# MATE ATTENTIVENESS, SEASONAL TIMING OF BREEDING AND LONG-TERM PAIR BONDING IN THE HOUSE FINCH (CARPODACUS MEXICANUS)

by

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## Summary

In seasonally breeding birds, natural selection favors individuals that begin breeding earlier in a year because they produce more or higher quality offspring than those that begin breeding later. Among the factors that influence the timing of breeding, which include the age, health, competitive ability, or mate quality of individuals, is the longevity of the pair bond, with birds that remain mated across years initiating breeding earlier in the season than newly formed pairs. The behavioural interactions between pair members that may facilitate long-term pair bonding and early breeding onset have infrequently been studied, however. Here we report the relationship between male-female affiliative behaviour, pair-bond duration, and breeding date in house finches (*Carpodacus mexicanus*), a short-lived, socially monogamous passerine species in which the duration of pair bonds is highly variable within and among seasons. Finches that initiated breeding earliest in the season were those that had bred with one another in previous years. Early breeding males from returning pairs maintained significantly closer contact with their mate during the first egg-laying period of the year than did males from late-breeding, newly formed pairs. Similarly, early-breeding females from returning pairs followed their mate more closely in nest-vicinity flights during the fertile period than

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females from late-breeding, newly formed pairs. These results suggest that attributes of and interactions between both pair members may help to maintain stable breeding pairs and influence the timing of breeding in seasonally nesting, short-lived songbirds. Rather than advertising for or seeking extra-pair fertilization opportunities, high-quality pairs of finches may invest heavily in their mate to secure the pair bond and ensure high intrapair reproductive success.

## Introduction

Seasonally breeding birds are faced with the challenge of producing as many offspring as possible in a limited amount of time. One strategy to maximize annual reproductive output may be to begin breeding as early in the season as possible, which allows more time for offspring production and development during the year (Lack, 1968; Perrins, 1970). Since Darwin (1871) and Fisher (1958) formulated hypotheses to explain the evolution of sexually selected traits in monogamous species, the fitness consequences of early breeding have been both modeled (O'Donald, 1972; Kirkpatrick *et al.*, 1990; Price *et al.*, 1993) and tested empirically (*e.g.* O'Donald *et al.*, 1974; Verhulst & Tinbergen, 1991), and results from these studies support the idea that animals breeding earliest in the season realize the highest annual reproductive success.

If early seasonal breeding has such selective advantages, however, why do some individuals in the population still initiate breeding later in the season than others? Studies of variability in breeding onset among individuals within a species have revealed a suite of proximate factors that accelerate or delay the timing of breeding in birds. Female traits such as nutritional state (Jones & Ward, 1976; Yom-Tov & Hilborn, 1981; Martin, 1987), age (Saether, 1990), breeding experience (Fowler, 1995), and competitive ability (O'Donald, 1980; Kelly & Van Horne, 1997) all have been shown to advance laying date in birds. The phenotypic or genotypic quality of male mates, as measured by ornamental traits such as song (Kroodsma, 1976; Wright & Cuthill, 1992) and courtship feeding (Nisbet, 1973), may also bring females into reproductive condition sooner during the year.

Characteristics of the male-female pair, such as the duration of the pair bond (in years), are also regarded as important determinants of breeding onset, with birds remaining paired together across seasons initiating breeding earlier than newly formed pairs (reviewed in Fowler, 1995). Under these circumstances, however, it is not always clear how males and females equally or differentially contribute to pair bonding and early breeding onset. Socially monogamous and long-term pair-bonded males and females might be expected to show mutual interest in attending to, feeding, and/or defending their mate (as in zebra finches, *Taeniopygia guttata*; reviewed in Zann, 1996). Alternatively, monogamous pair members may show a conflict of interest and invest time in breeding behaviours not directed at his/her mate (Birkhead, 1981). Time spent away from a mate will depend upon the value of factors such as territory defense (Westneat, 1993), food acquisition (Neudorf *et al.*, 1997), extra-pair mating opportunities (Currie *et al.*, 1998), and the quality of available mates (Hasselquist *et al.*, 1996).

Ultimately, it would be useful to quantify the acute behavioural interactions that occur between pair members in relation to the timing of reproduction, to better understand how early seasonal breeding and long-term pair-bonding is accomplished by certain pairs. These interactions are often difficult to observe in migratory passerines, where one sex (typically the male) returns from migration before the other, establishes a breeding territory, and forms a pair with a member of the opposite sex within a few days of their return. In contrast, resident, non-territorial species that exhibit substantial variation in breeding onset offer the opportunity to quantify intra-pair interactions and thus better understand whether mutual associations between male and female pair members may help facilitate pair stability and early breeding onset in birds.

In this study, we investigated the degree to which both sexes interacted at the start of the first breeding attempt of the year in relation to pair-bond duration and breeding date in the house finch (*Carpodacus mexicanus*). Most pairs in this short-lived (up to five years), non-territorial, socially monogamous passerine remain mated within a season, but some will remain paired across seasons (Hill, 1993, 2002). Pairs can produce up to four broods and fledge up to twenty offspring in a year, and those that begin breeding earlier in a season fledge significantly more offspring during the year than pairs that initiate breeding later (McGraw *et al.*, 2001). Between the onset of nest building and the completion of egg-laying, both pair members often actively attend to and follow their mates (Hill, 1993, 2002). In this study, we quantified the intra-pair interactions of male and female house finches during the female's first fertile period of the season and compared the intensity of mate attentiveness in both sexes to the duration of the pair bond and to breeding onset.

## Methods

### *Study area*

We studied the breeding biology of house finches on the campus of Auburn University in 1998 and 1999 (Hill *et al.*, 1999; McGraw *et al.*, 2001). We trapped birds at feeders and nests and banded each with a unique combination of one aluminum U.S. Fish and Wildlife Service band and three colored plastic leg bands for individual identification. Accessible nesting sites were provided in the form of open nest cups that we constructed from the bottom of 1.89 L (0.5 gallon) plastic milk containers and placed inside of small wooden boxes. We attached these boxes beneath overhangs on buildings and other structures that mimicked traditional nesting locations on campus. Greater than 80% of birds nesting on our site used these boxes (McGraw *et al.*, 2001). We monitored these boxes and nests found outside of our boxes on a bi-daily basis between February and August of each year for the presence of nest material, eggs, and nestlings.

### *Breeding behaviour*

The identity of breeding pairs was determined in the field with binoculars and confirmed on videos taken of incubation and parental behaviour (Nolan *et al.*, 2001). When eggs were found in a nest, we assigned dates of breeding onset for pairs of birds by scaling them relative to the day on which the first egg was laid in our study population (McGraw *et al.*, 2001). Because house finches lay one egg per day (Hill, 1993), we back-dated breeding-onset dates when we found nests with more than one egg.

Since the pairing status of birds that nested on our study site had been determined in previous years (Hill *et al.*, 1999; McGraw *et al.*, 2001), we were able to determine the longevity of pair bonds for 12 pairs in 1998 and 10 pairs in 1999. Pairs were characterized as either newly formed (when both birds were unpaired or paired with different birds during the previous year) or as long-term (when both birds had bred with one another for the duration of the previous season). For these pairs for which we assigned breeding-onset dates and pair-bond duration, we observed the affiliative behaviour of both sexes during the female's first fertile period of the season. We conducted two, 1-hr. observation periods within the first three hours of morning daylight for each first nest. These periods occurred between day 2 of the egg-laying sequence and the day on which the penultimate egg was laid. Because we could not predict the number of eggs that individual females would lay, we later ignored observation periods that we conducted on the day that females laid their last egg.

To quantify behavioral interactions within a pair, we positioned ourselves approximately 15 m from each nest in a concealed spot to follow the location and flight patterns of both pair members with binoculars. At 1-min. intervals, the distance between the two sexes was estimated to the nearest 0.1 m. Because house finches are non-territorial, both members of the pair often flew out of sight of the nest (*e.g.* around buildings, into the distance/horizon), and often did this without the presence of their mates. On occasion, however, pair members that were out of sight exchanged vocal contact calls to indicate their nearby presence. As a result, we calculated the proportion of 1-min. observations that pairs spent in visual or vocal contact with one another. We also determined the mean distance between the members of the pair when both could be located. Females generally spent time on and around the nest during her fertile period, but males only occasionally approached the nest to provision the female. Thus, we made a distinction between our two aforementioned measures of behaviour — contact time and separating distance — when females were on the nest and when females were active in the shrubs and trees and on the ground around the nest. Pair members often made short flights of 5-10 m in the vicinity of the nest, and were periodically followed by their mate immediately after the initial flight. We calculated the proportion of short flights around the nest for both males and females that were followed by a pursuit-flight by their mate.

### *Statistical procedures*

Although we collected data on affiliative behaviour, breeding date, and pair-bond duration for 22 pairs of house finches, sample sizes are smaller for certain behavioural attributes when we failed to collect more than 20 min. of observational data for a pair of birds in that particular behavioural category. Prior to analysis, we tested all variables for normal distributions (Shapiro-Wilk $W$-test) and equal variances (Equality-of-variance $F$-test). Because breeding initiation dates were normally distributed and the variances of newly formed and return pairs did not differ significantly (all $p > 0.25$), we used unpaired t-tests to examine the effect of pair-bond duration on breeding onset. Variances were unequal for all comparisons involving breeding onset and mate-guarding effort ($p < 0.05$), so we used non-parametric Spearman rank-correlations to determine if the earliest breeding birds spent the most time with and close to their mate. We used non-parametric Mann-Whitney $U$-tests ($Z$ reported) to compare behavioural interactions between return pairs and newly formed pairs because variables were not normally distributed. We found no effects of year on breeding onset, pair-bond stability, or any of our behavioural measures, so we pooled the two years of data for analysis. Birds appear only once in each comparison; when birds nested in both years of our study, we used data from that year for which we had the most breeding/behavioural information.

## Results

We detected a significant relationship between pair-bond duration and seasonal timing of breeding in house finches. Pairs returning to breed with one another across years began nesting significantly earlier in the season than did newly formed pairs (Fig. 1). Return pairs produced 10 of the first 12 nests in the population during the breeding seasons of 1998 and 1999.

We also found significant relationships between seasonal breeding onset and some of our measures of intra-pair affiliative behaviour (Fig. 2). Males from earlier-breeding pairs stayed in contact with their mate while she was on the nest significantly more often than did later-breeding males (Fig. 2A). Early-breeding males did not necessarily remain significantly closer to the nest than late breeders (Fig. 2B). Also, when females spent time off of the nest during the fertile period, early-breeding pairs remained in contact significantly more often than did late-breeding pairs (Fig. 2C). Again, there was no relationship between the date of first breeding and the distance between

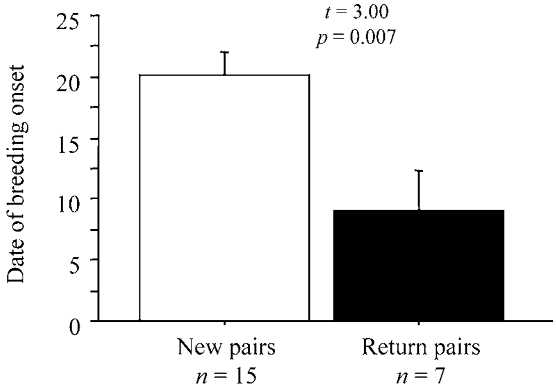

Fig. 1. Differences (means + standard error) in the seasonal onset of breeding for newly formed versus long-term pairs of house finches in east-central Alabama from 1998-1999. Pairs were identified in the field from 1997-1999 (*sensu* Hill *et al.*, 1999) to determine whether individuals formed new bonds with opposite-sex partners each season or retained the same mate across years. Timing of breeding is defined as the appearance of the first egg in a nest for each pair and measured as the number of days since the first egg was laid in the population each year (set at 1). Newly formed pairs began egg-laying significantly later in the season than long-term pairs.

pair members (Fig. 2D). Females from the earliest-breeding pairs were more likely to fly in pursuit of their mates than females from late-breeding pairs (Fig. 2E). Nearly all males always pursued their mates when they flew in the vicinity of the nest, so there was no relationship between male pursuit-flight frequency and breeding onset (Fig. 2F).

These relationships between affiliative behaviour and breeding date can be explained by the fact that return pairs of house finches spent more time in association with each other than did newly formed pairs (Fig. 3). Return pairs stayed in contact for significantly longer periods of time during the female's fertile period when she was off the nest than newly formed pairs (Fig. 3C). Females from long-term pairs pursued mates in nest-vicinity flights significantly more frequently than females from new pairs (Fig. 3E). There also was a non-significant tendency for males from stable pairs to remain in contact more often with their mates while she was on the nest than males from newly formed pairs (Fig. 3A). We found no effect of pair-bond duration on the distance between mates when females were either on or off the nest or on the proportion of female flights in which males followed (Fig. 3B, D, F). Our measures of intra-pair behaviour also did not depend on the stage of the egg-

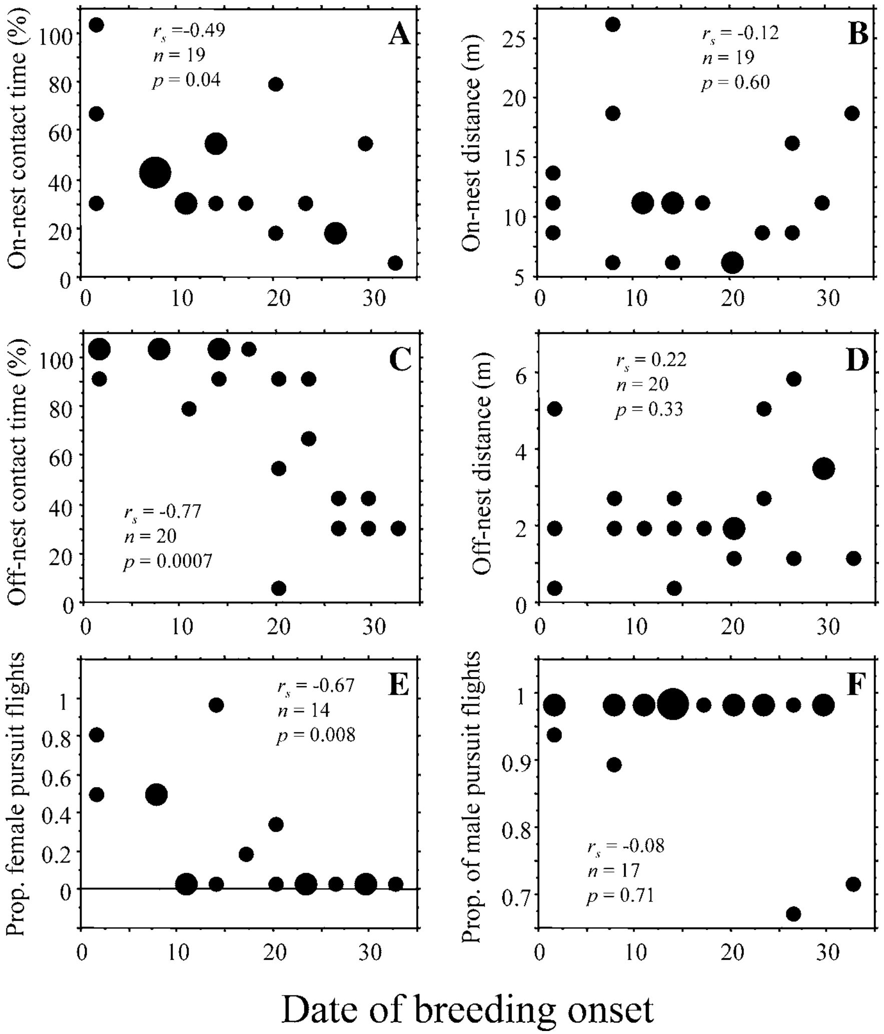

Fig. 2. Relationships between breeding onset (in days) and affiliative behaviours between mated pairs of male and female house finches: (A) percentage of time that the male and female spent in contact with one another while the female sat on the nest during her fertile period, (B) mean distance between partners while females sat on the nest, (C) percentage of contact time between pair members when females were not sitting on the nest, (D) mean distance between partners when females were off the nest, (E) proportion of flights taken by the male in which the female followed, and (F) proportion of female flights in which the male pursued her. Note the gross sex differences in mate attentiveness; males less frequently departed females (smaller n in panel E compared to F) but were more likely to follow females when they took flight (higher mean and narrower range of variation in panel F compared to E). Point size is proportional to the number of overlapping observations.

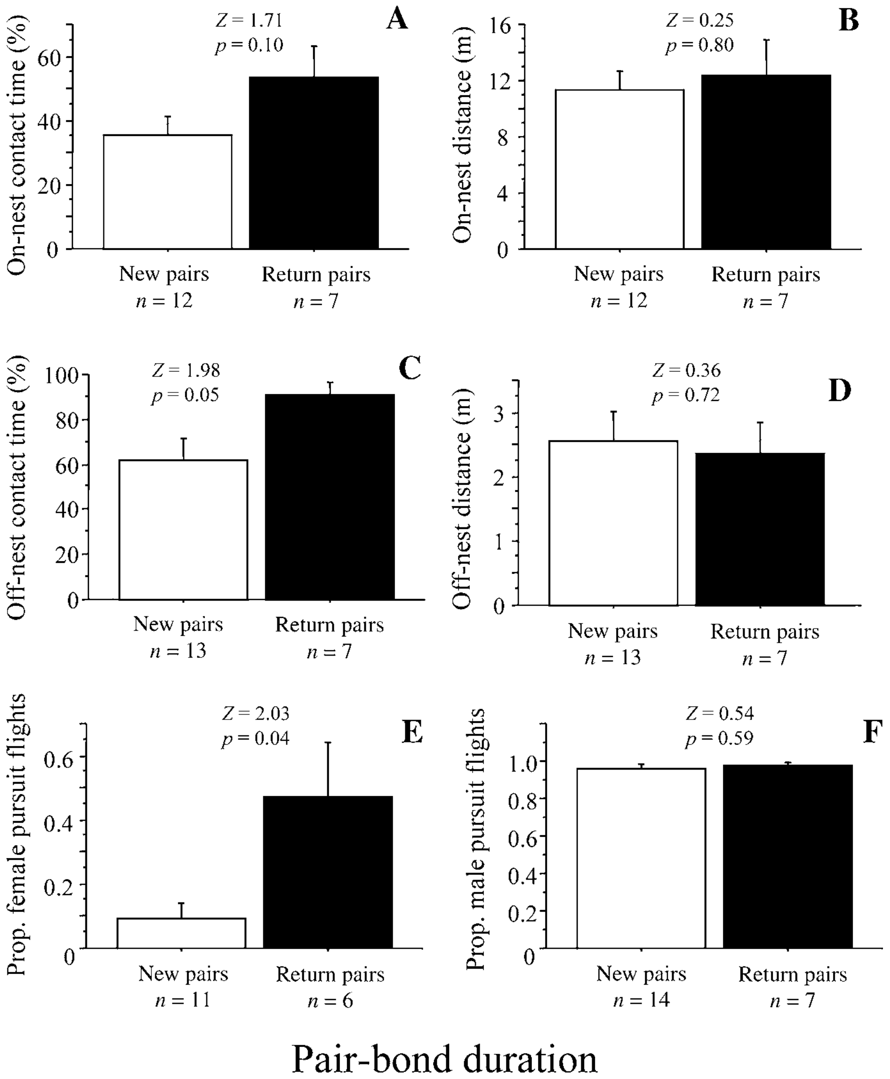

Fig. 3. Differences (means + standard error) in mate attentiveness between newly formed and long-term pairs of house finches during the first breeding attempt of the year (panels A-F follow those listed previously for Fig. 2). See Fig. 1 for methods of determining pair-bond stability. Much like the behavioural patterns observed for early-breeding pairs, stable pairs spent a greater percentage of time in contact with one another and females from long-term partnerships more often pursue their mates.

laying cycle during which observations were made or the density of nesting pairs in the area (Spearman rank-correlations, all $p > 0.10$).

## Discussion

In this study, we considered how the proximate behaviors of mated male and female house finches relate to the long-term stability of pairs as well as the seasonal onset of breeding. We found that pairs breeding earliest in a year were those that returned to breed across seasons. Most studies that have related pair-bond duration to breeding onset (reviewed in Fowler, 1995) have been conducted on long-lived species (*e.g.* procellarids, sulids, larids, spheniscids). Our results illustrate a similar relationship for a short-lived, socially monogamous passerine. Long-term pair bonding appears to confer considerable reproductive advantages in many species, with early breeding birds fledging more offspring in a year than later breeders (O'Donald, 1980; McGraw *et al.*, 2001).

We further explored the specific behaviours typical of long-term, early-breeding pairs. We found that members of both sexes in long-term pairs of house finches showed strong affiliative behaviors and begin breeding early in the season. During the female's fertile period, early-breeding males from returning pairs spent more time in contact with their mate when she was on the nest than later-nesting males from newly formed pairs. Males and females from long-term pairs also spent more time in contact with one another when near the nest. Last, early-breeding females from long-term pairs were significantly more likely to follow their mate in pursuit flights in the vicinity of the nest than later-nesting females from new pairs. One interpretation of these data is that long-term pairs may show similarly strong affiliative behavior prior to breeding, which allows them to initating nesting earlier than pairs that have not yet formed. However, we could not test this idea explicitly because we rarely can follow the behavior of individuals prior to pair-formation; house finches leave our study site during winter and characteristically return in mated pairs that begin inspecting for nest sites immediately (pers. obs.).

Mate-attentive behaviours by males during the female's fertile period (*e.g.* the amount of time spent in contact, distance between pairmates) are typically viewed as mate-guarding efforts to ensure paternity (Møller & Birkhead, 1991; Dickinson, 1997; Pagenkopf & Wesolowski, 2002). If extra-pair fertilization opportunities are high, however, (*e.g.* when breeding is synchronous within a population), males may forgo mate defense and seek additional copulations outside the pair (Stutchbury, 1998; Chuang-Dobbs *et al.*, 2001). The breeding season of house finches is characterized by largely asynchronous bouts of nesting and renesting (Hill, 1993), so there seem to be few predictable opportunities to encounter several fertile females at one time and make extra-pair mating a worthwhile tactic. These ecological conditions may be a selective force favoring strong within-pair interactions and limiting extra-pair fertilizations in this species (incidence of cuckoldry was estimated at 6.5% and 8% in two previous studies of house finches in Montana (Badyaev *et al.*, 2001) and Michigan (Hill *et al.*, 1994), respectively).

Studies of female behaviour during her fertile period are comparatively less common and more difficult (Cézilly *et al.*, 2000), particularly because of their typically cautious and cryptic habits designed to avoid predators, forage, or solicit extra-pair copulations (Neudorf *et al.*, 1997). The open, urban habitat of house finches in eastern North America, not too unlike the expansive deserts in which they breed natively in the western half of the continent, provided us the opportunity to track the location and flights of females in relation to her mate. The fact that females are so easily tracked by humans, and presumably by their social mates, on their breeding grounds may also play an important role in limiting extra-pair forays by females and maintaining close within-pair contact. Female pursuits of their long-term mates (Fig. 2E, 3E) may be a mechanism by which females restrict male extra-pair behaviors as well.

In addition to the social affiliations demonstrated in this study, there should be several other advantages to retaining mates across successive years. By definition, long-term pair members are older, have demonstrated their survival ability (Kokko & Lindström, 1996), and have acquired the breeding experience (Forslund & Pärt, 1995) necessary to maximize annual reproductive success. But if the benefits to stable partnerships are so high in house finches, why don't all pairs mate for multiple seasons or even for life? Certainly, individuals vary in mate quality, such that less-desirable pair members die or are abandoned by their mates sooner than others. Divorces are common both within and among seasons in house finches (Hill, 1993, 2002), and females use traits such as carotenoid-based plumage coloration to assess a male's potential worth as a mate and will desert less-colorful males more often (Hill, 1991). In fact, the degree to which males and females interact with and attend to their mates may serve as important sexually selected behaviours (*e.g.* Mills, 1994); those individuals that fail to show reliable affiliative behaviours may be poor candidates for long-term pair-bonding. Due to the correlational nature of this study, we cannot tease apart the cause-and-effect relationship between breeding onset, long-term pairing, and mate attentiveness. Only using future behavioural manipulations will we be able to determine whether the intrapair behaviours documented here are causes or consequences of early seasonal breeding and stable partnerships.

## References

Badyaev, A.V., Hill, G.E., Dunn, P.O. & Glen, J.C. (2001). Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. — Am. Nat. 158, p. 221-235.

Birkhead, T.R. (1981). Mate guarding in birds — conflicting interests of males and females. — Anim. Behav. 29, p. 304-305.

Cézilly, F., Preault, M., Dubois, F., Faivre, B. & Patris, B. (2000). Pair-bonding in birds and the active role of females: a critical review of the empirical evidence. — Behav. Proc. 51, p. 83-92.

Chuang-Dobbs, H.C., Webster, M.S. & Holmes, R.T. (2001). The effectiveness of mate guarding by male black-throated blue warblers. — Behav. Ecol. 12, p. 541-546.

Currie, D.R., Burke, T., Whitney, R.L. & Thompson, D.B.A. (1998). Male and female behaviour and extra-pair paternity in the wheatear. — Anim. Behav. 55, p. 689-703.

Darwin, C. (1871). The descent of man, and selection in relation to sex. — John Murray, London.

Dickinson, J.L. (1997). Male detention affects extra-pair copulation frequency and pair behaviour in western bluebirds. — Anim. Behav. 53, p. 561-571.

Fisher, R.A. (1958). The genetical theory of natural selection. — Dover, New York.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds — hypotheses and tests. — Trends Ecol. Evol. 10, p. 374-378.

Fowler, G.S. (1995). Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. — Am. Zool. 35, p. 318-328.

Hasselquist, D., Bensch, S. & von Schantz, T. (1996). Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. — Nature 381, p. 229-232.

Hill, G.E. (1991). Plumage coloration is a sexually selected indicator of male quality. — Nature 350, p. 337-339.

Hill, G.E. (1993). House finch (*Carpodacus mexicanus*). — In: Birds of North America, no. 46 (A. Poole & F. Gill, eds). Academy of Natural Sciences, Philadelphia.

— — (2002). A red bird in a brown bag: the function and evolution of ornamental plumage coloration in the house finch. — Oxford University Press, Oxford.

— —, Montgomerie, R., Roeder, C. & Boag, P. (1994). Sexual selection and cuckoldry in a monogamous songbird: implications for sexual selection theory. — Behav. Ecol. Sociobiol. 35, p. 193-199.

— —, Nolan, P.M. & Stoehr, A.M. (1999). Pairing success relative to male plumage redness and pigment symmetry in the house finch: temporal and geographic constancy. — Behav. Ecol. 10, p. 48-53.

Jones, P.J. & Ward, P. (1976). The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the red-billed quelea *Quelea quelea*. — Ibis 118, p. 547-574.

Kelly, J.F. & Van Horne, B. (1997). Effects of food supplementation on the timing of nest initiation in belted kingfishers. — Ecology 78, p. 2504-2511.

Kirkpatrick, M., Price, T. & Arnold, S.J. (1990). The Darwin-Fisher theory of sexual selection in monogamous birds. — Evolution 44, p. 180-193.

Kokko, H. & Lindström, J. (1996). Evolution of female preference for old mates. — Proc. R. Soc. Lond. B 263, p. 1533-1538.

Kroodsma, D.E. (1976). Reproductive development in a female songbird: differential stimulation by quality of male song. — Science 192, p. 574-575.

Lack, D.M. (1968). Ecological adaptations for breeding in birds. — Methuen, London.

Martin, T.E. (1987). Food as a limit on breeding birds: a life-history perspective. — Ann. Rev. Ecol. Syst. 18, p. 453-487.

McGraw, K.J., Stoehr, A.M., Nolan, P.M. & Hill, G.E. (2001). Plumage redness predicts breeding onset and reproductive success in the house finch: a validation of Darwin's theory. — J. Avian Biol. 32, p. 90-95.

Mills, J.A. (1994). Extra-pair copulations in the red-billed gulls — females with high-quality, attentive males resist. — Behaviour 128, p. 41-64.

Møller, A.P. & Birkhead, T.R. (1991). Frequent copulations and mate guarding as alternative paternity guards in birds — a comparative study. — Behaviour 118, p. 170-186.

Neudorf, D.L., Stutchbury, B.J.M. & Piper, W.H. (1997). Covert extraterritorial behavior of female hooded warblers. — Behav. Ecol. 8, p. 595-600.

Nisbet, I.C.T. (1973). Courtship-feeding, egg-size and breeding success in common terns. — Nature 241, p. 141-142.

Nolan, P.M., Stoehr, A.M., Hill, G.E. & McGraw, K.J. (2001). The number of provisioning visits to the nest predicts the mass of food delivered. — Condor 103, p. 851-855.

O'Donald, P. (1972). Sexual selections by variations in fitness at breeding time. — Nature 237, p. 349-351.

— — (1980). Sexual selection by female choice in a monogamous bird: Darwin's theory corroborated. — Heredity 45, p. 201-217.

— —, Wedd, N.S. & Davis, J.W.F. (1974). Mating preferences and sexual selection in the arctic skua. — Heredity 33, p. 1-16.

Pagenkopf, K. & Weslowski, T. (2002). Do male nuthatches (*Sitta europaea*) guard their mates? — J. Ornithol. 143, p. 145-154.

Perrins, C.M. (1970). The timing of birds' breeding seasons. — Ibis 112, p. 242-255.

Price, T., Kirkpatrick, M. & Arnold, S.J. (1993). Directional selection and the evolution of breeding date in birds. — Science 240, p. 798-799.

Saether, B.E. (1990). Age-specific variation in reproductive performance of birds. — Curr. Ornithol. 7, p. 251-283.

Stutchbury, B.J.M. (1998). Breeding synchrony best explains variation in extra-pair mating system among avian species. — Behav. Ecol. Sociobiol. 43, p. 221-222.

Verhulst, S. & Tinbergen, J.M. (1991). Experimental evidence for a causal relationship between timing and success of reproduction in the great tit *Parus m. major*. — J. Anim. Ecol. 60, p. 269-282.

Westneat, D.F. (1993). Temporal patters of within-pair copulations, male mate-guarding, and extra-pair events in eastern red-winged blackbirds (*Agelaius phoeniceus*). — Behaviour 124, p. 267-290.

Wright, J. & Cuthill, I. (1992). Monogamy in the European starling. — Behaviour 120, p. 262-285.

Yom-Tov, Y. & Hilborn, R. (1981). Energetic constraints on clutch size and time of breeding in temperate zone birds. — Oecologia 48, p. 234-243.

Zann, R.A. (1996). The zebra finch. — Oxford University Press, Oxford.