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Intersexual differences in age-specific parental effort in the house finch (*Carpodacus mexicanus*)

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Abstract. Although age-specific improvements in reproductive performance are common in iteroparous organisms, they are by no means universal. Reproductive tradeoffs are integral features of the life-histories of animal populations and may lead to complex breeding strategies among birds of different age. In particular, asymmetries in the costs and benefits of different components of reproduction for males and females may result in contrasting patterns of age-related parental investment between the sexes. We examined age-specific patterns of parental care in an eastern North American population of house finches (*Carpodacus mexicanus*) over a three-year period and found pronounced differences in the degree to which males and females provisioned young as they aged. Younger male house finches provided more care to offspring than did older males, yet in females it was the middle-aged mothers that provisioned young most often. This pattern of paternal care is inconsistent with condition- and experience-dependent investment, and instead may reflect male compensation for decreased maternal performance or an attempt by males to secure future breeding attempts with their mate. In contrast, the pattern of maternal provisioning mimics age-related trends in other female breeding efforts (e.g. clutch size, fledging success) for short-lived passerines, which may be governed by condition, experience, and the onset of senescence. These data emphasize the variability in parental tactics that characterizes birds of different sex and age, and the importance of considering the allocation of reproductive effort to competitions for mates, egg-production, and parental care in relation to age so that we may better understand the evolution of male and female breeding strategies in birds.

Key words: age-specific reproduction, nestling provisioning, parental care, reproductive tradeoffs, sex differences

Resumen. *Diferencias intersexuales en el esfuerzo parental específico de la edad en el camachuelo mexicano* (Carpodacus mexicanus). Aunque las mejoras relacionadas con la edad en el éxito en la reproducción son comunes en los organismos iteróparos, no son completamente universales. Los compromisos reproductores son hechos integrales de las estrategias vitales de las poblaciones animales y pueden determinar estrategias reproductoras complejas entre aves de edades diferentes. En particular, las asimetrías en los costes y beneficios de los diferentes componentes de la reproducción para machos y hembras, pueden producir pautas contrastantes entre los sexos en la inversión parental relacionada con la edad. Nosotros examinamos las pautas de cuidado parental relacionadas con la edad en una población del este de Norteamérica de camachuelo mexicano (*Carpodacus mexicanus*) durante un período de tres años, y hallamos claras diferencias en el grado en que machos y hembras aprovisionan a los pollos a medida que crecen. Los camachuelos macho jóvenes proporcionaron mayor cuidado a la descendencia que los machos más viejos, pero en las hembras fueron las de edades intermedias las que alimentaron a los pollos más a menudo. Esta pauta de cuidado parental no es consistente con una inversión dependiente de la condición y la experiencia, y al contrario podría reflejar la compensación masculina de la disminución en la ayuda materna o un intento de los machos para asegurarse la reproducción futura con su pareja. Por el contrario, la pauta de aprovisionamiento materna imita las tendencias relacionadas con la edad en otros esfuerzos reproductores femeninos (p.e. tamaño de nidada, éxito de volantones) para paseriformes de vida corta, que podría estar bajo el control de la condición, experiencia e inicio de la senescencia. Estos datos enfatizan la variabilidad en las tácticas parentales que caracterizan a las aves de diferente sexo y edad, y la importancia de considerar la distribución del esfuerzo reproductor en la competencia por parejas, producción de huevos, y cuidado parental en relación con la edad, de tal forma que podríamos entender mejor la evolución de las estrategias reproductoras de machos y hembras en aves.

Introduction

Age-specific variation in breeding performance is a prominent feature of reproduction in animals that breed multiple times during their lifespan, particularly in passerine birds (Williams, 1966a,b, Pianka & Parker, 1975, Charlesworth & Leon, 1976, Charlesworth, 1980, Curio, 1983). Life-history theory predicts that reproductive effort will increase with age when there is a concomitant decrease in future survival probabilities and breeding opportunities (Roff, 1992, Stearns, 1992). Maturing individuals also acquire the foraging skills (Wunderle, 1991) and breeding experience (Forslund & Pärt, 1995) necessary to increase their reproductive output over time. Such conditions allow older males and females of many avian species to initiate breeding earlier in the year, produce more offspring with each attempt, and produce more offspring during a single breeding season (Sæther, 1990, Martin, 1995).

Comparatively less is known about patterns of parental investment (e.g. defending young from predators, provisioning young with food) in relation to age. Among the few studies that have been conducted in birds, both positive (Pugesek, 1981, 1995, Pärt et al., 1992, Wiebe & Martin, 1998) and negative (Sundberg & Larsson, 1994) relationships between parental age and offspring care have been documented. Theoretically, parents may follow a condition- or experience-dependent strategy when caring for young and invest more in offspring in each subsequent year (Kokko, 1997, 1998, Wolf et al., 1997). Conversely, because reproductive tradeoffs are integral life-history features of animals (Clutton-Brock, 1988, Ligon, 1999), there are situations in which parental investment is predicted to decline with age (Fagen, 1972, Schaffer, 1974). Breeding birds must allocate effort between mating and parental activities (Trivers, 1972, Westneat et al., 1990, Johnson & Burley, 1998), between producing more and higher quality offspring (Lack, 1954), and between current and future reproduction (Williams, 1966a,b, Gadgil & Bossert, 1970), and because birds of different age typically vary in their quality as a mate and in their reproductive potential (Kokko, 1997, Manning, 1985, Sæther, 1990), the balance of these tradeoffs may be markedly different for young and old birds. For example, older birds may be more attractive and invest more in securing as many matings as possible, but effort devoted to raising offspring may suffer.

This theoretical framework, under which two potential mechanisms – 1) condition- and experience-dependence, and 2) life-history and reproductive tradeoffs – drive age-specific changes in parental investment, warrants further empirical consideration. At a very basic level, it is not known whether males and females within a species adopt similar strategies of parental investment in relation to age. In species with biparental care, the relative importance of the various components of reproduction is not necessarily equivalent for the two sexes. Males typically invest more in mating effort than females, while females invest more in offspring production than males (Trivers, 1972). These and other fundamental differences in the allocation of reproductive effort between the sexes may lead to contrasting patterns of age-specific parental investment in males and females that are governed by completely different decision rules.

In this study, we examined patterns of maternal and paternal effort in relation to age during a three-year study of breeding house finches (*Carpodacus mexicanus*). Our goal was to test specifically whether age-specific food provisioning of nestlings by males and females represents a condition- or experience-dependent parental tactic or whether age-dependent provisioning behaviour in either sex is sensitive to reproductive or life-history trade-offs. The house finch is an appropriate species for such a test because they are socially monogamous with biparental care. Females select mates and defend nest sites early in the season, and pairs may breed for as long as six months and fledge offspring from up to four broods annually. Males do not maintain breeding territories, but pairs defend nest microsites and males defend their mates throughout the breeding season. Most pairs breed together for the duration of the season, but occasionally individuals will switch mates within a season or remain paired across years. Females complete nearly all of the nest building and incubation activities, and males provision their mates with food during these periods (reviewed in Hill, 1993a).

Methods

We studied the breeding biology of house finches on the campus of Auburn University in Auburn, Alabama, USA from 1997-1999 (see also Hill et al., 1999, McGraw et al., 2001). Starting in 1993, finches were attracted to feeding stations across campus and captured in hanging basket traps for marking and measurement. We trapped unbanded breeding birds at their nests using Potter traps. In each of the three years of this study, we banded approximately 90% of the individuals in the campus population during the breeding season. Each bird received a numbered US Fish and Wildlife Service metal band and a unique combination of three colored plastic leg bands.

Age determination

Juvenile house finches disperse away from their natal area in the fall, and only approximately 6% of males and 3% of females return to their natal site to breed (Hill, 1993a, G.E. Hill, unpublished data). Thus, we were unable to assign absolute ages to the majority of birds that bred on our site. Instead, we assigned minimum ages to each individual by assuming that unbanded birds were in their first year when they were captured and marked, and by counting the number of years since banding for previously marked birds. This technique is used commonly in field studies of those avian species for which morphological characteristics do not reveal age reliably (e.g. Veiga, 1993, Johnsen et al., 1996), and we felt confident that most unbanded breeding birds on our site were first-year individuals because breeding site fidelity was common among finches of all ages in our study. Of the birds that bred on campus during 1997 or 1998, 48% of the newly banded birds (*n*=33), 56% of the 2nd-year birds (*n*=27), and 64% of the 3rd- and 4thyear birds (*n*=11) returned to breed on our site the following year. Adult ages ranged from 1 to 5 years, but because there were so few older birds in our sample we used three age-classes in our analyses: 1 year-old, 2 years-old, and older than 2 years. We found no differences in male or female age-class distribution among the three years of our study for any of our measures of parental effort (Kruskal-Wallis *H*-tests and Mann-Whitney *U*-tests, all $p>0.2$). Additionally, the frequency with which each age-class was represented did not differ between the sexes (chi-square test, $p=0.7$). The ages of the birds were unknown to those collecting behavioural data throughout the study.

Nest monitoring

We monitored the breeding activity of house finches by drawing pairs to nest cups that we placed under the overhangs of campus buildings (see description in McGraw et al., 2001). Nest cups were checked every other day throughout the breeding season (February-August) for the presence of nests, eggs, and nestlings. We confirmed the identity of pairs using focal observations early in the breeding cycle and from videotapes of nestling provisioning behaviour (see below). For each nest found during the three years, we recorded the day on which the first egg appeared, clutch size, and brood size up until young fledged from the nest.

Nestling provisioning

We observed the nestling provisioning rates of house finch pairs by videotaping nests with small video cameras. These units were fastened to pipes and building ledges approximately 1-2 m from the nest so that we could accurately identify the colored band combinations on the legs of the parents. Although cameras were placed close to the nest cups, birds returned to their nests quickly after the cameras were set up, such that there was no difference between the latency to return to the nest to feed after we had set up the camera and the average interval between normal feedings for either males or females (Wilcoxon matched-pair signed-rank test, both $p>0.3$). Most importantly, birds from the three age classes did not respond differently to the cameras that were placed close to the nest, as the effect of age on the latency to return to the nest was not statistically significant for either males or females (Kruskal-Wallis *H*-tests, both $p>0.3$).

House finch parents regurgitate seed to their offspring in bouts that last for up to 1 min, during which food is delivered to all young in the nest (Hill, 1993a). Although sunflower seed feeders were scattered throughout campus, we inspected the crops of nestlings on a regular basis and found that they were typically fed green and brown weed seeds, not sunflower seeds. Furthermore, the random arrangement of feeders in relation to nest sites should not have biased food access toward any parental age class. Because we focused our cameras strictly on the nest cups themselves, we were unable to determine the location of parents when they flew away from the nest, which made it difficult to decide which visits to the nest were independent feeding trips. To alleviate this problem, we used data from previous field observations (Hill, 1991) and considered feeding trips to the nest as independent when they were separated by more than 20 min.

From the videotapes, we calculated the number of provisioning trips that males and females made per nestling per hr (hereafter referred to as per-nestling feeding rates). This is a commonly used index of absolute parental effort in birds (Filliater & Breitwisch, 1997, Stoehr & Hill, 2000), and is a reliable measure of food provided to offspring in this species. In a previous study of nestling provisioning in the house finch, in which electronic balances were placed beneath nest cups to measure the number of grams of food that parents delivered to their young, we found that the number of feeding trips to the nest by each parent significantly and linearly predicted the overall mass of food delivered to offspring across all brood sizes (Stoehr et al., 2001). To investigate the relative effort of paired birds, we calculated the proportion of feedings within a pair that were provided by the male. Among the possible time periods that could be used to calculate provisioning rate from the videotapes (e.g. the entire length of the observation period, the time from the first feeding to the end of the observation period, the time between the first and last feedings), all were intercorrelated for both males and females (all $r>0.5$, all $p<0.001$). We chose to use the time period between the first feeding and the end of the tape in all of our calculations because we had no idea how recently parents had fed their offspring before we began taping each morning.

House finch nestlings typically spend 17-21 days in the nest before fledging (Hill, 1993a). We filmed provisioning behaviour in all three years on day 11 of the nestling period. All filming sessions began within the first hr of morning daylight. We filmed nests for 2 hr in 1997, and because we upgraded our video equipment in 1998 we filmed nests for 8 hr in 1998 and 1999. Despite these methodological differences, we found no overall effect of year on any of our measures of nestling provisioning (Kruskal-Wallis *H*-tests, all $p>0.2$). We also found no significant changes in provisioning behaviour across nests within a season for pairs (Wilcoxon matched-pair signed-rank tests, all $p>0.3$), and there was no general effect of time of year on any of the provisioning measures (Kendall's rank correlations, all $p>0.1$). Thus, we used nests spread throughout the year in our analyses. In all, we collected nestling provisioning and age data for 34 unique pairs over the three years.

Statistical procedures

All analyses were performed using the statistical program StatView® 5.0.1 (SAS Institute, 1998). Tests are two-tailed, the assumed level of significance is $p<0.05$, and means ± SD are reported in all cases. Birds appear only once in each comparison, and when birds were observed in multiple years or nested multiple times in a year, we used data from that nest for which we had the most information (e.g. age of both pair members, paternal and maternal care data). We tested for age-assortative mating in our population by

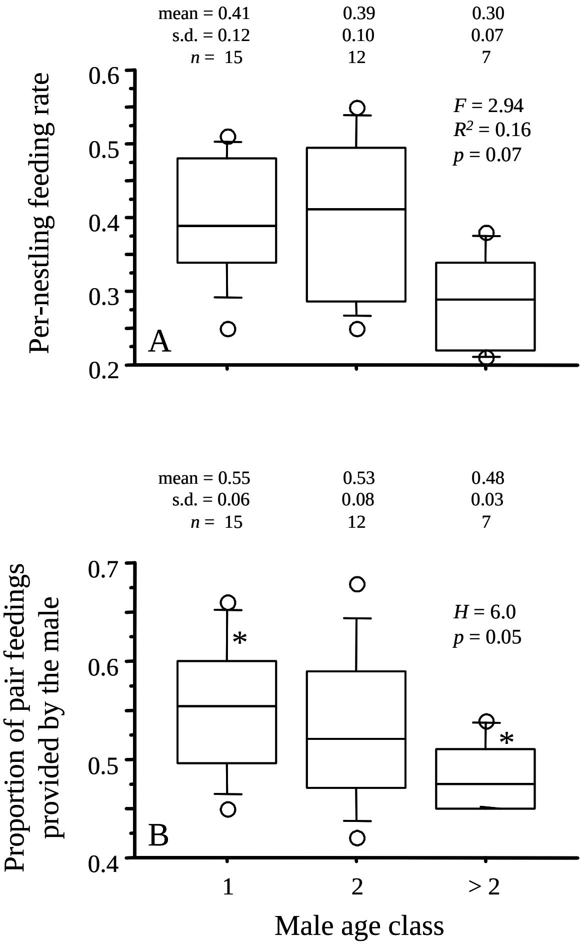

Figure 1.- Boxplots illustrating the relationships between male age and A) the per-nestling feeding rates of fathers, and B) the proportion of feedings within the pair that were provided by the male. Horizontal bars in box plots indicate the 10th, 25th, 50th, 75th, and 90th percentiles and points give data for individuals outside of these ranges. Means, standard deviations, and sample sizes for each age class are given at the top of the plots. Asterisks denote the two groups that differed in post-hoc planned comparisons at α= 0.05.

comparing the ages of mated members within a pair with a non-parametric rank correlation (Kendall's T).

Using analyses of variance (ANOVAs), we considered the effect of parental age on the aforementioned measures of provisioning effort. We used non-parametric ANOVAs (Kruskal-Wallis H-tests) when data were not normally distributed (Shapiro-Wilk W-tests, p<0.05) or when variances differed among the three age classes (Equality-of-variance F-tests, p<0.05). If tests were significant, we conducted post-hoc analyses to determine particular differences among the age classes; we used Fisher's PLSD test for parametric ANOVAs, and non-parametric tests follow Siegel & Castellan (1988).

Results

General patterns of parental care

House finch pairs mated positively assortatively by age (T=0.70, n=46, p<0.0001). On average, pairs of finches provided 0.71±0.17 feedings per nestling per hr on day 11 of the nestling period. Males had significantly higher per-nestling feeding rates than their mates (t_{33}=2.71, p=0.01), amounting to 53.0±0.07% of the feedings within a pair. Per-nestling feeding rates for members of a pair were significantly correlated (r=0.50, n=34, p=0.002).

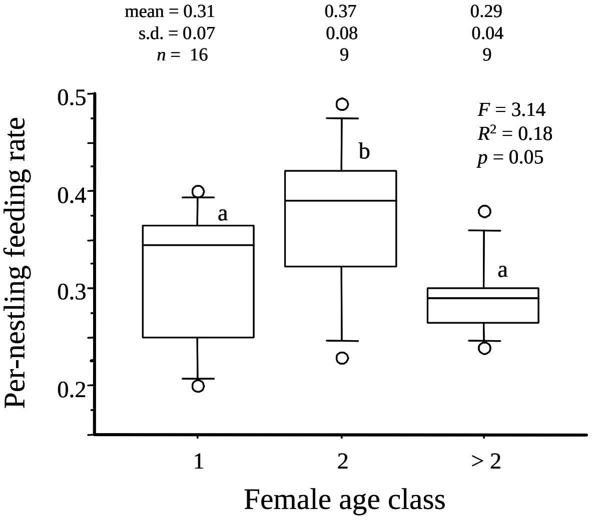

Figure 2.- Effect of maternal age on the per-nestling feeding rates of mothers. Letters denote significant differences in provisioning between age-classes. See Fig. 1 for additional details of the boxplots.

Male provisioning

A male's age was marginally related to his per-nestling feeding rate on day 11 of the nestling period, with younger males tending to feed offspring more often than older males (Fig. 1A). Male age was significantly associated with the proportion of feedings that males provided within pairs, such that younger males provided a greater proportion of feedings than did older males (Fig. 1B). Post-hoc comparisons revealed significant differences between the proportion of pair feedings provided by 1st-year males and males >2 years of age (p=0.02). There was a marginal difference in the proportion of male feedings between 2nd-year males and males >2 years of age (p=0.06), but there was no difference between 1st- and 2nd-year males (p=0.68).

Female provisioning

There was a significant overall effect of maternal age on the rates at which females provisioned 11-day-old nestlings (Fig. 2). However, inter-age-class patterns of investment were different from those found in males. Post-hoc tests revealed no difference in feeding rates between 1st -year females and those >2 years of age (p=0.47). Instead, 1st-year females and females >2 years of age fed significantly less often than 2nd-year females (both p<0.05).

Discussion

Here we document age-specific sex differences in parental effort in a short-lived passerine species. Investment in offspring provisioning was significantly related to age in both male and female house finches, but it followed different age-specific patterns in the two sexes. Younger males fed nestlings more often than did older males. This was true for relative parental investment (within-pair proportion) and marginally so for absolute provisioning effort (per-nestling feeding rate). In contrast, older and younger female house finches provisioned offspring significantly less often than females from the middle age class.

Our observations of paternal investment in house finches are inconsistent with the notion that all aspects of reproductive performance generally improve with age. These findings are similar to those of Sundberg & Larsson (1994), who documented a negative correlation between paternal provisioning and age in yellowhammers (*Emberiza citrinella*). Because older male house finches tend to be in better condition and more experienced than younger males (see below), these data fail to support the hypothesis that paternal provisioning is a condition-dependent tactic in this species. Carotenoid-based plumage pigmentation, which is known to reveal parasite burden (Brawner et al., 2000) and nutritional condition (Hill & Montgomerie, 1994, Hill, 2000) in male house finches, becomes brighter with age for some birds (Hill, 1992). Moreover, older male house finches breed earlier in a season (Hill, 1993b) and spend more time with and in closer proximity to their mates during her fertile period than do younger males (K.J. McGraw, unpublished data).

So why should older males in better condition provision offspring less often than younger males in poorer condition? The 'differential allocation hypothesis', as proposed by Burley (1986, 1988), offers one explanation for lower levels of parental effort by higher quality males. Under this idea, females obtain high-quality genes for their offspring from older males or those expressing elaborate ornamentation, and as a consequence are willing to compensate for the lack of paternal investment by high-quality mates. However, we found that per-nestling feeding rates were significantly positively correlated for pairs of house finches. Moreover, despite a negative relationship between male age and parental investment, there was no corresponding significant positive relationship between maternal age and provisioning effort. Thus, we find no support for the 'differential-allocation hypothesis' in this study.

A second explanation for these age-specific patterns of paternal behaviour is that male effort is directly sensitive to levels of parental care by his female mate. Again, we found that the feeding rates of house finch pair members were positively correlated, despite the fact that male and female provisioning behaviours were not associated with age in identical manners. However, when we separately considered intrapair similarities in provisioning effort among the age-classes, the significant intercorrelation for the per-nestling feeding rates of pair members broke down among first-year birds ($p>0.15$). This finding suggests that changes in the levels of parental effort with age in male house finches are not governed by single underlying mechanism (e.g. by assortative-mating in relation to quality, condition, or parental ability).

Instead, our observations of paternal care in the house finch may illustrate behavioural strategies that balance certain reproductive tradeoffs at different life-stages. Specifically, young males find themselves at a reproductive disadvantage because they typically are paired with younger females (Hill, 1993b, this study) who begin nesting significantly later in a season (Hill, 1993b, McGraw, 1999), complete only a few nesting attempts during a year, and fledge fewer young over a year than do older pairs (McGraw, 1999). Thus, compared to older males, there may be an immediate need for young males to elevate parental effort to successfully raise the few offspring that are produced and poorly raised by their mate. The short-term fitness benefits of increased investment among first-year male finches are not great, however, as the likelihood of fledging offspring from a nest for the different age classes closely tracks age-specific patterns of clutch size and maternal care in this species (McGraw, 1999).

Added long-term benefits to young males investing heavily in parental care may come in the form of pair bond stability. Younger males also face the difficulty of securing a mate across years, as opposed to older males, who, in many species, are preferred as social and extra-pair mates (Weatherhead, 1984, Sundberg, 1995a,b, Sundberg & Dixon, 1996) and retain mates across years (Mock & Fujioka, 1990) because they advertise their survival capabilities (Manning, 1985). In fact, because long-term pair bonding traditionally confers a series of reproductive advantages in addition to those typical of older birds (e.g. advanced laying dates, higher intra-pair fertilization rates, Black, 1996), newly paired young birds may elevate parental efforts as a strategy to secure future breeding opportunities with the same mate (Hoelzer, 1989). In the house finch, some pairs breed together for nearly their entire lifetime, and pairs remaining together across years begin nesting earlier in a year and guard their mates more intensely than do newly formed pairs of similar age (K.J. McGraw, unpublished data). This hypothesis generates the prediction that, among newly paired birds, those younger males that provide the most care to young should subsequently be the most likely to remain paired into the following season. Unfortunately, we were unable to test this idea because there were too few newly paired males for which we had nestling provisioning data in the previous year. From this, it is clear that, in future work, it will be critical to experimentally manipulate reproductive parameters such as offspring production and pair bond stability to determine if age-specific paternal behaviour in the house finch or other biparental species is finely tuned to the costs and benefits of current versus future reproduction or mating versus parental activities.

Contrary to what we found for the age-specific provisioning efforts of male house finches, female parental effort did not decline directly with age. The nestling provisioning rates of female house finches were lower in first-year females, higher among middle-aged birds, but lower again in older individuals. The increase in investment between first- and second-year females is consistent with the hypothesis that age-specific maternal provisioning of offspring is a condition- and experience-dependent breeding tactic. This same first- to second-year pattern is true for a variety of other reproductive efforts in female house finches, including breeding onset, clutch size, and reproductive success (McGraw, 1999). However, the decrease in maternal care among females from the oldest age class suggests that the overall relationship between age and condition in female house finches is non-linear. Instead, this terminal decline in parental investment with age may be a consequence of senescence (Sanz and Moreno, 2000). Senescence is defined as the decrease in reproductive value and phenotypic expression, and increase in mortality rate, among older individuals (Fisher, 1930, Rose, 1991). Along with this age-specific pattern of maternal investment, trends in clutch size and reproductive success among female house finches mimic the senescent-typical changes in breeding parameters found in other short-lived songbirds (Gustafsson & Part, 1990, Møller & de Lope, 1999, G.E. Hill, unpublished data). Thus, unlike our findings for males, these results support the idea that nestling provisioning behaviour in female house finches closely reflects the condition of individuals at the time of breeding.

In conclusion, these data highlight the potential for male and female birds to use unique decision rules when investing in parental behaviours as they age. To our knowledge, this is one of the first studies to document differences in the patterns of male and female parental behaviours in relation to age or any other measure of mate quality. Because of intrinsic dimorphisms in gametic investment, differences in mate competition and reproductive potential (e.g. probability of both intra- and extra-pair matings) between the sexes may generate vastly different parental tactics in males and females from biparental species (Clutton-Brock, 1991). Paramount to understanding these sexual strategies is equal consideration of the mechanisms underlying and functions of various male and female reproductive behaviours. Unfortunately, although many studies of biparental investment have focused on understanding variation in male parental care, and how paternal efforts influence offspring survival (e.g. Bart & Tornes, 1989) or relate to sexual selection (e.g. Verner & Willson, 1969, Sætre et al., 1995), variation in maternal care has not received equal attention (Gowaty, 1996). Our study emphasizes the need for a more careful examination of the relative costs and benefits of reproduction as both sexes age and how these contribute to the diversity of avian mating strategies that exist in nature.

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