

## POLYTERRITORIAL POLYGyny IN THE AMERICAN REDSTART

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**ABSTRACT.**—The first six cases of bona fide polygyny are described in American Redstarts (*Setophaga ruticilla*), along with associated male song behavior, nesting and parental care, and a case of female-female aggression. Typically, older (than yearling) males sought secondary reproductive opportunities by traveling 100–400 m through continuous forest to advertise new territories using “repeat-mode” song, typical of genuinely unmated males; and fed primary nestlings and fledglings more than secondary ones. Estimated frequencies of polygynous mating were 15.8%, 5.3%, and 8.0%, respectively, in 1988, 1989, and 1990 (N = 63 color-banded males under close observation), but additional cases of polyterritorial advertisement behavior were noted. Polygyny appears to be a facultative strategy by which males obtain extra reproductive opportunities deceptively, on secondary territories far removed from sites of primary territories and nests. However, we have not ruled out the possibility that secondary females could compensate for reduced parental care by mating with higher quality mates or on better territories than otherwise available. Polygyny may have been facilitated in our study population by a relatively low abundance of males and an unusual abundance of yearlings. Received 30 April 1990, accepted 6 Feb. 1991.

Polygyny is widespread in passerine birds, even in predominantly monogamous species (Ford 1983). The evidence for polygyny in primarily monogamous species is often anecdotal, however, and even in well studied species often provides insufficient behavioral or ecological context with which to evaluate which of various forms polygyny has taken (Searcy and Yasukawa 1989). We document here the first bona fide cases of polygyny in the American Redstart (*Setophaga ruticilla*), and provide preliminary information with which to assess the form polygyny takes in this species. We describe associated territorial and song-advertisement behavior, nesting chronology, parental care, a case of female-female aggression, and a number of additional cases of males attempting to attract multiple mates. We then discuss the form polygyny takes in redstarts and the ecological circumstances favoring it in this species. Previous reports of polygamy in redstarts, describing cases of two unbanded females at one nest (Barney 1929, Hodges 1948), are insubstantial, because they provide no information on the reproductive contributions of these two females, and fail to rule out the possibility that one of these “females” was actually a yearling male, which can closely resemble a female (Rohwer et al. 1983).

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## STUDY AREA AND METHODS

Our study took place in a nearly mature and continuous northern hardwoods forest in the Hubbard Brook Experimental Forest (USDA, Forest Service Experiment Station) in West Thornton, New Hampshire. Locations of American Redstarts, their nests, and behaviors were studied in a 180-ha area, but concerted effort to color mark all individuals and find their nests was restricted to a 34-ha area, gridded at 50-m intervals. The study areas and avifauna have been described by Sherry and Holmes (1985) and Holmes et al. (1986). Most males and several females involved in these observations were identified by unique combinations of colored and aluminum leg bands, or by peculiarities or unique patterns of song types. This allowed detection and monitoring of their movements in heavily forested habitat. Nests were observed, usually without using a blind, from a minimum distance of 20 m. Numbers of trips made to the nest by both the male and female at each nest were recorded, usually in one-hour watch periods spread throughout the day. Song behavior terminology follows MacNally and Lemon (1985): "Repeat-mode" uses only one song type, usually the "accented-ending" song (Ficken 1962), whereas "serial-mode" involves series of alternating song types, usually exclusive of the repeat-mode type. Genuinely unmated male American Redstarts, prior to the arrival of females, characteristically broadcast continuous, relatively loud, high rate, repeat-mode songs (Ficken 1962, Ficken and Ficken 1970). Upon mating, the rate of repeat mode song slows, and the serial mode begins to occur more frequently as nest building progresses. Those males remaining unmated after arrival of females rarely, if ever, sing in serial mode. We refer to bouts of continuous, relatively loud, repeat-mode song behavior as "advertising," regardless of when in the season they occurred, and regardless of whether a bird was known to be mated.

## RESULTS

*Frequency of polygyny and territorial advertisement.*—We confirmed two cases of polygyny in each of 1988 and 1990, and found two other likely cases in 1988 and one in 1989. These numbers represent 15.8% ( $N = 19$ ; only three of the four 1988 cases were on the 34-ha area), 5.3% ( $N = 19$ ), and 8.0% ( $N = 25$ ) of all males in 1988, 1989, and 1990, respectively, on the 34-ha study area. We based these estimates of polygyny frequencies on our 34-ha study area, in which we were most likely to detect polygyny because of the color-banded males and intensive nest searches there. We first describe two 1988 cases in greatest detail, then describe briefly additional cases of polygyny and polyterritorial advertisement.

The two cases confirmed in 1988 involved a bigamous male (henceforth M1) and a trigamous male (M2), which were three and  $\geq 4$  years old, respectively, based on when they were banded. M1's primary female was banded the previous summer, and so was  $\geq 2$  years old. Two of the other four females mated to M1 and M2 were banded late in the 1988 season: The secondary mate of M1 was a yearling female, and the tertiary mate of M2 was probably a yearling as well, based on rectrix characteristics (Pyle et al. 1987).

Both M1 and M2 resumed advertising song behavior in at least two

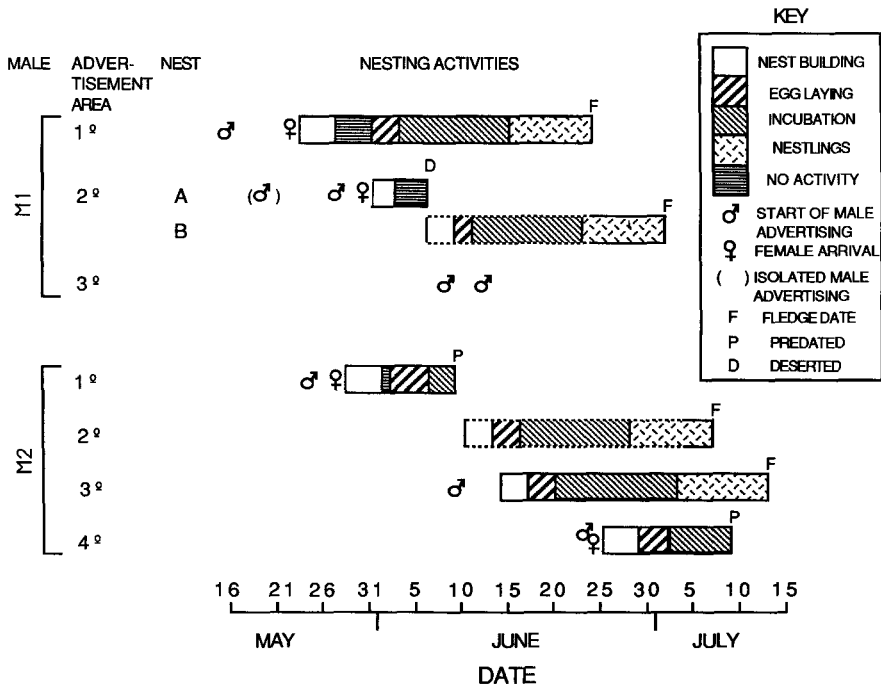


FIG. 1. Chronologies of breeding season activities for two polygynous male American Redstarts observed in 1988, Hubbard Brook Experimental Forest, New Hampshire. M1 and M2 designate male one and male two, respectively, and their home ranges are numbered chronologically, beginning with the first territory advertised. Dashed horizontal lines designate inferred dates of activities, based on typical redstart periods for the different nesting stages. Parentheses surrounding the first date that male M1 advertised at his 2° area indicate one isolated day in which this male sang at the site, but did not persist there until the female was observed on 31 May.

separate areas after mating with a female at another initial location. Both males resumed advertising on secondary and tertiary advertising areas no later than the late building phase of their previous nest (Fig. 1). The exception to this was M1's secondary advertising area, where we once observed him singing subsequent to establishment of his first advertising area, but before his first female was known to have arrived (Fig. 1). However, he was not observed in the second area again until the late building phase of his first nest.

Advertising areas were locations of repeat-mode singing prior to mating and nest building (Fig. 2). We hesitate to refer to these areas as territories, since no other males established themselves within the continuously suit-

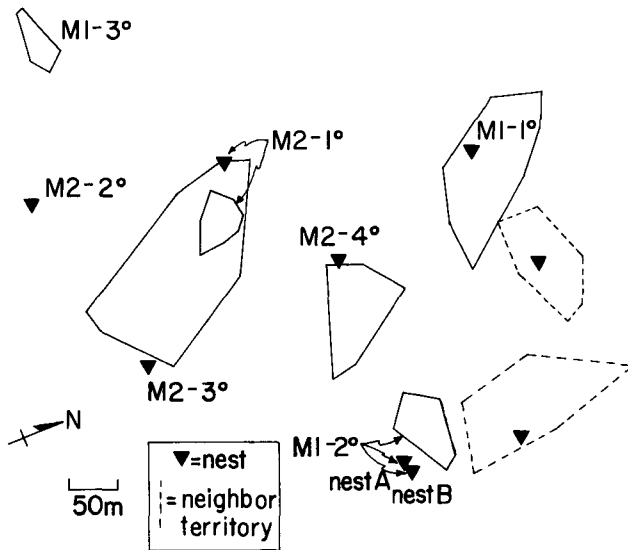


FIG. 2. Map showing locations of multiple advertising areas within home ranges of two polygynous male American Redstarts observed in 1988, Hubbard Brook Experimental Forest, New Hampshire. Nest locations are shown by triangle, and territories of two other neighboring males are shown with dashed lines. Arrows emanating from M1-2° and M2-1° indicate particular advertising territory and associated nest(s). See legend to Fig. 1 and text for descriptions of other symbols.

able habitat between the advertising areas of either M1 or M2, such that both of these males had relatively wide corridors in which to travel between their different display areas and nests (Fig. 2). One can argue that the area inclusive of all nests and advertising areas for either of these males was that male's territory (e.g., DellaSala 1986), even though these latter areas were larger than the territories of other males. However, these males did not sing throughout their home ranges, but instead concentrated advertising behavior in the smaller areas indicated (Fig. 2). M1 attracted a mate in two of his three advertising areas. His primary display area was less than 100 m from where he had been banded as a yearling in 1986; and his tertiary advertising area, to which he never successfully attracted a mate in 1988, was the area in which he had successfully mated and in which young were fledged in both 1986 and 1987. M2 succeeded in mating at all three of the areas where we observed him advertising. We did not observe M2 advertising in the vicinity of his secondary nest because this nest was not found until three days before its chicks fledged (Fig. 1). All females of both these males nested within or immediately adjacent to the

display areas of their respective mates (Fig. 2). If we define distances between advertising areas as the distance from a male's previously established nest to the nearest location where he subsequently resumed advertising that same breeding season, then distances between M1's advertising areas were 245–450 m, and those for M2 ranged from 120–180 m.

*Nesting chronology.*—Three nests were built on display areas where only male M1 sang or was otherwise observed repeatedly. M1's primary nest, and the second nesting attempt (B) on his secondary display area successfully fledged young (Fig. 1). The first nesting effort on his secondary display area (A) failed before we had ascertained whether laying had begun. Eighteen days after activity at this nest ceased we observed M1 feeding nestlings at the B nest, 10 m distant from the A nest (Fig. 2). Because these nests were so close together, were constructed in such similar sites, and building of nest B was inferred to have begun by 6 June (see below for modal chronologies at typical redstart nests), the day after the first nest was probably destroyed (Fig. 1), we believe that the two nests were built by the same female.

Four chicks fledged from M1's first nest on 24 June. During the period when he was feeding fledglings from this primary nest, he also fed nestlings in his secondary nest B. We simultaneously monitored recent fledglings from M1's primary nest and nestlings in his secondary nest (B) on nestling period days 5–7 (where day 0 was the first day in which any nestlings had hatched—see Fig. 1). Only 9% of the sightings of M1 bringing food to chicks were in the vicinity of secondary nest B ( $N = 391$  min). His secondary nest B fledged at least three chicks on 1–2 July.

Four nests were built in association with the display areas of male M2 (Fig. 1), and young fledged from his secondary and tertiary nests. Because his secondary nest was discovered when it contained nestlings, the transition dates for phases in the nest cycle were extrapolated backwards from the fledge date (Fig. 1). Modal nest phase lengths were used in these extrapolations (Sherry, unpubl. data): Nest-building = 4 days, egg laying = 4 days (or one day per egg in clutches with fewer or more eggs than four), incubation = 11 days, nestling-feeding = 9 days. M2's first nest became inactive during incubation. We do not know whether or not his secondary nest was built by his mate from his primary nest, but the female at the secondary nest could have been the same individual as the one which abandoned the primary nest, since M2's secondary mate had sufficient time (assuming modal durations of nesting stages described above) to accomplish all nesting tasks by July 7 if she had begun building on 10 June, the day after M1's primary nest was depredated (Fig. 1). M2's first successful nest, on his secondary display area (Fig. 2), fledged four young on July 7. M2 fed fledglings from this first brood while feeding the nestlings

TABLE 1  
COMPARISON OF NESTLING-FEEDING BEHAVIOR OF TWO POLYGYNOUS AND FIVE  
MONOGAMOUS AMERICAN REDSTART MALES IN THE HUBBARD BROOK  
EXPERIMENTAL FOREST, NEW HAMPSHIRE, 1988

Male	Nest	Nestling days <sup>a</sup>	Percent feeding trips by male (per nest)	Observation time (min)
M1	1°	2	85–100	57
	2°	1–7	4–10	617
M2	2°	7–8	59–72	291
	3°	3–10	34–50	720
Monogamous males		5–7	61–67	1440

<sup>a</sup> Days since at least one nestling hatched (=day zero).

of his second (tertiary nest, Fig. 1). During simultaneous surveillance of these fledglings and M2's tertiary chicks on their nestling period days 4–6 (nestling day 4 for tertiary chicks corresponded with the fledge day at his nest on his secondary display area—Fig. 1), only 33% of his sightings were near his tertiary nest ( $N = 291$  min). His tertiary nest fledged four young on 13 July. His quaternary nest was active during this period, but it was not observed concurrently to see if he visited the site. However, earlier, during the period that his tertiary female was incubating and his quaternary female laying, he was never sighted at either of their nests during simultaneous watches (150 min). He may have been attending nestlings at his secondary nest, which we had not yet discovered, during these 150 min of observation. M2's quaternary nest was deserted about half way through the incubation phase.

*Parental care.*—Both males contributed more to feeding dependent young at their earlier than their later nests, as quantified by percentage of trips made by the male (Table 1). M1 made 85–100% of the feeding trips at his primary nest, but this is based on a short observation period when cool weather may have increased his relative contribution to feeding nestlings (K. E. Omland and T. W. Sherry, unpubl. data). We do not know how many trips he contributed to this nest late in the nestling stage, but judging by his contribution to fledglings (see below) it was almost certainly more than the 4–10% he contributed to his secondary nest. M2 contributed more trips at his earlier (secondary) nest (59–72%) than at his later (tertiary) nest (34–50%—Table 1). The second trend to note is that both polygynous males contributed proportionately fewer feeding trips to nestlings at their secondary nests than five monogamous two-year-or-older males also observed in 1988, each of which contributed 61–67% of feeding trips (Table 1). Thus the females at M1's secondary nest and at M2's

tertiary nest fledged young with reduced feeding assistance from their mates. Three widowed redstart females and an older male without a mate during at least the final two days of the nestling period have all fledged young successfully (Sherry, unpubl. data). These observations indicate that redstarts can fledge young with reduced parental effort from a mate, unlike Black-throated Blue Warblers (Petit et al. 1988), although redstart nestlings starve in some years even with both parents attending nests (Sherry and Holmes, in press).

For most broods (M1's primary, and M2's secondary and tertiary ones) each parent fed half the brood exclusively, a brood division described previously in redstarts by Boxall (1983). We lost track of all females with broods on the second day after fledging.

The location of M1's primary nest fledglings shifted toward his secondary nest over several days. He spent most of his time singing serial mode songs, alternating with feeding his two fledglings. Periodically he moved away from these fledglings, switched to repeat mode song and made one or two short visits to his nestlings in the secondary nest B (Fig. 1), before returning to the fledglings from his primary nest. On the morning of fledging day at his secondary nest B, only his mate was observed feeding the three new fledglings. M1 spent most of his time about 100 m from his secondary nest, where he was probably feeding fledglings from his primary nest. Twice on that morning M1 came within a few meters of his secondary nest female, but we never saw him feed any of these new fledglings.

M2 fed two fledglings from his secondary nest from the day they fledged until we stopped observing him, two days after his tertiary nest fledged young. The female and at least one fledgling were being fed by the male at this nest on fledge day, but were not subsequently observed. As with M1's brood, the location of M2's fledged young gradually shifted toward his tertiary nest. Three days later, when the tertiary nest fledged young, we observed M2 feeding his two new fledglings while continuing to feed his two older ones from his secondary nest. On the following day we could account for only the four fledglings being fed by this same male.

*Other cases of polygyny and polyterritorial advertisement.*—Polyterritorial polygyny such as that of M1 and M2 are not isolated incidents in redstarts, as illustrated by a variety of less detailed examples, all involving older males. The first likely case of polygyny occurred in 1985, when a male was seen advertising and traveling with a female while she was building a nest on 7 June. We saw no other male at this nest site prior to 28 June, when this nest was depredated, but we saw this same color-banded male feeding young on the day they fledged (June 27) at a concurrent successful nest almost 200 m away (across the territory of another

redstart pair) from the depredated nest. We observed circumstances suggestive of two cases of polygyny in 1988 besides those involving M1 and M2. In the first instance, the male repeatedly left a nest site where he was feeding young, and traveled about 200 m to another site where he used advertisement song (much as M1 did when traveling to his secondary nest site); we also saw a female redstart and fledglings at this site, but were unable to confirm feeding of young here by this male. In the second case, intensive observations at the nest of one male revealed repeated periods during which he was absent from the nest site as though he were off at another nest or territory site. In 1989 we confirmed one case by observing an older male feeding a recently fledged young near the ground, fewer than 10 m away from a tree containing young (<four days old) chicks that this same male was helping to feed. We do not know where this lone fledgling came from, but certainly not from this nest, so that we think the simplest explanation is that this male had a secondary nest. In 1990 we confirmed two more cases by observations of banded males feeding nestlings at different nests. In the first case, the male alone fed four nestlings during the two days the nest was under observation until the chicks fledged on 1 July. This same male was subsequently seen feeding nestlings at a second nest found on 4 July, and depredated two days later. This second nest, on which a female must have been incubating eggs by 23 June to have nestlings hatched by 4 July, was 270 m from the first nest, and was located where this male had been observed courting a female on two different days starting on 8 June. In the second 1990 case, the male defended one relatively large (ca 1.25 ha) territory within which he helped feed young that fledged a first nest on 24 June. A second female built a nest in this territory 120 m from the first nest, began incubating on 20 June, began feeding chicks with the male's assistance when the first chick hatched on 4 July, and then abandoned the area when the nest was depredated on 5 July.

In addition to these cases of polygyny, we have observed numerous instances in which a male behaved as though he were trying to attract a second mate in a territory far removed from the primary one. One older male in 1986, and another in 1987 each advertised over 150 m from an active nest site at which each later fed young. In two instances in 1988 we observed older males advertising unsuccessfully up to 200 m away from their primary nest sites, then reverting within several minutes to serial mode song back at the primary nest site. In 1989 we observed an older male advertising in a secondary area with repeat mode song 450 m away from the site of an active nest where he had advertised and attracted a mate earlier in the season. In 1990 we observed two cases. First, a yearling male used advertisement displays on two different days in an



area approximately 415 m from the site of a nest at which it was later feeding nestlings. Second, an older male was seen repeatedly with a female at one site, then was subsequently observed advertising 150 m away to a second female on 2 June, the day this second female started to build a nest. The male shuttled between the two sites at least four times while under observation on this date. We also observed intensive female-female aggression at this second display site at 09:10 in the morning and again at about 12:00–12:44 h, when we observed extensive chases, aerial grapples, and fluttering descents of the two females to the ground. The female observed initiating nest-building never returned to this nest-site following the female-female aggression, but instead moved about 75 m further away from the primary site from which the male was shuttling initially, and built a nest there. We hesitate to call this latter example polygyny since we never confirmed that the first female nested.

#### DISCUSSION

The advertising behavior and occasional polygyny that we have observed in American Redstarts is remarkably similar to polyterritoriality described in the Wood Warbler (*Phylloscopus sibilatrix*, Temrin et al. 1984; Temrin 1986, 1989) and the Pied Flycatcher (*Ficedula hypoleuca*, Alatalo et al. 1981, 1982; Slagsvold and Lifjeld 1988). Monogamously mated Wood Warblers, for example, differed from unmated males in their song types and rates, with rates decreasing once mating occurred (Temrin 1986). By the time their first mates began laying, some Wood Warbler males established secondary territories within which the males resumed “unmated” song mode (Temrin et al. 1984). In both the Wood Warbler and Pied Flycatcher, secondary territories were generally not farther than a few hundred meters from primary ones, thus facilitating their defense by one male (Slagsvold and Lifjeld 1988). Similarly, redstart display territories and nests were usually at least 200–300 m apart, but occasionally up to 500 m apart (Fig. 2), with large expanses of intervening forest within which males did not display vocally. Finally, young of secondary mates in a variety of species received less parental care than those of primary mates (Alatalo et al. 1982, Temrin et al. 1984, Searcy and Yasukawa 1989, Lifjeld and Slagsvold 1989). Male redstarts, however, did not completely abandon secondary mates, as did Wood Warblers (Temrin et al. 1984) and male Red-winged Blackbirds (*Agelaius phoeniceus*) in some populations (Searcy and Yasukawa 1989, Whittingham 1989). Two-year-or-older males were involved in all but one case of polygyny or polyterritorial advertising behavior we observed in Redstarts, implying that older males are more likely than yearlings to be polygynous, much as in the Pied Flycatcher (Alatalo et al. 1981, 1982). However, we observed one

yearling male displaying polyterritorially, and Reid and Sealy (1986) observed a polygynous yearling Yellow Warbler (*Dendroica petechia*).

Although we have confirmed only six cases of polygyny, regular polyterritorial advertisement behavior and several other instances of likely polygyny suggest that the phenomenon was not infrequent, occurring in about 5–15% of males in the period 1988–1990. Polygyny may have gone undetected in our study until 1988 (even though a large number of color-banded males were under observation beginning in 1983) because we became more efficient at detecting it, but it may have been unusually frequent in the period 1988–1990 (see below). American Redstarts are thus best characterized by “facultative polygyny” (Ford 1983:340), in which males of a primarily monogamous species are polygynous whenever ecological or social circumstances allow it. We are not surprised to observe polygyny in redstarts, given their plumage sexual dimorphism and male plumage bimaturism, and given the association of these characteristics with polygyny in other birds (Rohwer et al. 1980, 1983).

Why are redstarts polygynous? We find no evidence in redstarts, as in all other birds studied to date, that male-coercion of females into polygynous relationships is possible, especially in forested habitats, implying that female-choice is more likely than male-choice (Searcy and Yasukawa 1989). We also note that the polyterritorial form of polygyny in redstarts, just as in Pied Flycatchers and Wood Warblers, precludes harem size-related benefits such as added defense against nest predators seen in Red-winged Blackbirds (Searcy and Yasukawa 1989). Redstart females that join an already mated male do risk receiving decreased male effort feeding nestlings (Table 1), and so there appears to be a net cost of polygyny to such females. The “skewed-sex-ratio” model, which conceives of females mating polygynously owing to the unavailability of monogamous males, does not apply to redstarts, because floating unmated males are generally available (Morris and Lemon 1988; Sherry and Holmes 1989; Sherry, unpubl. data). We are left with two possible models: (1) The compensation, or “polygyny-threshold” model, in which females are compensated by better reproduction when mating with older males, either because of higher quality territories held or higher genetic quality of the males; and (2) a “no-compensation model” (Searcy and Yasukawa 1989). The polygyny-threshold model could apply to redstarts, since females could easily use plumage differences to distinguish between yearling and older males, and since yearling males tend on average to advertise territories in poorer habitats than older males (Sherry and Holmes 1988, and unpubl. data; but see Morris and Lemon 1988). Also, habitats vary patchily at Hubbard Brook (Sherry and Holmes 1985), in such a way that older males could monopolize the preferred, deciduous habitats (Sherry and Holmes 1989),

facilitating polygyny if females tend to become concentrated in relatively preferred habitats (Wesolowski 1987). However, yearling males appear to care for young and fledge them as successfully as older males (Procter-Gray and Holmes 1981; Morris and Lemon 1988; Omland and Sherry, unpubl. data), and so females should gain little advantage by mating preferentially with an older male. Finally, aspects of Searcy and Yasukawa's (1989) "no-compensation" model would seem to apply to redstarts and explain aspects of polygyny in this species: There could well be a search cost to females traveling through large areas of forest trying to locate mates during a short breeding season, in which clutch size declines each year (Sherry, unpubl. data). The polyterritorial form of polygyny in redstarts also allows for the possibility that females are deceived about the mating status of males, as appears to be the case in Pied Flycatchers (Lifjeld and Slagsvold 1989, Searcy and Yasukawa 1989). Our observation of redstart female-female aggression suggests that primary females may suffer when their mates establish secondary mating relationships, perhaps because primary females lose the help feeding their own nestlings that their mates provide at secondary nests (Table 1). Primary female Pied Flycatchers receive less help feeding nestlings from a polygynous than a monogamous mate (Lifjeld and Slagsvold 1989), and their aggression towards other females provides an explanation for why males display secondary territories far from primary ones, i.e., are polyterritorial (Breie-hagen and Slagsvold 1988). However, female-female aggression also occurs on territories of polygynous Yellow Warblers, which are not poly-territorial (Hobson and Sealy 1989).

We are puzzled by the fact that none of the earlier studies of redstarts have observed polygyny, given its frequency at Hubbard Brook. Several explanations are possible. First, polygyny is probably difficult to detect in species such as redstarts with home-ranges occupying many hectares of heavily forested habitat, particularly when males are not color-banded. Second, relatively high nesting success of Hubbard Brook redstarts in the late 1980s (Sherry and Holmes, in press) may have facilitated confirmation of polygyny via detection of male parental care at multiple simultaneously active nests. Third, polygyny may be more frequent in some populations than others. Polygyny may have been relatively prevalent at Hubbard Brook in the late 1980s, for example, due to peculiar ecological circumstances. The redstart population at Hubbard Brook in the period 1988–1990 was at its lowest abundance since we began mapping territories in 1981 in our 180-ha area (Sherry and Holmes, in press), and the population on a 10-ha part of the 180-ha area was as low in 1988 as anytime in the previous 18 years (Holmes and Sherry 1988). Low abundance would have facilitated males' uncontested movement within suitable habitat, and all six cases of confirmed or likely redstart polygyny involved territories

connected by unoccupied corridors of appropriate deciduous habitat (e.g., Fig. 2). Moreover, the low-abundance populations in 1988–1990 were comprised disproportionately of yearling males (Sherry and Holmes, in press), and presumably also of yearling females. Older males might have experienced decreased competition for mates from the relatively few older males and from the less experienced yearling males (which are generally unsuccessful in competition with older males for territories and mates—Sherry and Holmes 1989). The secondary female of male M1 and the tertiary female of M2 were both almost certainly yearling females, which are likely to be inexperienced at assessing mating status of males (see, e.g., Alatalo et al. 1981). Since American Redstarts appear to be invariably single-brooded at Hubbard Brook (T. W. Sherry, unpubl. data), our observations are consistent with the hypothesis of Slagsvold and Lifjeld (1988) that polyterritorial polygyny is promoted by conditions of low intraspecific competition for mates in single-brooded species with a short reproductive season.

In conclusion, our data and observations suggest that polygyny in American Redstarts results from a facultative strategy used primarily by older males to increase mating opportunities in a female-mate-choice system. Polygynous matings in redstarts appear to be facilitated both by males' locating secondary territories far from primary nesting sites, i.e., polyterritoriality, and by relatively low levels of intraspecific competition among males for mates. Secondary females received less assistance from males feeding nestlings than primary females, and an instance of female-female aggression suggests that primary females may attempt to restrict polygynous matings by their mates. To our knowledge this is the first reported case of polyterritorial polygyny in a North American bird.

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