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Author(s): Kevin E. Omland and Thomas W. Sherry

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PARENTAL CARE AT NESTS OF TWO AGE CLASSES OF MALE AMERICAN REDSTART: IMPLICATIONS FOR FEMALE MATE CHOICE¹

KEVIN E. OMLAND

Department of Biology, State University of New York–Albany, Albany, NY 12222

THOMAS W. SHERRY

*Department of Ecology, Evolution and Organismal Biology, Tulane University,
310 Dinwiddie Hall, New Orleans, LA 70118*

Abstract. We compared food provisioning at nests of two age classes of male American Redstarts (*Setophaga ruticilla*). Older male redstarts are more likely to obtain a mate than yearling males. We hypothesized that females actively choose older males as mates because of direct benefits due to increased rates of nestling provisioning. Lack of foraging experience or low food availability on their territories might cause yearling males and their mates to deliver less food to their nestlings. Our results did not support this hypothesis. Nestling provisioning rates did not differ between nests of yearling and older males in number of feeding trips per hour, average load size, estimated mass delivered per hour, nor prey taxa. Direct benefits to the female (at least with regard to nestling provisioning) do not explain why older male redstarts are more likely to obtain a mate. We discuss alternative hypotheses that might explain the lower mating success of yearling male redstarts.

Key words: *Parental care; mate choice; delayed plumage maturation; nestling provisioning.*

INTRODUCTION

Most recent literature on female mate choice has focused on species in which the male contributes only genes to his offspring (e.g., Bradbury and Andersson 1987). However, in species in which the male contributes resources, such as parental care and a territory, females should pay more attention to these direct benefits (Trivers 1972). Studies in numerous taxa show that females do choose males based on such attributes as courtship feeding load and territory quality (reviewed in Halliday 1983). In passerine birds, female Great Tits (*Parus major*) may use stripe size as an indicator of male parental care (Norris 1990). Lemon et al. (1992) showed that among adult male American Redstarts, females tended to choose males with smaller bills, which had higher reproductive success probably due to male parental quality. In addition, females of several species have been shown to choose males based on territory quality (e.g., Searcy 1979, Alatalo et al. 1986).

We studied a species of wood warbler, American Redstarts, in which there is a strong skew in age-specific mating success. We hypothesized

that female redstarts may actively choose older males because mating with an older male would increase their reproductive success. Older male American Redstarts are much more likely to obtain a mate than yearling males, as shown by Morris and Lemon (1988). They also suggested older males might be more attentive than yearlings. At our study site, from 1981 to 1989 nearly all (>95%) older males mated, but only about half of the yearling males paired. Systematic mist-netting confirmed that few males of either age class go undetected (T. W. Sherry, pers. observ.). Most male-removal studies done on birds indicate that male parental care improves at least some measures of female reproductive success (reviewed in Wolf et al. 1988). A female redstart that chooses an older male may thereby increase her fitness if he provides her offspring with more care, or if his territory has more food available.

Yearling male redstarts exhibit delayed plumage maturation (Rohwer et al. 1983). Older males have jet black feathers with bright orange patches on their flanks, wings and tails. Females have olive-grey plumage with yellow patches in the same areas. Yearling males are similar to the females, except that most have small patches of black feathers on their heads and throats that distinguish them from females (Rohwer et al.

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1983). Female redstarts could use plumage as a cue to choose adult males, or could choose based on more direct indicators of male and territory quality.

Low food availability or lack of foraging experience may constrain the amount of food yearling males and their mates deliver to their nests. Several lines of evidence suggest that yearling male redstarts may hold lower quality territories. First, older males exclude yearling males from mutually preferred territories (Sherry and Holmes 1989). Second, older males arrive on the breeding grounds earlier than yearlings (Procter-Gray and Holmes 1981, Francis and Cooke 1986, Morris and Lemon 1988) and settle preferentially in deciduous forest, whereas yearlings arrive just before or at the same time as females and are more likely to settle in mixed deciduous-coniferous forests (Sherry and Holmes, unpubl. manuscript). Third, older males are less likely to settle in the presence of Least Flycatchers (*Empidonax minimus*), which are behaviorally dominant to redstarts and compete for the same types of food, so yearlings that are apparently constrained to settle with them are at a disadvantage (Sherry and Holmes 1988). Lack of foraging experience may also constrain younger redstarts, as has been shown in several passerine species (Grant 1986, Desrochers 1992). Yearling males may make fewer feeding trips, deliver less prey mass, and overall make less of a relative contribution than older males.

Although the aim of this project was to document the effects of male age on provisioning rates, we also expected to find direct and indirect effects of male provisioning on the provisioning behavior of females. If food were more limiting on territories of yearlings than older males, this scarcity would directly lower both male and female provisioning rates. If on the other hand, yearling males were poor foragers relative to adult males, we might expect females paired with yearlings to provision at the same rate as adult paired females, or for females mated to yearlings to increase their provisioning rates in response to their mate's behavior.

METHODS

We conducted this study in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, U.S.A. (44°57'N, 71°44'W) during the summers of 1988 and 1989. See Sherry and Holmes (1985) for a description of the study site.

When yearling males were particularly female-like, we color banded at least one member of the pair to facilitate rapid identification of the sexes at the nest. (We color banded 58% of the males and 32% of the females in this study.) We located nests by following parents, usually during nest building, and monitored nests subsequently to establish clutch size, hatching date, nest fate, number of nestlings, and fledging date.

We observed provisioning behavior at nests with video cameras (Panasonic AG-450 Camcorders) and directly from blinds using a spotting scope. In 1989 all nests lower than five meters (8 of 18) were videotaped. The spotting scope was used at the remaining higher nests in 1989, and at all nests in 1988. We recorded the frequency of feeding trips to the nest by both the male and the female, and where possible the length and type of prey delivered. Prey were identified to order whenever possible.

We then converted lengths of individual prey or prey loads to mass estimates for two different situations. First, for videotaped observations, we stopped the tape to measure prey and bill length on the screen, converted prey length to absolute length using average exposed bill length (10 mm) as a standard, then converted to dry mass directly using mass-length regressions specific to order (R. T. Holmes and J. Schultz, pers. comm.; Schoener 1980). Whenever loads contained more than one item we summed individual prey masses to obtain total load mass. Second, for observations conducted directly from blinds, we estimated prey length, again using exposed beak length as a reference. We then assigned prey to one of five size classes we had established based on the mass-length regressions, and converted to mass by using the mean mass for that size class (Table 1).

When using either the video camera or the spotting scope, about 50% of all prey loads consisted of one or more small prey items that we could not individually distinguish and/or identify. We estimated the size and number of prey items such small loads contained, then established qualitative criteria for assigning these loads to a size class (Table 1). (We could always distinguish prey in the largest loads, classes 4 and 5, so we only established qualitative criteria for the first three size classes.) Although this method was quite subjective, we needed to use it for only the smallest loads, which contributed little to total mass delivered. We pooled data from video

TABLE 1. Load size classes used for watches conducted with spotting scopes to estimate mass of prey delivered.

Size class	Ranges of prey lengths (mm)			Mean mass (mg) ^a	Subjective criteria for assigning loads to a size class when prey not distinguishable ^b
	Lepidoptera larva	Lepidoptera adult	Diptera adult		
1	1–7	1–5	1–4	1	Load barely visible in bill
2	8–14	6–10	5–9	2	Load protrudes from sides of bill, extends up to half of bill length
3	15–21	11–15	10–14	8	Load protrudes from sides, extends greater than half of bill length
4	22–28	16–20	15–19	20	—
5	29–35	21–25	20–24	38	—

^a Mean mass = hypothetical mean mass of prey (sum of mass of one item of each 1 mm interval, divided by the number of intervals in that size class, rounded to nearest integer).

^b Used for loads with prey not distinguishable using either the spotting scope or video cameras.

camera and spotting scope watches for analysis since both techniques yielded similar estimates of mass delivered per hour, and we used video tape to document loads at a similar proportion of yearling male nests (two of four) as older male nests (six of 11).

We conducted one to four 90 min nest watches between days 4 and 9 of the nestling cycle (hatch date = day 0, fledge date = day 9 or 10, T. W. Sherry). Nestling provisioning rates (for males, females and combined) tended to increase prior to day 4, but leveled off and remained relatively constant thereafter (Omland, pers. observ.; see also Knapton 1984). We observed nests between 07:00 and 16:00 hr, and sampled both age classes equally with respect to time of day and day of nestling cycle. We excluded watches conducted during cold weather (below 16°C) or rain storms, since the female usually remained on the nest and the male did all the feeding under these conditions (Omland, pers. observ.). We observed broods containing 3–5 nestlings ($\bar{x} = 3.6$). The number of nestlings for the two age classes of males did not differ significantly in this study (older males 3.7 ± 0.6 , $n = 16$, yearling males 3.5 ± 0.5 , $n = 11$, $U = 105.5$, ns). We conducted watches at all nests we located, except when weather or numerous synchronous nests made observing every nest impossible.

We analyzed four measures of parental feeding at the nest: number of feeding trips per hour, load sizes, prey mass delivered per hour, and prey types. We report pooled means ± 1 SD of all variables for 1988, 1989, and data from both years pooled. All within-year comparisons were conducted using Mann-Whitney U tests (except where noted) using two-tailed probabilities at the

0.05 level of significance. The number of feeding trips per hour and prey mass delivered per hour differed significantly between years for several comparisons. Therefore we first analyzed each year's data separately, then combined probabilities (Sokal and Rohlf 1981) for 1988 and 1989 to determine if the two age classes differed when we included data from both years.

We aged as many females as we could (as first year or older, using methods of Pyle et al. 1987) in order to determine if female age affected female provisioning rates. We did not include data from nests of several polygynous males observed during the study (see Secunda and Sherry 1991). This would have confounded our analysis since polygynous males feed nestlings at several nests. Furthermore, polygyny occurs at a relatively low rate (10% of all males 1988–1990), and has involved both yearling and older males (Sherry, pers. observ.).

RESULTS

FEEDING TRIPS

Yearling and older males did not differ significantly in the number of feeding trips per hour, in either year or when we combined probabilities from the two years (Table 2). We also found no significant differences between (1) the number of trips made by females mated to males of the two age classes, (2) the total number of parental trips made to nests of older versus yearling males, nor (3) the percentage of total trips made by males. Thus we conclude that either the number of trips made to nests of yearling versus older males did not differ, or that any differences present were not large.

TABLE 2. Feeding trip and biomass delivery rates to nests of yearling and older male American redstarts 1988–1989.^a

	Number of feeding trips/hour ($\bar{x} \pm SD$)			Estimated mass (mg) delivered/hour ($\bar{x} \pm SD$)		
	Yearling males	Older males	Significance	Yearling males	Older males	Significance
1988						
Male	6.0 ± 1.7	5.3 ± 1.9	ns	45 ± 14	49 ± 24	ns
Mate	5.1 ± 1.1	4.5 ± 1.5	ns	33 ± 12	29 ± 26	ns
Total	11.1 ± 2.8	9.8 ± 2.2	ns	78 ± 15	78 ± 21	ns
% by male	53 ± 4	54 ± 12	ns	56 ± 16	63 ± 24	ns
1989						
Male	9.9 ± 5.5	7.5 ± 2.0	ns	69 ± 19	72 ± 41	ns
Mate	7.8 ± 3.2	7.3 ± 2.0	ns	26 ± 12	52 ± 23	ns
Total	17.7 ± 8.7	14.8 ± 3.5	ns	95 ± 28	124 ± 57	ns
% by male	54 ± 5	51 ± 10	ns	73 ± 7	57 ± 12	<i>P</i> < 0.05
1988 + 1989						
Male	8.2 ± 4.6	6.8 ± 2.2	ns	56 ± 20	65 ± 37	ns
Mate	6.6 ± 2.8	6.4 ± 2.6	ns	30 ± 12	46 ± 27	ns
Total	14.9 ± 7.5	13.2 ± 3.9	ns	86 ± 22	111 ± 59	ns
% by male	54 ± 4	52 ± 10	ns	63 ± 15	59 ± 16	ns

^a Sample sizes: yearling: 1988 *n* = 5, 1989 *n* = 7 (trips), *n* = 4 (biomass); older: 1988 *n* = 5, 1989 *n* = 11.

LOAD SIZES

Load sizes generally did not differ significantly between the two age classes for either males or their mates (Fig. 1). The one exception was that in 1989 females mated to older males delivered significantly larger loads per trip to the nest than

did females mated to yearling males (*U* = 40.0, *df* = 11, 4, *P* = .02). This *P* value, like the others presented in this paper, is a per-comparison probability value. We conducted thirteen comparisons for each year’s data, and if we use a conservative Bonferoni correction to account for the multiple comparisons and obtain a family-

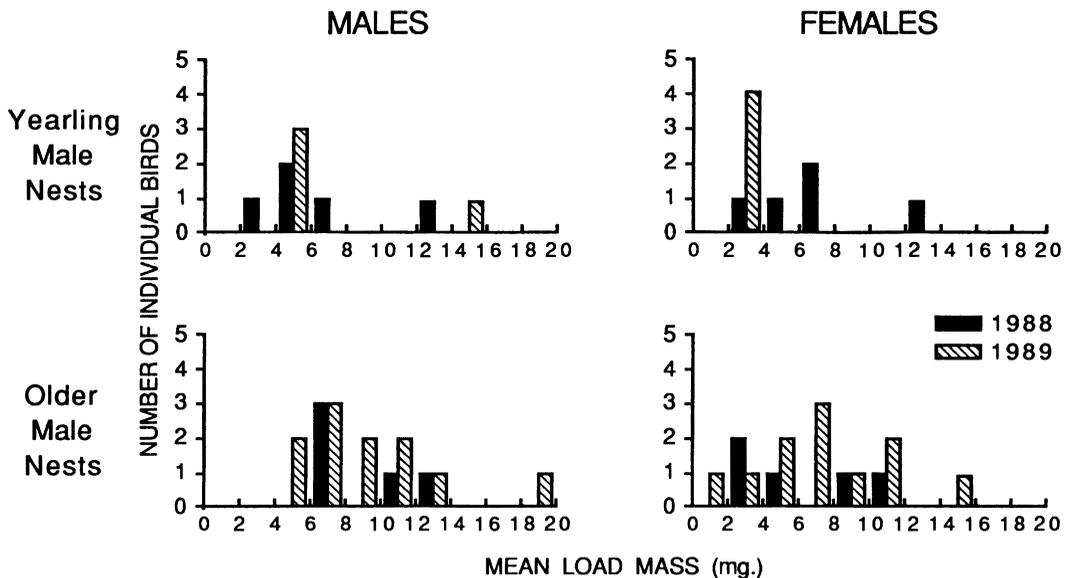


FIGURE 1. Comparison of mean load mass (estimated, milligrams) delivered by males and females to yearling and older male nests. Load sizes only differed significantly between nests of the two age classes for females in 1989.

TABLE 3. Distribution of identified prey types delivered to nests of yearling and older male American Redstarts.^{a,b}

	1988 nests of		1989 nests of		1988 + 1989 nests of	
	Yearling males	Older males	Yearling males	Older males	Yearling males	Older males
Males						
Lepidoptera	64%	80%	39%	60%	53%	67%
Diptera/other ^c	36%	20%	61%	40%	47%	33%
Females						
Lepidoptera	64%	59%	43%	55%	59%	56%
Diptera/other	36%	41%	57%	45%	41%	44%
Total						
Lepidoptera	64%	72%	40%	58%	55%	62%
Diptera/other	36%	28%	60%	42%	45%	38%

^a All comparisons between age classes not significant. Chi-square tests conducted on the mean number of items of each type delivered to nests of each age class.

^b Data based on average of percentages of prey types delivered to nests of the two age classes. Sample sizes: yearling: 1988 $n = 5$, 1989 $n = 4$; older: 1988 $n = 5$, 1989 $n = 11$.

^c Less than 3% of all loads contained prey in three other taxa: Hymenoptera, Coleoptera, and Arachnida.

wide alpha of 0.05 (Hays 1988), the revised per-comparison alpha level should be 0.004. Viewed in this context, the difference in the amount of mass delivered is not significant.

Males fed nestlings significantly larger loads than females did. (Data from both years and age classes pooled; $8.6 \text{ mg} \pm 3.6$ vs. $6.2 \text{ mg} \pm 3.6$. Paired t -test on square-root transformed data, $t = -3.38$, $df = 50$, $P < .001$.) This accounts for the fact that males generally delivered a higher proportion of the mass ($\bar{x} = 55.3\%$) even though males made a slightly lower proportion of the feeding trips than females ($\bar{x} = 48.9\%$).

PREY MASS DELIVERED

When we analyzed delivery rates in terms of estimated mass delivered per hour, we obtained results similar to the results for number of trips. In neither year did yearling and older males deliver significantly different amounts of mass per hour to their nests (Table 2). However, in 1989 yearling males were responsible for a significantly greater percentage of the total mass delivered to their nests than older males ($U = 38$, $df = 11$, 4 , $P < .05$). Again if we account for the multiple comparisons, this difference is not significant. The greater percentage mass delivered by 1989 yearling males compared to older ones probably results because females mated to yearlings tended to deliver less mass per hour than females mated to older mates ($U = 36$, $df = 11$, 4 , $P = .10$).

PREY TYPES

If yearling and older males differed strongly in territory quality, we suspected that some differences in prey types might have been evident. We identified the prey to order in 52% of the loads, and found the nestling diet consisted mostly of two orders of insects: Lepidoptera (caterpillars and adult moths) and Diptera (mostly craneflies, Tipulidae) (Table 3). We calculated the mean number of items in each order delivered to nests of each age class. We conducted inferential tests on these data using chi-square tests on contingency tables. Once again, we found no significant differences between the two age classes for males, females, or both sexes combined. Thus we found no evidence based on prey types for age-specific differences in territory quality.

FEMALE AGE

Of the females involved in this study, nine were of known age: seven yearlings and two older females. We compared feeding rates of the two age classes of females, without regard to the age of their mates. Yearlings and older females made a similar number of trips per hour (yearling $\bar{x} = 6.8 \pm 2.5$ vs. older $\bar{x} = 6.7 \pm 3.4$) and delivered a similar amount of mass per hour. Although the sample size of known age females is small, these data suggest that the two age classes of females did not differ in their nestling-feeding rates, thus did not confound our comparisons between the two age classes of males. Furthermore, females

of the two age classes seem to have mated randomly with respect to male age; four of the yearling females were mated to yearling males and three to older males, while one of the older females was mated to a yearling and the other to an older male. These data combined with data from 1990–1992 suggest that redstarts do not mate assortatively by age (Table 4). Pyle et al. (1987) caution that the reliability of their methods for aging females needs further evaluation. However, since their criteria are probably reliable in most cases, even if one age class of females did deliver significantly less food, it probably would not have affected one age class of males more than the other.

PREDATION RATE

We also analyzed predation rates and showed that another major factor affecting female fitness is similar between yearling and older male nests. Data from 1981 to 1989 show that predation events per day of nest exposure do not differ. Older male nests had a mean per day survival probability of 0.9668 (± 0.0028 , 343 nests) vs. 0.9699 (± 0.0055 , 82 nests) for yearling male nests ($\chi^2 = 0.25$, $P = 0.62$).

DISCUSSION

Results of this study suggest that yearling male American Redstarts and their mates provision nestlings at rates that are similar to the provisioning rates of older males and their mates. Therefore age-related differences in male parental care do not appear to explain differences in mating success between the two age classes of males. It is possible that our methods and sample sizes were not capable of detecting minor differences in provisioning rates between the two age classes, thus causing us to falsely accept the null hypothesis. However, since our methods did successfully detect differences in provisioning rates between years, they are capable of detecting real differences between nests. Even if there were some undetected difference, it probably is too small to account for the large disparity in mating success. Our data show that territory quality did not cause any overall differences in provisioning rates. We did not measure prey abundance directly, but our results suggest that if yearling territories did have lower food levels, yearlings and their mates compensated. Similarly, although we did not directly examine male foraging, our data suggest that

TABLE 4. Ages of mated pairs of male and female American Redstarts. Data from 1990–1992. There is no tendency for Redstarts to mate assortatively by age, $\chi^2 = 0.25$ ns. Data within each year reveal a similar pattern.

Male age	Female age	
	Yearling	Older
Yearling	11	9
Older	30	31

yearling and older males do not differ in foraging skill, or that yearlings compensated if differences exist.

Lack (1968) and others suggested that differences in foraging efficiency could cause younger breeders to have lower reproductive success. Many studies have now documented lower reproductive success for young birds (reviewed in Saether 1990, Clutton-Brock 1991). However, most of these studies focused on the age of females or the age of both parents and did not address the effect of male age. In agreement with our findings, several other studies failed to document an effect of male age on male provisioning rate (Yellow Warblers, *Dendroica petechia*, Studd and Robertson 1989) or on fledging success (Northern Orioles, *Icterus galbula*, Flood 1984; European Blackbirds, *Turdus merula*, Desrochers 1992). A study of Northern Orioles (which have delayed plumage maturation) showed that yearling males fledged significantly fewer young (Labeledz 1984). Also, Hill (1988) showed yearling male Black-headed Grosbeaks (*Pheucticus melanocephalus*, another species with delayed plumage maturation) had lower fledging success than older males. However, when Hill removed effects of nest predation, the number of young fledged did not differ between age classes.

After 39 comparisons between nests of the two age classes, we found only two differences significant at the 0.05 level. (1) In 1989, yearling males delivered a significantly greater percentage of the mass (perhaps due to the nearly significant tendency for females mated to yearlings to deliver less food than females mated to older males). (2) Mates of older males delivered significantly larger loads than mates of yearlings in 1989. As mentioned earlier, if we account for multiple comparisons within years, even these differences are not significant. However, these minor differences could be due to underlying differences in territory food abundance that could influence re-

productive success during some years. We plan future work to determine if differences between nests of yearling and older males do occur in years with low food availability.

FEMALE MATE CHOICE

Our results fail to demonstrate that females gain any advantage, with respect to the provisioning of their nestlings, by mating with older males. This is consistent with studies that demonstrated similar fledging success for yearling and older male redstarts (Procter-Gray and Holmes 1981; Morris and Lemon 1988). Our data also demonstrate that predation rates do not differ between yearling and older male nests. However, our results are unexpected in light of the findings of Lemon et al. (1992) that female redstarts choose among adult males, and apparently increase their reproductive success as a result.

We suggest five possible explanations for why older males enjoy higher mating success than yearling males, given the absence of age-related differences in parental care. First, older males arrive about a week earlier than females and yearling males. Females may be more likely to pair with older males because they have established territories and are advertising (singing) when the females arrive. Females may not be actively choosing older males. They may randomly pair with older males or may actively choose to initiate breeding sooner, and thereby end up paired with older males. In several other species with delayed plumage maturation, yearling males arrive later than older males (Lanyon and Thompson 1986, Slagsvold and Lifjeld 1988, Hill 1989, Stutchbury 1991) and have lower pairing success (Flood 1984, Lanyon and Thompson 1986, Hill 1989, Stutchbury 1991). However, Enstrom (1993) found that yearling male Orchard Orioles (*Icterus spurius*) arrived with older males, but still had lower pairing success. Second, female redstarts may gain a genetic advantage for their offspring by mating with older males if selection has eliminated inferior individuals at earlier ages (Trivers 1972, Halliday 1978, Weatherhead and Robertson 1979). Third, females may choose only those yearlings that can be good providers or have high quality territories. Fourth, mating with an older male may have conferred an advantage that this study did not address such as better post fledging care. Finally, female redstarts may be more likely to pair with older males because the females have an innate

preference for bright plumage. Such a preference may or may not have functional significance (Bradbury and Andersson 1987). In captive choice experiments, female Orchard Orioles preferred older males over males with subadult plumage when either live or stuffed birds were used (Enstrom 1993). Future work on redstarts and other species with delayed plumage maturation should be aimed at understanding which of these factors, if any, cause the observed differences in age-specific male mating success.

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