Early arrival, initiation of nesting, and social status: an experimental study of breeding female red-winged blackbirds

Red-winged blackbirds (*Agelaius phoeniceus*) arrive at breeding sites several months before nests are constructed. Males in this highly polygynous species presumably return early to defend desirable territories. Females, however, also begin to arrive almost two months before nesting is attempted. Early return to breeding sites could enhance reproductive success by increasing a female's social status and thereby allowing earlier nesting. I measured the effect of experimentally delayed arrival on the timing of nesting, reproductive success, and social status of females. Birds were captured as they arrived in early spring and detained in an aviary. These experimental females were later released at their capture sites before control females began construction of nests; controls had arrived during the same period as experimentals but were not detained. Experimental females nested, on average, more than a week later than controls, although I could detect no effect of timing on reproductive success during this study. By manipulating arrival date, but not covariates of arrival time such as age or experience, this result indicates that timing of arrival directly influenced laying date. Delayed females were subordinate to control females with the same mate. This decline in social status may have been responsible for the delay in nesting and could have fitness consequences for females in some years, because the offspring of earlier nesting, dominant birds are more likely to receive male parental care in this population. *Key words*: *Agelaius phoeniceus,* clutch initiation, delayed arrival, female arrival time, red-winged blackbird, social dominance, timing of reproduction. *[Behav Ecol 6:87–93 (1995)]*

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Early nesting can potentially enhance a female bird's fitness. In species for which multiple-brooding is a possibility an early first nest increases the chances of having time to produce a second nest. Even in single-brooded species, an early female will have more chances to replace a failed nest. In many species, early nesting results in higher reproductive success (Klomp, 1970; Nolan, 1978; Perrins, 1970). In addition, early-hatched young have the highest likelihood of surviving to breeding age in some species (e.g., Cooke et al., 1984). Studies from several populations of red-winged blackbirds (*Agelaius phoeniceus*) have shown that nesting success is generally higher early in the season (Langston et al., 1990; Orians, 1980; Robertson, 1973; Westneat, 1992).

Red-winged blackbirds are among the earliest migrants to return each spring, arriving as early as the first week of February at my study site. Males presumably return early to defend high-quality territories in this polygynous population. Yet many females also return nearly two months before the first eggs are laid, and before abundant food or nest sites are available. The wetland study site is normally covered with ice at this time of year, and little of the previous year's vegetation is left standing. Because female red-winged blackbirds do not appear to defend territories (Yasukawa and Searcy, 1981), it is unclear why they return to breeding sites so early. The goal of this study was to test whether early arrival at breeding sites is advantageous to females. By experimentally delaying females I could assess the importance of arrival date for female reproductive success. If early arrival is adaptive, then experimentally delayed birds should have poorer reproductive success than nondelayed controls arriving at the same time.

Intrasexual aggression occurs frequently among female red-winged blackbirds and could influence breeding date (Langston et al., 1990). Thus, I also examined the role of arrival date in determining the outcome of social interactions among females. By experimentally manipulating arrival time I was able to determine whether arrival date influences social status directly, or whether the reported relationship between arrival and social status is the result of covariation with another variable such as age (Roberts and Searcy, 1988).

METHODS

The study site was a cattail (*Typha latifolia*) marsh at the north end of Yellowwood Lake, Yellowwood State Forest, Brown County, Indiana, USA (39° 10′ N, 86° 20′ W). Red-winged blackbirds have been studied and color-banded at this site since 1969, and the habitat remains nearly as described by Yasukawa (1979). In 1990 and 1991, I determined the natural arrival date and nesting success of all females breeding at the site (1990, $n = 90$; 1991, $n = 56$) and carried out a delay-of-arrival experiment on 27 of these females (1990, $n = 17$; 1991, $n = 10$). Females were assigned a minimum age of one year when banded for the first time.

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Arrival

I censused the entire study area from dawn to 0900 h EST either every day (1990) or every second or third day (1991). In both years censuses began before any females were sighted (8 February 1990; 5 February 1991) and lasted until well into the nesting season (25 June 1990; 31 July 1991). In 1990, several males had arrived before the first census, but that was not the case in 1991. I plotted each sighting on a detailed map. The probability that I would detect all newly arriving birds was high because: (1) until June the marsh was only sparsely vegetated with residual vegetation and (2) female redwings that were perched in the vegetation often called conspicuously when I approached. Birds were captured in treadle traps and, if they had not been banded in a previous year, were given unique combinations of anodized aluminum leg bands (yellow, pink, blue, or silver). Traps were baited with corn and placed on platforms above the water or on the ground in nearby communal feeding areas. Traps were cleared of bait following use so that supplemental food was available for only a few hours in the morning and only to captured birds. In each year of the study all of the males and more than 85% of the females were captured and banded before nesting. I included data from unbanded birds only in analyses of dominance interactions.

Delay of arrival

Most females were captured within a few days of being detected by the census ($\bar{x} = 4.5$ days, range = 0–15 days). Captured females were weighed to 0.5 g with a 50-g Pesola spring balance. They were then either removed to an aviary (experimental treatment) or released immediately (control treatment). Only females that arrived first on a male's territory were used as experimental birds, and they were used only if capture occurred before any other females had arrived on that territory. Females were assigned to treatment groups haphazardly in 1990 and randomly in 1991, with the constraint that no female was included in the experimental treatment group in both years. Control groups for the various comparisons are described at the appropriate points in the Results section.

Experimental birds were housed together in a large (7 × 5 × 3 m) outdoor cage located 24 km from the study site. They were provided ad libitum with corn, sunflower, millet, turkey mash, and vitamin-fortified water, and each day a dish containing 10 live mealworms per bird was placed in the cage. The birds' only contact with humans was during their brief daily feeding. An artificial stream provided constant running water for bathing. Numerous dowel perches and cut evergreen trees were present for roosting. For most of the captivity period one or more male red-winged blackbirds from another population were housed in a cage within sight and hearing of the females in an attempt to mimic the social environment present in mixed-sex migratory flocks. In 1990, all experimental females were released at site of capture at dawn on 23 April, three days after the peak of arrival of females at the study site. In 1991, females were not released all on one day. Instead, each experimental female was released at dawn one to two days after another female had settled on the territory from which she had been removed. Throughout this article the term *release date* refers to the time of release for experimental females, and *natural arrival* refers to the day that experimental or control females were first sighted. In both years females were released before any construction of nests had begun on their mates' territories. Females were held for an average of 17.5 days (range: 3–41 days), and, except for one that died shortly after capture, all appeared healthy upon release.

Reproductive success

Nest searches were conducted every 2 to 3 days, and nests were checked daily when laying, hatching, and fledging were expected. To minimize the risk of predation, nest locations were not marked in the field; rather each nest site was plotted on a map. Within 12 h of laying, eggs were measured to 0.01 cm with a dial calipers and weighed to 0.1 g with a 10-g Pesola spring balance. Egg volume (V) was calculated as:

$$V = 0.51 \cdot LB^2$$

where L was egg-length and B was breadth at the widest point on the egg (Hoyt, 1979). The date that the first egg was laid was recorded or calculated from its hatching date. In most cases the date the female began building the nest could not be determined accurately because the period of nest-building in this species is highly variable (3–12 days in the present study, unpublished data; see also Teather et al., 1988). The male that behaved aggressively toward me as I checked nest contents was assumed to be the mate of the female at that nest.

Because of the openness of the habitat and because newly fledged red-winged blackbirds remain near the nest, the fate of nests (failure or success, with success defined as producing at least one fledgling) could usually be determined with confidence. To assess seasonal variation in nest success, I calculated the probability of success as a function of the number of days since the first egg of the year was laid on the study area. To calculate probabilities I divided the number of successful nests begun in each 2-day period by the total number begun during that period.

Dominance status

In 1991, aggressive interactions among females were recorded on the morning censuses and also during occasional hour-long watches at lightly baited platforms within male territories. Only chases were included, as these have a clear initiator, winner (the pursuer), and loser (the displaced female). Because no reversals or ties were observed in 99 interactions, a female was classified as dominant to an opponent if she displaced it one or more times.

Statistical analyses

All dates have been adjusted so that the date of the first breeding female to arrive in each year is day 0, the following day 1, etc. Nonparametric statistics are used, unless otherwise noted, to avoid assuming normality of the underlying distributions and because in most cases the sample sizes of controls and experimentals differed (Siegel and Castellan, 1988). All correlations are presented as Spearman rank correlation coefficients. Fisher exact probabilities were used in place of χ^2 when expected values were less than five. Multiple regression was used to determine how much of the variance in laying date was explained by age and arrival date. A significance level of $\alpha = 0.05$ was employed, all tests were two-tailed, and corrections for ties or continuity were used when necessary. Throughout this article mean values are followed by standard deviations. The arrival schedules and methods were similar in both years, so I have combined them for analysis.

RESULTS

Numbers, arrival dates, and ages of females

In 1990, I captured 126 females, of which 78 remained at the study site and laid at least one clutch of eggs. In addition, nests were built by 12 unbanded females that were never captured. The 90 females that bred were distributed on the territories of 27 males in groups (hereafter called breeding groups) of 1–8 females ($\bar{x} = 3.4 \pm 2.0$ females). The population was smaller in 1991, probably because of destruction of some nesting habitat by an unusually large population of muskrats (*Ondatra zibethica*) during the winter of 1990–1991. In 1991, I captured 65 females, of which 49 remained at the study site and nested at least once. Seven additional unbanded females nested. The resulting 56 breeding females did so on the territories of 20 males, and breeding group size ranged from one to six females ($\bar{x} = 3.0 \pm 1.4$ females).

In 1990, the first breeding female arrived on 10 March, and the median, as well as the modal, arrival date was day 41 (20 April). In 1991, the first breeding female arrived on 19 March, and the median, as well as the modal, arrival date was day 19 (7 April). In each year, females arrived later than males (male median 1990 = day −18, 1991 = day −27), and female arrivals took place over a longer period of time (Figure 1A,B). Minimum ages ranged from 1–8 years ($\bar{x} = 2.1 \pm 1.2$ years). During 1991 only one banded female was present that had been present earlier than, but not during, 1990. This suggests that females generally return each year so that minimum age and years of experience at the study site should be highly correlated.

Condition of control and experimental females

In comparing experimental and control females, I assumed that captivity did not affect breeding condition and that any differences between treatment groups resulted from manipulating the arrival date. To test this assumption I compared experimentals and controls for change in mass during the period that experimentals were in captivity, size of the first clutch, and volume of the first-laid egg. All control females that arrived during the same period as experimental birds were used as controls for the clutch size and egg volume comparisons, but only those captured more than once during the time experimentals were in captivity were included in the comparison of change in mass. Treatment groups had nearly identical mean values for change of mass during the period when experimental birds were in captivity (controls $\bar{x} = -0.2 \pm 2.3$ g, $n = 22$; experimentals $\bar{x} = -0.2 \pm 1.5$ g, $n = 17$), clutch size (controls $\bar{x} = 3.66 \pm 0.54$ eggs, $n = 35$; experimentals $\bar{x} = 3.65 \pm 0.49$ eggs, $n = 17$), and egg volume (controls $\bar{x} = 3.95 \pm 0.41$ cm^3, $n = 29$; experimentals $\bar{x} = 3.86 \pm 0.38$ cm^3, $n = 17$). The date of laying the first egg by experimental females was not significantly correlated with the duration of captivity ($r_s = .26$, $p = .27$, $n = 20$). It is possible that some unmeasured parameter, such as hormone titers, differed as a result of the treatment, but the measures I used give no indication that there were physiological effects of captivity.

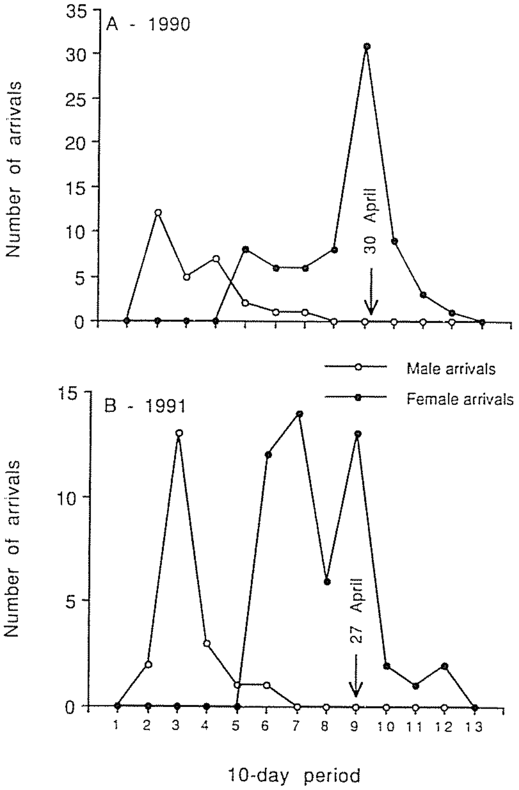

Figure 1
Male and female arrival dates in (A) 1990 and (B) 1991. In 1990, range was 51 days for males and 72 days for females ($n = 27$ males, 72 females); in 1991, range was 41 days for males and 67 days for females ($n = 20$ males, 49 females). Arrows indicate the date of the first egg in each year.

Relationship between arrival, age, and laying date

Among control birds (all nonexperimental females), arrival date was significantly correlated with the date the first egg was laid (Figure 2A). Minimum age was also significantly correlated with the date of the first egg ($r_s = -.64$, $p < .001$, $n = 89$) and arrival date ($r_s = .57$, $p < .001$, $n = 90$). Multiple regression analysis indicates that arrival date and age, together, explain 64% of the variation in date of the first egg (regression line = $46.9 + 0.345 \cdot$ arrival date $- 1.83 \cdot$age; ANOVA, $F = 79.1$, $p < .001$, $n = 89$). Control females (only those that arrived during the same period as experimental birds' natural arrivals in each year) laid their first eggs, on average, significantly earlier than experimentals (controls $\bar{x} =$ day 48, $n = 30$, experimentals $\bar{x} =$ day 57, $n = 20$, Mann-Whitney $U = 523$, $p < .0001$, Figure 2A,B).

The duration of the period between arrival of control females and laying of their first egg was

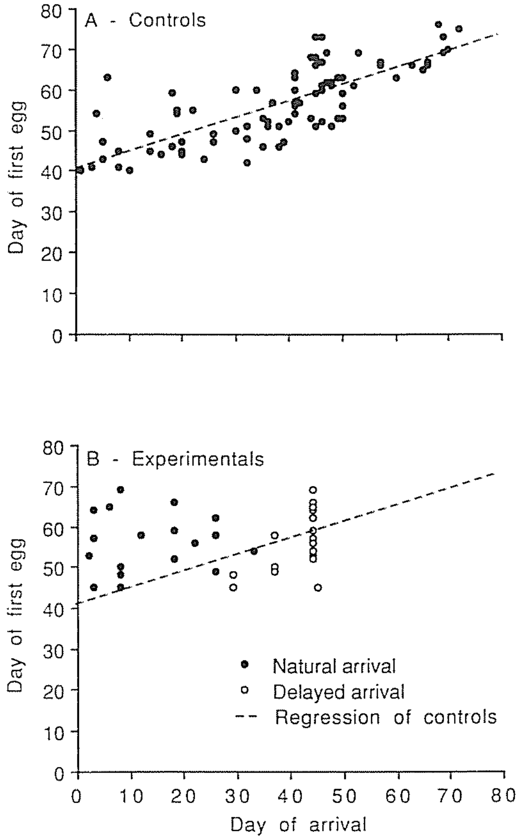

Figure 2
Date of arrival and first egg (in days since first female arrived) for (A) control and (B) experimental females for 1990 and 1991 combined. Regression line (dashed line, $Y = 0.41x + 40.70$, $r_s = .78$, $p < .001$, $n = 92$) was computed for controls only, and is also shown in (B) for comparison. Dots represent natural arrival and first egg dates. Circles represent the dates of release from captivity and first egg for the experimental females.

negatively correlated with arrival date ($r_s = -.85$, $p = .001$, $n = 92$), indicating that earlier females waited longer before nesting. For experimental birds the equivalent period is the time between release date and laying of their first egg. Considering as controls only females that arrived within 2 days of the release date of an experimental bird, the mean period between arrival (or release date for experimentals) and laying the first egg differed by less than 2% between experimentals and controls (controls $\bar{x} = 16.4 \pm 6.6$ days, $n = 20$; experimentals $\bar{x} = 16.1 \pm 4.8$ days, $n = 20$, Mann-Whitney $U = 197$, $p > .9$). Control females that arrived within 2 days of the dates when experimental females were released were significantly younger than the experimentals (controls $\bar{x} = 1.7 \pm 0.8$ years, $n = 20$; experimentals $\bar{x} = 2.4 \pm 1.0$ years, $n = 20$, Mann-Whitney $U = 123$, $p = .03$).

Within breeding groups consisting only of controls, the female that arrived first usually laid the earliest clutch (16 of 21 breeding groups). The proportion of first-arriving females that initiated a clutch before any other member of their breeding group was significantly greater for controls (76%) than for experimentals (28%, $n = 14$, $\chi^2 = 5.96$, $p = .015$). It should be remembered that each experimental female nested in a breeding group consisting of nonexperimental females.

Production of eggs and fledglings

The first egg was laid on day 51 (30 April) in 1990, and on day 40 (27 April) in 1991 (Figure 1). All experimental females built their first nests on the males' territories from which they had been removed. Including as controls all females that arrived during the period of experimental birds' natural arrivals in each year, the proportion of experimental females that laid at least one clutch was virtually the same as that of controls (controls = 0.85, $n = 48$; experimentals = 0.82, $n = 27$; $\chi^2 = 0.01$, $p > .9$).

Reproductive success was very low in both years, in 1990 as the result of a destructive flood on 16 May and nest predation thereafter, and in 1991, as the result of severe predation on eggs and nestlings. Only 22% of clutches successfully produced one or more fledglings in 1990, and 41% of females were successful, most because they repeatedly built replacement nests. In 1991, 20% of clutches produced one or more fledglings, and 51% of females were eventually successful. The success rate of first nesting attempts was 27% in 1990 and 16% in 1991. Experimental females were about as likely as controls to produce at least one fledgling (controls = 0.45, $n = 111$; experimentals = 0.43, $n = 20$, $\chi^2 = 0.01$, $p > .9$). Considering only the first nest, control females were slightly, but not significantly, more likely to produce at least one fledgling (controls = 0.22, $n = 104$; experimentals = 0.15, $n = 20$, $\chi^2 = 0.17$, $p = .68$). Control birds for these two comparisons included all non-experimentals that arrived during the same period as the experimental birds' natural arrival dates in each year.

Among control females the probability of producing any fledglings from the first nesting attempt was not significantly correlated with date (df = 9, $r_s = .27$, $p > .4$, $n = 93$ nests), and the probability of success also did not differ significantly among 2-day periods (range: 0–38% of nests successful in each period, Kruskal-Wallis ANOVA, $H = 9$, $p > .4$, $n = 93$ nests).

Social status

I recorded 99 aggressive interactions involving 30 different females that formed 20 dyads. These interactions consisted of one female chasing another from a perch ($n = 72$) or baited platform ($n = 27$) from 1 to 20 times ($\bar{x} = 5 \pm 6$ interactions/dyad). Experimental females had earlier natural arrival dates than their control opponents, but were released from captivity after their control opponents had arrived. In eight of ten dyads where both members were controls, the female with the earlier natural arrival date was dominant. In contrast, among six dyads involving a control female and an experimental female, the control females were always dominant, despite their later natural arrival dates. Thus, the probability of the female with the earlier natural arrival date being dominant differed significantly between dyads containing only control females and those consisting of one experimental and one control female (Fisher exact, $p = .007$). To state it another way, females with earlier natural arrival dates were usually dominant to later arriving birds, but if early females were experimentally delayed, they became subordinate to females that arrived in their absence. In the six cases where the relationship between control females of different ages was known, the older female was dominant in four and the younger was dominant in two.

DISCUSSION

Effects of delayed arrival on nesting success

Among unmanipulated female red-winged blackbirds there was a strong correlation between natural arrival date and the date of laying the first egg. Age was negatively correlated with both arrival date and date of laying, with older females arriving and laying early. Females that were removed from males' territories shortly after early spring arrival, and then released up to several weeks later, were less likely than controls to be the first female in their breeding group to lay eggs. Experimental females initiated clutches approximately 9 days later than controls with the same natural arrival dates, further indicating that experimentally delaying arrival delayed nesting. Experimental females did not nest earlier than the control females arriving at the time they were released, despite the younger age of the later-arriving control females. This result demonstrates that arrival date is causally related to laying date, while greater age alone does not enable birds to nest earlier.

Other studies have shown that nesting date is related to food availability in this species (Ewald and Rohwer, 1982; Wimberger, 1988); females receiving supplemental food tended to lay earlier clutches. One could argue that in the present study the laying dates of the experimental females were affected by nutritional condition or other factors resulting from captivity. Experimental females were housed together in a very large outdoor aviary, however, and care was taken to provide them with appropriate feeding, bathing, and roosting opportunities. Three indices of condition (change of mass during the time when experimentals were in captivity, clutch size, and volume of the first egg) suggested that the physiological condition of the treatment groups did not differ, so it is unlikely that differences in condition were responsible for the later nesting of experimentals. It is not immediately clear why experimentally delayed females nested later than controls with the same natural arrival dates. Experimentals did not require longer to prepare for egg laying than controls that arrived on the experimentals' release dates. In addition, because each experimental female was released well before any nests were initiated on her mate's territory, nesting delays were not simply the result of experimentals having been detained while controls were building nests. I suggest, below, that arrival date determines social status, which in turn influences order of nesting within breeding groups, potentially increasing reproductive success of early-arriving females.

Within-season prior residence and social status

Earlier-arriving females were nearly always dominant among dyads of control birds. When the usual association between early arrival and within-season prior residence was decoupled by the experimental delay of early females, later-arriving prior residents were dominant. Experimental females were subordinate to controls that had arrived after the experimentals' natural arrival dates but before their release dates in all six such cases. Although it has been shown that arrival date is correlated with dominance among unmanipulated female red-winged blackbirds (Roberts and Searcy, 1988), and that early females are more aggressive when presented with taxidermic mounts of female blackbirds (Langston et al., 1990), the present study is apparently the first demonstration that this relationship is not simply a byproduct of covariation between arrival date and other determinants of dominance such as age or size. Although factors such as experience or large size might increase a female's chances of being dominant to others in her breeding group, within-season prior residence appears sufficient for high social status. The underlying mechanism for the prior residence advantage among female red-winged blackbirds remains unclear. It has, however, been demonstrated in many species that being present at a site for some time prior to a social interaction increases status, and this advantage can outweigh many other potential determinants of dominance (e.g., Cristol et al., 1990).

For another population of red-winged blackbirds it has been proposed that the most aggressive females outcompeted others to settle earlier on choice territories, and therefore layed eggs earlier (Langston et al., 1990). This argument implies that aggressive behavior caused the earlier settling. My results, however, suggest reversed causation, as within-season prior residence (i.e., early settling) resulted in higher social status (i.e., more aggressive females). As Langston et al. (1990) did not have individually marked females, it is not clear whether their settling dates are analogous to arrival dates in the present study, or whether aggression toward taxidermic mounts corresponds to social status. Further studies will be needed to determine whether these contrasting results are due to real population differences or differences in interpretation.

Selection for early arrival

Although females that arrived later nested later, the period between arrival and nesting decreased with arrival date among control females (as in Westneat, 1992). Early females arrived long before nesting, while later females began nest construction almost immediately. Given that some females can construct nests shortly after arrival, why did many females arrive at the breeding site while it was still frozen, even though there appeared to be little food or nesting substrate available in the breeding marsh? Females may not be able to nest until some critical resource becomes available. They also may benefit from nesting synchronously with later-arriving females (Westneat, 1992). These factors would explain why females that happened to arrive early would wait before nesting, but they beg the question of why female red-winged blackbirds regularly arrive weeks to months before nesting.

In this population, males tend to feed only the offspring of first-hatched nests, which, as a result, grow faster and are more likely to survive than chicks receiving no male parental care (Patterson, 1991; but see Muldal et al., 1986; Whittingham, 1989). Males also defend first-hatched nests more aggressively than later nests (Knight and Temple, 1988). Thus, starting to lay eggs even one day earlier than other females in the same breeding group could increase a female's reproductive success. Although during the two years of this study there was no detectable reproductive advantage to early nesting, an earlier three-year study of this population showed that male assistance increased the output of females by 0.5–2.0 fledglings per nest. Thus, early nesting could have a selective advantage in years when early nests hatched first. Dominant females could enhance their fitness by even slightly delaying subordinates' nesting attempts (Yasukawa and Searcy, 1982). Such a mechanism is particularly plausible because dominant females in this population are most aggressive during the 2 weeks before they lay their first eggs (Cristol and Johnsen, 1994). The low overall nest success in 1990 and 1991 may have overshadowed benefits of early nesting or any advantage of first-hatched nests. In fact, for unknown reasons male feeding of any nestlings was very rare during the two years of this study (unpublished data).

One implication of the direct effect of arrival date on time of first egg in this population is that there could be a cross-seasonal interaction between selection for early arrival and migratory behavior. Like many passerines, red-winged blackbird populations in eastern North America exhibit differential migration, females migrating farther than males and arriving later in spring (Dolbeer, 1982; James et al., 1984). One proposed explanation for this phenomenon is that the selective pressure for early return to the breeding grounds between sexes results in one sex wintering farther north than the other (arrival-time hypothesis, Ketterson and Nolan, 1976; Myers, 1981). In this case, if early spring arrival were a more important correlate of fitness in males than in females, then males that wintered at more northerly latitudes might arrive earlier at breeding sites and achieve higher reproductive success than males from farther south. My results suggest that female red-winged blackbirds experience some selective pressure to return early to breeding sites to increase reproductive success. Yet males may have to arrive as soon as there is any chance of a rival male defending a territory, or perhaps forego the chance of producing young that year. Females, in contrast, are able to nest at their preferred sites even if they return late, so the intensity of selection for early arrival may differ between the sexes.

If females could always increase their social status and fitness by arriving and laying earlier, intrasexual competition for high social status might lead to directional selection for earlier female arrival. Laying date has been shown to have high heritability in some avian species (Findley and Cooke, 1982; van Noordwijk et al., 1981), so clearly there is potential in this system for selection to act on date of laying the first egg. It has been demonstrated theoretically, however, that even if early females have greater reproductive success, there will be no selection for early arrival if the relationship between laying date and reproductive success is the result of a correlation between these factors and a nonheritable variable such as nutritional status (Perrins, 1966; Price et al., 1988). Similarly, Westneat (1992) suggests that the correlation he found between early breeding and higher nesting success in red-winged blackbirds might be an artifact of covariation between breeding date, nesting success, and familiarity with the breeding site gained in previous seasons. Familiarity gained in previous seasons should be highly correlated with age, particularly in my study population where females are extremely site faithful (unpublished data). The results of the present study, which dissociated age from within-season prior residence, suggest that the latter is causally related to early nesting. Experimentally delayed females, with more years of previous experience than controls arriving on their release dates, did not nest earlier. Thus, older and experienced females still had to arrive early to nest earlier, perhaps because gaining prior residence was the surest way to increase social status.

Selection for early arrival should be expected if the reproductive advantages of early breeding result directly from early arrival through the mechanism of female dominance. Further experimental studies are needed to determine how female social status is related to laying date in this species. If arrival date determines social status, and status directly influences reproductive timing and success, then competition to attain the highest social rank within each breeding group might be a mechanism for directional selection on arrival time in females. There could, of course, be strong counter selection against early arrival because of factors such as cold weather and lack of food. Other potential costs of early arrival could include: lost opportunities for fattening in the warmer wintering area, greater risk of facing snow storms during the migratory journey, increased exposure to predators on the breeding site before regrowth of protective wetland vegetation (including migratory raptors that are not present later), and intensified interspecific competition for food and roost sites from migratory birds that have overwintered at the breeding site.

For female red-winged blackbirds, differential reproductive success may hinge on social status within a female breeding group and resulting access to male parental assistance. Arriving earlier than other females within a breeding group can ensure higher social status. Further detailed studies of prenesting females are now needed to elaborate the mechanisms linking social status, timing of breeding, and reproductive success.

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