THE EVOLUTION OF FEMALE BODY SIZE IN RED-WINGED BLACKBIRDS: THE EFFECTS OF TIMING OF BREEDING, SOCIAL COMPETITION, AND REPRODUCTIVE ENERGETICS

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Abstract.—We examined opposing selective forces on female body size in the sexually dimorphic red-winged blackbird: social competition favoring larger females, and energetic advantages favoring smaller females. Downhower proposed that selection might drive female birds to be smaller than the optimum for survival, if smaller females were able to exceed their energetic requirements for self-maintenance earlier in the season and therefore breed earlier. Since in most birds the earliest breeders fledge the most young, this could favor the evolution of smaller female size, and therefore contribute to the magnitude of sexual size dimorphism in these birds. We tested this hypothesis in 1987 and 1988 by comparing the size and breeding date of female red-winged blackbirds. Consistent with our preditions, early-nesting females had much higher nesting success, but contrary to prediction, larger females bred earlier. We then examined the effects of female size on competition. If large females have an advantage in social competition, and if competition influences breeding date and reproductive success, then larger females might breed earlier. Primary females, the first females to arrive and nest on a territory, were more aggressive than lower ranked females; more aggressive females settled on better territories and laid earlier than less aggressive females; and larger females were more aggressive. Social competition between females may therefore favor large females. Finally, we tested the prediction that selection favoring large females might be limited by energetic constraints on large females. We found that large females had less fat than small females during breeding, and that the levels of fat that females of a given size carried affected breeding date and egg size. Therefore, social competition may favor large females, but reproductive energetics favoring smaller females may constrain selection for large female body size.

We examined opposing forces of selection on body size in female red-winged blackbirds (*Agelaius phoeniceus*), first testing Downhower's hypothesis that smaller females are able to breed earlier for energetic reasons and therefore have a selective advantage (Downhower, 1976; Price, 1984*b*). In contrast to previous tests of this hypothesis, we found that larger, rather than smaller, female redwings bred earlier. We then considered the possibility that selection for advantages in social competition might favor large females and enable them to breed earlier, and analyzed the effects of body size on female aggression and reproductive success. In an effort to identify opposing selective forces that might counteract selection for large females, we analyzed energetic constraints on female body size. This is the first study to date to identify opposing directional forces of selection on female body size in birds.

Downhower's Hypothesis

Downhower (1976) argued that selection should drive females to be smaller than the optimum for survival, if smaller females are able to breed earlier and therefore have a higher reproductive success than larger females. He reasoned that if energy is limited early in the season, then smaller females should be able to satisfy their energetic requirements for self-maintenance earlier in the season and begin to shunt calories into reproduction before larger females. The hypothesis contains several assumptions. First, it requires that there is variance in breeding date, and that breeding date is energy-limited. Second, the hypothesis assumes that early breeding is advantageous, either because it increases the probability of offspring survival or raises the potential for renesting. Finally, the hypothesis assumes that females are producing eggs from food eaten on the breeding grounds, rather than from reserves accumulated elsewhere.

We tested Downhower's hypothesis on female red-winged blackbirds, a sexually dimorphic species which seemed likely to fulfill the assumptions of the hypothesis. Female redwings vary in their timing of breeding: initiation of first nests occurs over

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at least a five-week period each year. Early breeding is advantageous for most passerines (Perrins, 1970); we tested this assumption specifically for redwing females with data from our study population. Experiments demonstrating that supplemental feeding of redwing females advances timing of breeding significantly (Ewald and Rohwer, 1982; Wimberger, 1988) show that their breeding is energy limited, and that females are producing eggs from energy gathered at the breeding grounds.

Female Competition

Social competition may also affect the evolution of body size in females, driving body size larger than the survival optimum. Competition among females may evolve in a polygynous mating system, if competition allows some females to reduce costs of polygyny, thereby increasing their reproductive success. A major cost of polygyny to female redwings may be competition for resources, such as food and non-sharable male parental care. Females of western populations of redwings feed themselves and their young with food gathered from the territory, which they supplement with food from off the territory (Orians, 1980). In eastern populations, the males feed the young, and preferentially feed the young of the primary female (the first female to settle and nest on the territory; Yasukawa and Searcy, 1982), although in western populations, the males feed the young very little. Other forms of male parental care, such as defense of the young, may also be partially non-sharable, since redwing males defend nests of primary females more vigorously than they defend nests of their other females (Knight and Temple, 1988).

Females may reduce competition for these resources by preventing or delaying the settlement or nesting of additional females (Yasukawa and Searcy, 1981), and so females may gain reproductive benefits from aggression. Resident females are very aggressive towards both nonresident and resident females (Nero and Emlen, 1951; Nero, 1956; Hurly and Robertson, 1984; Searcy, 1986; Searcy, 1988; Roberts and Searcy, 1988). Dominant females may be able to settle and lay first, and therefore may be able to choose the best territories, males, and

nest sites. Aggressive females could potentially limit the numbers of females settling onto their territories, delay the nesting of subordinates, and decrease pressure on food resources during nesting. If aggressive females do better, and large females have an advantage in aggressive competition, then selection for increased female body size might drive females to be larger than the optimum based on energetic considerations.

We analyzed female competition first by examining female settlement patterns. We predicted that if there are advantages to being a primary female, then most territories should get one female before any territories get additional females. Alternatively, if primary status did not confer important benefits, then settlement should be random. We next predicted that if female aggression could delay or prevent additional settlement, then secondary females should begin to settle after primary female aggression levels begin to decline. We examined evidence that primary females became less aggressive after they began to nest, and that secondary females settled after primary females began to nest.

We measure aggression by recording responses to mount presentations of conspecific females (LaPrade and Graves, 1982; Yasukawa and Searcy, 1982; Searcy, 1988). We defined female rank as the order of settlement onto the territory, so that the first female to settle had the highest rank, and was the primary female. Nest rank was the order of nest initiation on the territory, so that the first nest on a territory had the highest rank (rank = 1). We tested several predictions about female aggression:

a. Nest rank and reproductive success: If female aggression has an adaptive basis, there should be reproductive benefits in competition. Since it is possible to obtain failure and nest rank data on large numbers of nests over several years, we tested the prediction that rank affects reproductive success by comparing the probability of nest failure and nest rank: did higher-ranked nests have lower probabilities of failure?

b. Female rank and aggression: If female rank affects reproductive success, and if

females compete for the highest rank, then primary females should be more willing to escalate contests, and therefore should be more aggressive towards mounts than lower-ranked females.

c. Female body size and aggression: If body size is an advantage in social competition, larger females should be more willing to escalate than smaller females, and therefore should show more aggression towards the mount.

d. Female aggression and reproductive success: If female aggression has an adaptive basis, then it should confer reproductive benefits on females. More aggressive females should get better breeding situations than less aggressive females, and should breed earlier in the season.

Reproductive Energetics

To analyze potential reproductive energetic contraints on female size, we measured fat and protein levels of females in three stages of reproduction: pre-laying, post-laying, and post-incubating. We predicted that if large body size placed a female at an energetic disadvantage during reproduction, then large and small females might show different patterns of nutrient storage and loss during egg-formation, egg-laying, or incubation.

Few studies have examined passerine nutrient requirements for reproduction (Ankney and Scott, 1980, Brown-headed Cowbirds; Jones and Ward, 1976, Red-billed Queleas; and Krementz and Ankney, 1988, House Sparrows), so it was not known if redwing females using body reserves of fat or protein for egg production. Therefore, we first asked if females deplete stored fat or protein during egg laying or incubation. We then asked if a female's reserves of fat affect her clutch size, egg size, or breeding date. Finally, we asked if female body size affects nutrient reserves during reproduction.

METHODS

All of our field work was done along the Winchester Wasteway in Grant County, Washington (47.1°N, 119.5°W).

Downhower's Hypothesis

In 1987, we collected 30 females nesting in one large marsh to assess the effects of body size on breeding date. The marsh was checked for nests every four days. When a nest was found with three or fewer eggs, we returned to check the nest every day until the clutch was complete (the same number of eggs on two consecutive days). The female was shot on this day, the day after the last egg was laid. First egg date (timing of breeding) was calculated by subtracting the number of eggs in the nest, less one, from the date on which the nest was found. All dates were converted to Julian dates for ease in analysis. We measured female mass to the nearest 0.5 gm with a 100 gm Pesola scale, and froze the carcasses for later analysis. We collected the eggs, measured egg length and width to the nearest 0.1 mm with vernier calipers and calculated egg volume (volume = 0.498 length × width^2; Spaw and Rohwer, 1987). We measured wing-chord and tarsus (from the bent ankle to the toes) to the nearest 0.5 mm with a 100 mm wing-chord ruler. We then prepared skeletal specimens from the carcasses, and took 13 bone measurements (measured as in Freeman and Jackson, 1990; listed in Table 1) with vernier calipers to the nearest 0.1 mm from each skeleton. With the exception of mass, NEL took all size measurements.

To estimate body size, we applied a principal component analysis with orthogonal rotation to the 13 bone measures (Robins and Schnell, 1971; Rohwer, 1972; Schluter, 1984; Rising, 1987; Rising and Somers, 1989; Freeman and Jackson, 1990). The first principal component (PC1) explained 79% of the variance in the 13 variables. Long bones, such as the humerus, ulna, and femur, loaded heavily onto PC1 (Table 1). Birds with large positive loadings were larger birds. We interpreted PC1 as a measure of structural size, and used the loadings from it to obtain a size score for each female. This measure of structural size correlated significantly with other traditional measures of size (Pearson Correlation Coefficients: wing-chord $r = 0.561$; tarsus $r = 0.471$; mass $r = 0.529$; $N = 30$). We also combined three external measures of size (wing, tarsus, and mass) in a principal component analysis without rotation to obtain an external estimate of size (loadings for PC1: wing = 0.43, tarsus = 0.56, mass = 0.45).

In 1988, we collected an additional 15

females for body size analysis from five marshes along the Winchester Wasteway. Treatment of these females differed slightly from the 1987 study since the females were also being used for the reproductive energetics study described below. Females were collected the day after laying their final egg (post-layers); we estimated first egg date as above. Mass, wing chord, and tarsus were measured as above. In the lab, three bones (femur, humerus, and ulna) which had loaded heavily onto PC1 in 1987 were dissected and measured, and the remainder of the carcass was set aside for energetics analyses (detailed below). Again, NEL took all size measurements. The internal bone measurements were combined in a principal component analysis to obtain an estimate of structural size; wing-chord, tarsus, and mass were combined in a principal component analysis to obtain an external estimate of size.

For a further comparison of external size measures and breeding date, we also used females that we decoy-trapped, measured, and released in the 1988 aggression experiments. We determined their breeding dates as above. Data from the two years were combined and analyzed after standardizing for differences in mean breeding date between the two years by adding three days to the 1987 Julian dates. Timing of breeding was regressed against the principal component scores for structural size, external size, and individual measures. The results from all the measures of size are reported to facilitate comparisons with studies where only one or two external measures of size are taken.

Age-effects would confound a comparison of size and timing of breeding, if larger birds were actually older birds. We controlled for this in two ways. First, we used bone measurements rather than wing-chord as our estimate of size, since bones do not increase after adulthood, although wing-chord measurements may. In addition, we excluded subadult females, thus controlling for much of the variance in size due to age. Second-year females, who are breeding for the first time, (hereafter called "subadult females") can be distinguished from adults because they usually lack the orange epaulets found on adult females. Payne (1969)

TABLE 1. Principal Component Analysis for 13 Bone Measures (1987). PC 1 and PC 2 show loadings onto each measure from the orthogonal solution. We interpret PC 1 as a measure of structural size.

Bone measure	PC 1	PC 2
Skull width	−0.229	0.77
Skull length	0.439	0.451
Sternum width	−0.367	0.654
Sternum length	0.574	0.307
Synsacrum width	0.423	0.396
Synsacrum length	0.617	−0.032
Coracoid	0.816	0.064
Humerus	0.908	−0.037
Ulna	0.933	−0.184
Femur	0.902	−0.146
Tibiotarsus	0.86	−0.088
Tarsometatarsus	0.848	−0.0059
Keel	0.237	0.539

found in a California population of redwings that 48 of 48 first-year females (aged by skull ossification) had no red or just a trace of red in the lesser marginal coverts of the upper surface of the wing, while 88 of 97 adult females had more than a trace of reddish coloration in these feathers. In a study of individually banded females in a population of redwings in Eastern Washington, Orians and Birks (unpubl. data) found that of 22 females lacking epaulets, 20 had been banded for the first time that year and were therefore likely to be subadults; while of 95 adult females (females recaptured at least one year after being first banded as adults, and therefore certain to be more than two years old), 93 had reddish epaulet coloration. Since age and experience may influence breeding date, we classified females lacking epaulets as subadults and analyzed their sizes and breeding dates separately.

Female red-winged blackbirds may renest if their first attempt fails. Inclusion of females attempting to nest for the second time in a test of Downhower's hypothesis would make it more difficult to see any effect of size on timing of laying. Since females were not banded, our only way to exclude renesting females from this analysis was to exclude the two adult females (one female in each year) who nested more than a week after all other females had initiated nests. Other renesting females are almost certainly included in the analysis.

Breeding Date, Nest Rank, and Nest Failure

To test whether timing of breeding or nest rank affects reproductive success, we analyzed nest records from a total of 1,321 red-winged blackbird nests during the breeding seasons of 1978 and 1986–1988. These nest records came from a total of 11 different marshes. Males on these marshes were individually color-banded. Male territories were mapped in 1986–1988 by placing grid markers at 10-meter intervals in the marshes and noting male display locations in relations to these markers on a map of each marsh. In 1978, nests were checked at least once a week during the breeding season, and in 1986–1988 nests were checked every three or four days. The contents of each nest were noted, and the location of the nest was mapped. Since the females that built these nests were unbanded, our data do not discriminate between first year and older females or distinguish first nest from renesting attempts.

We defined the start date of a nest as the date on which the first egg was laid. We considered a nest as failed if the contents disappeared before their earliest estimated fledging date. We considered a nest successful if feathered chicks were present at the nest check prior to finding the nest empty; in almost every instance we were able to confirm fledging by finding feather shafts and feces in the empty nest cup or newly fledged young nearby. Successful nests, then, were those from which at least one young fledged.

To determine whether females that nest earlier in the season have a higher probability of success than females that nest later, we grouped nest records from the four years by the 10-day interval in the season in which each nest was initiated. We defined the first day of the season as the date on which the first egg was laid in any of the nests studied in that year, unless this first nest was at least 10 days earlier than any other nest initiated that year, in which case the second nest started was used to mark the commencement of nesting. In each breeding interval, then, we compared the number of nests that failed with the total number of nests initiated in that breeding interval for all years combined.

To assess whether time in the season affects probability of nest failure, we used a logistic regression model, which is appropriate for the analysis of binomial data (such as number of nest failures compared to number of nest attempts) with unequal sample sizes and variances. The equation for the logistic regression can be expressed in two equivalent forms either as

$$Y = \frac{e(\text{grand mean} + \text{slope X})}{1 - e(\text{grand mean} + \text{slope X})},$$

where Y = the probability of nest failure, or as log (probability of failure/probability of success) = grand mean + slope X. We report the equations in the second form, since they more closely resemble the standard regression equations.

To assess whether nest rank affects probability of nest failure, we grouped the nests from 1986–1988 by the order in which they were initiated on a male's territory, so that the first nest to be initiated on a territory was assigned rank = one. We could confidently assign rank to 895 nests; rank varied from one to nine. We used a logistic regression to compare nest rank and the probability of nest failure. To examine the effects of nest rank independently of any effect of breeding date, we used a logistic multiple regression model to evaluate these data.

FEMALE COMPETITION

Female Settlement Patterns

To test whether female settlement onto male territories is random, we recorded settlement dates of females on six marshes, which had from 8 to 18 male territories. Since females land on territories and are chased off by males for some time before settlement, we considered that a female was settled when we observed her perched on a male's territory, and when a male ceased to chase her off the territory. In addition, if a female sang on a territory, we considered her settled. In the analysis, we compared the dates of primary settlement with the dates of secondary female settlement both within individual marshes and between all six marshes. To test whether females bred in the order they settled, we caught 33 females at six marshes in grain and decoy traps as soon as possible after they ar-

rived and individually color-banded them. Marshes were searched for nests every four days, and the progress of the nests was followed as above. Once each nest was found, we observed the nest until we were sure of the identity of the female using the nest. In the analysis, we categorized females as either settling first on a male's territory or not, and either as laying first on a male's territory or not.

Mount Presentations

To quantify levels of aggression, we presented taxidermic mounts of female redwings to 100 females of different status. Female redwings respond aggressively to mounts of conspecific females (Yasukawa and Searcy, 1982). Mounts were placed on territories where females had been active within the preceding 15 minutes, and the height was adjusted so that the mounts were at the level of the cattail heads, where females perch. After placing the mount, the observer retreated at least 30 meters and watched through binoculars. We waited three minutes after leaving the marsh to allow the birds to stop alarm-calling before recording the response. If our disturbance flushed the female off the marsh, and she did not return by the beginning of the presentation, we did not include her in the analysis. We ran each mount presentation for 15 minutes, and made a continuous record of the female's behavior and position. Controls included both poles placed in the marsh without the mounts inserted (to control for our disturbance in the marsh) and mounts of Eastern Kingbirds (a species common in the marshes during redwing nesting towards which redwings rarely show aggression). No females were exposed to a mount more than once, to prevent habituation bias. All mount presentations were done within two hours after dawn, during the hours of greatest activity; we did not do mount presentations during rain or heavy winds.

In the analysis, nine variables from each mount presentation (listed in Table 2) were combined into a single score of aggression using a principal component analysis without rotation, based on a Spearman Rank Correlation Matrix. PC scores are given in Table 2. We interpret PC1 as a measure of aggression and use the loadings from this factor to calculate a measure of aggression for each female ("aggression score"). More aggressive females have larger positive loadings on PC1. These aggression scores correlate strongly with traditional individual measures of aggression (Spearman Correlations: number of pecks, $r = 0.81$; seconds spent on the mount $r = 0.867$; seconds to hit the mount $r = -0.88$; seconds spent within 0.5 m of the mount, $r = 0.91$; number of flying hits $r = 0.79$; $N = 103$). We used the principal component score as our measure of aggression, since there are a variety of correlated ways a female can aggressively respond to a mount. For example, one female might hit the mount often, but never peck it, while another female might peck often, while a third female might simply glance at the mount and resume foraging. If we only looked at one variable such as number of pecks, the female who pecked often would have a high aggression score, while the female who specialized on flying hits would have the same low score as the female who ignored the mount. By combining variables, both females that attack the mount get a higher score than a female who merely watches. Principal component analyses allow an unbiased and repeatable method of combining variables (Rohwer, 1978), which seems preferable to the alternative method of arbitrarily deciding that one hit is worth two pecks, and adding up the variables to obtain an aggression score for each female.

Settling Females Versus Nesting Females

To examine whether females become less aggressive once they begin to nest, we compared 41 primary females before nesting with 31 nesting primary females. The prenesting females were adults tested within one week after settlement before nests were constructed; the nesting females were adults tested two meters from their nest, after completion of the nest but before eggs had been laid.

Primary Versus Secondary

To compare the aggression of primary versus secondary females, we did two tests. First, we placed mounts two meters from the nests of both primary and secondary females, after completion of the nest but before eggs were laid. We compared females

only during the first round of nesting, before renesting attempts were initiated on the marsh. All these mount presentations were done within 10 days of each other to control for seasonal effects. These are not paired comparisons within male territories, so variance in territory quality may affect the results, although it is unlikely that this biases the results in support of the hypothesis. While this analysis controls for female position on the territory, point in the nesting cycle, and season, it unfortunately compares females during nesting, after aggression levels have already largely declined. Therefore, we also compared all primary females ($N = 57$) with all secondary females ($N = 16$), including both settling and nesting females in the analysis.

Aggression and Size

To test whether size affects aggression, we controlled for female status, time of the season, and time of the breeding cycle, by comparing only primary adult females tested after settlement but before nesting. These females were captured in grain traps, individually color-banded, measured, and released. External measures of size (wing chord, tarsus, and mass) were taken, rather than internal structural sizes, as we wished to follow these females throughout the season. To ask whether more aggressive females laid earlier in the season, we compared the breeding dates and aggression score of primary adult females.

Aggression and Reproductive Success

To examine whether more aggressive females got better breeding situations, we experimentally altered territory quality for females by setting out open-tray feeders stocked with sunflower seeds at marshes before females arrived. This supplemental food has two effects: it increases male display rates (Gori and Rohwer, unpubl.), and it is also a resource which females use (Ewald and Rohwer, 1982). Therefore, females might choose territories with supplemental food either because they were choosing on the basis of high male display rates, or because they were choosing on the basis of territory quality as judged by seed availability. Either way, supplemental territories represent a higher quality breeding situation than un-

TABLE 2. Principal Component Analysis of female behavior in response to presentations of taxidermic mounts, showing the loadings onto PC 1 for each variable.

Variable	Loading
Seconds to hit the mount	−0.937
Closest distance to the mount	−0.93
No. pecks on the mount	0.955
No. bill-up displays[1]	0.612
No. song spreads[1]	0.24
No. precopulatory displays[1]	−0.24
Seconds spent on the mount	0.955
Seconds spent within 0.5 m of the mount	0.91
No. hits from a flying position	0.94

[1] Female song spread, bill-up, and pre-copulatory displays described in Orians and Christman (1968).

supplemented territories. We compared the external size measurements (wing, tarsus, and tail, but not mass because supplemental feeding may increase mass) of fed and unfed females. The fed females for this sample were primary females we caught in grain traps; the unfed sample consisted of three primary females we managed to catch in decoy traps and the primary females we collected for the 1988 reproductive energetics experiments.

REPRODUCTIVE ENERGETICS

We collected 45 females during three stages of breeding: after the completion of the nest but before laying the first egg (prelaying); after laying the final egg (post-laying); and at the end of incubation (post-incubation). Females of each stage in the cycle were collected from five marshes, to control for marsh effects. Wing-chord, tarsus, mass, and eggs (if already laid) were measured as above, the feathers were plucked, and carcasses were frozen. In the lab, contents of the gut were removed, and the reproductive tract (ovary, developing follicles, oviduct, and contents of the oviduct) was removed and dried to constant mass. The femur, humerus, and ulna were dissected, measured, and combined into a single estimate of structural size as above. We divided females into two size categories based on the structural sizes. Females above the mean size were put into the "large" category; females beneath the mean were put into the "small" category.

TABLE 3. Regressions of breeding date on size; data from 1987 and 1988 combined. "Structural size" is the principal component score for bone measures, adults only. Breeding dates for the two years are standardized by adding three days to the 1987 dates so that the means for both years are equal.

Size measure	r	Sample size	P (2-tailed)
Structural size	−0.35	37	0.04
Wing	−0.59	61	0.0001
Tarsus	⌐0.25	61	0.06
Mass	−0.44	61	0.001

The remaining carcass was dried to constant weight at 80°C for five days, then ground with a mortar and pestle. Lipids were extracted for six hours in a Soxhlet apparatus using petroleum ether, which does not extract membrane lipids (Krementz and Ankney, 1988). Lipid mass was calculated by subtracting the mass of the lean dry carcass from the mass of the dry carcass. The lean dry carcass was then ashed in a muffle furnace at 500°C for five hours. After ashing, we calculated the percentage of the lean dry carcass that remained, which represented the nonorganic mineral content of the carcass. We subtracted this from the lean dry mass to obtain an index of protein (Krementz and Ankney, 1988).

Both the fat and protein measures represent nutrients available for reproduction, since they do not include fat or protein already put into reproduction in the form of the oviduct, developing follicles, or eggs (Krementz and Ankney, 1988).

RESULTS

Downhower's Hypothesis

Downhower's hypothesis predicts that smaller females should breed earlier, yet our results showed the opposite in both years. Larger adult females bred earlier. Adult females with larger structural size, longer wings and greater mass laid significantly earlier in the season, while adult females with larger tarsi tend to do, although the regression was not quite significant (Table 3). When we combined external measures of size into a single size variable, the results are highly significant (Fig. 3). The results are similar when each year is considered separately (data not shown).

Age may confound a comparison of size and timing of breeding, since adult females may be larger in external measures and breed earlier. We found that adult females do have longer wings and tails than subadult females, and do breed earlier (Table 4). Surprisingly, adult females had significantly smaller structural sizes than subadult females (Table 4). By excluding subadult females from our test of Downhower's hypothesis, and by using bone measures rather than external measures as an estimate of size, we have controlled for much of the variance in size due to age, which might confound the test. The variance in size due to differences in age that remains within our adult age-class data is probably minimal, since female mortality is quite high (40% a year in one population of redwings, Searcy and Yasakuwa, 1981).

Breeding Date, Nest Rank, and Nest Failure

Breeding date does significantly affect reproductive success. In a test with 1,325 nests from 10 marshes over four years, early nests have a lower probability of nest failure (Fig. 1, $P < 0.001$). We combined data from different marshes and years in the analysis, because the probability of failure varied

TABLE 4. Subadult females versus adult females: size and laydate. 1987 and 1988 data combined. Breeding dates are in Julian dates. Significance values are from two-tailed t-tests.

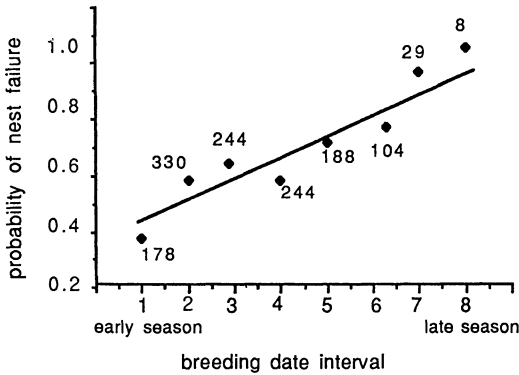| Variable	Adult		Subadult		P
	(N)	Mean ± SE	(N)	Mean ± SE	
Tarsus	(152)	30.4 ± 0.09	(24)	30.2 ± 0.198	0.5
Mass	(148)	48.5 ± 0.284	(24)	48.0 ± 0.5	0.6
Wing	(152)	105.0 ± 0.184	(24)	101.8 ± 0.323	0.0001
Structural size	(63)	−0.1 ± 0.128	(11)	0.6 ± 0.179	0.04
Breeding date	(85)	118.3 ± 0.72	(15)	122.9 ± 0.73	0.001

FIG. 1. Regression of the probability of nest failure on breeding date. The logistic regression equation is: Log (probability of failure/probability of success) = $-0.56 + 0.28X$; $P < 0.001$; $df = 7$; this regression is based on 1,325 nest records. Breeding date interval is explained in the methods. Sample sizes for each breeding interval are next to each data point.
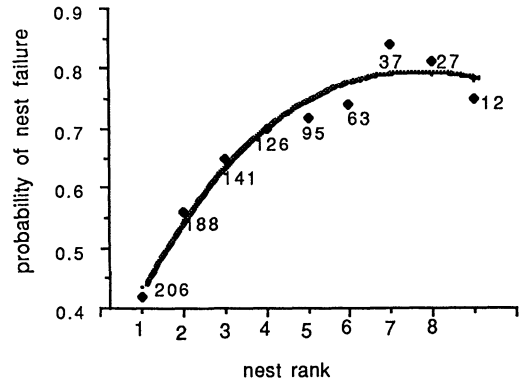
FIG. 2. Regression of the probability of nest failure on nest rank. Nest rank is the order a nest appeared on a male's territory; rank 1 is the first nest to appear. The polynomial logistic regression equation is: log (prob. success/prob. failure) = $-0.77 + 0.55X - 0.04X^2$. Rank $P < 0.001$; rank^2 $P < 0.025$; $df = 8$; this regression is based on 895 nest records. Sample sizes for each nest rank category are next to each data point.

enormously between marshes in any given year, and between years for any given marsh, so that we could not detect a "marsh" or "year effect." Overall, nest failure was 59% but varied from 21% to 93%. In a single marsh over a three-year period, nest failure varied from 35% to 93%. Almost all failure seemed due to predation, and the increase in failure with season was probably due to increased predation pressure by snakes, mice, magpies, marsh wrens, and ravens. Overall, there was great stochastic variation in nest success.

Nest rank on the territory has a strong effect on reproductive success (Fig. 2, $P < 0.001$). The first nests on a territory have a lower probability of failure than later nests. The regression of nest rank against nest failure has a significant polynomial effect, suggesting that the effects of rank are most pronounced for the first nests, and then drop off. For example, the difference between the first and second nest on a territory is greater than the difference between the fourth and fifth nest. Furthermore, both the linear and quadratic effects of nest rank remain significant when the effect of breeding date is controlled in a multiple regression (Table 5). Therefore, highly ranked females have a higher probability of nest success not just because they tend to breed earlier, but because of additional factors related to female rank.

Female Settlement and Aggression

In this population of redwings, as in Teather et al.'s study population (1988), females that settled first on a male's territory tended to be the first to lay eggs on that territory. Out of 19 primary females, 18 were the first to lay on the territory; while out of 14 nonprimary females, only one was the first to lay on her territory (Fisher exact test, $P < 0.001$).

Female settlement onto male territories is not random in relation to other females. For all six marshes considered individually, one female settled onto each male territory before any territory received a second female. In addition, when we pool the six marshes, one female settled onto each territory before a second female settled onto any territory on all of the six marshes, which is clearly not random (Poisson distribution, $N = 74$, $X^2 = 127.2$, $P < 0.001$). Primary females settled, on the average, 29 days earlier than secondary females (primary female settlement Julian date: 73.1 ± 0.3, secondary female: 101.9 ± 0.3; 2-tailed t-test, $P = 0.0001$). Secondary females settled almost exactly when primary females began nesting (Julian date = 102). This pattern may be due to aggression by primary females, since when primary females began to nest, their levels of aggression dropped (aggression scores: pre-nesting females 0.37
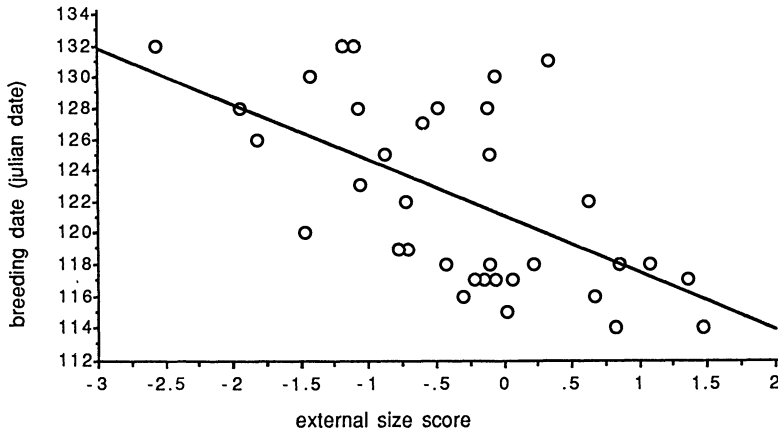
FIG. 3. Regression of breeding date versus external size score (PC analysis of wing, tarsus, and mass). Data from 1987 and 1988 combined. Adult females only. $r = -0.57$, $Y = -3.6X + 121.1$; $df = 52$; $P = 0.0001$.

$\pm$ 0.13, nesting females -0.18 ± 0.13; 2-tailed t-test, $P = 0.004$).

The aggression scores of control females presented with poles and Eastern Kingbird mounts were significantly lower than aggression scores of females presented with female redwing mounts (aggression scores: poles -0.82 ± 0.06; kingbird mounts -0.85 ± 0.05; female redwing mounts 0.43 ± 0.13; ANOVA $F = 22.1$, total $df = 57$, $P < 0.001$).

Nesting primary adult females were significantly more aggressive at their nests than were secondary adult females at their nests (Table 6). While this analysis controls for female position on the territory, point in the nesting cycle, and season, it compares females during nesting, after aggression levels have already largely declined. Therefore, we did a second test, in which we included both settling and nesting females, with the result that primary females were far more aggressive than secondary females (Table 6). This test does not control for factors that may be affecting aggression (such as the presence of absence of a nest), but it does more accurately reflect the natural situation, in which primary females spent a great deal of time before nesting showing aggression towards female intruders, while secondary females settled later and rapidly began nesting without ever showing much aggression.

Larger females were more aggressive (Table 7). Females with longer wings, tarsi, and exernal size scores had higher aggression scores, although mass did not correlate with aggression. Females did seem to compete for the best breeding situations. Females that settled at territories with feeders were larger, and spent more time attacking the mount and hit the mount more often than unfed females (Table 8).

Aggression seemed to affect when a female bred. More aggressive primary adult females bred earlier in the season than less aggressive primary adult females (Fig. 4). Since more aggressive females were also larger, and larger females bred earlier, we asked whether more aggressive females bred earlier only as a function of size, rather than aggression. Controlling for size by using the residuals of the regression of aggression on wing-chord, we still found that more aggressive females bred earlier ($r^2 = 0.26$, $Y = -6.2X + 116.7$, $P = 0.048$).

Reproductive Energetics

Females significantly depleted both fat and protein during laying. They regained fat

TABLE 5   Multiple Regression of Probability of Nest Failure on Rank and Breeding Date. Logistic Regression Equation: Log(prob failure/prob success) $= -0.97 + 0.39$ nest rank -0.03 nest rank$^2 + 0.19$ lay date. $df = 33$; 895 observations.

Variable	Coeff	SE	P
Grand mean	−0.97	0.23	<0.001
Rank	0.39	0.14	0.004
Rank^2	−0.03	0.02	0.04
Date	0.19	0.07	0.004

TABLE 6. Comparisons of primary females and secondary females: aggression at the nest, external size (from PC analysis of tarsus, wing, and mass), and breeding date. Sample sizes differ for tests because the size and breeding date comparisons include females to which mounts were not presented. Significance values are from two-tailed *t*-tests, adults only.

| | Primary female | | Secondary female | | |
Variable	(N)	Mean ± SE	(N)	Mean ± SE	P
Nesting female aggression score	(16)	0.1 ± 0.2	(15)	−0.4 ± 0.1	0.05
Settling and nesting female aggression score	(57)	0.3 ± 0.1	(16)	−0.53 ± 0.1	0.0004
Wingchord (mm)	(14)	107.2 ± 0.7	(30)	105.1 ± 0.5	0.03
Mass (gm)[1]	(14)	49.1 ± 0.7	(25)	46.8 ± 0.6	0.02
External size score[1]	(14)	0.64 ± 0.3	(25)	−0.1 ± 0.21	0.04
Breeding date (Julian)	(14)	110.0 ± 1.8	(30)	119.0 ± 1.7	0.003

[1] Excludes five females with mass > 54 gm whose masses are elevated because of egg formation.

during incubation, but did not regain protein (Fig. 5).

Relative amounts of fat reserves also affected breeding date and egg size. When controlled for size, females with more fat bred earlier (Pearson correlation $r = -0.67$, $N = 17$, $P = 0.002$). Again, controlling for size, fatter females laid bigger eggs (Pearson correlation $r = 0.87$, $N = 8$, $P = 0.02$). Females that bred early in the season laid smaller eggs (Pearson correlation, $r = 0.37$, $N = 23$, $P = 0.05$).

The amount of fat and protein on a female significantly varies with female body size. As expected, large females have more protein than small females (protein index: large females $9.6 ± 0.1$, small females $9.3 ± 0.1$; 2-tailed *t*-test, $P = 0.04$). Surprisingly, large females have fewer grams of fat, and a smaller percentage of body fat, than small females during pre-laying, post-laying, and post-incubation periods (Fig. 6).

DISCUSSION

Downhower's Hypothesis

Previous tests of Downhower's hypothesis have largely supported the hypothesis. Perrins' work on the great tits (*Parus major*) shows that over many years, smaller females generally lay earlier (Perrins, 1979). Price (1984a) found that female Darwin's finches (*Geospiza fortis*) with smaller bills bred earlier in one particularly severe year, although not in the majority of years. Järvinen and Väisänen (1984) showed that in good years, larger female pied flycatchers (*Ficedula hypoleuca*) laid earlier, while in poor years there was no effect of size on breeding date. Murphy (1986) found that

lighter female eastern kingbirds (*Tyrannus tyrannus*) laid earlier, and females with smaller internal structural sizes tended to lay earlier.

We found the opposite in red-winged blackbirds: larger females bred earlier in two years. Since early breeders have a far higher probability of nesting success, selection should favor early breeding. Why then do larger, rather than smaller, female redwings tend to lay earlier in our study population? The observation that female redwings are very aggressive towards each other suggests that competition among females may affect female size and breeding. Larger females might be able to lay earlier if females compete for breeding resources or males, and if larger females are favored in social competition. Smaller females may indeed have a metabolic advantage, but the effects of female competition favoring larger female redwings may override this advantage in this polygynous species.

Female Competition

In six marshes, all territories got one female before a second female settled at any territory. This extreme pattern of settle-

TABLE 7. Correlation of Aggression Score and Size, Pearson Correlations. Females tested include only fed, primary, adult females tested within one week after settlement. $N = 18$.

Size measure	r	P
Wing	0.58	0.01
Tarsus	0.50	0.03
Mass	0.01	0.95
External size	0.44	0.056

TABLE 8. Comparisons of fed and unfed females: size and aggression, adults only, 2-tailed t-tests.

Variable	Fed females		Unfed females		P
	(N)	Mean ± SE	(N)	Mean ± SE	
Seconds on mount	(12)	295.2 ± 62	(26)	129.4 ± 37	0.02
No. pecks	(12)	99.0 ± 28	(26)	45.0 ± 12	0.04
Wing	(34)	106.7 ± 0.4	(54)	104.7 ± 0.26	0.0001
Tarsus	(34)	30.9 ± 0.1	(54)	30.5 ± 0.12	0.026

ment may result from several possibilities. Settling females may be choosing to settle as primaries before settling as secondaries, or the aggression of primary females may delay the settlement of additional females. A third possibility is that if mated males sing less than unmated males, the nonsettling of females on territories where a male already has a mate may be a result of decreased singing, and hence decreased attractiveness to the settling female. Secondary female settlement began during the same week that primary females began nesting, when primary female aggression dropped sharply, which suggests that primary female aggression may have been delaying secondary female settlement. The settlement pattern suggests that it is preferable to be a primary female.

We found that primary females were more aggressive than secondary females. If females are competing to be primary females, then the most aggressive females should do best in the competition and settle first as primary females. There is an alternative explanation for this result: primary females may be not be intrinsically more aggressive, but females may adjust their levels of aggression to suit their rank. One could test this by removing primary females from territories after secondaries have settled. If the ex-secondaries (now raised to the rank of primary females) increased their levels of aggression to the primary level, this would imply that levels of aggression are not intrinsic, and that females may not be competing to be the primary female. However, our findings that primary females are larger than other females, and that larger primary females are more aggressive than smaller females, suggests that females do compete to be primary, and that larger females have an advantage in competition.

Competition may exist between females,

but unless we can show that it has reproductive advantages (Searcy, 1988), there is no reason to expect that selection for advantages in competition would act on female size. Rather than attempt to establish direct correlations between aggression and nesting success, we have several indirect measures that support the hypothesis that female competition is adaptive in redwings. First, more aggressive females (controlling for the effects of body size) laid earlier in the season, and females that laid earlier had a higher probability of nest success. Second, females settling at territories with supplemental food were more aggressive than unfed females. Finally, nest rank strongly predicts nest success, and aggressive females tend to initiate the first nests on a male's territory.

The result that fed females were more aggressive than unfed females could support either of two hypotheses. There may be competition for these food-supplemented territories, and more-aggressive females may fare better in the competition and therefore be able to settle at the better territories. Alternatively, the supplemental food may raise the levels of aggression after females have already settled, implying that females at food-supplemented territories might not have been any more aggressive than unfed females before they settled. One way to test this possibility is to put out feeders before primary females have settled, let the primary females settle, and then close half the feeders. If primary females were more aggressive only because of the presence of food, primary females whose food was withdrawn would be less aggressive than primary females whose food remained. However, if primary females had been able to settle at fed territories because they were more aggressive, then feeder-withdrawn primary females should still be as aggressive as the fed
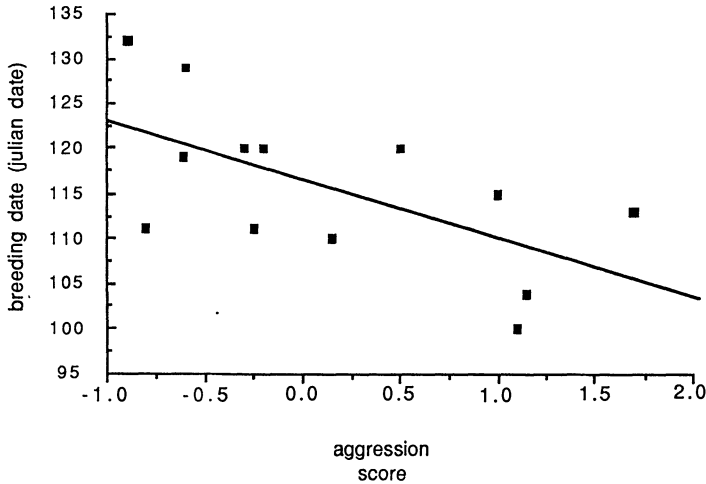
FIG. 4. Regression of the effects of aggression on breeding date. The linear regression equation is: $Y = 116.6 - 6.6X$; $r^2 = 0.38$, $P = 0.01$, $df = 11$.

primary females. Primary females that settled at fed territories were larger (in wing and tarsus) than unfed primary females, suggesting that there was female competition for the best breeding situations, and that larger, more aggressive females fared better in this competition.

Finally, the strongest argument that female competition may affect reproductive success comes from the nest rank and failure data. Nest rank has a very pronounced effect on the probability of failure, and primary females usually own the first nests. Part of this effect is due to timing of breeding: the

first nests on the territory tend to be built early in the year. However, the multiple regression of rank and timing of breeding on failure shows that the effects of nest rank remain significant even when the effects of date are controlled. Therefore, highly ranked females have a higher probability of nest success not just because they tend to breed earlier, but because of additional factors that may be related to female quality, male parental care, or greater freedom in the choice of nest sites. Even though males in this population of redwings rarely feed the young, they do offer parental care in the form of
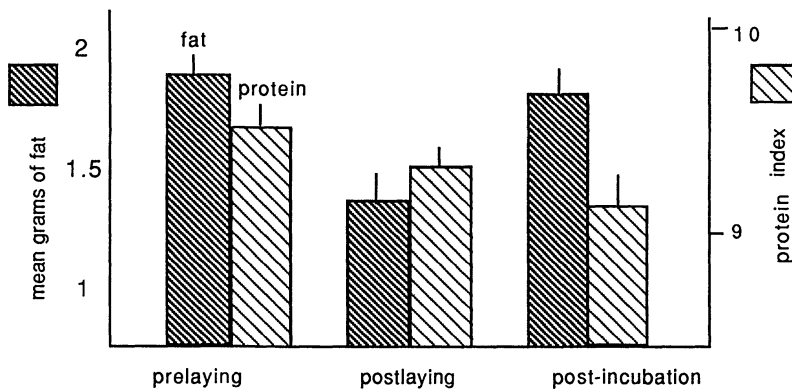

FIG. 5. Fat and protein depletion during laying and incubation. Each category of reproductive stage contains 15 females; total $N = 45$. The protein index is the lean dry weight of the carcass minus the percentage of mineral ash. Fat: ANOVA $P = 0.04$; prelaying versus post-incubating NS; other comparisons significant. Protein index: ANOVA $P = 0.04$; prelaying versus post-incubating significant; other comparisons NS.
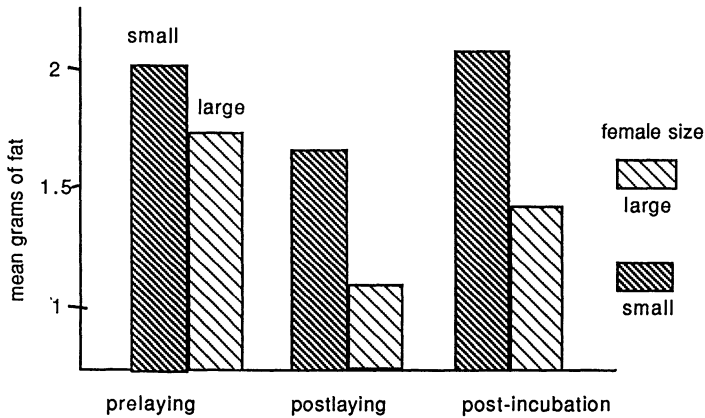
FIG. 6. The effect of female structural size on fat levels during reproduction. Each category of reproductive stage contains 15 females; total $N = 45$. 2-factor ANOVA: size, $P = 0.004$; reproductive stage, $P = 0.04$.

protection from predators, and Knight and Temple (1988) have shown that redwing males preferentially protect the young of primary females.

Several studies have found evidence of female competition in polygynous birds. Female aggression has been shown in dunnocks (Davies, 1985), marsh wrens (Leonard and Picman, 1987) and yellow-headed blackbirds (Lightbody and Weatherhead, 1987), in addition to female redwings. Support for an adaptive basis for female competition in redwings was found by Hurly and Robertson (1985), whose removal experiments suggested that redwing female aggression may limit the number of additional females settling onto a territory. Yasukawa and Searcy (1982) also found that primary female redwings were more aggreessive than secondary females, and that more-aggressive females were more likely to receive male parental care. Roberts and Searcy (1988) found that priniary females tended to be dominant within a harem, although age or size did not predict dominance relationships. However, Searcy was not able to find any adaptive basis for female aggression in eastern redwing females (1988). He found no correlations between levels of female redwing aggression and harem size, inter-nest distance, or number of young fledged.

Our results may differ from Searcy's because of differences between our study populations. In addition, we have used different indices of aggression and reproductive suc-cess. Instead of directly comparing aggression and nest failure for a given female, we did a two step process: for samples of 10 to 40 females, we assessed the effects of aggression on timing of breeding and nest rank. For larger samples, of 895 to 1,321 females, we then assessed the effects of timing of breeding and rank on nest failure. Although this method is indirect, it may be preferable to directly examining correlations between scores on mount presents and annual nest success. Since nest success has an extremely large stochastic variation, one needs enormous sample sizes to statistically assess the effects of any variable on nesting success, and the probability of committing Type II statistical error is quite high. However, since timing of breeding and rank are less susceptible to random variations, we can assess the effects of aggression on timing of breeding or rank with sample sizes that are reasonable for behavioral experiments.

Reproductive Energetics and Female Size

Since more aggressive females have higher status, are larger, lay earlier, and may get better breeding situations, selection for social competition should favor larger, more aggressive females. In that case, what constrains female body size? We tested the hypothesis that energetic constraints might limit the advantages of increased female size, if reproduction places increased energetic demands on large females.

Our most surprising result regarding re-

productive energetics is that large females had less fat than small females during reproduction. These results suggest that larger females may be unable to maintain themselves in good condition for laying. Alternatively, females of different sizes may have different reproductive strategies, which may affect the fat stores they need for reproduction. In other words, the low levels of fat that large females carry may not represent a constraint, but an alternative strategy. However, our analyses suggest that even small differences in fat levels may affect female redwing reproductive success. Since egg size and timing of breeding are positively correlate with fat for females of a given size, lower levels of fat may represent a direct within-season constraint. Larger females may do better in social competition, but their physiological ability to breed early may be limited by increasing body size. The observation that females breeding early lay smaller eggs also suggests an energetic constraint on female size during the breeding season. Finally, low levels of fat may also affect survival in large females, since adult females were smaller in structural size than birds breeding for the first time, suggesting that natural selection may be operating against large females after their first breeding attempt.

There appear to be at least two opposing forces of selection on female redwing body size: social competition favoring large size, and reproductive energetic constraints favoring small females. However, we cannot yet say if these forces represent stabilizing selection on female size, for two reasons. First, we have not measured the magnitude of either selective force. More importantly, there may well be other forces acting on female size which we have not yet identified. These results point to the importance of examining selection on female size as well as male size when considering sexual size dimorphism.

ACKNOWLEDGMENTS

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