

Patterns of Provisioning in Known-aged *Spizella pusilla* (Field Sparrow): A Multi-year Study

Jennie M. Carr^{1,*}, Maren E. Gimpel², and Daniel M. Small²

Abstract - Lack of experience in young adult birds may exacerbate the costs of parental care. Thus, birds may modify their behavior over time to balance the costs and benefits of parental care. We observed a population of *Spizella pusilla* (Field Sparrow) with individuals of known age and identity over multiple years to examine how age of parents affected feeding rates and overall nesting success. Parents fed larger and older broods at higher rates. Feeding rates of paired individuals were also correlated with one another. However, males provisioned offspring at a consistently faster rate than females. Ordinal date and year were the only factors that influenced nest success, with nests failing more frequently early in the summer. These findings may indicate that environmental factors—and less so intrinsic factors—may dictate overall nest success. Although we were unable to detect an effect of parent age on feeding rates, our ability to detect such trends is likely limited by considerable behavioral variation in the population and relatively few birds that were monitored across consecutive years.

Introduction

Parental care is associated with direct and indirect costs to breeding birds, including missed opportunity costs, greater predation risk, reduced energy for self-maintenance, and lowered future reproductive success (Clutton-Brock 1991, Gustafsson and Sutherland 1988, Parejo and Danchin 2006, Santos and Nakagawa 2012). In birds, demands on parental care change depending on the characteristics of the nest; birds invest increasingly more time and energy in feeding offspring throughout the nesting period (Sanz and Tinbergen 1999) and return with food more often when attending to larger and older broods (Alder and Ritchison 2011, Filliater and Breitwisch 1997). In addition, parents may also return to the nest with larger or higher quality food items as provisioning demands increase (Haggerty 1992).

Prior experience may allow birds to more adequately balance the costs and demands of parental care; Curio (1983) suggested that an accumulation of general life experiences may account for greater parenting success over time because young parents may be inefficient foragers with inferior territories. Older birds tend to invest more resources into offspring care and provisioning (Daunt et al. 2007, Dearborn et al. 2008, but see Lagassé and Ryder 2016). Limmer and Becker (2009) found that feeding rates in *Sterna hirundo* L. (Common Tern) were not associated with breeding experience. However, first-time breeders brought a higher proportion of low-energy food to their chicks. Thus, young parents produced fewer fledglings

¹Department of Biology, Washington College, Chestertown, MD 21620. ²Center for Environment and Society, Washington College, Chestertown, MD 21620. *Corresponding author - jcarr2@washcoll.edu.

per season than experienced breeders (Limmer and Becker 2009). Woodard and Murphy (1999) demonstrated that *Tyrannus tyrannus* L. (Eastern Kingbird) with prior breeding experience had the greatest reproductive success when paired with another experienced bird. Nest success of *Melospiza melodia* (Wilson) (Song Sparrow) also increased as females matured up to the age of 3 y, though success declined as birds aged beyond 3 y, an observation that may be attributed to senescence (Crombie and Arcese 2018). These findings suggest that parents may become more attentive and efficient in their parental efforts with greater experience. However, there is also evidence that aspects of parental behavior are perhaps innate or condition-dependent, for instance, as the result of social status (Laubach et al. 2015), and not directly influenced by age (Wheelwright and Beagley 2005).

Despite any increase in individual attentiveness or efficiency resulting from the accumulation of experience, the high costs of avian reproduction typically prohibit a single parent from successfully rearing offspring on its own. Thus, many species of birds have evolved a system of biparental care in which attention from both the male and female is often required to successfully raise offspring to independence (Clutton-Brock 1991), particularly in poor environmental conditions (Bart and Tornes 1989). The benefit of biparental care also applies to polygynous species, such as *Agelaius phoeniceus* L. (Red-winged Blackbird), which had greater reproductive success when chicks received care from both parents (Whittingham 1989, Yasukawa et al. 1990). In some instances, females of biparental species have managed to raise young without a male partner but produced lower quality offspring; female *Junco hyemalis* L. (Dark-eyed Junco) fledged young alone, though their chicks gained mass more slowly and fledged at slightly lower mass than those raised by 2 parents (Wolf et al. 1988). Biparental care divides the costs of care between both parents, although parental effort is seldom shared evenly between males and females (Yoon et al. 2016). For instance, male *Vermivora chrysoptera* L. (Golden-winged Warbler) consistently provisioned at higher rates than females (Reed et al. 2007). In a study on *Cardinalis cardinalis* L. (Northern Cardinal), males also fed at higher rates, maintaining those rates for each nestling in their brood and increasing their effort as nestlings aged (Filliater and Breitwisch 1997). In contrast, male *Passerina cyanea* L. (Indigo Bunting) only fed at 19% of nests studied and primarily on days 7–9 post-hatching (Ritchison and Little 2014).

In addition to the direct energetic costs of parental care, nesting is also a period of elevated predation risk for adult birds, reflecting a complex balance of ecological tradeoffs that may determine seasonal survival and lifetime fecundity (Lima 2009). Woodard and Murphy (1999) found that the nestlings of inexperienced parents suffered greater predation risk, implying that parental experience yields some degree of antipredator benefit. Skutch (1949) proposed that parental behavior may alter predation risk at the nest, as frequent return trips to the nest may draw the attention of predators, although this hypothesis has received conflicting experimental support (Martin et al. 2000a, b). Regardless, several studies have clearly demonstrated that perceived risk leads to changes in parental behavior. Experimental manipulations of perceived predation risk caused adults to reduce their feeding rates (Ghalambor

and Martin 2001) and produce fewer offspring (Zanette et al. 2011) in high-risk conditions, while investing more effort in the production and care of young when predators were removed (Fontaine and Martin 2006).

Nest success is affected by a complicated interplay of direct and indirect costs to the parents, energetic demands of offspring, and response to extrinsic factors. Although sufficient experimental evidence is lacking, existing literature suggests that age and experience of the parents may have wide-reaching effects on parental care in ways that affect reproductive success. Thus, we predicted that older and presumably more experienced birds would be able to balance the aforementioned indirect and direct costs of breeding more effectively than young birds, manifesting in the form of more attentive parental behavior (measured here as feeding rate and brooding time). Therefore, we expected that older birds would have higher nesting success than younger birds. We used breeding *Spizella pusilla* (Wilson) (Field Sparrow) as a system in which to address these age-related questions. Field Sparrows exhibit biparental care and are a common site-faithful grassland species at our study site in rural Maryland (see Methods for more details). Females begin brooding chicks immediately after they hatch and spend more time on the nest when attending small broods compared to larger broods that require frequent trips to the nest with food (Carey 1990). Females reduce their time spent brooding as chicks age (Crooks and Hendrickson 1953) and become capable of maintaining their own body temperatures (Dawson and Evans 1957). Both parents contribute to feeding young (Best 1977, Carey et al. 2008, Walkinshaw 1968), and males and females provide more and larger food items to larger and older broods (Crooks and Hendrickson 1953, Walkinshaw 1939, but see Best 1977), though male feeding rates are lower than females' while attending small, young broods (Carey 1990), leading us to expect sex differences in feeding behavior. Extensive prior bird-banding efforts of both chicks and adults have been conducted in our study population; thus, many individuals were of known age, which provided a unique opportunity to examine parental care for a range of known-aged birds across several years of breeding attempts. We sought to examine whether older parents would be more attentive by feeding chicks at a faster rate and spending more time brooding, thus potentially resulting in greater nesting success than their younger counterparts. In addition to these age-related questions, we predicted that Field Sparrows attending older and larger broods would return more frequently with food for their young—a trend well established in this species and across avian taxa, as noted above.

Field-site Description

We conducted our study on a 91.7-ha Conservation Reserve Program warm-season grassland at the Chester River Field Research Station (CRFRS) in Queen Anne's County, MD (39°13'51.6792"N, 76°0'21.0708"W). The grassland is under extensive habitat management for the purposes of habitat restoration and maintenance, the details of which can be found in Gill et al. (2006). We conducted research on 4 study plots, each averaging 9.7 ha, that were representative of the larger grasslands.

Methods

We conducted field work from May through July of 2014–2016. We captured all non-color-banded adult Field Sparrows using standard targeted mist-netting techniques. We employed an audio lure of a conspecific song to capture males defending territories; incubating or brooding females were captured by placing 2 mist-nets in a “V” shape around the nest. We banded all captured adults with a US Geological Survey (USGS) aluminum band (USGS permit #21885), with 1 color band on the left leg, and 2 color bands on the right leg. We color-coded the band on the left leg to indicate the sex of the bird to assist in behavioral observations (female = red, orange, yellow; male = teal, blue, black, purple) and used combinations of these colors as well as grey, lime, pink, and white to create unique color combinations for each individual. We used plumage criteria to age unbanded birds as 2nd year, after hatch year, and after 2nd year (Pyle 1997). We back-dated previously banded birds to the original banding date, which allowed us to age birds up to 9 y of age. For the purposes of this study, we assigned all birds a “minimum age” because the exact age was not known for all birds. For example, we assigned a bird aged as “after 2nd year” in 2014 a minimum age of 3 for that calendar year, thus providing a conservative estimate of age for these birds in the analysis. We aged 4 birds as “after hatch year” indicating that when first banded, these individuals were already adults of unknown minimum age; minimum age could easily be determined for birds in the other age groups (i.e., 2nd year, after 2nd year). Thus, we excluded these 4 from our study because we could not determine their age.

We searched nests and mapped territories on a daily basis. We made an effort to find nests while females were incubating eggs, though we detected nests throughout the incubation and brooding stages. To find most nests, we observed parents, e.g., by following a female returning to a nest for incubation or following either parent making food deliveries. We marked nests with colored flagging 1.5 m to the north of the nest; subsequent nest checks were conducted every 3 d, increasing to every other day as hatch date approached and video monitoring commenced. We banded nestlings between days 5 and 7, with day 1 counted as hatch-day. We banded nestlings with a USGS aluminum band on the left leg. We considered a nest successful if at least 1 nestling fledged (Galligan et al. 2006, Sutter and Ritchison 2005).

Video monitoring of nests

We used video cameras to record activity of provisioning parents at each nest approximately every other day (with each day of video recording at a nest hereafter referred to as a “nest day”) with a concerted effort to film nestlings on post-hatch days 3, 5, and 7. The precise day of video recordings was influenced by weather conditions and the stage at which the nest was found. When we found nests that contained older chicks, we filmed them 2 days in a row until the age of the nestlings coincided with day 5 or 7. The day prior to filming a nest, we placed a tripod covered with burlap and hidden with natural vegetation at least 2 m from the nest to acclimatize the adults to its presence. We used a curved piece of plastic covered in burlap and vegetation to conceal and protect cameras when mounted on the tripod.

These camera covers remained on the tripods during the acclimation period, thus minimizing the change in visual conditions when cameras were mounted on the tripods for video recording. The tripods and camera covers remained in place near the nest until the last nest day was recorded. For each nest day, we placed cameras on the tripods ~1 h after local sunrise time (~0700 h EST); recordings were ~2.5 h in duration. We used each nest-day video recording to confirm the color combinations of the parents' leg bands and to quantify and characterize parental behavior. We recorded the number of times that each parent returned with food throughout the course of the video as well as the proportion of time that the female spent brooding the chicks. We classified a provisioning attempt as "unknown" if obstructed views prevented the positive identification of the parent. To calculate an hourly feeding rate for each parent, we totaled feeding attempts and divided by the total video length for each nest day. We did not monitor nests that contained *Molothrus ater* (Boddaert) (Brown-headed Cowbird) chicks, a nest parasite at our site. Methods were approved by the Washington College Institutional Animal Care and Use Committee (Protocol #Su14-002).

Statistical methods

We found a total of 90, 117, and 121 nests in 2014, 2015, and 2016, respectively. We detected nests at various stages, from nest construction to chicks near fledging. For the purposes of this analysis, we considered only video-monitored nests with both color-banded parents, ensuring the known identity, age, and sex of each bird. We included a nest day in the feeding-rate analysis if we were able to positively identify which parent was feeding the nest in at least 95% of the visits during that given video recording. Our final sample size ($n_{\text{nests}} = 95$) consisted of 20 nests with 64 nest days, 37 nests with 160 nest days, and 38 nests with 170 nest days in 2014, 2015, and 2016, respectively. A total of 128 unique individuals ($n_{\text{male}} = 63$, $n_{\text{female}} = 65$) were associated with these remaining 95 nests. Age varied from 2 y to 9 y (2.9 ± 0.08 years) for females and from 2 y to 7 y (3.4 ± 0.09 years) for males. We conducted all analyses in Program R 3.4.1 (R Core Team 2017). Where appropriate, data presented are described by means \pm SE.

We treated birds attending a nest as individuals ($n = 128$) to assess whether feeding rate was influenced by characteristics unique to an individual parent, hereafter referred to as a focal individual. In addition to the possibility of individual-specific variations in behavior, adults forage independently of one another in the sense that the male and female both have to navigate the environment and find food without the assistance of their mate. Furthermore, independence of these observations between nest days was a reasonable assumption because we monitored nests on alternating days with conditions in the nest changing between nest days (e.g., chick age, and occasionally, changes in brood size). Therefore, we treated the feeding rates of the parents at a nest day as statistically independent from one another both within and between nest days, yielding a total sample size of 394 feeding-rate observations. Examination of Q-Q plots of the standardized residuals of our feeding-rate values indicated a non-normal distribution (Komogorov–Smirnov test: $P = 0.003$; Shapiro–

Wilk: $P < 0.001$). Thus, we ran a generalized linear mixed model (GLMM) with a Gamma probability distribution and log-link function to analyze feeding rate. We included age and sex of the focal individual (0 = male, 1 = female) as continuous and categorical fixed factors, respectively, with the age of the chicks (days since hatching) and brood size as continuous covariates. We also included as a covariate the feeding rate of the focal individual's mate because the activity of the mate could conceivably be correlated with the feeding rate of the focal bird. We monitored each nest approximately every other day for the life of the nest; thus, feeding rates of a focal individual were recorded multiple times and were able to include individual identity as a random factor in the GLMM. As addressed in the introduction, we expected that the feeding rates might vary between the sexes (Carey 1990). Thus, feeding rates of males and females were further examined in sex-specific GLMMs to address how age of the focal individual, chick age, brood size, and feeding rate of the mate differentially influenced the feeding rates of males and females.

We used the logistic-exposure method (Shaffer 2004) to model factors influencing nest outcome (success = 1, fail = 0). The method used here considers the combined contribution of both parents as it relates to nest outcome. Thus, individual ages of the parents were not used in the logistic-exposure model, instead, we generated 2 variables to describe skew or disparity between the ages of the parents tending the same nest (e.g., combined age of the parents, difference between the age of the parents; see Woodard and Murphy 1999). Similarly, we included a measure of the total feeding rate of the nest, which considered the total number of provisioning visits made by the male, female, and undetermined individuals (i.e., an adult with food that could not be identified due to obstructed views of color bands in the video recording). We also included the number of visits of undetermined individuals, given our interest in the overall care of the nest and not the relative contributions of males and female to overall nest success, which allowed us to include a total of 110 nests in the logistic-exposure model. Additional variables included in this analysis were brood size, the brood size*feeding rate interaction term, the proportion of time the female spent brooding chicks, ordinal date, and year.

Results

Sex of the individual had a strong effect on feeding rate, with males feeding at faster rates than females (Table 1, Fig. 1). As expected, parents fed older chicks

Table 1. Results of a generalized linear mixed model of factors affecting the feeding rate of a focal Field Sparrow. Corrected model: $F_{5, 387} = 77.791$, $P < 0.001$. All significant factors are denoted by an asterisk (*). Identity of the focal individual was included as a random factor in the analysis

| Factor | $\beta \pm SE$ (95% CI) | $F_{1, 387}$ | P |
|----------------------|------------------------------------|--------------|---------|
| Sex | 0.269 \pm 0.051 (0.168, 0.370) | 27.341 | <0.001* |
| Age | -0.025 \pm 0.018 (-0.060, 0.011) | 1.862 | 0.173 |
| Chick age | 0.125 \pm 0.012 (0.101, 0.148) | 105.640 | <0.001* |
| Brood size | 0.106 \pm 0.029 (0.050, 0.162) | 13.720 | <0.001* |
| Feeding rate of mate | 3.974 \pm 0.628 (2.740, 5.208) | 40.097 | <0.001* |

(Fig. 1) and large broods (Fig. 2) at a faster rate (Table 1). The feeding rate of the mate was positively correlated with the feeding rate of the focal bird (Table 1), as represented by a positive slope between male and female feeding rates (Pearson's $r = 0.56$; Fig. 3). After examining each sex in more detail, we found that although

Figure 1. Feeding rate of male ($n = 63$) and female ($n = 65$) Field Sparrows as a function of the age of the chicks in the nest. Solid and open circles represent the feeding rate of a male or female during a given nest day. The solid and dashed lines represent the linear fit for male and female feeding rates, respectively. ($R^2_{\text{male}} = 0.29$, $R^2_{\text{female}} = 0.34$).

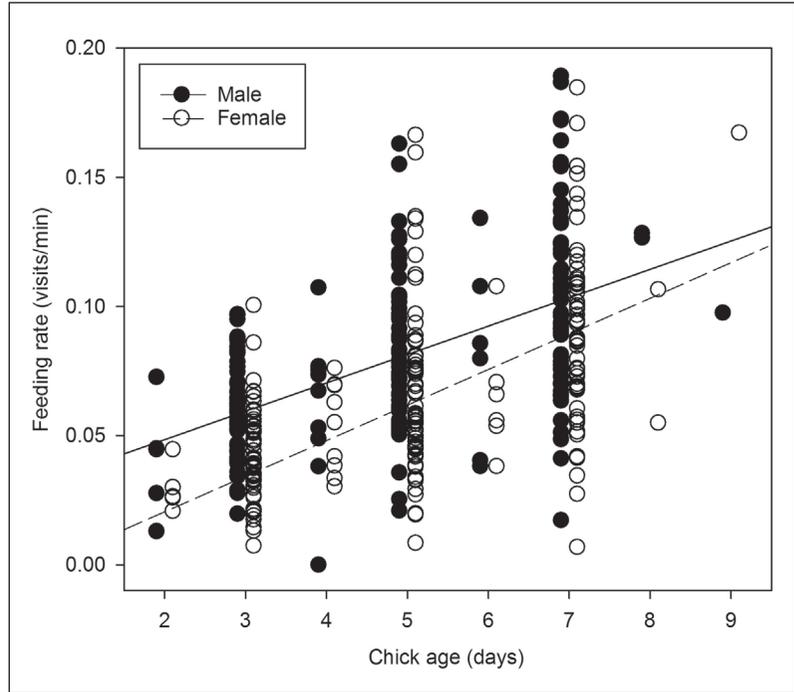
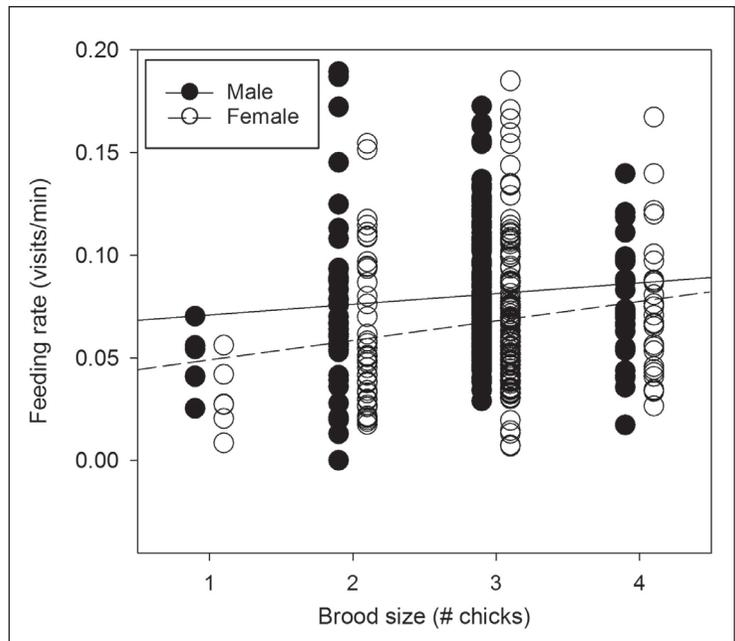


Figure 2. Feeding rate of male ($n = 63$) and female ($n = 65$) Field Sparrows as a function of brood size. Solid and open circles represent the feeding rate of a male or female during a given nest day while the solid and dashed lines represent the linear fit for male and female feeding rates, respectively. ($R^2_{\text{male}} = 0.01$, $R^2_{\text{female}} = 0.03$).



the feeding rates of males and females were both influenced by chick age and the feeding rate of the mate, brood size had a marked effect on female feeding rate only (Table 2).

The logistic-exposure model indicated that nest outcome was independent of all parent- and nest-specific factors, and that factors related to time and season (i.e., year and ordinal date) were the only factors associated with success or failure of a nest (Table 3). Most nests failed early in the summer, with 87% of failures occurring prior to the month of July (ordinal date 182; Fig. 4).

Figure 3. Feeding rate of male Field Sparrows as a function of the feeding rate of their mates. Each point represents feeding rates of mated pairs on a nest day. ($n = 126$, $R^2 = 0.315$).

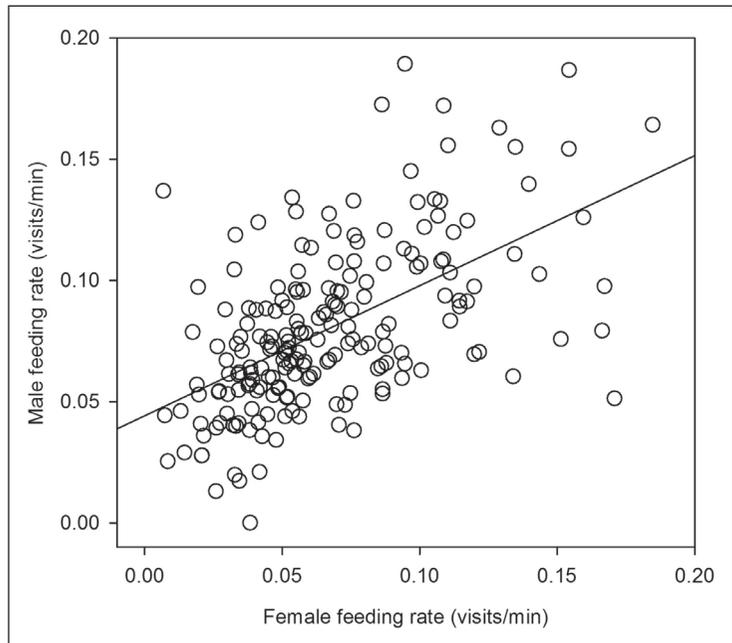


Table 2. Results of sex-specific generalized linear mixed models to determine the extent to which variables differentially affect male or female feeding rates at the nest. Corrected model (males): $F_{4, 191} = 40.481$, $P < 0.001$. Corrected model (females): $F_{4, 192} = 54.973$, $P < 0.001$. All significant factors are denoted by an asterisk (*). Identity of the focal individual was included as a random factor in the analysis.

| Sex/factor | $\beta \pm SE$ (95% CI) | $F_{1, 191}$ | P |
|----------------------|------------------------------------|--------------|---------|
| Males | | | |
| Age | -0.033 \pm 0.023 (-0.079, 0.012) | 2.061 | 0.153 |
| Chick age | 0.103 \pm 0.015 (0.073, 0.133) | 44.992 | <0.001* |
| Brood size | 0.049 \pm 0.037 (-0.023, 0.121) | 1.788 | 0.183 |
| Feeding rate of mate | 3.233 \pm 0.778 (1.700, 4.767) | 17.291 | <0.001* |
| Females | | | |
| Age | -0.007 \pm 0.028 (-0.062, 0.047) | 0.071 | 0.790 |
| Chick age | 0.143 \pm 0.018 (0.107, 0.179) | 60.996 | <0.001* |
| Brood size | 0.169 \pm 0.043 (0.085, 0.254) | 15.640 | <0.001* |
| Feeding rate of mate | 5.060 \pm 0.975 (3.137, 6.983) | 26.946 | <0.001* |

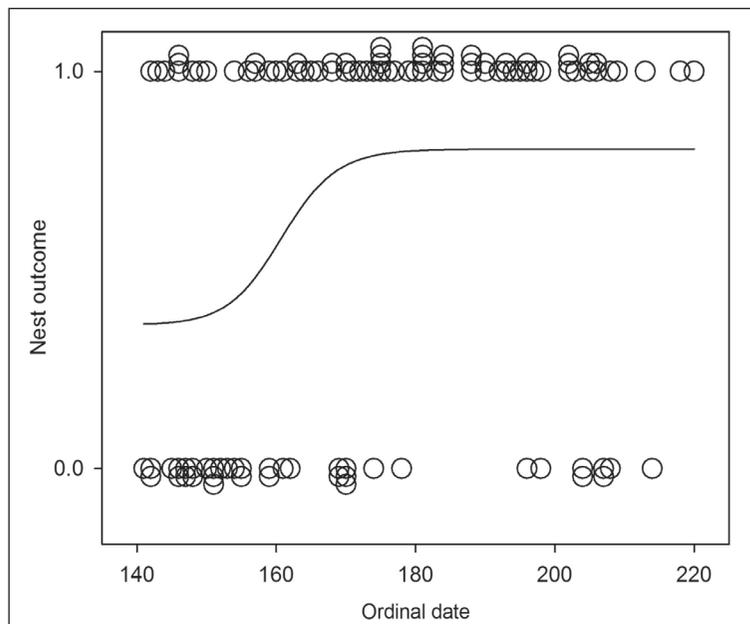
Discussion

As previous studies have concluded, we found that adult Field Sparrows fed larger and older broods at faster rates (Goodbred and Holmes 1996, Rauter et al. 2000). Furthermore, the males in our study fed offspring at a consistently higher rate than females, which may reflect that, unlike males, female Field Sparrows must divide their time between brooding and feeding nestlings (Carey et al. 2008). However, these results are contrary to previous findings in this species; Best (1977) reported that male Field Sparrows made fewer trips than females, a trend also detected by Carey (1990) but only for nests with small broods. The underlying causes between these conflicting results provide reason for speculation but may be associated with varying observation techniques (e.g., video monitoring in our study vs. firsthand in-field observations in Best [1977] and Carey [1990]). In our experience, some individuals would not be detected using in-field optics, yet were clearly observed feeding a nest in the video recordings. Thus, male provisioning rates may

Table 3. Factors affecting nest outcome (success = 1, fail = 0) as modeled using the logistic-exposure method. All significant factors are denoted by an asterisk (*).

| Factor | Log odds | SE (95% CI) | Z | P |
|-----------------------------|----------|-------------------------|--------|---------|
| Brood size | 0.549 | 0.482 (-0.409, 1.509) | 1.139 | 0.255 |
| Feeding rate | 12.244 | 10.598 (-8.270, 33.255) | 1.155 | 0.248 |
| Proportion of time brooding | -0.025 | 0.868 (-1.719, 1.683) | -0.029 | 0.977 |
| Pair age | 0.057 | 0.084 (-0.106, 0.226) | 0.676 | 0.499 |
| Age difference | 0.136 | 0.099 (-0.062, 0.328) | 1.366 | 0.172 |
| Day | 0.039 | 0.008 (0.024, 0.055) | 5.015 | <0.001* |
| Year | -0.879 | 0.218 (-1.321, -0.469) | -4.024 | <0.001* |
| Brood size x rate | -2.261 | 3.565 (-9.256, 4.727) | -0.634 | 0.526 |

Figure 4. Field Sparrow nest outcome as a function of ordinal date. Nests ($n = 110$) were determined to be successful (1) if they produced at least one fledgling; all others were determined to have failed (0). Values at 0 and 1 were offset to minimize overlapping data points while the line on the figure describes the data using a best-fit sigmoidal logistic curve ($R^2 = 0.140$).



have been underestimated in these earlier studies that were not supplemented by video-based observations.

Feeding rates of individual Field Sparrows were positively correlated with the feeding rates of their mate (Table 1, Fig. 3), a finding that is consistent with the “negotiation model”, whereby individuals may modify their feeding rates based on their mate’s effort (Hinde and Kilner 2006, McNamara et al. 1999). However, it is possible that the positive correlation between the feeding rates of a mated pair does not reflect a causal relationship, but perhaps is the byproduct of quality of the shared territory or other extrinsic factors not addressed here. Future studies would benefit from considering the repeatability of behaviors of an individual apart from its mate, as measures of repeatability may vary based on conditions, sex, and the behavior of interest (Bell et al. 2009).

Similarly, examining the repeatability of behaviors throughout the lifetime of an individual may provide additional insight into the effects of age on parental behavior. The behavior of the birds in our population was highly variable (Fig. 1). Thus, considerable variation among individuals in the population may make it difficult to detect any underlying age-related trends or variation in behaviors unless examined at the level of the individual over time. Despite our best efforts to locate and monitor the same individuals across years, relatively few birds in our study were monitored for more than 1 y; of the 128 birds in the study, only 14 males and 12 females were monitored for consecutive years. This absence of re-monitoring data is an obvious limitation of our study, but an unfortunate consequence of large field projects focusing on organisms with great capacity for movement, cryptic nests and behaviors, and relatively high annual mortality (Carey et al. 2008). Previous studies that suggested that feeding rate was not influenced by the age of the parent did not monitor individual birds over consecutive years nor did they assign known ages to the birds in their populations (Goodbred and Holmes 1996, Mitrus 2004, Omland and Sherry 1994). Thus, it is possible that improved parental behavior of an individual over time may be more widespread than expected yet difficult to quantify given the challenges of monitoring free-ranging birds of known age and identity over consecutive years.

Given the complexity of factors that contribute to breeding success, it is possible that other behaviors or processes not measured here may be influenced by age and/or alter reproductive success. For instance, different-aged parents may return to the nest with prey items of varying size, quantity, and quality (Limmer and Becker 2009). Age and experience may also influence nest-site selection (but see Hatchwell et al. 1999). Older birds may build better-concealed nests (Marzluff 1988) and hold higher-quality territories (Hill 1988, Norris et al. 2003). In addition, older males may have greater fitness due to more opportunities for extra-pair copulations (Perreault et al. 1997, Poesei et al. 2006), though opportunities for such copulations may come at the cost of reduced nest attentiveness (i.e., missed opportunity costs; Chutter et al. 2016).

Year and ordinal date were the only factors that predicted nest success in our study (Table 3). We suspect that both climactic conditions and seasonal variation

in nest predation likely contributed to our findings of greater nest failure in early summer (Fig. 4). The rate of nest predation is typically higher early in the breeding season (Benson et al. 2010, Evans et al. 1997, Shustack and Rodewald 2011, Vickery et al. 1992). Such temporal variation in predation risk may be attributed to the changing energetic demands of the predator community, which, in itself, is dynamic and variable. Unfortunately, identifying the source of nest predation is notoriously difficult (Larivière 1999, Renfrew and Ribic 2003) and further complicated by the fact that adult Field Sparrows carry deceased young away from the nest (Gimpel and Carr 2017). Climactic conditions can also result in nest failure due to thermal and energetic stress on eggs and chicks in the nest (Bowman and Woolfenden 2001, Heltzel and Earnst 2006) and a greater likelihood of poor breeding conditions earlier in the season (e.g., brief periods of below-average temperatures), with much variation in conditions between years.

Provisioning behavior of Field Sparrows in our study seems largely driven by characteristics of the brood with overall nest success dictated by extrinsic factors associated with annual and seasonal variation. At the population level, the behaviors of the adult birds in our study were highly variable. Unfortunately, we were unable to collect sufficient data for individual birds over multiple years to comment on whether the behaviors of a single individual are similarly variable. Further studies focusing on repeated behavioral measures of a known individual over time may provide valuable insight into the overall plasticity and predictability of behaviors at an individual-level (Biro and Stamps 2015) and whether variations in feeding rate may be correlated with other reproductive behaviors or represent personality, plasticity, individual quality, or a combination thereof (Westneat et al. 2011).

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