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A POSSIBLE RELATIONSHIP BETWEEN REVERSED SEXUAL SIZE DIMORPHISM AND REDUCED MALE SURVIVORSHIP IN THE RUBY-THROATED HUMMINGBIRD[1]

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Abstract. An examination of 28 years of banding data from Powdermill Nature Reserve in southwestern Pennsylvania showed the following trends in the sex ratio (female : male) of Ruby-throated Hummingbirds (*Archilochus colubris*): 1.1:1 for immature hummingbirds caught in late summer and fall; 1.4:1 for adults in spring (April–May); 3.1:1 for adults in summer (June–7 August); and 4.1:1 for adults in fall (8 August–October). Hypotheses to explain these increasingly female-biased sex ratios include differential migration, capture bias and differential mortality. Banding data from eight other stations in eastern North America provided no evidence of different fall migration routes for males and females. We detected no capture bias at Powdermill, with respect to mesh size of mist nets, net wariness or net avoidance ability, but there was seasonal variation in the number of overlapping captures of males and females at individual mist nets: spring (81.5%); summer (27.6%); fall (44.7%). A capture bias resulting from differences between the sexes in the use of habitats sampled by our mist nets has likely contributed to observed sex ratio variation. Differential mortality, with males suffering greater losses than females, probably also contributed to this variation. Estimated annual survivorship calculated from returns of banded hummingbirds to Powdermill was lower for males (0.294) than females (0.446), but this difference was not significant. The mean minimum known age for returning male hummingbirds at Powdermill was significantly less than that for females; furthermore, the oldest known age for a returning male (three years) was half that observed for a female. The lower inferred survivorship for males may be related to reversed sexual size dimorphism in this species. The body mass of female Ruby-throated Hummingbirds was significantly greater than that of males and did not vary between May and August, whereas males weighed significantly less in June and July than they did in May and August. Low mid-summer mass in males, coupled with increased metabolic demands during the breeding season, may lead to a fatal "energy crisis" in this sex during nocturnal fasting or periods of inclement weather.

Key words: Sex ratio; reversed sexual size dimorphism; differential mortality; capture bias; Archilochus colubris; *Ruby-throated Hummingbird; body mass.*

INTRODUCTION

The Ruby-throated Hummingbird (*Archilochus colubris*) exhibits pronounced reversed sexual size dimorphism. The ratio of mean adult wing lengths of males and females is 0.87 (from data in Mulvihill and Leberman 1987), a value that is apparently near the extreme for hummingbirds (cf. Payne 1984:26). A similar ratio (0.88) exists for mean mass during May (Mulvihill and Leberman 1987), when most individuals of both sexes are nearly fat-free and before most females are gravid. A promiscuous mating system characterized by large variation in male reproductive success and a lack of pair bond formation or male parental care (Orians 1969, Selander 1972, Wittenberger 1981, Payne 1984), along with acrobatic aerial courtship and territorial displays (Pitelka 1942), has presumably resulted in sexual selection for smaller size in adult male Ruby-throats (Stiles 1973, Payne 1984, Jehl and Murray 1986). Some sexual selection theory implies that this will carry with it a counter-selective cost such as increased risk of mortality (Trivers 1972). Evidence for such counter-selection in birds is scarce and mostly limited to cases of normal, not reversed, sexual size dimorphism (Selander 1965, Wittenberger 1978, Searcy and Yasukawa 1981, Yasukawa 1987).

We analyzed (1) sex ratios across seasons and between adult and immature age classes, (2) return records of banded birds, and (3) trends in male mass during the breeding season at Pow-

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dermill Nature Reserve, to determine whether lower survivorship might be one cost of smaller size in male Ruby-throated Hummingbirds. We also evaluated several possible sources of capture bias that might confound interpretation of our data.

STUDY AREA

The study was conducted at Powdermill Nature Reserve, an 890 ha field research station of the Carnegie Museum of Natural History in Westmoreland County, Pennsylvania (40°10′N, 79° 16′W). The Reserve includes foothills along the northwestern slope of Laurel Hill (elev. 600 m) and adjacent lowlands (elev. 400 m). The site is dominated and mostly surrounded by mature mixed-deciduous forest. The bird banding area is located in a moist lowland area of about 25 ha and includes a variety of early successional habitats. Within the banding area are several small ponds, streams and wetlands. In general, mist nets for capturing birds are situated near streams, roads and pond or field edges in proximity to thickets of dogwood (*Cornus amomum, C. racemosa*), hawthorn (*Crataegus* sp.), wild crabapple (*Pyrus coronaria*), black willow (*Salix nigra*), speckled alder (*Alnus rugosa*), multiflora rose (*Rosa multiflora*), autumn olive (*Elaeagnus umbellata*) and Tartarian honeysuckle (*Lonicera tatarica*). Comparatively few nets sample birds moving within or at the edge of mature forest. Net placements have changed only slightly during the study. Plant succession has been somewhat retarded by selective cutting of tall trees and mowing of some open areas in the vicinity of mist nets. No sugar-water feeders have ever been used to attract hummingbirds to the banding area. A number of native hummingbird food plants occur commonly in the banding area, especially spotted jewelweed (*Impatiens capensis*) and cardinal flower (*Lobelia cardinalis*).

METHODS

A total of 4,208 unbanded Ruby-throated Hummingbirds was captured in up to 60 mist nets, along with 58 captures of birds returning to Powdermill one or more years after their original banding, between 1963 and 1990. For details of the banding procedures at Powdermill see Leberman and Wood (1983).

The age (HY = hatching year or AHY = after hatching year) of hummingbirds was determined by mouth color and plumage. HY birds were caught in the same calendar year in which they hatched. AHY birds were caught in a later calendar year than the one in which they hatched. Sex was determined by emargination of the sixth primary and wing length (Leberman 1964, 1972). Body mass (to the nearest 0.1 g, using an Ohaus triple-beam or electronic balance) and fat score (ranked from 0 to 3; Leberman 1967) were also recorded for most individuals.

For the purpose of analyzing sex ratios of adult (AHY) hummingbirds ($n = 2{,}000$), we used the following seasonal cutoffs: spring (22 April–31 May); summer (1 June–7 August), and fall (8 August–2 October). As delimited, the summer season probably excludes most migrant hummingbirds (Mulvihill and Leberman 1987). The sex ratio of immatures ($n = 2{,}116$) was based on all birds caught in their hatching year. To assess possible existence of capture bias between the sexes with respect to mist net mesh size and possible spatial separation of the sexes in the banding area, we recorded the mesh size and exact net location for every hummingbird caught during 1987 and 1988 ($n = 401$). We calculated the percent overlap of the sexes at each season by totalling the number of hummingbirds at mist net sites where both sexes were captured and comparing this to a total obtained based on an artificial distribution of the less numerous sex (male) at the actual capture sites of the more numerous sex (female). In order to compare Powdermill sex ratio data with results from other sites in eastern North America, a summary of hummingbird bandings by state through 1982 was obtained from the U.S. Fish and Wildlife Service's Bird Banding Laboratory. Additional records, through 1991, were obtained directly from banders in Maryland and Ohio. Sex ratios were calculated from data generated by eight banding programs in Maryland, Ohio, North Carolina, Louisiana, Missouri, and Oklahoma, for seasonal subsamples with $n \geq 20$. In analyzing all sex ratios, we used chi-square tests to detect departures from an expected 1:1 ratio of females to males.

Minimum annual survivorship of male and female hummingbirds was estimated on the basis of recapture or inferred survival of birds one or more years after banding, through 1990, using the weighted mean method (Spendelow 1984). We assumed (1) that all birds in the sample were site faithful residents, based on their having returned at least once; (2) that recapture did not affect subsequent survival or likelihood of recapture, or that the sexes were affected equally in this regard; and (3) that there was no significant variation in the survival rate of different age classes. Survivorship was calculated as equal to:

$$\sum_{i=2}^{a} X_i \Bigg/ \sum_{i=1}^{a-1} X_i$$

To test whether survivorship was equal for the sexes we compared the proportions of returning males and females, using a chi-square test. Sex differences in the mean minimum age of returning hummingbirds were assessed with a *t*-test. The minimum known age of returning hummingbirds was simply the number of years after banding, for birds that were HY when banded, or this plus one for AHY birds.

Comparisons of adult hummingbird body mass by sex and month were made using analysis of variance (ANOVA) and the GT2 method of pairwise multiple comparisons of means (Sokal and Rohlf 1981). Excluded from the adult female May, June, and July samples was a small number of individuals ($n = 17$) that were probably gravid, based on their physical appearance or large body mass (≥ 4.0 g) in the absence of visible fat deposits. ANOVA and GT2-tests were performed with BIOM (Rohlf 1987).

RESULTS

POWDERMILL SEX RATIOS

The ratios of female to male hummingbirds captured at different seasons at Powdermill are shown in the first line of Table 1. The ratio of immature birds, 1.1:1, was slightly, but significantly, female-biased ($\chi^2 = 6.14$, 1 df, $P < 0.05$). Annual totals were similar between the sexes in all years except 1963, when about twice as many immature males were recorded as immature females. During 1963, however, age and sex criteria were still being evaluated for the species (Leberman 1964): the sex of 26 immature birds and the age of 66 females was listed as unknown (Mulvihill and Leberman 1987). Results from subsequent years, when the age and sex of virtually every bird was determined, suggested that most "unknown" birds in 1963 were immature females. The greater difficulty in distinguishing this age/sex class has important implications for comparisons of Powdermill sex ratios to those from other stations, as discussed below.

The ratio of AHY females to males, averaged over all years, was significantly different from 1:1 in all seasons, and became progressively more skewed from spring through fall. During spring, total captures of males and females were similar in about half of the years, but the overall ratio was 1.4 (different from 1.0, $\chi^2 = 30.34$, 1 df, $P < 0.01$). The spring sample included both adult (AHY in the previous fall season) and immature (HY in the previous fall season) birds, because these two age classes are indistinguishable in the spring following a complete molt by all birds on the wintering grounds (Tyler 1940). The numbers of adults captured during the summer and fall seasons were biased in favor of females in all years and the overall ratios (summer, 3.1; fall, 4.1) were significantly different from 1.0 (summer, $\chi^2 = 100.28$; fall, $\chi^2 = 201.03$, 1 df, P's < 0.01). Fewer than five females were caught in only one fall season, while five or fewer males were caught in 23 of 28 years.

SEX RATIOS AT OTHER SITES IN THE EASTERN U.S.

Hummingbird data from eight banding operations in six states in the eastern and midwestern United States are compared with Powdermill in Table 1. Four of the operations were classified as "feeder-type." The hummingbirds in these samples were caught in feeder traps or in mist nets placed near feeders or other artificially concentrated food sources (e.g., ornamental flower gardens). Two stations were classified, along with Powdermill, as "nonfeeder-type." The hummingbirds in these samples were incidentally captured in mist nets placed in natural habitats as part of a generalized banding program. The capture method used for two samples was unknown.

In contrast to Powdermill, the sex ratio of immatures was male-biased for six of eight samples in Table 1, by as much as 2.5:1. The difference was significant for five samples. As noted above in connection with the anomalous immature sex ratio at Powdermill in 1963, male-biased immature sex ratios are probably due to the difficulty of assigning female hummingbirds to their proper age class. Young males lack the complete iridescent-red gorget of adult males, but they usually have streaked throats or a few red throat feathers that are distinctive. Immature females, on the other hand, differ only slightly from adult females in general appearance.

TABLE 1. Ratio of female to male Ruby-throated Hummingbirds for different ages and seasons at banding sites in the eastern United States. Samples from theses sites are designated as nonfeeder-type (NF), feeder-type (F), or type unknown (U). Asterisks (*) denote significant departure ($P < 0.05$) from expected ratio of 1.0. No ratios are given for samples with <20 birds.

Site	Years	Type	*n*	HY	AHY		
					Spring	Summer	Fall
Powdermill	28	NF	4,116	1.1*	1.4*	3.0*	4.1*
Maryland—A	23	NF	527	0.8*	1.4		5.1*
Maryland—B	12	NF	131	0.5	1.4		5.2*
Ohio	2	F	194	1.0	0.5	1.5*	
North Carolina	18	U	491	0.5*	0.7*	2.1*	
Louisiana	4	F	348	0.4*	0.5*	1.3	
Missouri	12	F	1,454	0.4*	1.2	1.3*	2.0*
Oklahoma—A	13	U	271	0.5*		1.2	3.3*
Oklahoma—B	6	F	849	1.0	0.5*	1.2	1.0

Spring ratios of adult hummingbirds favored males at two feeder stations. Significantly male-biased capture also occurred at one station where the trapping method was unknown. Twice as many males as females were caught in Ohio, but the difference was not quite significant ($\chi^2 = 3.48$, $0.05 < P < 0.10$). At the nonfeeder stations in Maryland, more females than males were caught, in a ratio similar to that at Powdermill, but the difference was not significant.

Summer totals at the other banding stations consistently favored females, although the difference was significant only in Ohio, Missouri, and North Carolina, where the bias was less than at Powdermill. Unfortunately, there were no summer data from the two nonfeeder stations. The fall ratio of adult females to males was significantly skewed in favor of females at every site but one (an Oklahoma feeder-trap station). At the Missouri feeder-trap station, the female-biased capture ratio was only half that observed at Powdermill. At the two Maryland sites, where hummingbirds were banded away from feeders, the ratio was similar to that observed at Powdermill. In general, the feeder samples produced adult sex ratios that were increasingly female-biased from spring through fall, like Powdermill and the other nonfeeder samples. The primary difference between feeder and nonfeeder samples was their beginning sex ratio: female-biased at nonfeeder sites; nearly equal to strongly male-biased at feeders.

RETURNS OF POWDERMILL HUMMINGBIRDS

Annual survivorship rate estimates based on the return data in Table 2 were 0.446 for females and 0.294 for males. A comparison of the proportions of returning males and females showed no significant difference ($\chi^2 = 1.28$, 1 df, $P > 0.05$), but the mean (±SD) minimum known age of returning males (1.83 ± 0.71 years; $n = 18$) was significantly less than that of returning females (2.47 ± 1.10 years; $n = 66$) ($t = 2.01$, 82 df, $P < 0.05$). Among the female returns are proportionately many more birds initially banded as AHY compared to males (Table 2). The greatest minimum known age for a returning female (six years) was twice that recorded for any male at Powdermill.

SEX DIFFERENCES IN BODY MASS

Mean masses for adult Ruby-throated Hummingbirds by month are given in Table 3. Adult females were significantly heavier than adult males ($F_{1,1746} = 17.553$, $P < 0.001$); both sexes differed significantly across months (females: $F_{4,1134} = 17.607$, $P < 0.001$; males: $F_{4,612} = 17.633$, $P < 0.001$) (Table 3). In females, mass did not change significantly between sequential months

TABLE 2. Return records (through 1990) of Ruby-throated Hummingbirds banded at Powdermill Nature Reserve. Number in each cell is the sum of actual returns and inferred presences based on later returns of banded individuals.

Age/sex when banded	Number of years after banding				
	1	2	3	4	5
AHY/F	27	15	6	3	1
HY/F	10	3	1		
AHY/M	7	2			
HY/M	6	2	1		
Total F	37	18	7	3	1
Total M	13	4	1		

TABLE 3. Body mass (grams) of Ruby-throated Hummingbirds, 1963–1990. Asterisks (*) denote a significant change ($P < 0.05$) from the previous month.

Month	*n*	Mean	SD	Range
		Male		
May	426	3.0	0.349	2.3–4.1
June	38	2.8*	0.302	2.4–3.4
July	46	2.9	0.288	2.4–3.7
August	88	3.2*	0.326	2.6–4.1
September	15	3.3	0.248	2.9–3.8
		Female		
May	591	3.4	0.287	2.7–4.7
June	76	3.4	0.286	2.8–4.0
July	124	3.3	0.309	2.6–4.2
August	275	3.3	0.354	2.7–4.5
September	165	3.5*	0.369	2.7–5.0

from May through August (GT2-test; *P*'s > 0.05); it increased from August to September (GT2-test; $P < 0.01$). In males, mass showed a significant decrease from May to June (GT2-test; $P < 0.01$), no difference between June and July (GT2-test; $P > 0.05$), an increase from July to August (GT2-test; $P < 0.01$), and no difference between August and September (GT2-test; $P > 0.05$).

DISCUSSION

IMMATURE SEX RATIOS

Of the four age/sex classes that can be recognized in the fall, adult and immature females are the most difficult to distinguish (Leberman 1972). We believe that the slightly (but significantly) skewed sex ratio in HY birds at Powdermill probably can be attributed to the incorrect age determination of a small number of adult females as immatures. We suspect that the male-biased sex ratios for immatures shown by most stations listed in Table 1 are also the result of the difficulty of determining the age of females; a great many immature females were probably coded as unknown age.

ADULT SEX RATIOS

The dramatic change in sex ratio for AHY birds from spring (1.4:1) through fall (4.1:1) can be explained in several ways: (1) adult males may migrate south in the late summer and fall by a different route than that taken in the spring; (2) there may be a capture bias that increasingly favors females from spring through fall; (3) males may suffer greater mortality than females, perhaps as a consequence of their smaller size. The reverse trend from fall (4.1:1) to spring (1.4:1) can be entirely explained by the inclusion in the spring "adult" sample of immature birds from the previous fall season. At Powdermill, immature birds outnumber adults by 3.4:1 in the fall (total fall samples for Powdermill are AHY-M, 109; AHY-F, 450; HY-M, 919; HY-F, 1002). A spring "adult" sample comprised of adults from the previous fall in a 4.1:1 ratio of females to males and nearly three and a half times as many immatures in a 1.1:1 sex ratio, has a ratio of 1.4:1 females to males, which is precisely that observed at Powdermill. This suggests that mortality rates for males and females and adults and immatures may, on average, be similar between breeding seasons.

THE DIFFERENTIAL MIGRATION HYPOTHESIS

Although data are not available for many sites in eastern North America, the localities represented in Table 1 are geographically widespread. At none of these sites is there the suggestion of a sex-ratio pattern complementary to Powdermill (i.e., more adult males than adult females captured in the summer or fall). With few exceptions, adult sex ratios at other stations are similar in direction and magnitude to those at Powdermill, particularly when possible biases associated with the "feeder-type" capture method are considered (see below). At present we have no evidence that adult male hummingbirds migrate south by a different route than adult females.

CAPTURE BIAS

Sex ratios are difficult to determine accurately for most species, due to differences in the detectability of males and females (Trivers 1972). We considered several possible sources of capture bias that might have contributed to the observed trend in sex ratios at Powdermill. The fact that male Ruby-throated Hummingbirds were smaller than females, combined with the fact that two different mist net mesh sizes (30 mm and 36 mm) were used at Powdermill, raised the possibility that we simply captured females more efficiently than males. If either mesh or hummingbird size was a factor, then proportionately more females should have been caught in 36 mm mesh nets. In 1987 and 1988, 16 of

112 adult females and 4 of 58 adult males were caught in 36 mm nets; there was no significant difference between the sexes in the proportion of birds caught in each mist net size ($\chi^2 = 2.01$, 1 df, $P > 0.05$). Among the less size dimorphic immatures, there was also no difference in the proportion of each sex caught in the two mist net sizes ($\chi^2 = 1.68$, 1 df, $P > 0.05$).

Another form of capture bias could have resulted from intersexual behavioral differences, if these somehow exposed females to capture more often than males. Differences in net wariness or net avoidance might have brought females into contact with mist nets more often than males, whose shorter wings and higher wing-disc loading make them more agile fliers (Feinsinger and Chaplin 1975, Rayner 1988). Furthermore, resident males could have improved in this regard as they became more familiar with the banding area. We tested this hypothesis by comparing the frequency of single and double recaptures of males and females within the same year (no individual was recaptured more than twice within a year). There was no difference between the sexes (males: 31, 3; females: 28, 2; $\chi^2 = 0.021$, 1 df, $P > 0.05$). Furthermore, when we corrected for differences in the number of males available for recapture compared to females (through the addition of a zero-recapture category), based on our overall female-biased adult sex ratio of 2:1, then significantly more males were recaptured ($\chi^2 = 14.31$, 2 df, $P < 0.05$). These data suggested that males were not more net wary or skilled at avoiding nets than females; in fact, they were probably less so. Direct observation at the Ohio station listed in Table 1 also suggest that females may be more skilled at escaping or avoiding nets and traps than males (S. J. Peters, pers. comm.).

It is plausible that seasonal patterns of habitat use by males may have differed from females such that males became less abundant in habitats sampled by our mist nets from spring through fall. Sex differences in habitat use during the breeding season are known for several species of North American hummingbirds (Stiles 1973, Armstrong 1987). A plot of capture locations for males and females during 1987 and 1988 showed that the greatest amount of overlap in captures of adult male and female hummingbirds (as a proportion of the maximum possible overlap) occurred in the spring (81.5%). We recorded much less overlap in summer (27.6%) and fall (44.7%). This suggested that something might be contributing to separation of the sexes in the banding area especially during summer and fall, and that our nets might better sample the habitats used by females. Since male hummingbirds generally are behaviorally dominant to females and demonstrate more distinctly food-centered territoriality (e.g., Pitelka 1942, Stiles 1973), the absence of males from the banding area would suggest that richer, or more concentrated food sources were available elsewhere. Two such food sources, in particular, might draw males away from the banding area. One is natural and one is associated with human activity. Mesic woodlands containing dense stands of bee balm (*Monarda didyma*) are widely available around Powdermill but were not sampled by our nets. *M. didyma,* which has been singled out as a key ecological feature of Ruby-throated Hummingbird territories (Saunders 1936), blooms from June to September (Jennings and Avinoff 1953). This coincides with the largest decline in the proportion of males in our banding samples. Another widely available food source not sampled at Powdermill are sugar-water feeders.

If we are correct concerning our hypothesis of greater energy stress in males due to their smaller size and vigorous territoriality (see below), then males would be expected to avail themselves more than females of concentrated, predictable food sources. Captures at such sites would be even more male-biased in the spring and summer if females require a greater proportion of insect food during the periods of egg-laying and nestling care (cf. Stiles 1973). Pickens (1944) found yellow poplar (*Liriodendron tulipifera*) near all Ruby-throated Hummingbird nests, and suggested that the abundant aphids typically found on this tree may have been the attraction for nesting females. To whatever extent rich, concentrated natural and artificial food sources are disproportionately attractive to or dominated by males during the breeding season (creating a female capture bias at Powdermill), we would expect hummingbird samples taken at such sites to have a reciprocal male capture bias.

EVIDENCE FOR MALE-BIASED MORTALITY

A third possible explanation for the change in adult sex ratio through the year is that males have a significantly higher mortality rate than females. At Powdermill, the lower survivorship estimate for males, based on a small sample, was not significantly different from an estimate of female survivorship. However, the significantly lower age of returning males (in large part due to the much smaller proportion of returning males that were AHY when initially banded, compared to females), and observed longevity differences between the sexes supported a hypothesis of lower male survivorship. Although sex differences in site fidelity could have affected these results, we minimized this possibility by restricting our analyses to birds that already demonstrated site fidelity by returning to Powdermill at least once.

In another banding study of Ruby-throated Hummingbirds, estimated annual survival rates based on a larger number of return records (female: $\hat{S} = 0.594$, $n = 106$; male: $\hat{S} = 0.250$, $n = 44$), were significantly different ($\chi^2 = 14.75$, 1 df, $P < 0.05$) (from data in Baumgartner 1989), and the greatest minimum known age of a returning female (nine years) was almost twice that of any male. This was despite the fact that adult sex ratios at the station where the study was done were either equal (summer and fall) or male-biased (spring) (Table 1; last entry). In the case of the Broad-tailed Hummingbird (*Selasphorus platycercus*), Calder et al. (1983) dismissed male-biased mortality as an explanation for lower rates of return by males than females, since the mean age of recaptured males and females did not differ significantly. Although they did not compare survivorship estimates based on returns of known site-faithful males and females, Calder et al. (1983) concluded that female bias among recaptures was mostly due to greater female site fidelity. Like the Baumgartner study, the greatest minimum age of a returning female (eight years) was nearly twice that recorded for males, while overall banding totals were slightly male-biased. The discrepancy between the sex ratio of birds banded (biased toward males) and possible differences between the sexes in survivorship (biased toward females) in these two studies may be linked to the fact that both employed feeders to attract birds for banding. If there is a male capture bias associated with this method, as we suggest, then female-biased sex-ratio differences would be masked to some degree, and apparent differences in survivorship favoring females would be, if anything, conservative.

REVERSED SEXUAL SIZE DIMORPHISM AND MALE SURVIVAL

If a sex-related difference in survival exists, then the smaller size of males may be an important contributing factor to mortality in this sex. Powdermill sex-ratio data suggest that there is a substantial loss of hummingbird males over the course of the nesting season, more so than over winter or during the migration periods (cf. Yasukawa 1987). In fact, our sex-ratio data support a parsimonious hypothesis of no relative change in the number of male and female and adult and immature hummingbirds between fall and spring. If this is the case it suggests that the smaller body mass of males places them at a relatively greater mortality risk only under energetics parameters associated with the breeding season.

During the breeding season, in particular, males may experience more energy stress than females. Their smaller body mass means that males have higher metabolic requirements per unit weight, more rapid heat loss, and lower fasting endurance than females, all other things being equal; therefore, they may develop an "energy crisis" more quickly (Calder 1974a, 1975). Behavioral differences between the sexes may add to this inequality. Male Ruby-throated Hummingbirds have an energetic aerial display that is used in both aggressive and courtship contexts (Whittle 1937, Pitelka 1942); display behavior is not well-developed in females (Pitelka 1942). Furthermore, male hummingbirds may need to both defend large breeding territories and commute to distant feeding areas, if areas with high concentrations of nectar-rich flowers are not best for encountering nesting females, or if the males' breeding territories do not contain sufficient energy reserves to sustain them (Stiles 1973, Armstrong 1987). Females apparently limit territorial behavior to the immediate vicinity of their nest site, foraging off-territory as needed (Pitelka 1942), and their territorial behavior is generally not as vigorous as that of males (Pitelka 1942, Stiles 1973). While they are nesting, the microenvironment surrounding their nests and the insulative qualities of their nests may give females a more favorable energy balance overnight than do the roost sites chosen by males (Calder 1974a, 1974b). During the breeding season, similar-sized male and female Anna's Hummingbirds (*Calypte anna*) were calculated to have similar daily energy requirements only if males became torpid overnight (Calder 1975), a condition that carries with it the risks of coordination loss, non-arousal, or cold death (Calder 1974a).

That the nesting season is energetically expensive for male Ruby-throated Hummingbirds is

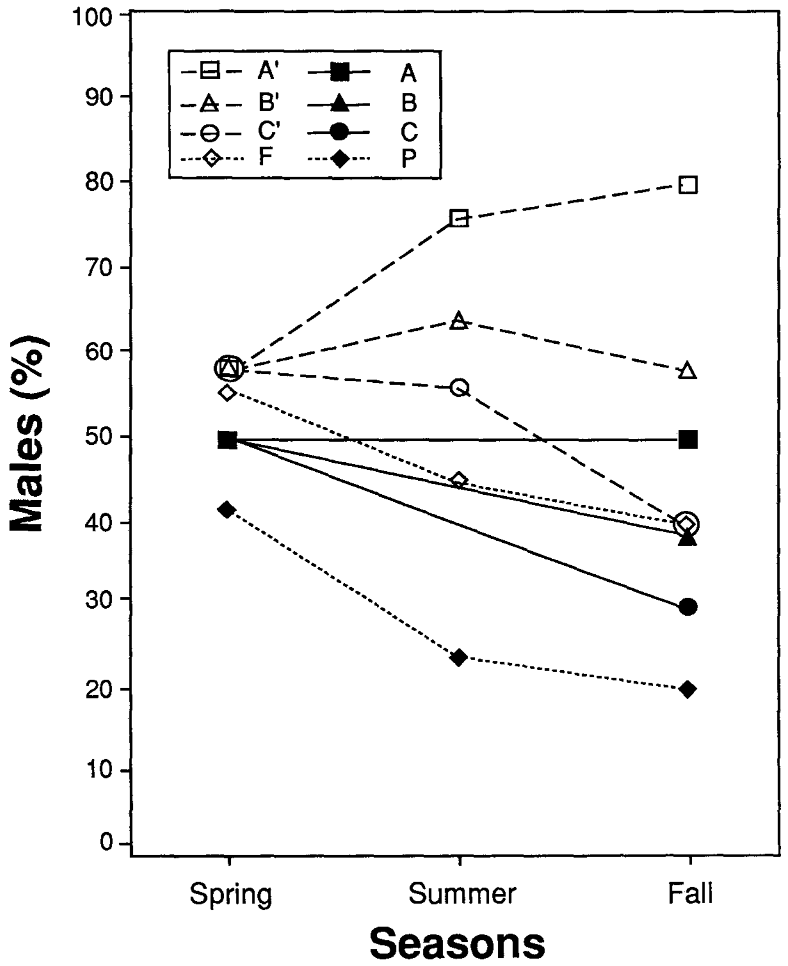

FIGURE 1. Increasingly female-biased Powdermill sex ratios (P) viewed as the sum of different levels of male mortality during the breeding season (A, B, C) and female capture bias resulting from disproportionate use by males of habitats not sampled at Powdermill (A − [A − P]; B − [B − P]; C − [C − P]). We considered three levels of male mortality: A—equal mortality (null hypothesis); B—male-biased mortality based on Powdermill returns (this study); C—male-biased mortality based on Oklahoma returns (from data in Baumgartner [1989]). A′, B′, and C′ are the predicted ratios at sites with a male capture bias exactly corresponding to female capture bias at Powdermill for each level of male mortality (A + [A − P]; B + [B − P]; C + [C − P]). Line F represents the average seasonal sex ratios calculated from all feeder stations in Table 1 (in calculating these averages non-significant values were treated as 1.0).

suggested by significantly lower masses for males in June compared to May and the maintenance of this mass depression through July. As a species, the Ruby-throated Hummingbird is near the extreme of small size that is physiologically possible for an endothermic vertebrate. It is conceivable that males approach a critical body mass during the summer. Below this critical mass they may have to abandon nocturnal homeothermy for hypothermic torpor (Lasiewski 1963, Hainsworth et al. 1977), and may starve overnight (i.e., they may have insufficient reserves to elevate their metabolism or to fly to food sources following overnight torpor) or during periods of inclement weather. Ironically, energy stress resulting in breeding season mass loss and concomitant increased mortality risk has been proposed as an important cost associated with sexual selection for *increased* male size in the Red-winged Blackbird (*Agelaius phoeniceus*) (Yasukawa 1987). Recently, Calder et al. (1990) reported a diurnal pattern of voluntary control of body mass through feeding restraint in a territorial male Rufous Hummingbird (*S. rufus*). They argued that this was adaptive for improved aerial performance in territorial defense and courtship. This supported a hypothesis that breeding male hummingbirds give priority to courtship-related activities, not energy intake. At dusk this restraint was replaced by hyperphagia, which resulted in a dramatically increased intake of sucrose solution that provided energy sufficient to preclude the need for overnight torpor. The generality of this pattern of energy intake is not known, even for Rufous Hummingbirds, but there is some evidence that male Ruby-throated Hummingbirds may also increase their feeding activity late in the day (Pitelka 1942, Lasiewski 1963). Whether or not the reduced summer mass of male Ruby-throated Hummingbirds at Powdermill reflects an adaptive, diurnal pattern of weight restriction (something that our data do not address), we argue that it nevertheless carries with it an attendant mortality risk, particularly when ad libitum food supplies are not insured (cf. Calder et al. 1990).

CONCLUSIONS

The increasingly female-biased sex ratio of Ruby-throated Hummingbirds from spring through fall at Powdermill is probably a consequence of both capture bias and differential mortality during the breeding season. In order to assess the possible contributions of each to observed sex ratio variation at Powdermill and elsewhere, we apportioned the female sex ratio bias at Powdermill between these two causes based on three combinations of male-biased mortality and female-biased capture (Fig. 1). As mentioned above, we view sex ratios based on samples taken at feeders, or other concentrated food sources, as incorporating a reciprocal capture bias to that hypothesized for Powdermill. From this model, a combination of the most unequal survivorship (favoring females) and the least amount of capture bias (favoring females at Powdermill and males elsewhere) best reconciles the overall seasonal sex ratios from Powdermill and average sex ratios calculated from feeder samples. Of course, the relative contributions of mortality and capture bias to observed sex ratios in this species are doubtless labile, in response to annual and geographical variation in population size, food availability, climate and other factors.

Smaller size in male Ruby-throated Hummingbirds, exaggerated by a reduction in body mass during the breeding season, appears to represent a trade-off of survival for potentially greater access to females during the nesting season; this is consistent with the widely held belief that traits that are under sexual selection are stabilized by natural selection. Recognizing the gaps and shortcomings in existing data, we offer this conclusion tentatively, primarily as a springboard for additional study. A clearer understanding of the possible relationship between reversed sexual size dimorphism in some hummingbirds and lower male survivorship awaits detailed comparative studies of habitat selection, time-energy budgets, reproductive success, and mortality between the sexes and among different-sized males in a population.

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