IS THERE A SEXUAL CONFLICT OVER HATCHING ASYNCHRONY IN AMERICAN ROBINS?

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ABSTRACT.—Many hypotheses have been proposed to explain the occurrence of hatching asynchrony in altricial birds. According to one hypothesis, parents would benefit from hatching asynchrony because the offspring would spend less energy on sibling rivalry. Another hypothesis states that there is a sexual conflict over hatching spread, with one parent trying to minimize investment at the expense of its mate. The latter hypothesis was suggested from a study where males survived better following asynchronous than following synchronous hatching of the brood, with opposite results for females. I tested this hypothesis by manipulating hatching spread in another altricial bird with biparental care, the American Robin (*Turdus migratorius*), and by observing food provisioning late in the nestling period. The hypothesis was supported because males seemed to contribute less, and females more, to asynchronous broods. Males did not take less care than females of the smaller nestlings within the brood, but when the brood had partially fledged it was mostly the female that fed the young that remained in the nest. Provisioning of the parents combined did not seem to be less with asynchronous than with synchronous hatching, lending no support to the sibling-rivalry reduction hypothesis. *Received 14 October 1996, accepted 31 March 1997.*

THE YOUNG OF MOST ALTRICIAL BIRDS do not hatch simultaneously but over a period of one or more days. Many hypotheses have been proposed to explain hatching asynchrony (Magrath 1990, Stoleson and Beissinger 1996). For instance, the cost to the parents may be reduced because less energy is spent on sibling rivalry (the Sibling Rivalry Reduction Hypothesis; Hahn 1981), and any offspring mortality that occurs may take place at an early stage of breeding so that little energy is wasted (Lack 1954). Hatching asynchrony also may help to spread out the peak demand for food of individual offspring (Hussell 1972, Mock and Schwagmeyer 1990). Evidence suggests that parents need to work less with asynchronous than with synchronous hatching in some species (Fujioka 1985, Mock and Ploger 1987) but not in others (Bryant and Tatner 1990).

The best way of assessing the costs of breeding would be to follow the subsequent survival and fecundity of the parents. When this was done in a study of Blue Tits (*Parus caeruleus*), there was no evidence that parents benefitted from hatching asynchrony (Slagsvold et al. 1994, 1995). In the study of Blue Tits, data for the two parents were combined. However, males and females seemed to differ in their re-

sponses, males having improved survival with asynchronous hatching, females with synchronous hatching. We therefore suggested that a sexual conflict exists between the sexes over the degree of hatching spread, with one parent trying to minimize investment at the expense of its mate (the Exploitation of Mate Hypothesis; Slagsvold et al. 1995). In Blue Tits, the conflict apparently is won by the female because hatching is rather synchronous despite a large clutch size. The female alone incubates, and by delaying incubation until most eggs have been laid, she can reduce the hatching span.

Why would a female benefit from synchronous hatching of her brood? One possibility is that with synchronous hatching, the male may contribute more because otherwise the whole brood would starve to death. Breeding success may be more variable with synchronous than with asynchronous hatching (Amundsen and Slagsvold 1997) such that synchronous broods may be more sensitive to the amount of male parental care. The male may invest less if the brood contains some small, undernourished young with low survival prospects. Relative to the female, then, he may give greater priority to molting and territory defense than to parental care (e.g. Svensson and Nilsson 1997). In addition, males may be less certain of paternity of later-hatched young and hence reduce investment in these offspring. In support of these

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TABLE 1. Characteristics of study broods of American Robins.

Nest no.	Hatching date[b]	Diff. in wing length (mm)[c]	Age at filming (days)[d]	Duration of filming (min)	No. of feedings[a]							
					Males				Females			
1	24	32.0	11, 12	414	1	4	6	0	17	16	8	5
2	25	27.0	10	182	3	2	—	—	6	5	—	—
3	25	11.0	12	375	10	9	4	—	1	3	0	—
4	26	16.5	11	339	3	6	6	—	3	3	4	—
5	28	15.0	11, 12	369	6	12	—	—	11	6	—	—
6	30	12.0	11, 12	368	17	12	—	—	15	7	—	—
7	30	13.0	11, 12	369	15	10	—	—	5	11	—	—
8	32	10.5	11	251	4	2	5	—	7	9	5	—
9	32	15.5	11	298	7	7	6	—	13	7	6	—
10	39	14.0	10, 11, 14	609	32	20	—	—	11	20	—	—
11	66	10.5	10, 12, 14	537	29	26	33	—	38	38	34	—
12	71	23.0	9, 10, 12, 14	641	8	9	9	—	27	24	25	—
13	72	17.5	8, 9, 11, 13	649	25	29	—	—	16	30	—	—
14	74	13.5	9, 11	365	18	15	8	—	13	8	7	—

[a] Oldest to youngest chick from left to right.
[b] Of oldest chick; 1 = 1 April.
[c] Between oldest and youngest chick after manipulation.
[d] Of oldest chick.

ideas, when the Blue Tits had fledged, it was the female and not the male that took care of the smallest young within the brood (Slagsvold et al. 1994).

Here I present a study of parental care in American Robins (*Turdus migratorius*) in relation to hatching asynchrony. Soon after hatching, I swapped young between nests to increase the hatching span in some broods. This was done to increase the difference in the reproductive value of the young, their competitive ability, and the ease with which the parents could assess these values and traits. Observations of parental care occurred late in the nestling period when little brooding of the young was needed and when the demand for food was high. I asked: (1) Do males contribute less than females to asynchronous than to synchronous broods? (2) Do males take less care than females of the smaller offspring, in particular in asynchronous broods?

METHODS

The study was conducted during May and June 1994, in woodland areas near Seattle, Washington. Because of heavy predation on adults and nests, most breeding attempts failed (ca. 75%), leaving only 14 broods for study. Hence, sample size did not allow a group design (e.g. synchronous, asynchronous, and control broods). When the nestlings were three to six days old, I interchanged them among nests to increase the age difference in some, but without chang-

ing brood size (Table 1). Results were analyzed with regression techniques. One brood (no. 14) was left unmanipulated because no other brood was available at that time for an exchange of chicks. Partial mortality occurred only at one nest, where one of four young disappeared after the manipulation but before observation of food provisioning. Nestlings within a brood were ranked in size according to wing length, which was recorded before and after manipulation.

Repeated visits to nests showed that unmanipulated broods hatched over a period of less than two days. Hatching spread was measured as the difference in wing length between the largest and smallest young (log-transformed values in tests). Multiple regression analysis showed that hatching spread in 12 broods measured in this way before manipulation tended to be positively correlated with brood size ($t = 2.33$, $P = 0.045$) and nearly so with hatching date ($t = 1.74$, $P = 0.12$). Hatching spreads measured before and after manipulation were not correlated ($r = 0.35$, $n = 12$, $P = 0.27$; range before manipulation, 3 to 19 mm, $n = 12$; range after manipulation, 10.5 to 32 mm, $n = 14$). For convenience, nests with the greater values of hatching spread are termed asynchronous broods, and those with the lower values are termed synchronous broods.

American Robins are suitable for study because their small brood size (two to four) made it easy to tell which young was receiving food. Their habit of nesting in the open facilitated recording of parental and nestling behavior (cf. Weatherhead and McRae 1990, Smith and Montgomerie 1991, McRae et al. 1993). A video camera on a tripod was placed 1 to 3 m from the nest. Spots of white correction fluid were

TABLE 2. Parental care by male and female American Robins. Values are $\bar{x} \pm$ SD, with n in parentheses.

Variable	Males	Females	t^a	P
No. feeding visits per h per young	1.63 ± 0.86 (14)	1.70 ± 0.88 (14)	0.31	0.76
No. feeding visits per h per young[b]	0.50 ± 0.53 (6)	3.12 ± 2.84 (6)	2.03	0.10
Prey length[c]	1.32 ± 0.54 (14)	1.24 ± 0.45 (14)	0.75	0.47
Proportion earthworms in prey	0.51 ± 0.33 (14)	0.50 ± 0.30 (14)	0.23	0.82
No. fecal sacs removed per h per young	1.04 ± 0.61 (14)	1.30 ± 0.51 (14)	1.29	0.22
No. fecal sacs removed per feeding visit	0.64 ± 0.23 (14)	0.83 ± 0.32 (14)	2.07	0.06
Proportion fecal sacs eaten	0.61 ± 0.30 (14)	0.70 ± 0.32 (14)	1.80	0.10

[a] Paired *t*-test.
[b] After part of the brood had fledged.
[c] Relative to length of parent's bill (1 = bill length).

dabbed on the head and bill of the chicks to aid in individual identification. The adults were sexed from their head and breast coloration. Most or all food was delivered to a single chick at each visit. Because it was difficult to observe how much food was received by each chick when more than one was fed, I followed Smith and Montgomerie (1991) in presenting only analyses for nestlings that were fed first.

My goal was to analyze parental care in relation to hatching spread and nestling size when offspring demands were high. Hence, nests were filmed close to fledging time, when the oldest chick in each nest was 8 to 14 days old (Table 1). No observations were made before brood manipulation because this may have increased nest predation, and because early in the nestling period, before manipulation, chicks were small and females spent much of their time brooding. I wanted to study how parents divided their efforts when both were busy collecting food.

Each of the 14 nests was filmed for a period of 182 to 649 min (total of 96.1 h), with 16 to 198 observations of feeding visits per nest (total of 880; Table 1). Low sample sizes at some nests resulted from predation of the entire brood. Filming occurred during one to four days per nest (Table 1), and at any time of day (range 0537 to 1910 hours PST). Video observations also were made at six nests where the brood had partly fledged, with one ($n = 4$) or two young ($n = 2$) remaining in the nest. These nests were filmed for periods ranging from 43 to 238 min (total of 16.6 h, 80 observations of feeding visits; data not included in Table 1).

From the videotapes the following information was obtained for each parent: (1) number of visits to the nest with food; (2) size rank of the young that was first offered the food at each nest visit; (3) position of each young (i.e. nearest, next nearest, etc.) relative to the site of entry of the parent at each nest visit; (4) length of the longest prey item brought at each nest visit measured in proportion to bill length of parent (1 = bill length); (5) prey type at each nest visit (i.e. earthworms, berries, and "other prey"); (6) number of fecal sacs removed; (7) size rank of the nestling that voided the fecal sac; (8) whether the parent swallowed a fecal sac or took it away when

leaving the nest; and (9) time spent on the nest. When estimating prey length and prey type of the youngest chick, data for the second youngest were used in the case at one nest where the male did not feed the youngest chick, and at one nest where the female did not feed the youngest one. The proportion of fecal sacs eaten of those removed was negatively correlated with brood size (see below). This suggests that there was a cost of eating feces, at least in large broods. In all statistical tests, proportions were arcsine square-root transformed in order to achieve normality so that parametric tests could be used.

RESULTS

General care by males and females.—The number of feeding visits to the nest per hour per young was similar for males and females, as was prey length, proportion of earthworms in prey, number of fecal sacs removed per hour per young, and the proportion of sacs eaten of those removed by the parent (Table 2). Females tended to remove slightly more fecal sacs per feeding visit than males, but the difference was not significant (Table 2).

Parental care in relation to hatching spread.—Total feeding frequency for the two sexes combined was negatively correlated with hatching spread but not significantly so (Table 3). However, parents tended to bring larger prey and more earthworms in cases of asynchronous broods (Table 3). Hence, there was no evidence that total food demands were lower in asynchronous broods.

Males made fewer feeding visits to asynchronous than to synchronous broods, both relative to females (Fig. 1), and in absolute terms (Table 3). Females did not compensate by feeding at a higher rate in asynchronous broods (Table 3). However, they tended to bring larger prey items and a higher proportion of earthworms to asynchronous broods (Table 3). In males,

TABLE 3.   Correlations between selected variables and degrees of hatching spread[a] in American Robins (n = 14 broods in each case).

Variable	Males		Females		Total	
	r	P	r	P	r	P
No. feeding visits per h per young	−0.58	0.03	−0.01	0.98	−0.33	0.25
No. feeding visits per h per young[b]	−0.54	0.02	0.04	0.88	−0.28	0.22
Mean prey length	0.18	0.53	0.44	0.11	0.40	0.16
Mean prey length[b]	0.12	0.49	0.38	0.02	0.33	0.01
Proportion earthworms in prey	0.29	0.31	0.42	0.13	0.44	0.11
Proportion earthworms in prey[b]	0.23	0.22	0.37	0.06	0.38	0.03
No. fecal sacs removed per h per young	−0.55	0.04	0.38	0.18	−0.17	0.56
No. fecal sacs removed per feeding visit	−0.05	0.86	0.31	0.28	0.30	0.30
Proportion fecal sacs eaten	0.16	0.59	0.28	0.34	0.29	0.32
Proportion fecal sacs eaten[b]	0.32	0.16	0.46	0.01	0.47	0.01

[a] Hatching spread measured as log (difference in wing length between largest and smallest nestling in brood).

[b] Multiple regression showing standardized beta coefficient instead of r.

prey length and prey type did not correlate with hatching spread (Table 3).

In cases of asynchronous hatching, males not only reduced the number of feeding visits but also the number of fecal sacs removed per hour per young (Table 3). However, they removed a similar number of fecal sacs per feeding visit. They also swallowed a similar proportion of the fecal sacs they removed in asynchronous and synchronous broods, in contrast to their
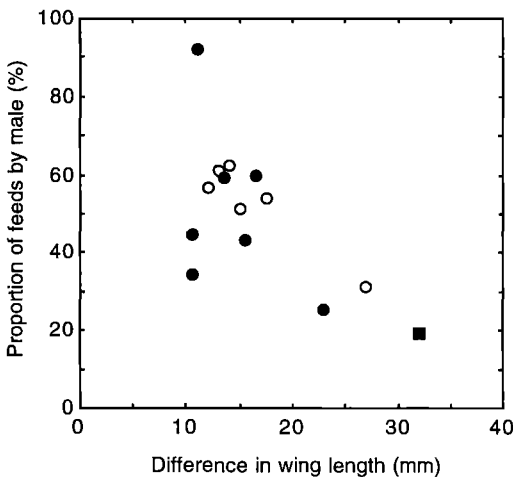

FIG. 1.   Proportion of the total number of feeding visits by male the parent in relation to degree of hatching asynchrony in American Robins. Asynchrony was measured as the difference in wing length between the oldest and youngest nestling of the brood. Broods contained two (open circle), three (solid circle), or four (solid square) young ($r = -0.69$, $n = 14$, $P = 0.006$).

mates, who tended to eat more of fecal sacs in asynchronous broods (Table 3).

When analyzing data for both parents combined, the number of feeding visits per hour per young was positively correlated with date ($r = 0.65$, $n = 14$, $P = 0.012$), mean prey length ($r = -0.87$, $n = 14$, $P = 0.0001$) and proportion of earthworms in prey ($r = -0.77$, $n = 14$, $P = 0.001$) were negatively correlated with date, and proportion of fecal sacs eaten of those removed was negatively correlated with brood size ($r = -0.73$, $n = 14$, $P = 0.003$). Accordingly, I performed multiple regression tests to account for the confounding variables date and brood size (Table 3).

Parental care of oldest and youngest nestling.— There were no indications that males provided more care to the oldest than to the youngest nestling within the brood, either relative to females or in absolute terms. Measures of care were feeding rate per hour (Fig. 2, Table 4), prey length, proportion of earthworms in prey, and number of fecal sacs removed per hour (Table 4).

I also examined the possibility that male provisioning was related to hatching spread, testing whether males skewed their care in favor of older nestlings in asynchronous broods. This was not the case because in asynchronous broods, males contributed less than females both to the oldest and to the youngest nestling (Fig. 3).

Finally, I determined if males consistently fed particular chicks within the brood. This was tested by looking at the proportion of feeds provided by the male (relative to the female) to
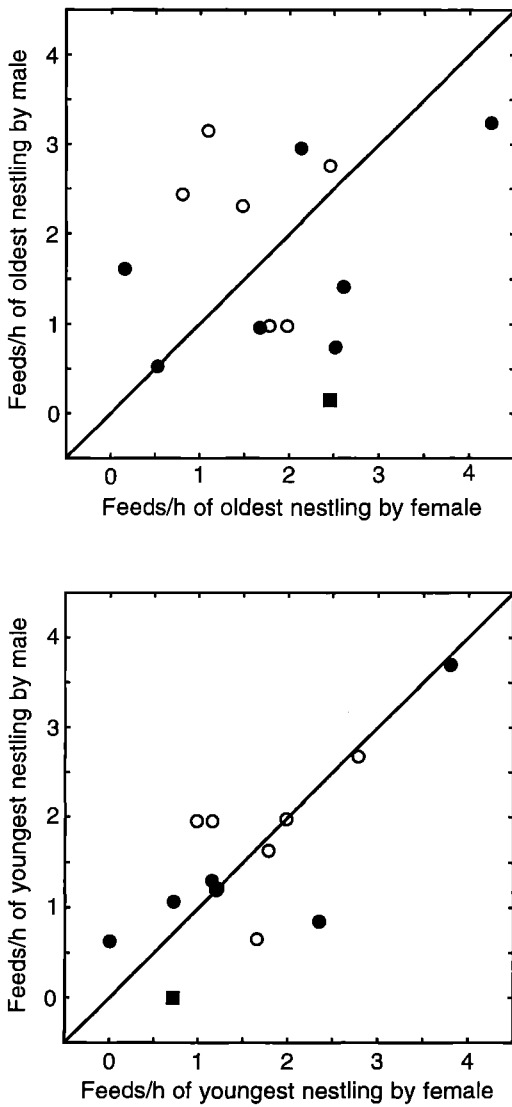
FIG. 2. Feeding frequency by male and female American Robins of the oldest (upper) and the youngest (lower) nestling of the brood. Broods contained two (open circle), three (solid circle), or four (solid square) young.
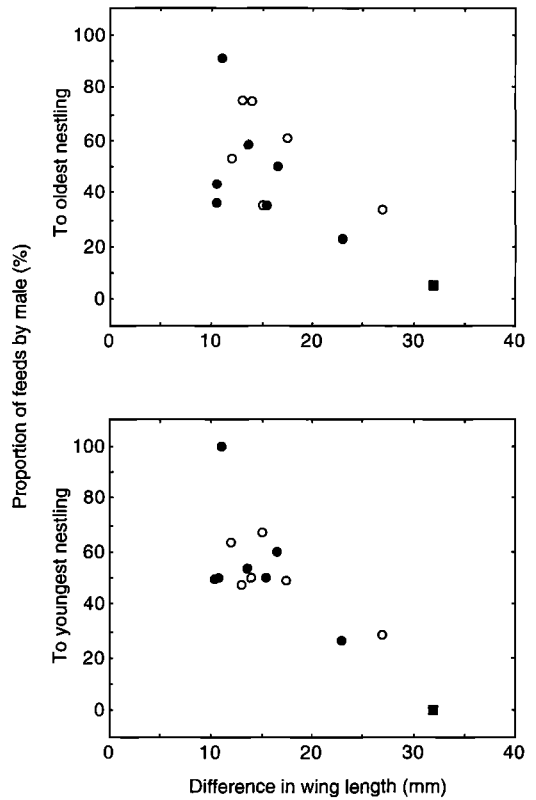

FIG. 3. Proportion of the feedings to oldest (upper) and youngest (lower) nestling of the brood by male relative to female parent plotted in relation to degree of hatching asynchrony in American Robins. Asynchrony was measured as the difference in wing length between the oldest and youngest nestling. Broods contained two (open circle), three (solid circle), or four (solid square) young. Upper: $r = -0.66$, $n = 14$, $P = 0.010$; lower: $r = -0.74$, $n = 14$, $P = 0.003$.

the oldest chick on two separate days (separated by one to three days; $n = 9$ nests). The second day was when the oldest chick was 11 to 14 days old. The values obtained were not correlated ($r = -0.16$, $n = 9$, $P = 0.68$), meaning that knowledge of which young a male was feeding on one day could not predict which young he would feed on a later day. The mean proportions of feeds were not significantly different

on the two days ($\bar{x} = 50.6 \pm$ SD of 18.1%, and $\bar{x} = 30.4 \pm 9.8\%$ for first and second day, respectively; paired t-test, $t = 1.24$, $n = 9$, $P = 0.25$). Hence, males did not seem to skew their care, relative to their mate, in favor of the oldest chick towards the end of the nestling period.

Nestling positions.—The position of a particular nestling (hereafter POS) relative to a particular parent was calculated for each nest as the number of times the nestling was closest to the parent bringing the food divided by the number of times expected from random. The measure was independent of brood size and number of feeding visits, and a score of unity meant that the position was as expected from random. The position score of the oldest chick

TABLE 4. Parental care ($\bar{x} \pm$ SD) provided to oldest and youngest nestling in brood by male and female American Robins ($n = 14$ broods in each case).

Variable	Males		Females		P[a]			
	Oldest (A)	Youngest (B)	Oldest (C)	Youngest (D)	A vs. B	C vs. D	A vs. C	B vs. D
No. feeds per hour	1.73 ± 1.06	1.49 ± 0.94	1.85 ± 1.04	1.53 ± 0.97	0.24	0.21	0.74	0.81
Prey length	1.32 ± 0.58	1.28 ± 0.68	1.20 ± 0.45	1.30 ± 0.58	0.78	0.45	0.32	0.92
Proportion earth-worms in prey	0.58 ± 0.23	0.43 ± 0.23	0.51 ± 0.18	0.55 ± 0.16	0.17	0.68	0.59	0.25
No. fecal sacs removed per hour	1.04 ± 0.67	1.00 ± 0.69	1.40 ± 0.77	1.22 ± 0.55	0.80	0.23	0.19	0.29

[a] Paired t-tests.

for male arrivals did not differ significantly from that of the same chick for female arrivals ($\bar{x} = 0.80 \pm 0.51$ and $\bar{x} = 0.95 \pm 0.38$, respectively; paired t-test, $t = 1.42$, $n = 14$, $P = 0.18$). Similarly, the youngest chick was no less (or more) in front when the male than when the female arrived ($\bar{x} = 1.14 \pm 0.48$ and $\bar{x} = 1.03 \pm 0.46$, respectively; paired t-test, $t = 1.25$, $n = 14$, $P = 0.24$).

If males tried to feed the oldest chick more selectively in asynchronous than in synchronous broods, I expected to find a positive relationship between POS_{male} for this young and hatching spread. The correlation was negative ($r = -0.58$, $n = 14$, $P = 0.030$), however, meaning that it was rather the younger nestlings that were in front when the male arrived with food at asynchronous broods.

Broods partly fledged.—When a brood had partly fledged, the female more often than the male tended to bring food to the remaining young in the nest, although the difference was not significant (Table 2). The female fed more often than the male at five of six nests.

Brooding.—Only the females were seen brooding chicks (observed in 7 of 14 nests). They often stayed at the nest for long periods (up to 35 min), mostly brooding or covering the young. Including only those cases when females stayed for more than one minute, they spent on average $8.8 \pm 12.0\%$ ($n = 14$) of the total observation time at the nest. This percentage was much higher for broods of two ($\bar{x} = 19.6 \pm 11.2\%$, $n = 6$) than for broods of three or four chicks ($\bar{x} = 0.7 \pm 1.5\%$, $n = 8$; $t = 6.70$, $P = 0.0001$). The percentage was not correlated with hatching spread ($r = -0.01$, $n = 14$, $P = 0.98$). No brooding was seen when the brood had partly fledged. However, it may well have occurred at this stage of breeding because fe-

males brooded chicks at six nests close to the time of fledging (oldest chicks were 12 to 14 days old).

DISCUSSION

The combined efforts of both parents were not lower with asynchronous than with synchronous hatching, which lends little support to the Sibling Rivalry Reduction Hypothesis. However, sample size was small and data were collected during only a part of the nestling period. Perhaps more importantly, the conditions for breeding seemed good. Larger chicks did not occupy more front positions than smaller chicks, and no nestling mortality occurred. This is different from a study of another population of American Robins (McRae et al. 1993).

There was some evidence in favor of the Exploitation of Mate Hypothesis because males seemed to contribute less to asynchronous broods, and females seemed to compensate by bringing presumably more high-quality food. During the nestling period, females did not provide more care to smaller chicks than did males, but they tended to do so at the time of fledging, as found in some other species (Slagsvold 1997). Because I did not follow the subsequent survival and fecundity of the parents, I do not know whether differences in parental care between the sexes had any long-term effects and whether provisioning was an appropriate measure of parental care.

Why did male robins provide less care to asynchronous broods? The problem cannot be solved because relevant data are missing on life-history aspects, timing of molt, territoriality, and extent of extrapair paternity. The suggestion that males invest less in asynchronous broods because of reduced confidence of pater-

nity in later-hatched chicks is questionable because males did not avoid feeding younger chicks in the brood. Moreover, females presumably would have fewer rather than more opportunities for extrapair copulations when commencing incubation early (as is the case with asynchronous hatching).

In the most asynchronous broods, size differences among the young were greater than under natural circumstances (measured before manipulation). Studies of other species have shown that the reproductive value of broods with extreme degrees of hatching spread is lower than that of broods with moderate hatching spread (e.g. Slagsvold 1986, Amundsen and Stokland 1988). Hence, male robins may have reduced their care to asynchronous broods because of low brood values. To avoid the risk that young would leave the nest early (preventing further observations of parental care), I did not record nestling body mass and wing length close to fledging time, which would be necessary to estimate the reproductive value of the brood (e.g. Magrath 1991).

Finally, a problem in explaining the results is that American Robins are multibrooded. Because the study occurred in May and June, most pairs probably had time for another brood. In this species, females may start laying a second clutch 15 to 16 days after the young from the first brood have left the nest (Weatherhead and McRae 1990). Hence, it should not pay a male robin to reduce his efforts so that his mate becomes exhausted. Instead, he might take special care of late-hatching young so that the female can start laying as soon as possible. I do not know why it was the female parent that tended to provide more care for chicks remaining in the nest when the brood had partly fledged. However, one possibility is simply that these chicks usually need more brooding than the older chicks and brooding was done by the female (see Slagsvold 1997).

I conclude that in American Robins, there may be a sexual conflict over parental investment in relation to hatching spread. Males contributed less care with increasing hatching asynchrony despite no evidence that the total demand of the brood was reduced in asynchronous broods. In this species, it is the female that incubates and so controls hatching spread. Hence, under natural circumstances, she may avoid costs by hatching relatively synchronous-ly. Optimal hatching spread probably is a compromise between several selection pressures (e.g. Stoleson and Beissinger 1996). My sample sizes were small, and further studies are needed to determine the generality of my results and especially to find out why males would reduce their share of care in asynchronous broods.

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