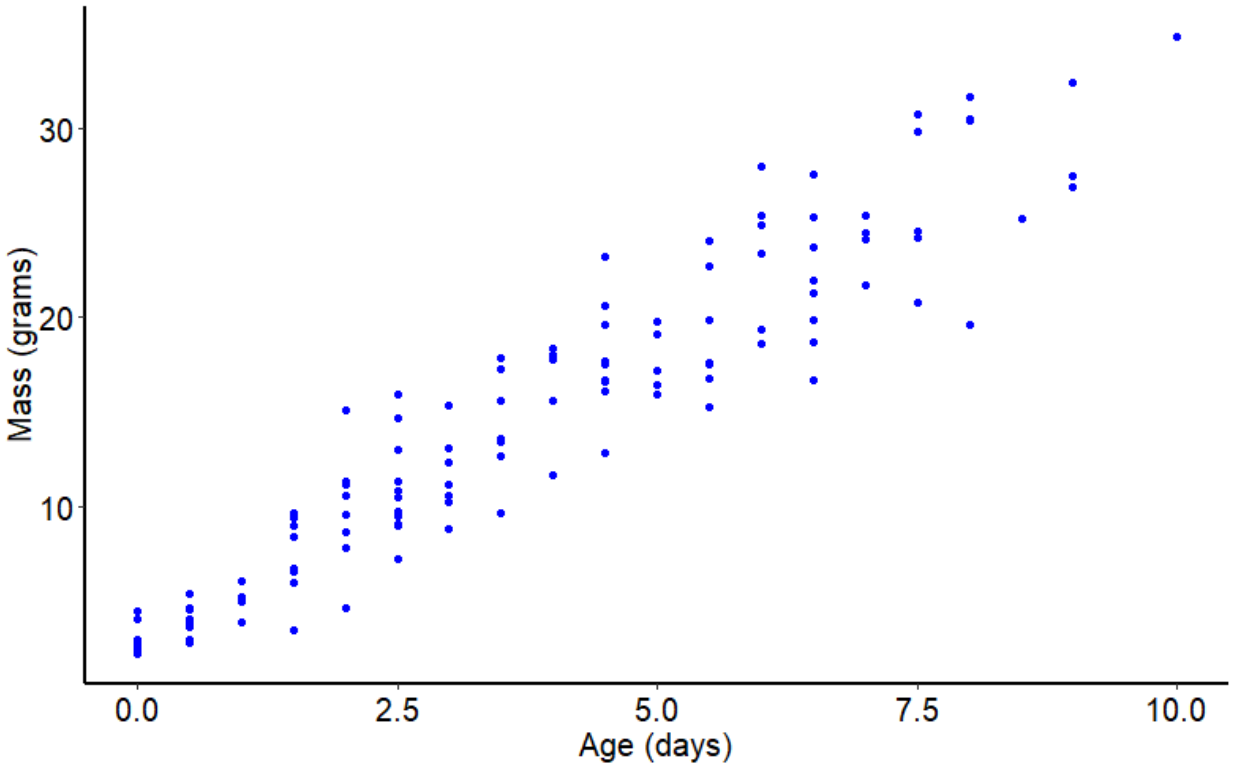

Figure 3-2. Cowbird mass measurements (in grams) over time (in days from hatch day=0).

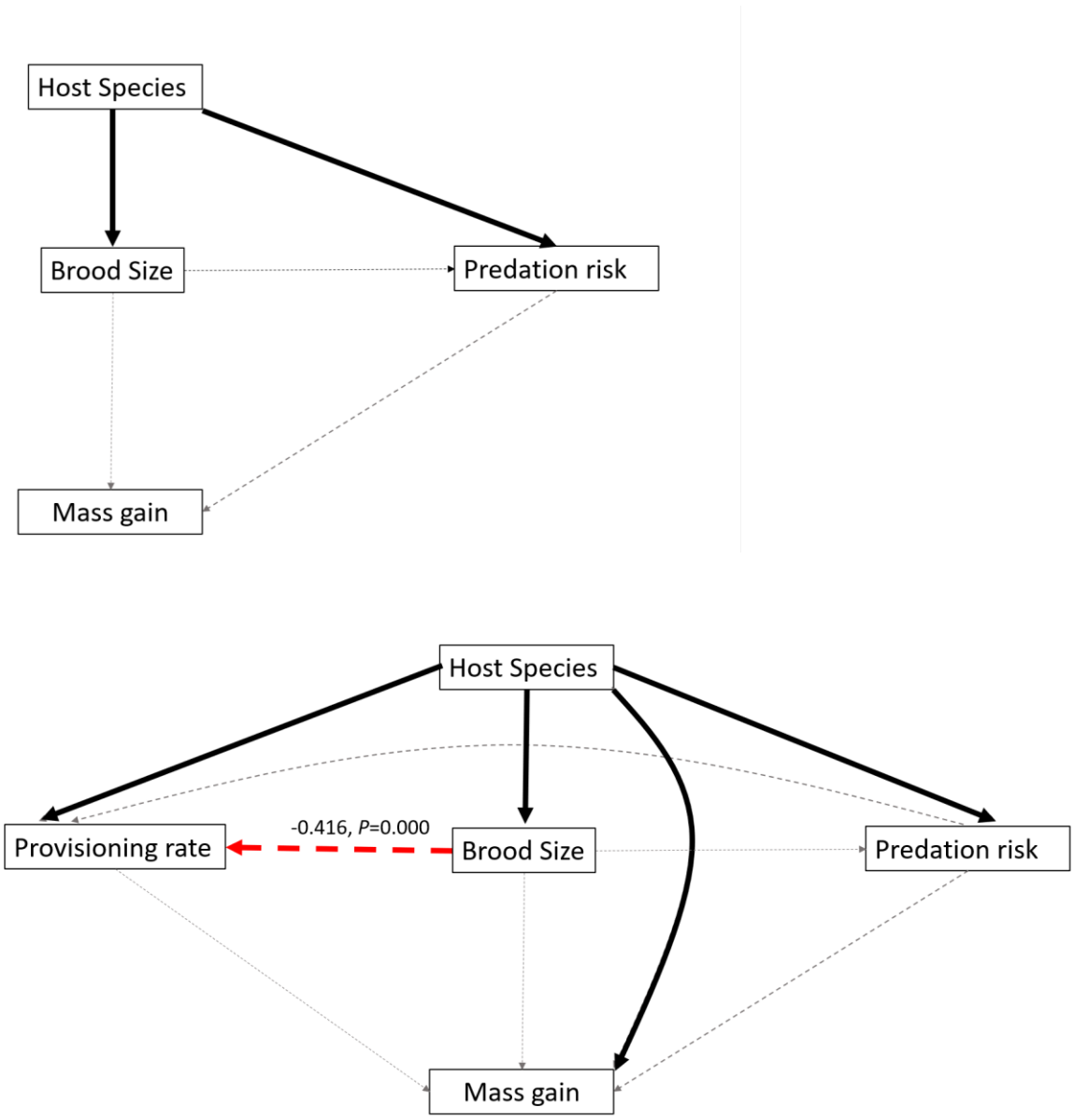

Figure 3-3. Results of structural equations modelling variation in cowbird mass gain. Red dashed lines indicate negative (β<0) relationships (*P*<0.05) and black solid lines indicate relationships (*P*<0.05) with categorical variables. Dashed gray lines represent tested paths that were not related. Each directional relationship includes the estimated β value for that effect and the estimated P-value. A) shows the full model for all nestlings (54 nestlings, 128 measurements; Fisher's C_6=1.936, *P*=0.926). B) shows the model restricted to only the nests with provisioning data (16 nestlings, 40 measurements; Fisher's C_6=7.82, *P*=0.252).

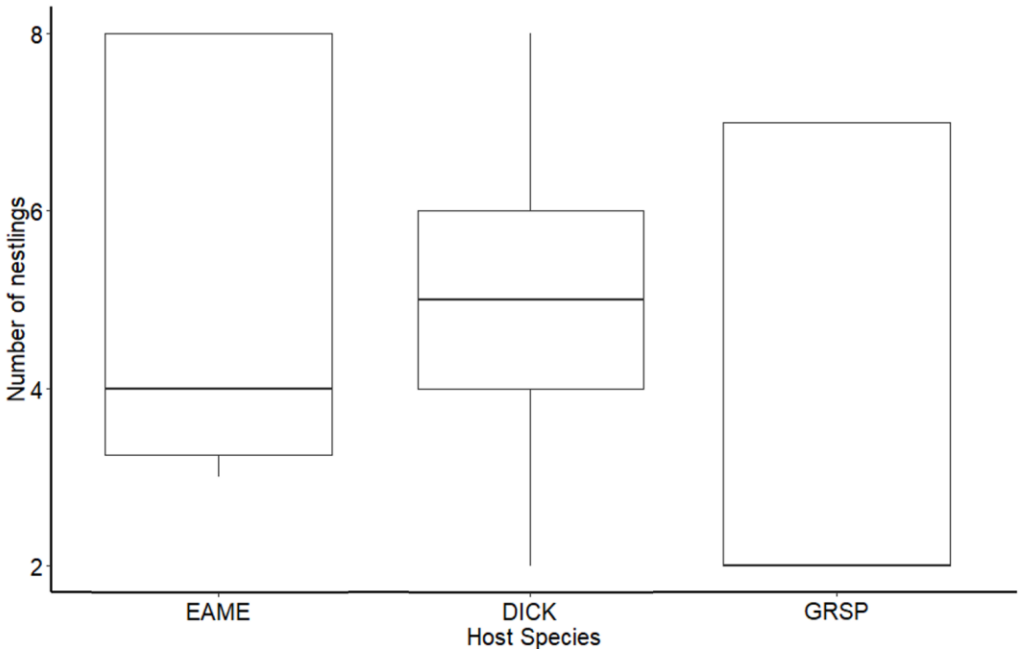

Figure 3-4. Dickcissels (DICK) have the highest average brood size overall, followed by Eastern Meadowlarks (EAME), and Grasshopper Sparrows (GRSP) have the lowest average brood size when parasitized, although ranges in brood sizes for each species broadly overlap.

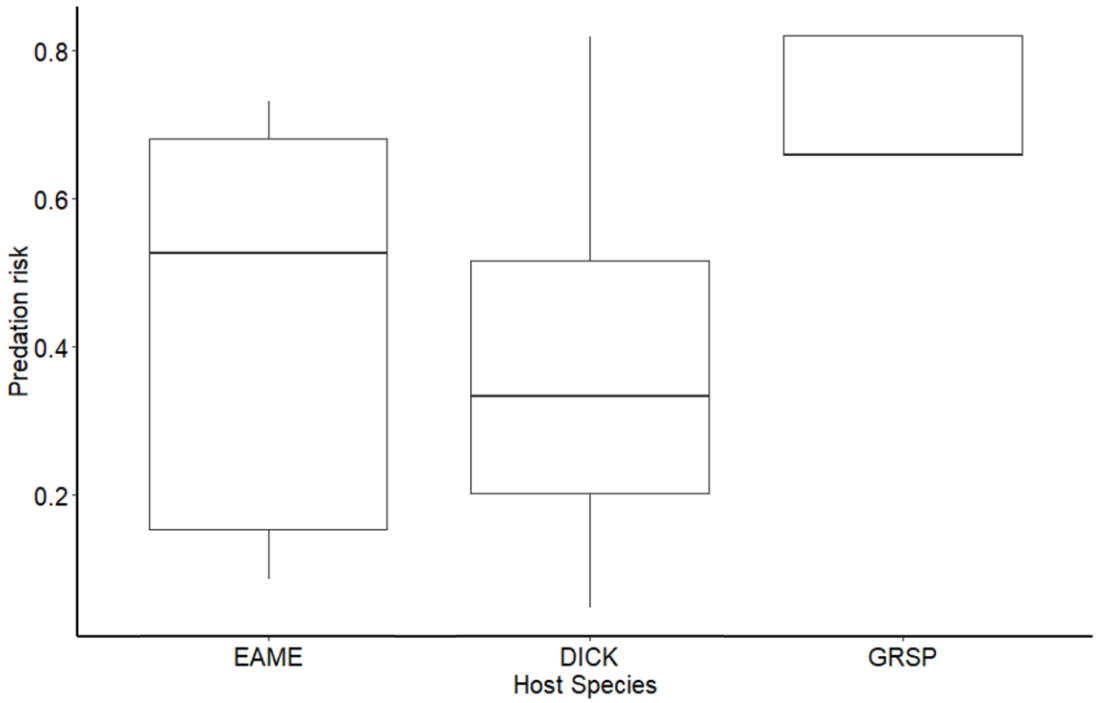

Figure 3-5. Dickcissels (DICK) build their nests in areas with the lowest predation risk (depredated nests/ha), followed by Eastern Meadowlarks (EAME) and Grasshopper Sparrows (GRSP).

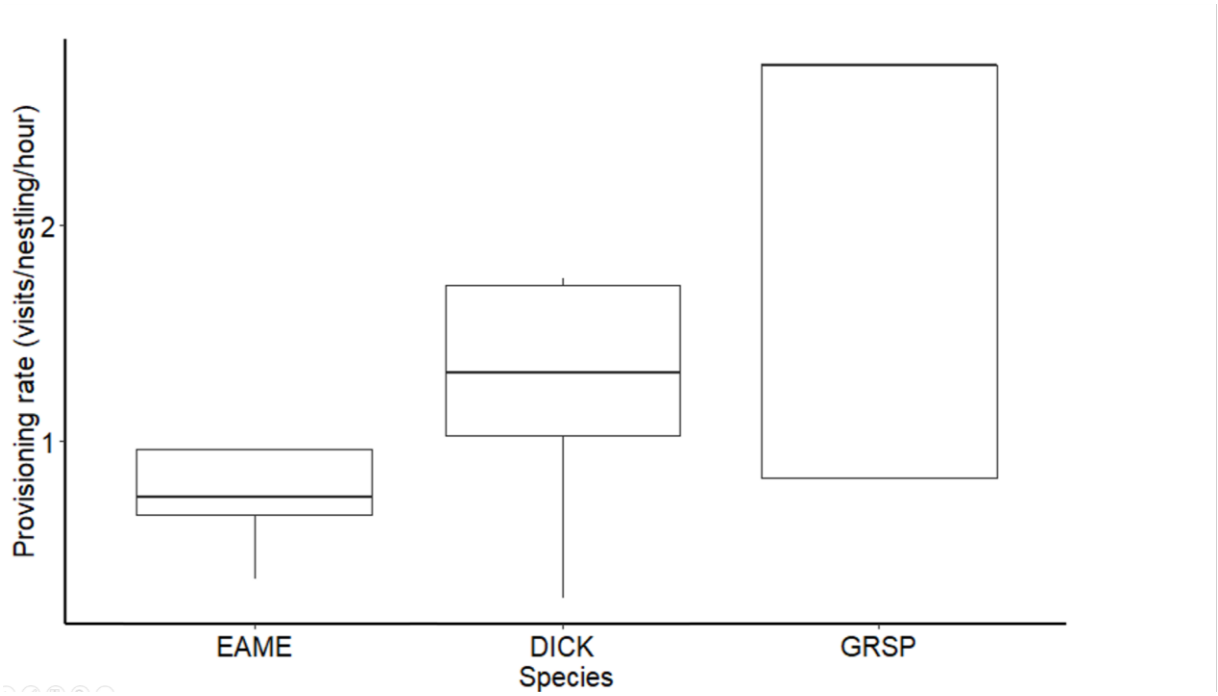

Figure 3-6. Host-specific differences in provisioning. Eastern meadowlarks (EAME) visit the nest the least frequently (visits/nestling/hour) ($F_{2, 37}$=14.7, *P*<0.001), followed by Dickcissels (DICK), followed by Grasshopper Sparrows (GRSP).

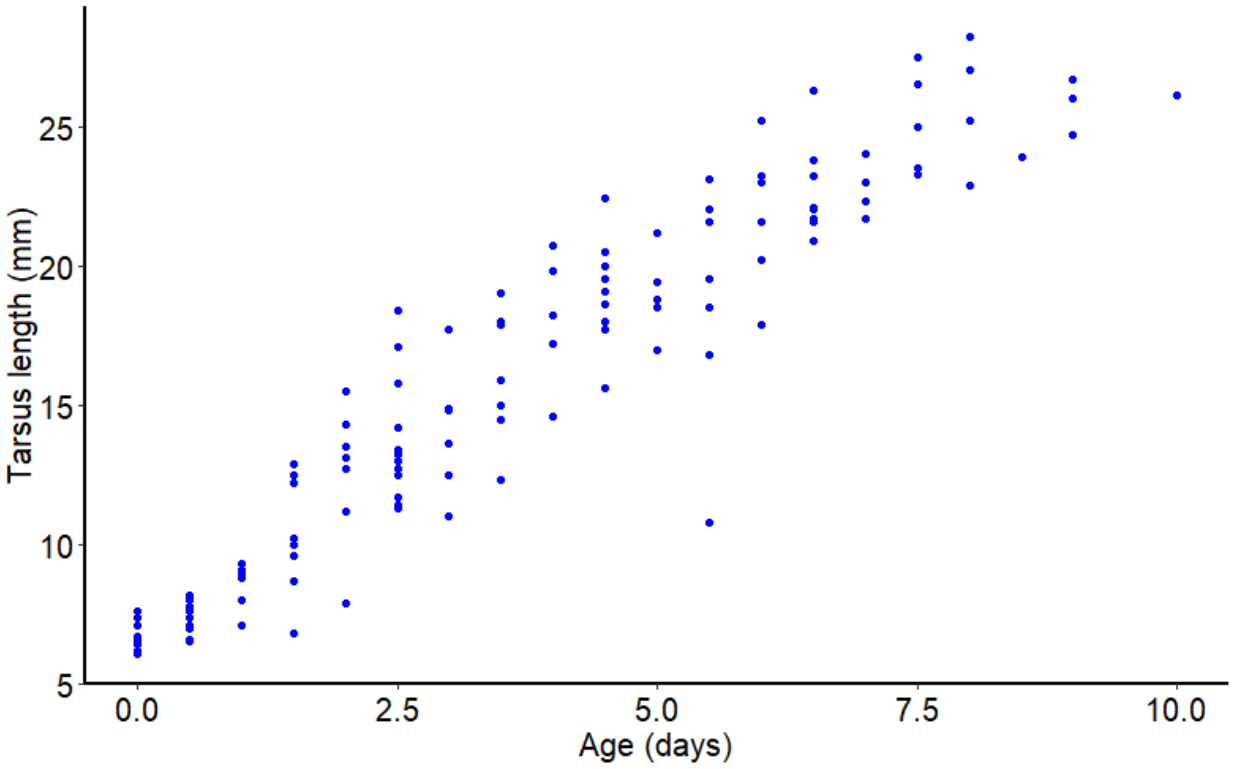

Figure 3-7. Cowbird tarsus measurements (in mm) over time (in days from hatch day=0).

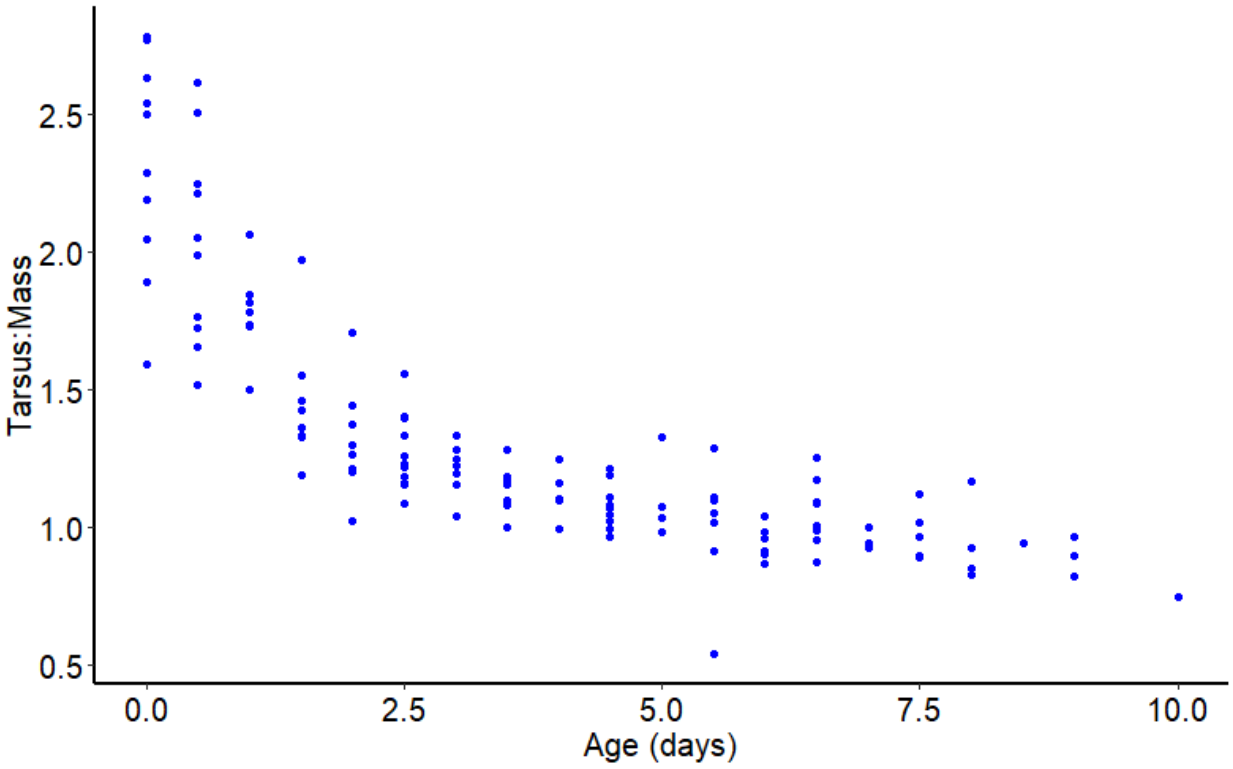

Figure 3-8. Cowbird mass-corrected tarsus scores over time (in days from hatch day=0).

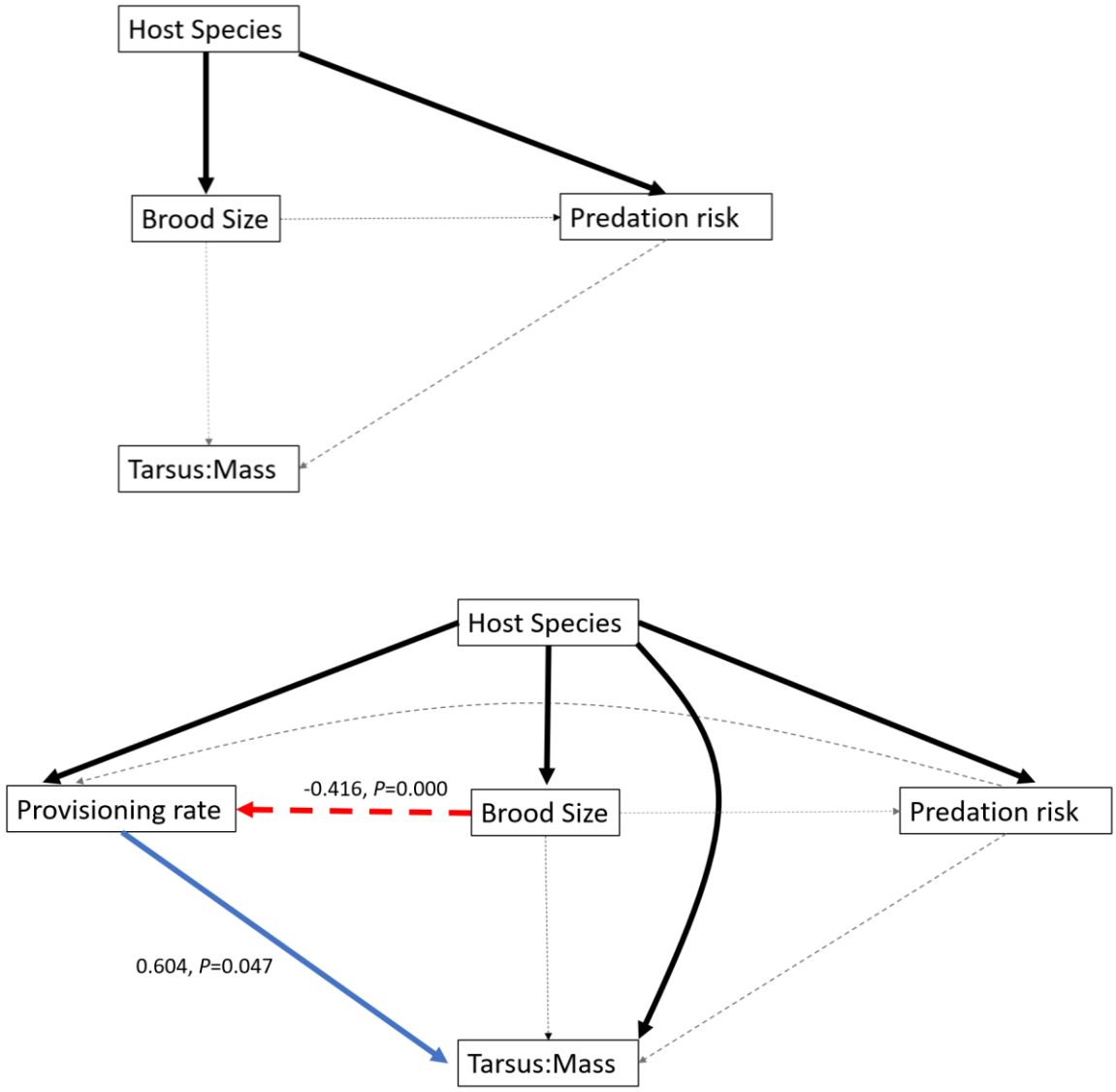

Figure 3-9. Results of structural equations modelling variation in cowbird mass-corrected tarsus lengths over time. Red dashed lines indicate negative (β<0) relationships (*P*<0.05), blue solid lines indicate positive (β>0) relationships, and black solid lines indicate relationships (*P*<0.05) with categorical variables. Dashed gray lines represent tested paths that were not related. Each directional relationship includes the estimated β value for that effect and the estimated P-value. A) shows the full model for all nestlings (54 nestlings, 128 measurements; Fisher's C_6=1.936, *P*=0.926). B) shows the model restricted to only the nests with provisioning data (16 nestlings, 40 measurements; Fisher's C_6=7.82, *P*=0.252).

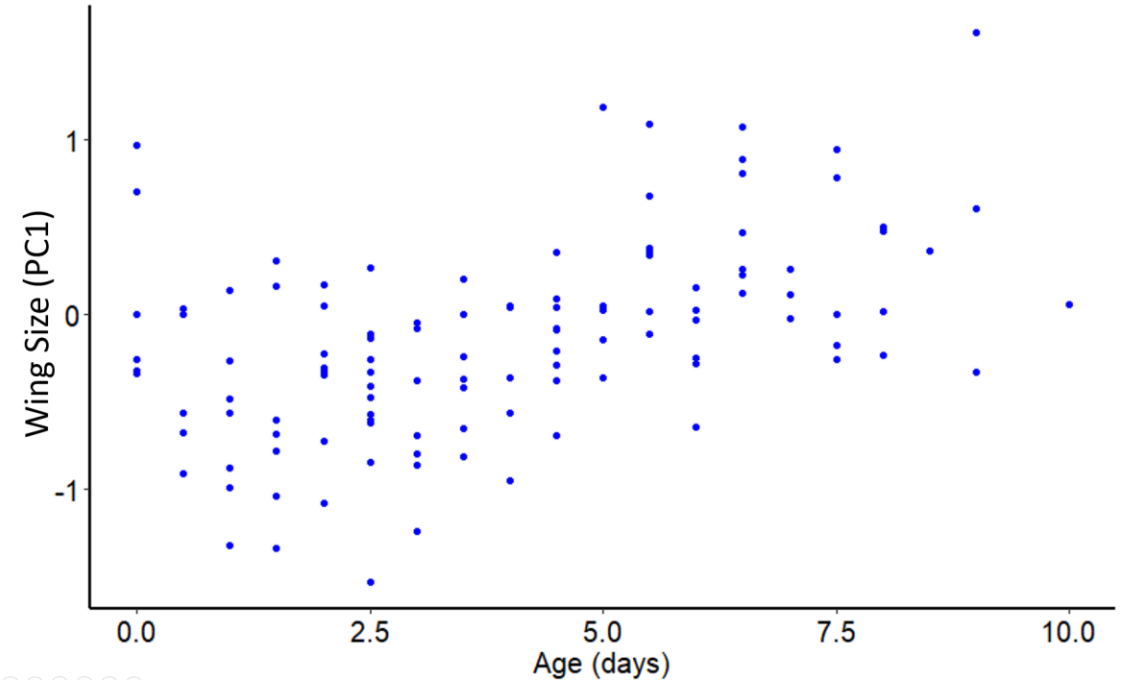

Figure 3-10. Cowbird Wing Principal Component 1 scores over time (in days from hatch day=0). Principal component 1 represents the ratio of mass-corrected wing size, with larger numbers indicating significantly larger wing composite scores than expected based on the nestling's mass.

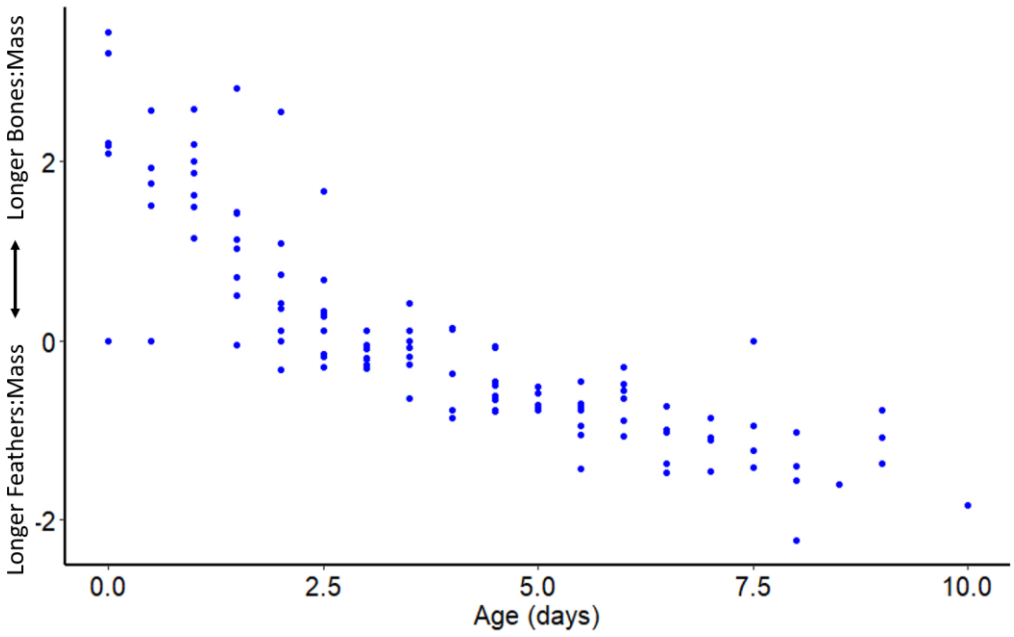

Figure 3-11. Cowbird Wing Principal Component 2 scores over time (in days from hatch day=0). Principal component 2 represents a tradeoff between mass-corrected feather lengths and mass-corrected wing bone lengths.

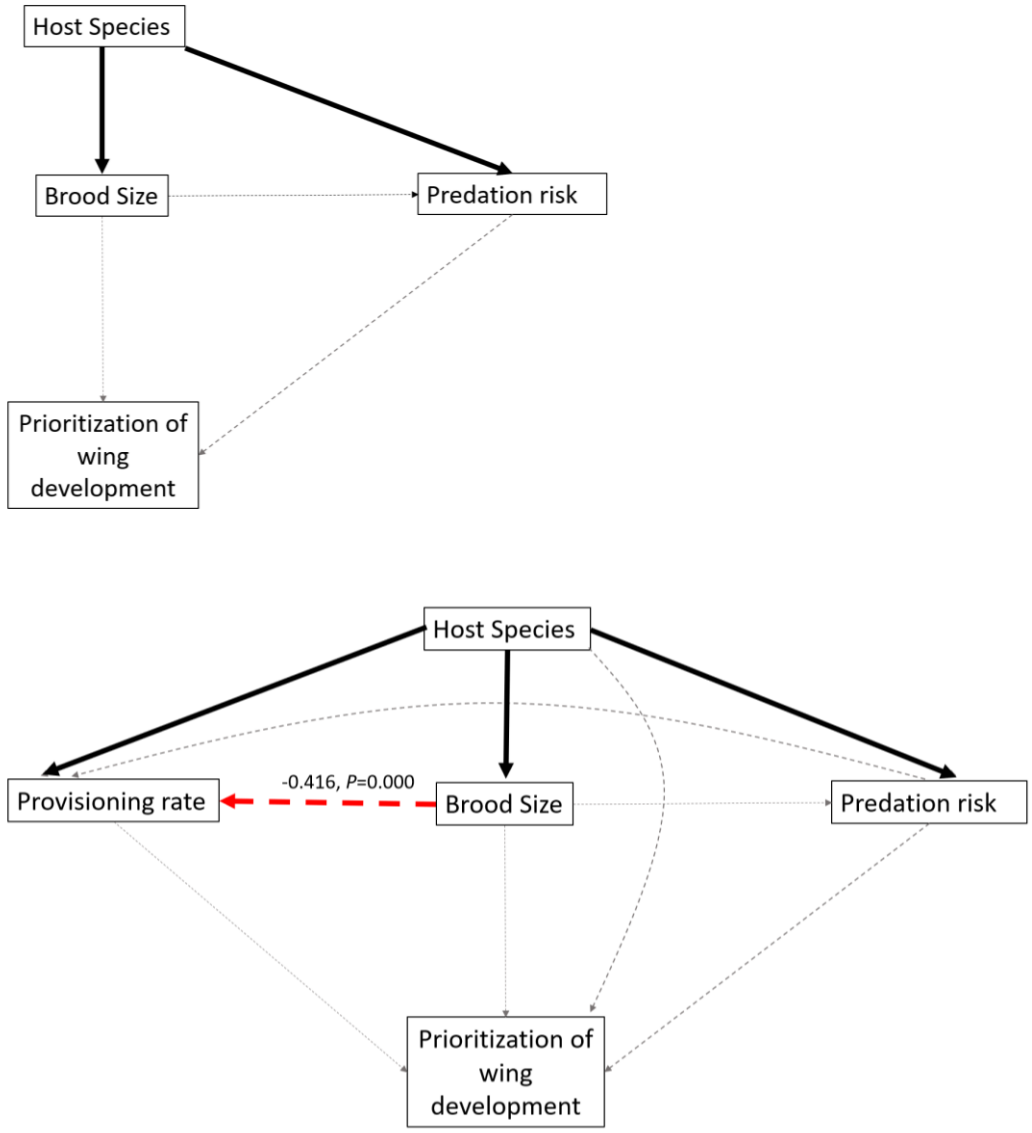

Figure 3-12. Results of structural equations modelling variation in the second principal component axis (PC2), which describes a spectrum from longer mass-corrected feather lengths to longer mass-corrected bone lengths. Results of structural equations modelling variation in cowbird mass gain. Red dashed lines indicate negative (β<0) relationships (*P*<0.05) and black solid lines indicate relationships (*P*<0.05) with categorical variables. Dashed gray lines represent tested paths that were not related. Each directional relationship includes the estimated β value for that effect and the estimated P-value. A) shows the full model for all nestlings (54 nestlings, 128 measurements; Fisher's C_6=1.936, *P*=0.926). B) shows the model restricted to only the nests with provisioning data (16 nestlings, 40 measurements; Fisher's C_6=7.82, *P*=0.252).

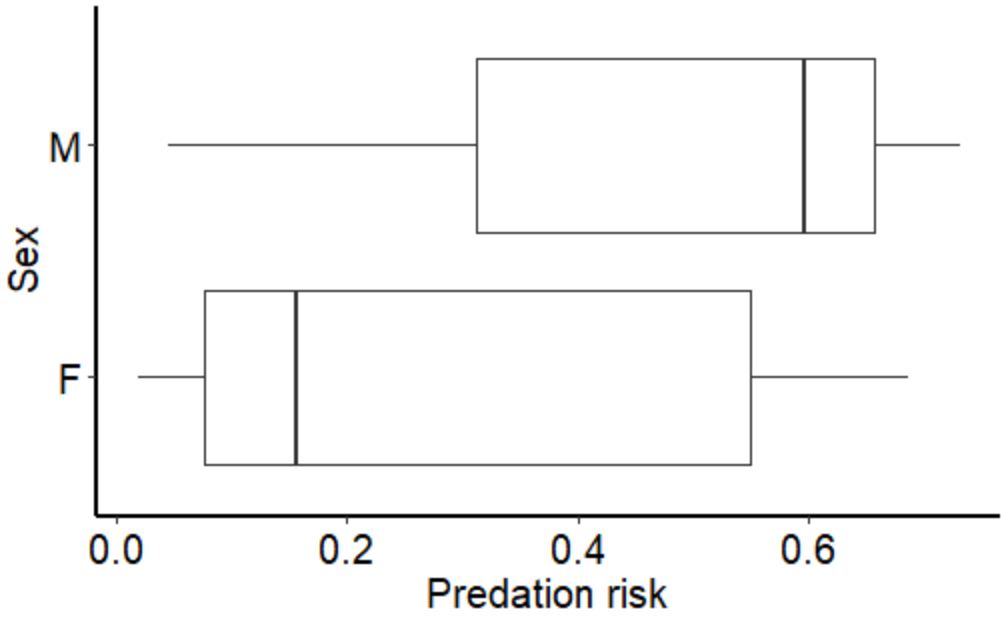

Figure 3-13. Nests with lower predation risk values (depredated nests/hectare) are more likely to have female cowbird nestlings than male cowbird nestlings, controlling for host species differences in cowbird sex ratios (z_{36}=2.388, *P*=0.017).

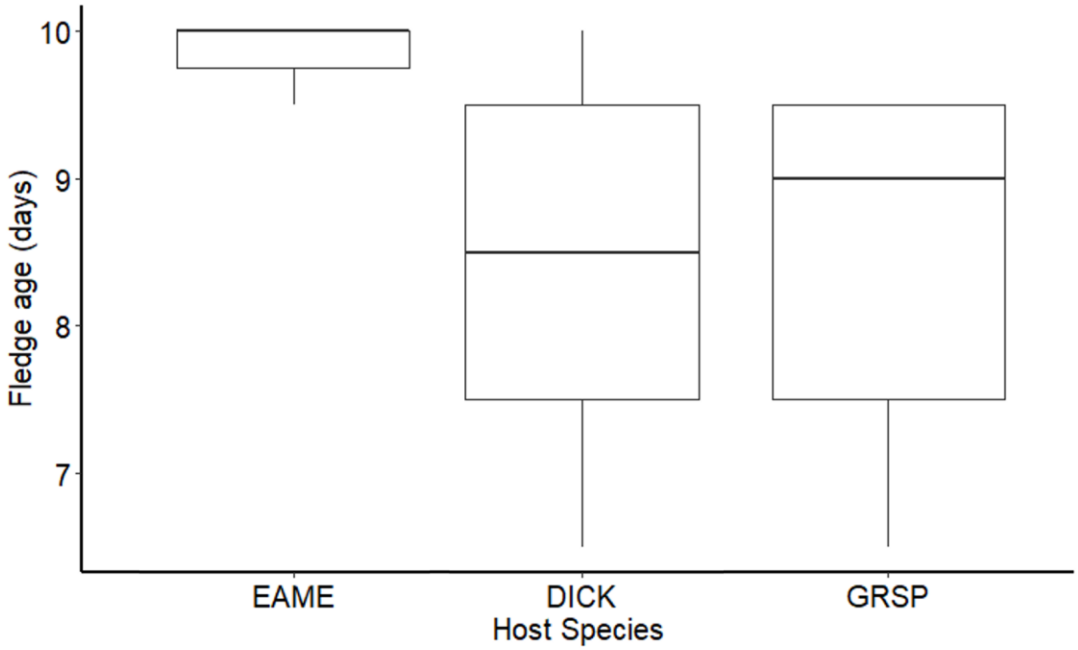

Figure 3-14. Fledge age of cowbirds (in days) from the nests of different hosts, with nestlings in Eastern Meadowlark nests fledging later than nestlings in Dickcissel or Grasshopper Sparrow nests ($F_{2,83}$=20.92, *P*<0.001).

Chapter 4 - Appendices

Chapter 1 Supplementary Material

Nestling growth and development scales:

We scored the nestlings' eye, dorsal feather, and activity level development by assigning each nestling to categories. During the first summer of research we scored the nestlings' eye development on a three-point visual scale ranging from 0: eyes unopen to 2: eyes fully opened. We scored their dorsal feather development on a four-point scale ranging from 0: no feathers present, feather tracts not visible to 3: feathers fully unsheathed. We scored their activity level on a six-point scale ranging from 0: cannot lift head or beg to 5: attempts to escape during handling. We expanded each of these scales during the second summer. Our eye scores ranged from 0: eyes unopened to 3: eyes fully opened, with the new category: eye slit open, eyeball visible. We expanded the dorsal feather score to a six-point scale including "feather tracts visible below skin," and "feathers starting to unsheathe." Instead of an activity scale, we answered five yes or no questions, asking whether the nestling can beg, flinch, lift its head, sit upright, and escape. We reclassified our less complete data from the first year with the expanded scales using photos of the nestlings, notes taken during handling when possible and assigned the nestling an intermediate score between the categories which would have been lumped together in the first years' classifications (e.g. 0=eyes unopened becomes 0.5 to fall between the new categories 0=eyes unopened and 1=slit visible). To check that this method was not biasing our results, we also ran the significant analyses with data reclassified in the opposite direction; we collapsed the data collected in the second summer to fit the first summer categories.

Nest success model selection tables

Table S1-1. Model table assessing the effect of nestling measurement visits, visits/day, host species, and year on nest success.

model	npar	AICc	DeltaAICc	weight	Deviance
Visits(Y/N)	2	487.871	0	0.425	483.864
Species * Visits(Y/N)	8	487.933	0.061	0.412	471.849
Visits(Y/N) * Year	4	490.705	2.833	0.103	482.682
Species	4	493.274	5.402	0.028	485.251
Visits/day	2	494.346	6.474	0.016	490.339
Camera(Y/N)	2	495.582	7.711	0.008	491.575
Year	2	498.207	10.335	0.002	494.200
Camera(Y/N) * Year	4	498.784	10.912	0.001	490.760
Species * Year	8	499.996	12.125	0.000	483.913

[1]number of parameters, [2]Akaike's Information Criterion corrected for small sample size, [3]difference in AICc between the model and the top-ranked model

Table S1-2. Beta values from the top nest success model.

	estimate	se	lcl	ucl
Intercept	2.378	0.240	1.907	2.848
Visits:Yes	0.974	0.278	0.428	1.520

Eastern Meadowlark growth model selection tables

Table S1-3. Model selection table for Eastern Meadowlark fledge age.

	df	logLik	AICc	delta	weight
age*parasitism(Y/N)	5	117.631	-224.888	0	0.960
size	5	113.185	-215.996	8.892	0.011
PCA 2	5	113.124	-215.874	9.014	0.010
constant	4	111.981	-215.714	9.174	0.009
PCA 1	5	112.884	-215.393	9.495	0.008

Table S1-4. Eigenvalues for the Multiple Factor Analysis for Eastern Meadowlark size.

	eigenvalue	percentage of variance	cumulative percentage of variance
dimension 1	13.058	68.727	68.727
dimension 2	2.002	10.540	79.268
dimension 3	1.403	7.384	86.653
dimension 4	0.666	3.509	90.162
dimension 5	0.488	2.569	92.732

Table S1-5a. Model selection table for the first round of Eastern Meadowlark size modeling.

	df	logLik	AICc	delta	weight
year*age	7	-308.474	631.377	0	0.817
year*age+N host nestlings	9	-308.385	635.465	4.088	0.105
year*age+N host eggs	10	-307.752	636.357	4.980	0.067
age*N host nestlings+ year	10	-309.911	640.674	9.297	0.007
age*N host eggs+ year	12	-309.453	644.125	12.747	0.001
age	5	-318.898	648.024	16.646	0.000
age*N host nestlings	9	-318.129	654.952	23.575	6.21E-06
age*N host eggs	11	-317.709	658.444	27.067	1.08E-06
constant	4	-724.971	1458.093	826.716	2.47E-180

Table S1-5b. Model selection table for the first round of Eastern Meadowlark size modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
year*age	7	-186.897	388.507	0	0.510
year*age+N host nestlings	11	-183.137	389.999	1.491	0.242
year*age+sex	8	-186.897	390.716	2.209	0.169
year*age+N host eggs	10	-185.489	392.405	3.898	0.072
age*sex+year	8	-190.884	398.691	10.184	0.003
age*sex*N host nestlings+year	12	-187.029	400.109	11.602	0.001
age*sex*N host eggs+ year	11	-189.383	402.490	13.983	0.000
age*N host eggs+ year	12	-189.736	405.523	17.016	0.000
age*N host nestlings+ year	14	-187.935	406.669	18.162	5.81E-05
age	5	-198.338	407.052	18.545	4.80E-05
age*sex*N host eggs+year	13	-189.733	407.876	19.369	3.18E-05
sex	7	-196.715	408.144	19.636	2.78E-05
age*N host nestlings*sex+year	15	-187.907	409.035	20.528	1.78E-05
age*sex+N host nestlings	11	-194.818	413.361	24.854	2.05E-06
age*sex+N host eggs	10	-196.572	414.572	26.065	1.12E-06
age*N host eggs	11	-196.869	417.463	28.956	2.63E-07
age*sex*N host nestlings+year	22	-183.481	418.088	29.581	1.93E-07
age*N host nestlings	13	-195.593	419.597	31.090	9.05E-08
age*sex+N host eggs	12	-196.865	419.783	31.276	8.25E-08
age*sex+N host nestlings	14	-195.592	421.983	33.476	2.75E-08
age*sex*N host nestlings	21	-191.692	431.845	43.338	1.98E-10

Table S1-6. Model selection table for the final round of Eastern Meadowlark size modeling.

	df	logLik	AICc	delta	weight
year*age	7	-308.474	631.377	0	0.604
year*age+parasitism(Y/N)	8	-308.428	633.410	2.032	0.218
year*age+N cowbird nestlings	9	-308.338	635.370	3.993	0.082
year*age+N all nestlings	10	-307.534	635.920	4.543	0.062
year*age+N cowbird eggs	10	-308.212	637.275	5.898	0.031
age*parasitism(Y/N)	7	-318.647	651.723	20.345	2.31E-05

age* N cowbird nestlings	9	-318.154	655.002	23.625	4.48E-06
age* N cowbird eggs	10	-318.231	657.314	25.937	1.41E-06
age*N all nestlings	11	-318.249	659.526	28.148	4.67E-07

Table S1-7. Model selection table for Eastern Meadowlark within-nest deviations in size.

	df	logLik	AICc	delta	weight
N all nestlings	7	-51.711	118.413	0	0.371
N host nestlings	6	-53.070	118.878	0.464	0.294
year*parasitism(Y/N)	7	-52.894	120.779	2.366	0.113
Year	5	-55.750	122.021	3.608	0.061
year+N host nestlings	9	-51.215	122.053	3.639	0.060
constant	4	-57.124	122.593	4.180	0.045
year+N all nestlings	11	-49.509	123.440	5.026	0.030
parasitism(Y/N)	5	-57.116	124.753	6.339	0.015
sex score	7	-56.271	127.533	9.119	0.003
N host eggs	7	-56.874	128.740	10.326	0.002
year+N host eggs	10	-54.068	130.136	11.722	0.001

Table S1-8. Eigenvalues for the Principle Components Analysis for Eastern Meadowlark prioritization.

	eigenvalue	percentage of variance	cumulative percentage of variance
component 1	4.394	36.622	36.622
component 2	2.501	20.844	57.466
component 3	1.224	10.206	67.673
component 4	0.845	7.044	74.717
component 5	0.694	5.790	80.508
component 6	0.551	4.598	85.106
component 7	0.479	3.993	89.100
component 8	0.374	3.122	92.223
component 9	0.330	2.753	94.976
component 10	0.308	2.574	97.551
component 11	0.201	1.675	99.226
component 12	0.092	0.773	100

Table S1-9a. Model selection table for the first round of Eastern Meadowlark PC1 modeling.

	df	logLik	AICc	delta	weight
year*age+N host nestlings	9	-551.778	1122.251	0	0.406
year*age	7	-553.947	1122.323	0.071	0.392
age*N host eggs	11	-550.81	1124.648	2.397	0.122
age*N host eggs+ year	12	-550.715	1126.648	4.396	0.045
year*age+N host eggs	10	-553.291	1127.434	5.183	0.030
age*N host nestlings	9	-556.95	1132.594	10.343	0.002
age*N host nestlings+ year	10	-556.756	1134.364	12.113	0.000
age	5	-564.861	1139.95	17.699	5.83E-05
constant	4	-571.737	1151.626	29.375	1.70E-07

Table S1-9b. Model selection table for the first round of Eastern Meadowlark PC1 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
year*age+N host nestlings	11	-352.384	728.493	0	0.693
year*age+sex	8	-357.205	731.333	2.840	0.167
year*age	7	-359.69	734.093	5.599	0.042
year*age+N host eggs	10	-356.356	734.140	5.647	0.041
age*sex+N host eggs	12	-354.511	735.074	6.581	0.025
age*N host eggs	11	-356.401	736.527	8.034	0.012
age*sex*N host eggs+year	13	-354.222	736.854	8.361	0.010
age*N host eggs+ year	12	-356.275	738.602	10.108	0.004
age*N host nestlings*sex+year	15	-354.519	742.259	13.766	0.000
age*sex+N host nestlings	14	-355.801	742.401	13.907	0.000
age*N host nestlings	13	-357.526	743.462	14.969	0.000
age*N host nestlings+ year	14	-356.722	744.244	15.751	0.000
age*sex*N host nestlings+year	12	-360.47	746.992	18.498	6.67E-05
age*sex+N host nestlings	11	-361.95	747.625	19.131	4.86E-05
age*sex+N host eggs	10	-364.323	750.073	21.580	1.43E-05
age*sex*N host nestlings	21	-350.996	750.453	21.960	1.18E-05
age*sex*N host eggs+ year	11	-363.546	750.816	22.323	9.85E-06

age*sex*N host nestlings+year	22	-350.006	751.138	22.644	8.39E-06
age*sex+year	8	-367.357	751.637	23.143	6.54E-06
sex	7	-368.544	751.801	23.308	6.02E-06
age	5	-371.728	753.833	25.339	2.18E-06

Table S1-10. Model selection table for the final round of Eastern Meadowlark PC1 modeling.

	df	logLik	AICc	delta	weight
year*age+N all nestlings	10	-550	1120.853	0	0.546
year*age	7	-553.947	1122.323	1.469	0.262
year*age+parasitism(Y/N)	8	-553.859	1124.272	3.418	0.098
year*age+N cowbird nestlings	9	-553.158	1125.012	4.158	0.068
year*age+N cowbird eggs	10	-553.446	1127.745	6.892	0.017
age*N host nestlings+N all nestlings	12	-553.611	1132.44	11.587	0.001
age*N host nestlings	9	-556.95	1132.594	11.741	0.001
age* N cowbird nestlings	9	-557.075	1132.844	11.991	0.001
age*N host nestlings+N cowbird nestlings	11	-555.588	1134.204	13.351	0.000
age*N host nestlings+parasitism(Y/N)	10	-556.686	1134.224	13.370	0.000
age*parasitism(Y/N)	7	-561.285	1136.999	16.146	0.000
age*N all nestlings	11	-557.341	1137.709	16.855	0.000
age*N host nestlings+N cowbird eggs	12	-556.524	1138.267	17.413	9.05E-05
age* N cowbird eggs	10	-561.067	1142.987	22.133	8.54E-06

Table S1-11. Model selection table for Eastern Meadowlark within-nest deviations in PC1.

	df	logLik	AICc	delta	weight
year	5	-138.422	287.365	0	0.921
constant	4	-142.622	293.589	6.224	0.041
parasitism(Y/N)	5	-142.551	295.622	8.257	0.014
N host nestlings	6	-141.881	296.499	9.134	0.009
N all nestlings	7	-141.487	297.966	10.601	0.004
sex score	7	-141.532	298.055	10.690	0.004
N host eggs	7	-141.685	298.360	10.995	0.003

Table S1-12a. Model selection table for the first round of Eastern Meadowlark PC2 modeling.

	df	logLik	AICc	delta	weight
constant	4	-504.645	1017.442	0	0.245
age*N host nestlings+ year	10	-498.448	1017.748	0.306	0.210
age	5	-503.93	1018.088	0.645	0.177
age*N host nestlings	9	-499.716	1018.127	0.685	0.174
year*age	7	-502.479	1019.387	1.945	0.092
year*age+N host nestlings	9	-500.575	1019.844	2.402	0.073
year*age+N host eggs	10	-500.982	1022.817	5.375	0.016
age*N host eggs	11	-501.26	1025.547	8.105	0.004
age*N host eggs+ year	12	-500.498	1026.214	8.771	0.003

Table S1-12b. Model selection table for the first round of Eastern Meadowlark PC2 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age	5	-312.157	634.690	0	0.637
sex	7	-311.627	637.967	3.276	0.123
year*age	7	-312.028	638.768	4.077	0.082
age*sex+year	8	-311.617	640.157	5.467	0.041
year*age+sex	8	-311.687	640.296	5.605	0.038
age*sex+N host eggs	10	-310.049	641.525	6.834	0.020
year*age+N host eggs	10	-310.242	641.912	7.221	0.017
age*sex*N host eggs+ year	11	-309.99	643.706	9.015	0.007
age*N host eggs	11	-310.038	643.801	9.110	0.006
age*sex+N host nestlings	11	-310.198	644.121	9.431	0.005
year*age+N host nestlings	11	-310.321	644.366	9.675	0.005
age*N host nestlings	13	-308.409	645.229	10.538	0.003
age*sex+N host eggs	12	-309.809	645.671	10.980	0.002
age*N host eggs+ year	12	-309.95	645.952	11.261	0.002
age*sex*N host nestlings+year	12	-310.184	646.420	11.729	0.001
age*sex+N host nestlings	14	-308.3	647.399	12.708	0.001
age*N host nestlings+ year	14	-308.365	647.530	12.839	0.001

age*sex*N host eggs+year	13	-309.752	647.914	13.223	0.000
age*N host nestlings*sex+year	15	-308.263	649.746	15.056	0.000
age*sex*N host nestlings	21	-306.23	660.921	26.231	1.28E-06
age*sex*N host nestlings+year	22	-306.117	663.360	28.669	3.79E-07

Table S1-13. Model selection table for the final round of Eastern Meadowlark PC2 modeling.

	df	logLik	AICc	delta	weight
age*N all nestlings	11	-494.449	1011.924	0	0.605
age*N host nestlings+N cowbird nestlings	11	-496.496	1016.02	4.095	0.078
age*parasitism(Y/N)	7	-501.099	1016.627	4.702	0.057
year*age+parasitism(Y/N)	8	-500.306	1017.167	5.242	0.044
age*N host nestlings+parasitism(Y/N)	10	-498.286	1017.425	5.500	0.038
constant	4	-504.645	1017.442	5.517	0.038
age*N host nestlings+N all nestlings	12	-496.364	1017.946	6.021	0.029
age	5	-503.93	1018.088	6.163	0.027
age*N host nestlings	9	-499.716	1018.127	6.203	0.027
age* N cowbird nestlings	9	-500.283	1019.26	7.335	0.015
year*age	7	-502.479	1019.387	7.462	0.014
age* N cowbird eggs	10	-499.477	1019.807	7.882	0.011
age*N host nestlings+N cowbird eggs	12	-497.65	1020.519	8.594	0.008
year*age+N all nestlings	10	-500.696	1022.245	10.320	0.003

Table S1-14. Model selection table for Eastern Meadowlark within-nest deviations in PC2.

	df	logLik	AICc	delta	weight
constant	4	-73.275	154.895	0	0.422
year	5	-73.098	156.718	1.823	0.169
parasitism(Y/N)	5	-73.172	156.866	1.970	0.157
N host nestlings	6	-72.660	158.058	3.163	0.086
N all nestlings	7	-71.691	158.374	3.479	0.074
sex score	7	-72.140	159.271	4.376	0.047
N host eggs	7	-72.266	159.523	4.628	0.041

Dickcissel growth model selection tables

Table S1-15. Model selection table for Dickcissel fledge age.

	df	logLik	AICc	delta	weight
sex	5	-224.347	459.100	0.00	0.956
constant	3	-230.613	467.390	8.28	0.015
parasitism(Y/N)	4	-229.824	467.922	8.82	0.012
PCA 2	4	-230.513	469.299	10.19	0.006
PCA 1	4	-230.546	469.365	10.26	0.006
size	4	-230.569	469.412	10.31	0.006

Table S1-16. Eigenvalues for the Multiple Factor Analysis for Dickcissel size.

	eigenvalue	percentage of variance	cumulative percentage of variance
dimension 1	12.586	66.245	66.245
dimension 2	1.931	10.168	76.413
dimension 3	1.599	8.418	84.831
dimension 4	0.648	3.414	88.246
dimension 5	0.534	2.811	91.057

Table S1-17a. Model selection table for the first round of Dickcissel size modeling.

	df	logLik	AICc	delta	weight
age	6	-329.285	670.954	0	0.469
year*age	7	-328.405	671.324	0.370	0.389
age*N host eggs	15	-321.052	674.389	3.435	0.084
age*N host eggs+ year	16	-321.02	676.642	5.688	0.027
year*age+N host eggs	12	-325.824	677.113	6.159	0.021
year*age+N host nestlings	12	-326.926	679.317	8.363	0.007
age*N host nestlings	14	-326.924	683.838	12.884	0.000
age*N host nestlings+ year	15	-326.784	685.854	14.900	0.000

Table S1-17b. Model selection table for the first round of Dickcissel size modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight

sex	7	-169.196	353.459	0	0.264
year*age	7	-169.452	353.970	0.511	0.204
age*sex+N host nestlings	8	-169.032	355.449	1.990	0.097
year*age+N host nestlings	8	-169.111	355.606	2.147	0.090
age*sex+year	8	-169.195	355.773	2.314	0.083
year*age+sex	8	-169.203	355.790	2.331	0.082
age	5	-173.067	356.695	3.235	0.052
age*sex+N host eggs	10	-167.692	357.541	4.082	0.034
age*sex*N host nestlings+year	9	-169.028	357.803	4.344	0.030
year*age+N host eggs	10	-167.982	358.12	4.660	0.025
age*sex*N host eggs+ year	11	-167.626	359.866	6.407	0.010
age*N host nestlings	7	-172.727	360.521	7.061	0.007
age*N host eggs	11	-168.694	362.001	8.542	0.003
age*sex*N host nestlings	11	-168.854	362.322	8.863	0.003
age*sex+N host nestlings	8	-172.532	362.448	8.989	0.002
age*N host nestlings+ year	8	-172.726	362.836	9.377	0.002
age*sex+N host eggs	12	-168.308	363.736	10.277	0.001
age*N host eggs+ year	12	-168.693	364.506	11.047	0.001
age*N host nestlings*sex+year	9	-172.531	364.810	11.351	0.000
age*sex*N host nestlings+year	12	-168.85	364.819	11.360	0.000
age*sex*N host eggs+year	13	-168.29	366.256	12.797	0.000
constant	4	-306.146	620.661	267.202	2.51E-59

Table S1-18. Model selection table for the final round of Dickcissel size modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
sex	7	-169.196	353.459	0	0.203
Year*age+N cowbird nestlings	9	-167.072	353.891	0.432	0.163
Year*age	7	-169.452	353.970	0.511	0.157
sex*age+ N cowbird nestlings	9	-167.128	354.003	0.544	0.154
sex*age+ parasitism(Y/N)	8	-169.071	355.526	2.067	0.072
sex*age+N all nestlings	10	-166.998	356.153	2.693	0.052
Year*age+parasitism(Y/N)	8	-169.384	356.153	2.694	0.052

Year*age+N all nestlings	10	-167.108	356.372	2.912	0.047
age	5	-173.067	356.695	3.235	0.040
age*N all nestlings	11	-166.529	357.672	4.213	0.024
age*parasitism(Y/N)	7	-172.171	359.408	5.949	0.010
age* N cowbird nestlings	9	-170.288	360.323	6.864	0.006
age*N host nestlings	7	-172.727	360.521	7.061	0.005
age*N host nestlings+N cowbird nestlings	9	-170.992	361.732	8.273	0.003
age*N host nestlings+N all nestlings	10	-169.919	361.994	8.534	0.002
age*N host nestlings+parasitism(Y/N)	8	-172.481	362.346	8.887	0.002

Table S1-19. Model selection table for Dickcissel within-nest deviations in size.

	df	logLik	AICc	delta	weight
N all nestlings	7	-36.156	87.661	0	0.394
constant	4	-39.915	88.296	0.635	0.287
parasitism(Y/N)	5	-39.770	90.246	2.584	0.108
year	5	-39.826	90.359	2.697	0.102
N host nestlings	6	-39.672	92.344	4.682	0.037
year+N all nestlings	10	-35.422	93.594	5.932	0.020
N host eggs	7	-39.184	93.717	6.055	0.019
year+parasitism(Y/N)	7	-39.657	94.664	7.002	0.011
sex score	7	-39.812	94.974	7.312	0.010
year+N host nestlings	8	-38.935	95.626	7.964	0.007
year+N host eggs	10	-38.208	99.166	11.504	0.001

Table S1-20. Eigenvalues for the Principle Components Analysis for Dickcissel prioritization.

	eigenvalue	percentage of variance	cumulative percentage of variance
component 1	4.111	34.261	34.261
component 2	2.017	16.812	51.073
component 3	1.204	10.038	61.111
component 4	1.146	9.555	70.666
component 5	0.703	5.866	76.532
component 6	0.607	5.062	81.594

component 7	0.517	4.313	85.908
component 8	0.483	4.031	89.939
component 9	0.435	3.626	93.566
component 10	0.361	3.013	96.580
component 11	0.288	2.400	98.980
component 12	0.122	1.019	100

Table S1-21a. Model selection table for the first round of Dickcissel PC1 modeling.

	df	logLik	AICc	delta	weight
age	5	-473.758	957.789	0	0.427
year*age+N host nestlings	11	-468.05	959.334	1.544	0.197
year*age	7	-472.841	960.194	2.405	0.128
age*N host nestlings	13	-466.265	960.246	2.456	0.125
age*N host nestlings+ year	14	-465.294	960.579	2.789	0.106
age*N host eggs	15	-466.935	966.155	8.365	0.006
age*N host eggs+ year	16	-466.2	967.002	9.212	0.004
year*age+N host eggs	12	-470.949	967.361	9.572	0.003

Table S1-21b. Model selection table for the first round of Dickcissel PC1 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*sex+N host nestlings	8	-253.667	524.718	0	0.437
age*N host nestlings	7	-255.794	526.654	1.936	0.166
age*N host nestlings*sex+year	9	-253.573	526.893	2.174	0.147
age*N host nestlings+ year	8	-255.332	528.048	3.330	0.082
age	5	-259.584	529.729	5.010	0.035
sex	7	-257.656	530.377	5.659	0.025
year*age+sex	8	-256.687	530.758	6.039	0.021
year*age	7	-257.975	531.015	6.297	0.018
age*sex*N host nestlings	11	-253.536	531.685	6.966	0.013
age*sex+N host nestlings	8	-257.368	532.120	7.402	0.010
age*sex+year	8	-257.404	532.192	7.474	0.010
year*age+N host nestlings	8	-257.625	532.634	7.916	0.008

age*sex*N host nestlings+year	12	-253.431	533.981	9.263	0.004
age*sex*N host nestlings+year	9	-257.166	534.078	9.360	0.004
year*age+N host eggs	10	-256.284	534.724	10.006	0.002
age*sex+N host eggs	12	-253.926	534.971	10.253	0.002
age*sex+N host eggs	10	-256.551	535.259	10.541	0.002
age*N host eggs	11	-255.765	536.144	11.426	0.001
constant	4	-264.074	536.518	11.800	0.001
age*N host eggs+ year	12	-254.752	536.624	11.905	0.001
age*sex*N host eggs+year	13	-253.54	536.756	12.038	0.001
age*sex*N host eggs+ year	11	-256.105	536.823	12.104	0.001

Table S1-22. Model selection table for the final round of Dickcissel PC1 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*sex+N host nestlings	8	-253.667	524.718	0	0.448
age* N host nestlings	7	-255.794	526.654	1.936	0.170
age*N host nestlings*sex+year	9	-253.573	526.893	2.174	0.151
age* N host nestlings+ parasitism(Y/N)	8	-255.61	528.604	3.885	0.064
age* N host nestlings+N cowbird nestlings	9	-254.924	529.596	4.877	0.039
age*sex	7	-257.656	530.377	5.659	0.026
age*sex+parasitism(Y/N)	8	-256.796	530.977	6.258	0.019
age*parasitism(Y/N)	7	-258.244	531.555	6.836	0.014
age* N cowbird nestlings	9	-255.965	531.676	6.958	0.013
age*sex+N host nestlings	11	-253.536	531.685	6.966	0.013
age* N host nestlings+N all nestlings	10	-254.984	532.124	7.406	0.011
age*sex+N cowbird nestlings	9	-256.257	532.260	7.542	0.010
age*sex*N host nestlings+parasitism(Y/N)	12	-253.135	533.389	8.670	0.005
age*N all nestlings	11	-254.47	533.554	8.835	0.005
age*sex*N host nestlings+N cowbird nestlings	13	-252.377	534.431	9.713	0.003
age*sex+N all nestlings	10	-256.726	535.608	10.890	0.001
age*sex*N host nestlings+N all nestlings	14	-252.741	537.767	13.049	0.000

Table S1-23. Model selection table for Dickcissel within-nest deviations in PC1.

	df	logLik	AICc	delta	weight
N host nestlings	6	-130.803	274.605	0	0.474
year	5	-132.697	276.099	1.494	0.224
constant	4	-134.23	276.925	2.320	0.148
N all nestlings	7	-131.799	278.946	4.341	0.054
parasitism(Y/N)	5	-134.199	279.104	4.499	0.049
N host eggs	7	-132.351	280.051	5.446	0.031
sex score	7	-132.926	281.201	6.596	0.017

Table S1-24a. Model selection table for the first round of Dickcissel PC2 modeling.

	df	logLik	AICc	delta	weight
year*age	7	-395.203	804.920	0	0.703
age	5	-399.288	808.848	3.927	0.098
age*N host nestlings	14	-390.302	810.595	5.674	0.041
age*N host eggs+ year	16	-388.015	810.632	5.711	0.040
age*N host nestlings+ year	15	-389.358	811.001	6.080	0.033
age*N host eggs	15	-389.408	811.101	6.180	0.032
year*age+N host eggs	12	-392.92	811.305	6.384	0.028
year*age+N host nestlings	12	-393.231	811.926	7.006	0.021

Table S1-24b. Model selection table for the first round of Dickcissel PC2 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*sex+N host nestlings	8	-253.667	524.718	0	0.437
age*N host nestlings	7	-255.794	526.654	1.936	0.166
age*N host nestlings*sex+year	9	-253.573	526.893	2.174	0.147
age*N host nestlings+ year	8	-255.332	528.048	3.330	0.082
age	5	-259.584	529.729	5.010	0.035
sex	7	-257.656	530.377	5.659	0.025
year*age+sex	8	-256.687	530.758	6.039	0.021
year*age	7	-257.975	531.015	6.297	0.018
age*sex*N host nestlings	11	-253.536	531.685	6.966	0.013

age*sex+N host nestlings	8	-257.368	532.120	7.402	0.010
age*sex+year	8	-257.404	532.192	7.474	0.010
year*age+N host nestlings	8	-257.625	532.634	7.916	0.008
age*sex*N host nestlings+year	12	-253.431	533.981	9.263	0.004
age*sex*N host nestlings+year	9	-257.166	534.078	9.360	0.004
year*age+N host eggs	10	-256.284	534.724	10.006	0.002
age*sex+N host eggs	12	-253.926	534.971	10.253	0.002
age*sex+N host eggs	10	-256.551	535.259	10.541	0.002
age*N host eggs	11	-255.765	536.144	11.426	0.001
constant	4	-264.074	536.518	11.800	0.001
age*N host eggs+ year	12	-254.752	536.624	11.905	0.001
age*sex*N host eggs+year	13	-253.54	536.756	12.038	0.001
age*sex*N host eggs+ year	11	-256.105	536.823	12.104	0.001

Table S1-25. Model selection table for the final round of Dickcissel PC2 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*sex+parasitism(Y/N)	8	-214.506	446.396	0	0.296
year*age* N cowbird nestlings	9	-213.783	447.313	0.917	0.187
age*sex	7	-216.487	448.040	1.644	0.130
age*sex+ N cowbird nestlings	9	-214.264	448.275	1.878	0.115
age	5	-219.382	449.325	2.929	0.068
year*age*parasitism(Y/N)	8	-216.392	450.168	3.772	0.044
year*age	7	-217.595	450.257	3.861	0.043
age*parasitism(Y/N)	7	-217.754	450.574	4.177	0.036
age*sex+N all nestlings	10	-214.681	451.519	5.122	0.022
year*age*sex+ N cowbird nestlings	13	-211.379	452.435	6.039	0.014
year*age*N all nestlings	10	-215.277	452.711	6.315	0.012
year*age*sex+ parasitism(Y/N)	12	-213.26	453.640	7.244	0.007
age*N all nestlings	11	-214.71	454.033	7.636	0.006
age* N cowbird nestlings	9	-217.242	454.231	7.835	0.005
year*age+sex	11	-214.982	454.577	8.181	0.004
year*age*sex+N all nestlings	14	-213.005	458.296	11.900	0.000

Table S1-26. Model selection table for Dickcissel within-nest deviations in PC2.

	df	logLik	AICc	delta	weight
year	5	-73.378	157.462	0	0.451
constant	4	-75.399	159.263	1.800	0.183
N host nestlings	6	-73.232	159.465	2.002	0.165
N all nestlings	7	-72.649	160.648	3.185	0.091
parasitism(Y/N)	5	-75.172	161.051	3.588	0.075
sex score	7	-74.083	163.515	6.052	0.021
N host eggs	7	-74.859	165.068	7.606	0.010

Grasshopper Sparrow growth model selection tables

Table S1-27. Model selection table for Grasshopper Sparrow fledge age.

	df	logLik	AICc	delta	weight
constant	4	-51.188	110.753	0	0.331
size	5	-50.486	111.545	0.791	0.223
PCA 2	5	-50.644	111.861	1.107	0.190
PCA 1	5	-51.026	112.623	1.869	0.130
parasitism(Y/N)	5	-51.070	112.712	1.958	0.124

Table S1-28. Eigenvalues for the Multiple Factor Analysis for Grasshopper Sparrow size.

	eigenvalue	percentage of variance	cumulative percentage of variance
dimension 1	12.556	66.085	66.085
dimension 2	1.959	10.311	76.396
dimension 3	1.439	7.574	83.971
dimension 4	0.726	3.825	87.797
dimension 5	0.565	2.976	90.773

Table S1-29a. Model selection table for the first round of Grasshopper Sparrow size modeling.

	df	logLik	AICc	delta	weight
age*N host nestlings	9	-243.484	506.046	0	0.660

age*N host nestlings+ year	10	-243.48	508.284	2.237	0.215
year*age+N host nestlings	9	-246.017	511.110	5.064	0.052
year*age	7	-248.846	512.354	6.307	0.028
age	8	-248.085	513.027	6.980	0.020
age*N host eggs	11	-245.019	513.638	7.591	0.014
age*N host eggs+ year	12	-244.809	515.520	9.473	0.005
year*age+N host eggs	10	-248.031	517.387	11.341	0.002
constant	4	-468.11	944.453	438.406	4.18E-96

Table S1-29b. Model selection table for the first round of Grasshopper Sparrow size modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age	5	-138.539	287.745	0	0.680
year*age	7	-138.094	291.46	3.714	0.106
sex	7	-138.175	291.623	3.877	0.097
age*sex+year	8	-137.749	293.153	5.408	0.045
year*age+sex	8	-138.088	293.831	6.085	0.032
age*sex+N host nestlings	11	-135.794	296.730	8.984	0.007
year*age+N host nestlings	11	-136.063	297.267	9.522	0.005
age*N host nestlings	13	-133.485	297.408	9.662	0.005
age*N host eggs	12	-135.179	298.117	10.371	0.003
age*N host eggs+ year	13	-134.215	298.868	11.123	0.002
age*sex*N host nestlings+year	12	-135.681	299.120	11.374	0.002
year*age+N host eggs	11	-137.045	299.232	11.486	0.002
age*N host nestlings+ year	14	-133.415	300.014	12.268	0.001
age*sex+N host nestlings	14	-133.481	300.147	12.401	0.001
age*sex+N host eggs	11	-137.661	300.464	12.718	0.001
age*sex+N host eggs	13	-135.155	300.75	13.004	0.001
age*sex*N host eggs+ year	12	-136.662	301.082	13.336	0.000
age*sex*N host eggs+year	14	-134.214	301.613	13.867	0.000

age*N host nestlings*sex+year	15	-133.415	302.829	15.083	0.000
age*sex*N host nestlings	21	-130.108	314.702	26.956	9.54E-07
age*sex*N host nestlings+year	22	-129.7	317.263	29.518	2.65E-07

Table S1-30. Model selection table for the final round of Grasshopper Sparrow size modeling.

	df	logLik	AICc	delta	weight
age*N host nestlings	9	-243.484	506.046	0	0.462
age*N host nestlings+parasitism(Y/N)	10	-243.198	507.720	1.673	0.200
age*N host nestlings+N cowbird eggs	12	-241.01	507.921	1.875	0.181
age*N host nestlings+N cowbird nestlings	11	-243	509.600	3.553	0.078
age*parasitism(Y/N)	7	-248.095	510.852	4.806	0.041
age* N cowbird eggs	10	-245.479	512.283	6.236	0.020
age* N cowbird nestlings	9	-247.224	513.526	7.479	0.010
age*N all nestlings	11	-245.747	515.093	9.047	0.005

Table S1-31. Model selection table for Grasshopper Sparrow within-nest deviations in size.

	df	logLik	AICc	delta	weight
N all nestlings	7	-22.139	59.950	0	0.306
constant	4	-25.906	60.385	0.434	0.246
year	5	-25.343	61.556	1.605	0.137
parasitism(Y/N)	5	-25.657	62.184	2.234	0.100
year+N host nestlings	9	-21.207	63.183	3.233	0.060
N host nestlings	6	-24.985	63.205	3.255	0.060
N host eggs	7	-24.417	64.505	4.555	0.031
year+N all nestlings	10	-20.982	65.402	5.451	0.020
year+parasitism(Y/N)	7	-25.008	65.688	5.737	0.017
sex score	7	-25.088	65.848	5.897	0.016
year+N host eggs	10	-22.561	68.560	8.609	0.004

Table S1-32. Eigenvalues for the Principle Components Analysis for Grasshopper Sparrow prioritization.

	eigenvalue	percentage of variance	cumulative percentage of variance

component 1	4.061	33.846	33.846
component 2	1.753	14.613	48.460
component 3	1.211	10.096	58.556
component 4	1.093	9.112	67.668
component 5	0.976	8.136	75.805
component 6	0.655	5.466	81.271
component 7	0.581	4.849	86.121
component 8	0.504	4.201	90.323
component 9	0.449	3.749	94.072
component 10	0.335	2.793	96.866
component 11	0.276	2.306	99.172
component 12	0.099	0.827	100

Table S1-33a. Model selection table for the first round of Grasshopper Sparrow PC1 modeling.

	df	logLik	AICc	delta	weight
age*N host nestlings	9	-243.484	506.046	0	0.660
age*N host nestlings+ year	10	-243.48	508.284	2.237	0.215
year*age+N host nestlings	9	-246.017	511.110	5.064	0.052
year*age	7	-248.846	512.354	6.307	0.028
age	8	-248.085	513.027	6.980	0.020
age*N host eggs	11	-245.019	513.638	7.591	0.014
age*N host eggs+ year	12	-244.809	515.520	9.473	0.005
year*age+N host eggs	10	-248.031	517.387	11.341	0.002
constant	4	-468.11	944.453	438.406	4.18E-96

Table S1-33b. Model selection table for the first round of Grasshopper Sparrow PC1 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*N host nestlings	13	-189.854	410.146	0	0.572
age*sex+N host nestlings	14	-189.807	412.799	2.653	0.152
age*N host nestlings+ year	14	-189.849	412.883	2.736	0.145
age	5	-202.285	415.236	5.090	0.044
age*N host nestlings*sex+year	15	-189.807	415.613	5.467	0.037

year*age	7	-201.066	417.405	7.258	0.015
sex	7	-201.296	417.863	7.717	0.012
year*age+sex	8	-200.824	419.303	9.157	0.005
age*sex+year	8	-200.87	419.394	9.248	0.005
age*sex+N host nestlings	11	-197.724	420.590	10.444	0.003
year*age+N host nestlings	11	-197.794	420.731	10.584	0.002
age*sex*N host nestlings+year	12	-197.685	423.129	12.983	0.000
age*sex*N host nestlings	21	-184.866	424.217	14.071	0.000
age*sex+N host eggs	11	-199.969	425.080	14.934	0.000
year*age+N host eggs	11	-199.991	425.125	14.979	0.000
age*N host eggs	12	-199.851	427.460	17.314	9.96E-05
age*sex*N host eggs+ year	12	-199.853	427.465	17.318	9.94E-05
age*sex*N host nestlings+year	22	-184.858	427.579	17.432	9.39E-05
age*sex+N host eggs	13	-199.776	429.990	19.844	2.81E-05
age*N host eggs+ year	13	-199.784	430.006	19.860	2.79E-05
age*sex*N host eggs+year	14	-199.675	432.536	22.389	7.87E-06

Table S1-34. Model selection table for the final round of Grasshopper Sparrow PC1 modeling.

	df	logLik	AICc	delta	weight
age*N host nestlings	9	-342.411	703.899	0	0.650
age*N host nestlings+parasitism(Y/N)	10	-342.406	706.138	2.238	0.212
age*N host nestlings+N cowbird nestlings	11	-342.324	708.247	4.348	0.073
age*N host nestlings+N cowbird eggs	12	-341.594	709.090	5.190	0.048
year*age+N all nestlings	10	-346.265	713.855	9.956	0.004
age*parasitism(Y/N)	7	-349.786	714.235	10.336	0.003
age*N all nestlings	11	-345.463	714.526	10.627	0.003
year*age	7	-350.626	715.914	12.014	0.001
year*age+parasitism(Y/N)	8	-350.337	717.531	13.631	0.000
age* N cowbird nestlings	9	-349.306	717.689	13.789	0.000
year*age+N cowbird nestlings	9	-350.012	719.102	15.203	0.000
age* N cowbird eggs	10	-348.972	719.268	15.369	0.000
year*age+N cowbird eggs	10	-349.832	720.988	17.089	0.000

Table S1-35. Model selection table for Grasshopper Sparrow within-nest deviations in PC1.

	df	logLik	AICc	delta	weight
constant	4	-59.888	128.348	0	0.414
year	5	-59.484	129.837	1.489	0.196
parasitism(Y/N)	5	-59.811	130.493	2.144	0.141
N host nestlings	6	-59.252	131.739	3.390	0.076
sex score	7	-58.100	131.873	3.524	0.071
N all nestlings	7	-58.108	131.888	3.540	0.070
N host eggs	7	-58.997	133.667	5.318	0.029

Table S1-36a. Model selection table for the first round of Grasshopper Sparrow PC2 modeling.

	df	logLik	AICc	delta	weight
age*N host eggs	11	-287.524	598.648	0	0.457
age*N host eggs+ year	12	-287.277	600.457	1.808	0.185
year*age+N host nestlings	9	-291.259	601.595	2.947	0.104
year*age+N host eggs	10	-290.731	602.786	4.137	0.057
year*age	7	-294.149	602.961	4.313	0.052
age	5	-296.345	603.041	4.392	0.050
constant	4	-297.478	603.189	4.540	0.047
age*N host nestlings	9	-292.64	604.357	5.708	0.026
age*N host nestlings+ year	10	-291.97	605.265	6.616	0.016

Table S1-36b. Model selection table for the first round of Grasshopper Sparrow PC2 modeling with the sex-only dataset.

	df	logLik	AICc	delta	weight
age*N host nestlings	13	-147.335	325.109	0	0.329
year*age+N host nestlings	11	-151.096	327.335	2.225	0.108
age*sex+N host nestlings	11	-151.104	327.350	2.240	0.107
age*sex+N host nestlings	14	-147.192	327.570	2.460	0.096
age*N host nestlings+ year	14	-147.256	327.697	2.588	0.090
age*N host eggs	12	-150.118	327.994	2.884	0.077
age*sex+N host eggs	13	-149.428	329.294	4.185	0.040
age*sex*N host nestlings+year	12	-150.831	329.420	4.311	0.038
age*N host nestlings*sex+year	15	-146.999	329.998	4.888	0.028

age*N host eggs+ year	13	-149.948	330.334	5.225	0.024
age*sex*N host eggs+year	14	-148.926	331.036	5.927	0.017
age*sex+N host eggs	11	-153.055	331.253	6.144	0.015
year*age+N host eggs	11	-153.639	332.420	7.311	0.008
age*sex*N host eggs+ year	12	-152.65	333.059	7.949	0.006
age	5	-161.202	333.069	7.960	0.006
year*age	7	-160.138	335.548	10.438	0.001
year*age+sex	8	-159.659	336.972	11.862	0.000
age*sex+year	8	-159.714	337.083	11.973	0.000
sex	7	-160.953	337.178	12.069	0.000
age*sex*N host nestlings	21	-144.768	344.022	18.913	2.58E-05
age*sex*N host nestlings+year	22	-144.404	346.671	21.562	6.86E-06

Table S1-37. Model selection table for the final round of Grasshopper Sparrow PC2 modeling.

	df	logLik	AICc	delta	weight
age*N host eggs+ N cowbird eggs	14	-281.861	594.314	0	0.494
age*N host eggs+ N cowbird nestlings	13	-283.804	595.841	1.527	0.230
age*N host eggs+parasitism(Y/N)	12	-285.181	596.265	1.951	0.186
age*N host eggs	11	-287.524	598.648	4.334	0.056
age*N all nestlings+N host eggs	14	-285.042	600.676	6.362	0.020
age	5	-296.345	603.041	8.727	0.006
age*parasitism(Y/N)	7	-295.256	605.175	10.861	0.002
age*N all nestlings	11	-290.804	605.208	10.894	0.002
age* N cowbird nestlings	9	-293.807	606.690	12.376	0.001
year*age+N cowbird eggs	10	-293.194	607.714	13.400	0.000
age* N cowbird eggs	10	-293.843	609.010	14.696	0.000

Table S1-38. Model selection table for Grasshopper Sparrow within-nest deviations in PC2.

	df	logLik	AICc	delta	weight
N host nestlings	6	-68.436	150.107	0	0.631
N all nestlings	7	-67.801	151.274	1.167	0.352
constant	4	-75.123	158.819	8.711	0.008
parasitism(Y/N)	5	-74.663	160.196	10.088	0.004

year	5	-75.015	160.900	10.792	0.002
sex score	7	-73.664	163.001	12.893	0.001
N host eggs	7	-75.071	165.814	15.706	0.000

Full PCA tables

Table S1-39. Contribution of each measurement to the Eastern Meadowlark PCA dimensions (full table).

	Dim1	Dim2	Dim3	Dim4	Dim5
tarsus/mass residuals	0.513	0.164	0.015	0.031	0.000
bill length/mass residuals	0.357	0.002	0.050	0.402	0.007
gape width/mass residuals	0.065	0.569	2.38E-06	0.009	0.053
ulna length /mass residuals	0.408	0.027	0.070	0.290	0.001
carpometacarpus length /mass residuals	0.259	0.122	0.378	0.001	0.002
primary 9 length /mass residuals	0.742	0.000	0.008	0.007	0.021
unsheathed primary 9 length /mass residuals	0.433	0.332	0.098	0.020	0.004
secondary 1 length /mass residuals	0.659	1.37E-06	0.078	0.002	0.006
unsheathed secondary 1 length /mass residuals	0.491	0.309	0.040	0.023	0.028
eye score/mass residuals	3.16E-06	0.612	0.136	0.006	0.025
feather score/mass residuals	0.201	0.304	0.114	0.000	0.255
activity score/mass residuals	0.262	0.057	0.232	0.049	0.285

Table S1-40. Contribution of each measurement to the Dickcissel PCA dimensions (full table).

	Dim1	Dim2	Dim3	Dim4	Dim5
tarsus/mass residuals	0.571	0.461	0.265	0.024	-0.356
bill length/mass residuals	0.511	0.194	0.183	0.582	-0.304
gape width/mass residuals	-0.209	0.364	0.640	0.415	0.313
ulna length /mass residuals	0.641	0.219	-0.302	-0.233	0.189
carpometacarpus length /mass residuals	0.335	0.565	-0.450	0.291	0.345
primary 9 length /mass residuals	0.813	-0.018	-0.185	0.229	0.135
unsheathed primary 9 length /mass residuals	0.588	-0.653	0.138	0.155	0.188
secondary 1 length /mass residuals	0.723	0.246	-0.280	0.004	-0.231
unsheathed secondary 1 length /mass residuals	0.687	-0.613	0.064	0.054	-0.035
eye score/mass residuals	0.318	0.560	0.327	-0.444	0.204

feather score/mass residuals	0.673	0.044	0.300	-0.463	-0.105
activity score/mass residuals	0.628	-0.291	0.246	-0.061	0.261

Table S1-41. Contribution of each measurement to the Grasshopper Sparrow PCA dimensions (full table).

	Dim1	Dim2	Dim3	Dim4	Dim5
tarsus/mass residuals	0.029	0.428	0.063	0.113	0.010
bill length/mass residuals	0.085	0.087	0.354	0.038	0.302
gape width/mass residuals	0.056	0.092	0.013	0.600	0.054
ulna length /mass residuals	0.610	0.000	3.00E-05	0.007	0.003
carpometacarpus length /mass residuals	0.006	0.185	0.482	0.116	0.025
primary 9 length /mass residuals	0.673	0.000	0.017	0.015	0.008
unsheathed primary 9 length /mass residuals	0.695	0.062	0.003	0.024	0.019
secondary 1 length /mass residuals	0.521	0.005	0.022	0.084	0.043
unsheathed secondary 1 length /mass residuals	0.692	0.073	0.003	0.035	0.022
eye score/mass residuals	0.000	0.660	0.058	0.042	0.060
feather score/mass residuals	0.316	0.072	0.059	0.013	0.386
activity score/mass residuals	0.372	0.085	0.131	0.000	0.040

Chapter 2 Supplementary Material

Table S2-1. Nest success model rankings for both years

model	Number of parameters	AICc	DeltaAICc	weight	Deviance
Nest visits	2	177.777	0.000	0.658	173.750
Nest visits*Year	4	180.468	2.691	0.171	172.379
Average visits/day	2	182.671	4.895	0.057	178.645
Constant	1	183.395	5.618	0.040	181.386
Camera (Y/N)	2	183.423	5.646	0.039	179.396
Year	2	184.725	6.948	0.020	180.698
Camera (Y/N)*Year	4	185.346	7.569	0.015	177.256

Table S2-2. Mass-corrected wing measurements principal component analysis contributions by measurement.

Mass-corrected Measurements	PCA1	PCA2	PCA3	PCA4
Ulna Length	0.525	0.411	0.028	0.035
Carpometacarpus length	0.521	0.417	0.023	0.040
Primary 9 Length	0.528	0.406	0.044	0.022
Secondary 1 Length	0.451	0.484	0.043	0.022

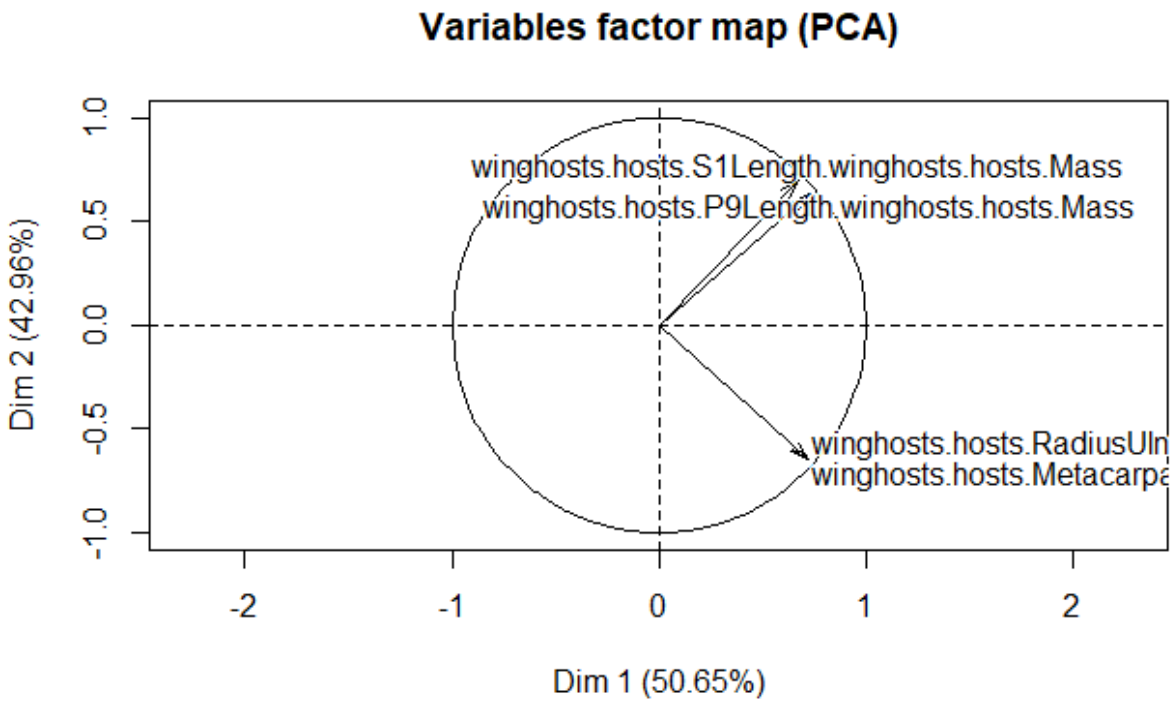

Figure S2-1. Map of the first two dimensions of the mass-corrected wing measurement principal component analysis.

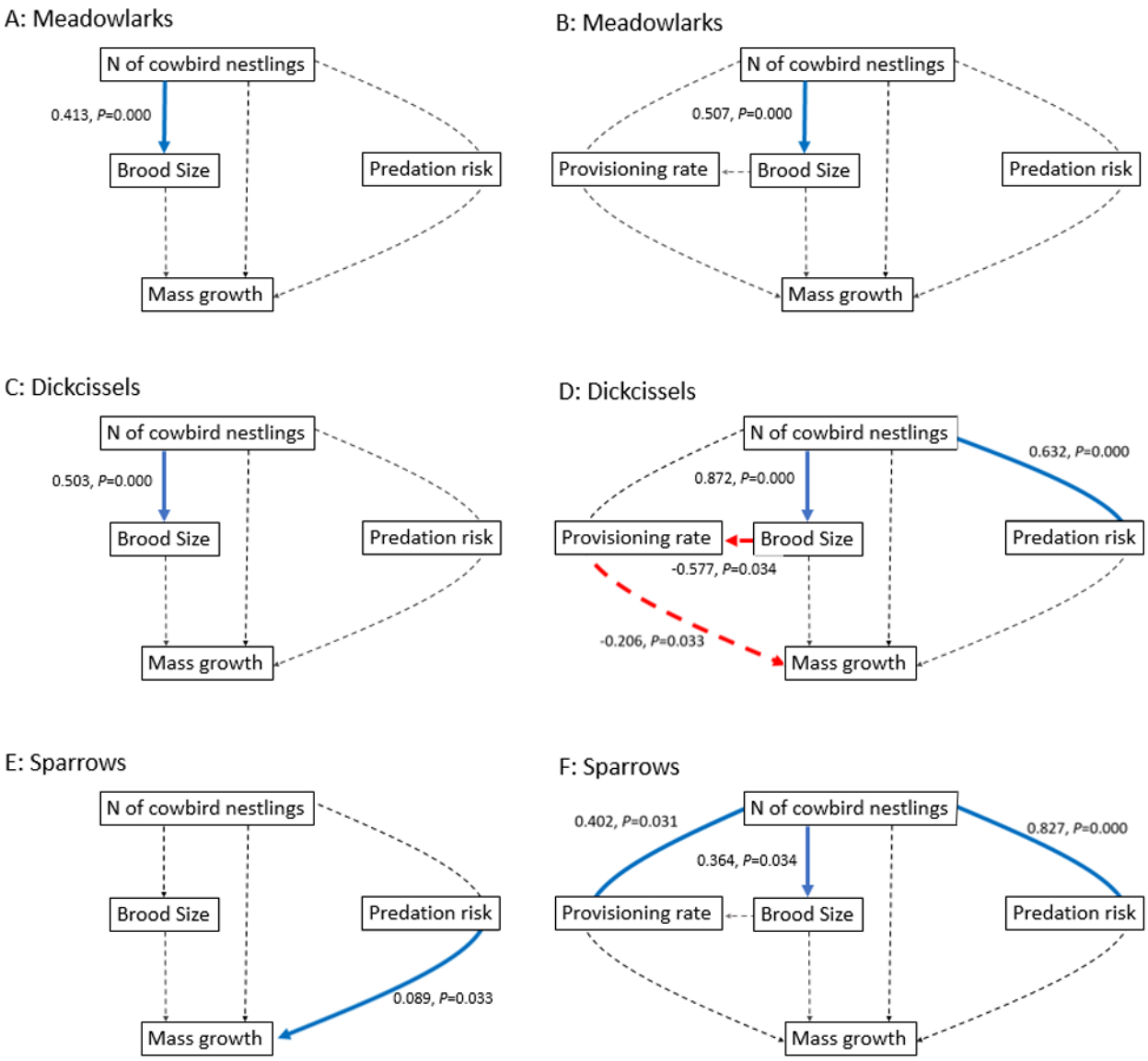

Figure S2-2. Mass growth SEMs, but labelled the betas from the additive effects instead of the effect*age interactions that account for change over time.

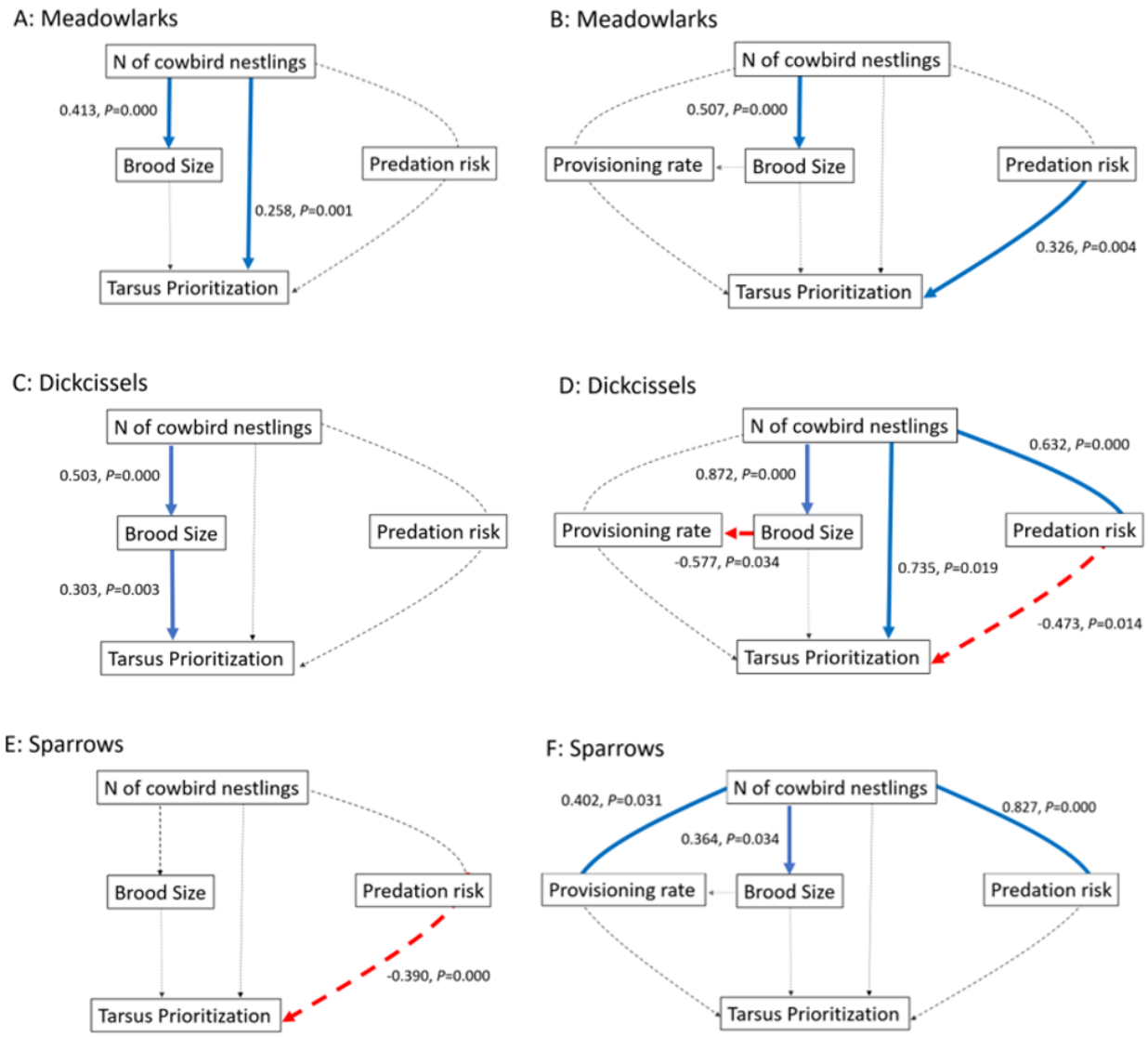

Figure S2-3. Tarsus prioritization SEMs, but labelled the betas from the additive effects instead of the effect*age interactions that account for change over time.

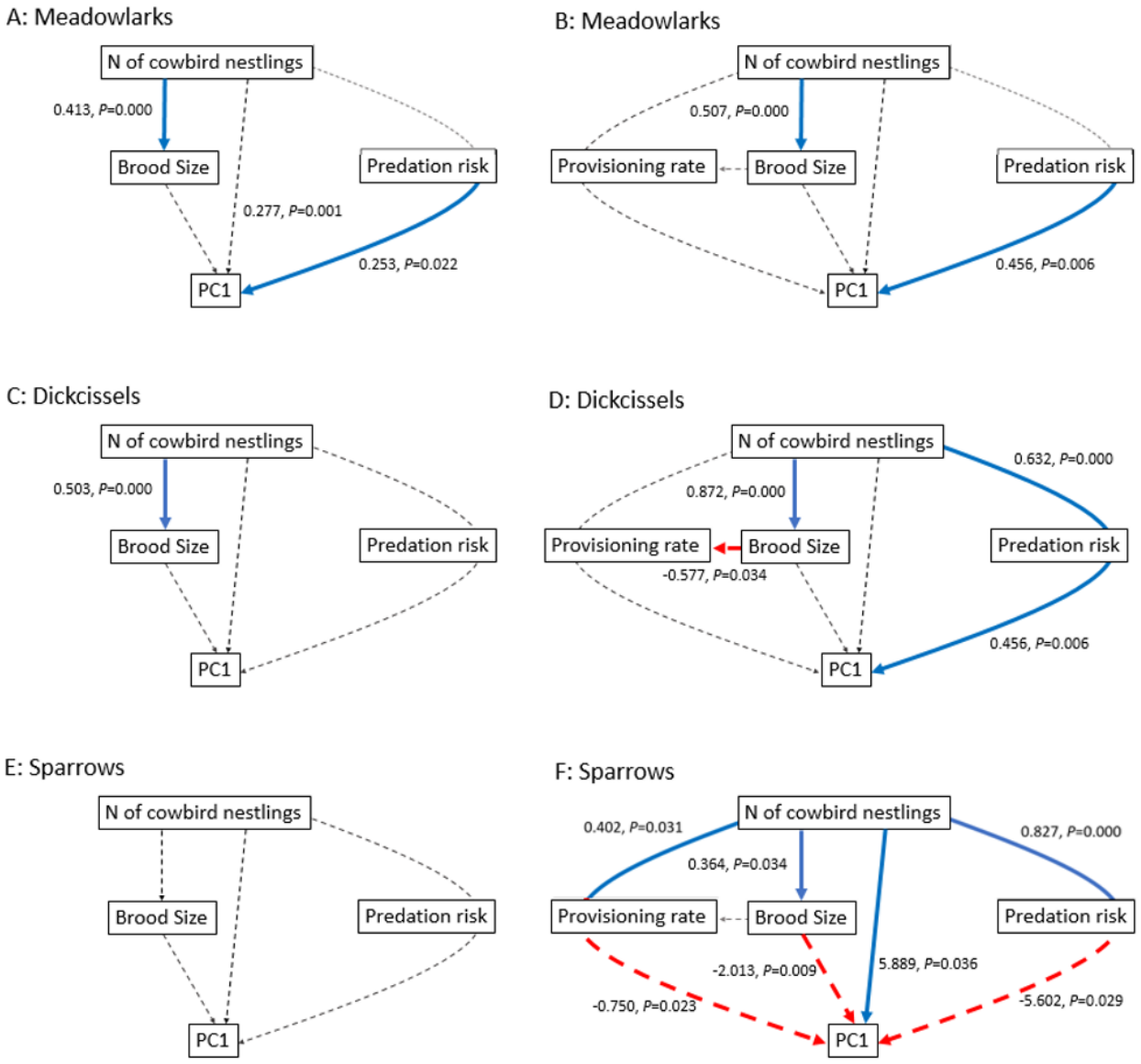

Figure S2-4. Wing size (PC1) prioritization SEMs, but labelled the betas from the additive effects instead of the effect*age interactions that account for change over time.

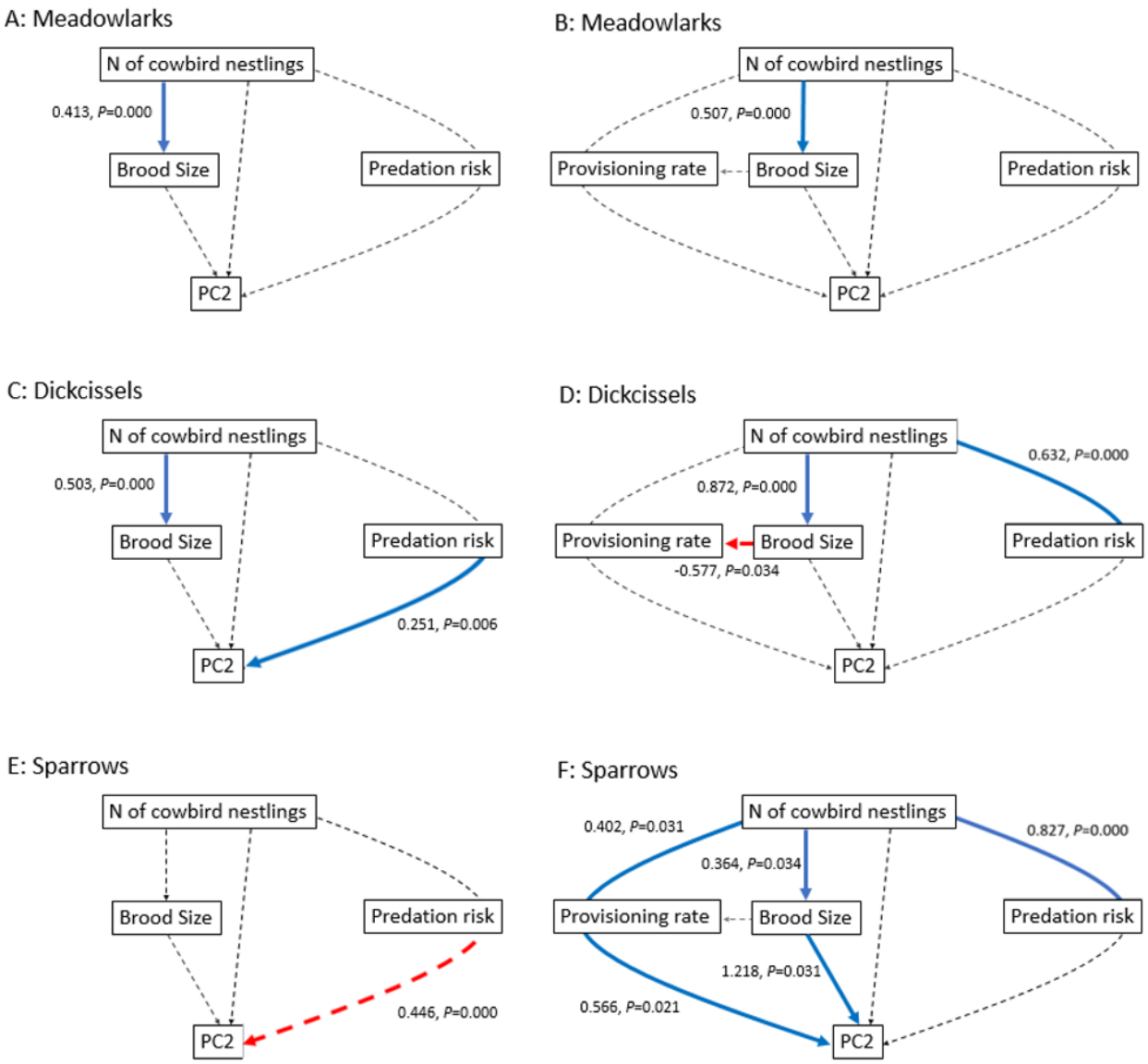

Figure S2-5. Feather growth (PC2) prioritization SEMs, but labelled the betas from the additive effects instead of the effect*age interactions that account for change over time.

Chapter 3 Supplementary Materials

Table S3-1. Mass-corrected wing measurements principal component analysis contributions by measurement.

Mass-corrected Measurements	PCA1	PCA2	PCA3	PCA4
Ulna Length	0.661	0.290	0.048	0.000
Carpometacarpus Length	0.585	0.370	0.044	0.001
9th Primary Length	0.633	0.344	0.000	0.022
1st Secondary Length	0.705	0.270	0.002	0.023

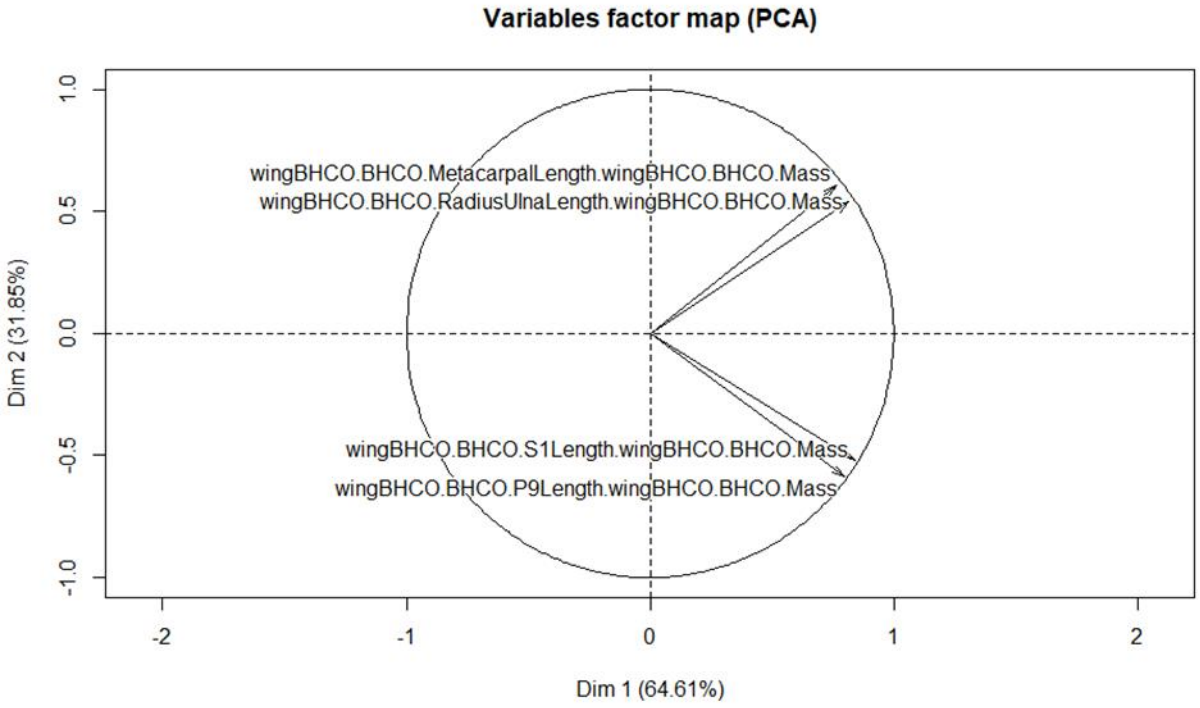

Figure S3-1. Map of the first two dimensions of the mass-corrected wing measurement principal component analysis.