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Skewed Sex Ratios in Cooper's Hawk Offspring

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The selective forces influencing avian sex ratios have received much recent attention (e.g. Bednarz and Hayden 1991, MacWhirter 1994, Weatherhead and Montgomerie 1995, Leroux and Bretagnolle 1996). Gowaty (1993) and Weatherhead and Montgomerie (1995) noted the paucity of information on sex ratios in avian offspring and called for more empirical data. Here, we provide new data for Cooper's Hawk (*Accipiter cooperii*) based on 16 years of study in Wisconsin.

Rosenfield et al. (1985) found that sex ratios did not differ significantly from unity (53.5% males, 46.5% females; χ^2 test, $P > 0.25$) in 71 broods of Cooper's Hawks in Wisconsin from 1980 to 1983. Further research through 1995 has increased this sample substantially and changed our earlier conclusion. Based on morphometric differences that are apparent at 11 to 12 days of age (Meng 1951, Rosenfield and Bielefeldt 1993a), we determined the sex of nestling Cooper's Hawks (ages 12 to 22 days; $\bar{x} = 16$ days) at 372 nests throughout Wisconsin from 1980 to 1995. We determined sex ratios at hatching (which we presume are the same as at fertilization) in nests where complete clutch sizes were known, all eggs hatched, and all young survived to an age at which sex could be

determined (see Newton and Marquiss 1979, Rosenfield et al. 1985). We also calculated sex ratio among fledglings (≥ 25 days of age) when, following banding and sexing of nestlings (and some subsequent mortality), we revisited nests opportunistically for other purposes (Rosenfield and Bielefeldt 1993a, b). For temporal analyses of offspring sex ratios, time of clutch completion was determined by back-dating from nestling age, assuming a 34-day incubation period (Rosenfield and Bielefeldt 1993a).

Because we found no significant differences in sex ratios among years at fertilization ($\chi^2 = 13.87$, df = 15, $P = 0.54$) or the nestling stage ($\chi^2 = 16.07$, df = 15, $P = 0.38$), we pooled data across years. We examined sex ratio at fertilization in 554 eggs at 130 nests (Table 1). Males were significantly more numerous (55%) at conception ($\chi^2 = 6.0$, df = 1, $P = 0.01$). We also examined sex ratio in 1,337 nestlings at 372 nests (Table 1). Again, males were significantly more numerous (54%) at this stage ($\chi^2 = 9.55$, df = 1, $P = 0.002$). We further examined sex ratios in 105 fledglings ($\bar{x} = 32$ days old, range = 25–56 days) at 33 nests. Once again, the sex ratio was significantly male-biased (60%; $\chi^2 = 4.2$, df = 1, $P = 0.04$). Annual samples of fledglings were too small for analyses of year-to-year sex ratios.

Sex ratio at fertilization did not vary significantly

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TABLE 1. Sex ratios in complete clutches and in broods of Cooper's Hawks in Wisconsin, 1980–1995.

	Clutches					Broods				
Year	n	No. males	No. females	Total	% Males[a]	n	No. males	No. females	Total	% Males
1980	2	3	4	7	43	9	14	15	29	48
1981	8	21	17	38	55	16	42	24	66	64
1982	9	17	19	36	47	20	30	37	67	45
1983	5	13	12	25	52	26	51	43	94	54
1984	8	21	13	34	62	23	49	41	90	54
1985	7	16	15	31	52	22	41	38	79	52
1986	9	16	18	34	47	22	39	44	83	47
1987	7	16	17	33	48	18	40	33	73	55
1988	9	19	21	40	48	21	42	36	78	54
1989	12	24	24	48	50	25	53	41	94	56
1990	7	18	11	29	62	26	59	37	96	61
1991	13	37	17	54	69	35	76	54	130	58
1992	10	26	18	44	59	27	53	40	93	57
1993	9	25	14	39	64	30	59	48	107	55
1994	7	18	9	27	67	22	38	28	66	58
1995	8	16	19	35	46	30	39	53	92	42
Total	130	306	248	554	55	372	725	612	1,337	54

[a] Presumed sex ratio at fertilization based on complete clutches with no egg or nestling mortality up to age that nestlings could be sexed.

with clutch size, nor did sex ratio among nestlings vary with brood size (Table 2). Nestling sex ratios did not differ temporally between 226 "early" nests (clutches completed ≤7 May; 53% males, $n = 863$ nestlings) and 146 "later" nests (clutches completed >7 May; 56% males, $n = 474$ nestlings; $\chi^2 = 0.64$, df = 1, $P = 0.42$). Overall, 16 years of data from Wisconsin indicated that sex ratios in Cooper's Hawk offspring at fertilization, and at the nestling and fledgling stages, were significantly and consistently skewed toward males (which accounted for 54–60% of offspring at all three stages).

It is possible that a loss of one or more eggs from some "complete" clutches went undetected because of the time lag between the completion of laying and our examination of nests. If so (and if laying sequences and egg losses were nonrandom with respect to sex), then our calculations of sex ratio at fertilization might be in error. We doubt that undetected egg loss affected our analysis of sex ratio at fertilization. As shown in Table 2, Cooper's Hawks in Wisconsin typically lay 4 or 5 eggs and only rarely lay 6 eggs (see also Rosenfield and Bielefeldt 1993a). Thus, it is highly unlikely that egg loss occurred in 5-egg clutches. Data from 5-egg clutches ($n = 49$; see Table 2) yielded a sex ratio at fertilization (56% males) that was virtually identical to our estimate for all complete clutches (55% males). Furthermore, even if we were to assume that *all* 4-egg clutches were the product of undetected egg loss, sex ratio is essentially unchanged (54%). These typical clutches of 4 or 5 eggs provided 88% of complete clutches and 91% of total eggs in those clutches (Table 2). Therefore, we suggest that our methods yielded reasonably accurate estimates of sex ratio at fertilization, at least for complete clutches.

Moreover, if adjustments in sex ratio do occur during incubation in reduced clutches (taken together), or clutches failing to show a full hatch, then these adjustments appear to act in a way that produces a nestling sex ratio (54%) almost equivalent to the ratio at fertilization (55%) for complete clutches (Table 1).

Skewed sex ratios apparently originate at fertilization, with little or no differential mortality in the sexes between conception and fledging. These results contrast with those of Wikman (1976) and Newton and Marquiss (1979), who failed to find skewed offspring sex ratios in their large samples from the congeneric Northern Goshawk (*A. gentilis*) and Eurasian Sparrowhawk (*A. nisus*), respectively. Male-biased offspring sex ratios have been reported in other falconiforms, including Montagu's Harrier (*Circus pygargus*; Leroux and Bretagnolle 1996), Harris' Hawk (*Parabuteo unicinctus*; Bednarz and Hayden 1991), Golden Eagle (*Aquila chrysaetos*; Edwards et al. 1988), and American Kestrel (*Falco sparverius*; Wiebe and Bortolotti 1992).

A long-term study was needed to document that offspring sex ratio in the Cooper's Hawk deviated significantly from unity. Indeed, we estimated through cumulative analyses that about 10 years (770 young from 228 nests) were required for a statistically reliable confirmation of a skewed sex ratios in nestlings. Our enlarged data set suggests that we committed a Type II error in our earlier short-term study (i.e. Rosenfield et al. 1985), partly because the study included two of the four years (out of 16 years total) in which offspring sex ratios favored females (Table 1).

Our results are consistent with Fisher's equilibrium hypothesis (1930). According to Fisher's theory, selection should favor equal parental expenditure in

TABLE 2. Sex ratios by clutch size and brood size of Cooper's Hawks in Wisconsin, 1980–1995.

	Clutches				Broods			
Size	*n*	No. males	No. females	% Males[a]	*n*	No. males	No. females	% Males
1	—	—	—	—	24	14	10	58
2	2	3	1	75	37	36	38	49
3	13	25	14	64	86	141	117	55
4	65	140	120	54	147	313	275	53
5	49	136	109	56	75	212	163	57
6	1	2	4	33	3	9	9	50
Total	130	306	248	55[b]	372	725	612	54[b]

[a] Presumed sex ratio at fertilization based on complete clutches with no egg or nestling mortality up to age that nestlings could be sexed.
[b] Sex ratios did not vary among clutch sizes (Fisher's exact test, $P = 0.54$) or brood sizes ($\chi^2 = 2.28$, df $= 5$, $P = 0.81$).

offspring of both sexes. Thus, offspring sex ratios at the termination of parental care should be skewed toward the less expensive sex (Howe 1977). Cooper's Hawks are highly dimorphic, with males being about two-thirds the mass of females at fledging (Meng 1951). Accordingly, males would require fewer resources during development and therefore would be the cheaper sex (cf. Bednarz and Hayden 1991). The turnover time among generations in the population we studied is six years (Rosenfield et al. 1995). Thus, our study encompassed approximately three generations of adults and their offspring. Skewed sex ratios in offspring did not appear to result from proximate factors operating on an annual, cohort, or other short-term basis.

According to Gowaty's (1993) differential dispersal hypothesis, sex differences in natal dispersal may lead to different degrees of competition between parents and their offspring such that offspring sex ratios should be skewed toward the sex that disperses the farthest. Our results do not support this hypothesis. Our data on natal dispersal for this population are limited, but median distance for males was 6.4 km (range 2.4 to 35.2 km, *n* = 10), whereas two females dispersed 14.4 km and 79.0 km (Rosenfield and Bielefeldt 1992, 1996). We suggest that natal dispersal distances of females are greater than those of males (at the very least, females do not appear to disperse shorter distances than males). Natal dispersal distances are greater for females in other raptor species as well (Newton 1979). If our inference about natal dispersal in Cooper's Hawks is correct, then the differential dispersal hypothesis would predict either an offspring sex ratio of unity (if natal dispersal is unbiased with regard to sex) or an excess of females (if females disperse farther than males). Our results, however, show a significant skew toward males.

We have been able to address only two of several hypotheses offered to explain avian sex ratios, as reviewed by Bednarz and Hayden (1991), Gowaty (1993), and MacWhirter (1994). Long-term empirical data on a wider variety of species are needed to elucidate the potential range of selective forces influencing avian

sex ratios. Whatever factors are affecting offspring sex ratios in the Cooper's Hawk population in Wisconsin, they appear to be operating on a long-term basis across generations, as Fisher's hypothesis predicts.

Another selective force that might operate across generations involves extrapair copulations (EPCs), now known to occur in many avian species (Birkhead and Møller 1992). Insofar as unpaired males are able (unlike unpaired females) to achieve reproductive output through EPCs, males will show greater future reproductive potential than females (Trivers and Willard 1973). Thus, it should be adaptive for parents to skew offspring sex ratios toward males in bird species where EPCs are prevalent. Studies of parentage in Cooper's Hawk broods (and in other species with male-biased sex ratios at fertilization) would be needed to test this prediction.

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Social Strategy and Cover in Savannah Sparrows

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In social vertebrates, group formation results from the collective response of individuals to environmental and social conditions. An individual's decision to join or leave a foraging group depends on the relative costs and benefits of group membership. Benefits to flock members include more effective predator detection (Powell 1974, Kenward 1978, Dekker 1980, Lindström 1989), an increase in foraging rate through reduced vigilance (e.g. Pulliam 1973, Caraco 1979, Barnard 1980), reduced probability of predation (Powell 1974, Dekker 1980, Lindström 1989), and an

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enhanced capacity to locate high-quality patches (Krebs et al. 1972). Costs to flock members include division of available food resources between flock members (Pulliam and Millikan 1982), a reduction in foraging rate due to increased social interference or aggression (e.g. Goss-Custard 1976, Caraco 1979, Barnard 1980, Caraco et al. 1980, Elgar 1987), and an increased probability of detection by predators (Vine 1973, Taylor 1979).

Both the costs and benefits of flock membership may increase with group size. Thus, changes in group size may be a dynamic response to the shape of specific cost/benefit functions (Pulliam 1976, Pulliam and Caraco 1984, Elgar 1987). Cost/benefit functions may change with environmental conditions. In heterogeneous or dynamic environments, flock size may