

(i.e. whether there was a less than expected number of mixed-sex versus single-sex broods [see Bortolotti 1986b] in years of low food abundance).

Edwards et al. (1988) present some interesting and provocative results: in particular, recognition of the coincidence in temporal patterns of prey abundance and sex ratios. However, sex ratios and prey numbers do not appear to coincide as closely as one might expect if brood reduction were the causal factor. In the first few years of study, prey abundance declined, yet the proportion of males increased. Similarly, in the last few years, prey numbers were low, yet the percentage of males was very high. A time-lag between prey abundance and proportion of males may even be evident (see their fig. 1).

The data presented by Edwards et al. (1988) allow additional statistical analyses. If a food shortage increased the frequency of brood reduction, then the mean brood size in low-food years should be less than in high-food years. A one-tailed Mann-Whitney U test of this is significant ($U = 10.5$, $P < 0.05$). According to the sex-biased siblicide hypothesis, the percentage of males that fledge in the population should be inversely related to the average brood size. A Kendall rank correlation was nearly significant ($\tau = 0.289$, $P = 0.069$, one-tailed), offering weak support for the general conclusions in the original paper.

One advantage of the previous analysis is that it does not require a prediction of what the sex ratio should be in the absence of siblicide. The assumption of a 1:1 sex ratio is problematic for Edwards et al. (1988) because their population has a disproportionate number of males. They propose that siblicide depresses the male bias, but they do not offer an explanation for why the bias exists in the first place. The

strongly skewed sex ratios could be artifacts of small samples, or the result of a bias in assigning sex to fledglings on the basis of size (Edwards and Kochert 1986). It seems plausible that something out of the ordinary is happening with eagle sex ratios; however, testing only the sex-biased siblicide hypothesis seems too limited for this phenomenon.

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Sex Ratios of Fledgling Golden Eagles and Jackrabbit Densities

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Edwards et al. (1988) documented significant ($P < 0.05$) male-biased deviations from a 1:1 sex ratio among fledgling Golden Eagles (*Aquila chrysaetos*) during three years (1979, 1981, 1983) and throughout their study (1970-1984). They suggested that biased sex ratios resulted from higher frequencies of facultative siblicide in mixed-sex broods. Female offspring are larger than similar-age males; siblicide should thus occur most frequently among mixed-sex broods in which the female hatches first, because nestling size disparities are largest in such broods (Edwards and Collopy 1983, see also Bortolotti 1986). Edwards et al. predicted that

if facultative siblicide is directed disproportionately towards male offspring and if it occurs most frequently when prey are scarce (but see Mock 1985, Simmons 1988), then the proportion of males in the fledgling population should increase with prey abundance.

Edwards et al. claimed that they found support for this prediction, but this support came by a very circuitous route. They fitted sine curves with 10-yr periodicities to 14 and 15 yr of data on black-tailed jackrabbit (*Lepus californicus*) abundances and fledgling sex ratios (proportion of males), respectively, and observed that both curves were explanatory ($P < 0.05$), and furthermore, that the two curves were not significantly different ($P = 0.57$). They therefore concluded that "fledgling sex ratio was highly correlated with jack rabbit density" (p. 795).

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Taking a more straightforward approach, I correlated fledgling sex ratios directly with jackrabbit abundances (visually estimated from Edwards et al. 1988: fig. 1) and detected no relationship (Spearman rank correlation, $r_s = -0.003$, $P = 0.99$). There was, however, a trend towards higher sex ratios during years of small fledged brood sizes ($r_s = -0.423$, $P = 0.12$; Edwards et al. 1988: table 1, fledged brood size = [males + females]/no. broods). This is contrary to Edwards et al.'s hypothesis that biased sex ratios were the result of higher siblicidal mortality among male offspring, because fledgling males were more prevalent during years in which many Golden Eagles fledged only one young.

During two additional years (1973, 1974), sex ratios were also strongly male-biased ($0.05 < P < 0.10$). Thus, male-biased sex ratios occurred during 3 of 9 yr of jackrabbit scarcity ($<25/\text{km}^2$) and 2 of 5 yr of jackrabbit abundance ($>25/\text{km}^2$).

Edwards et al.'s data are inconsistent with their hypothesis of sex-biased siblicide. Their hypothesis predicts sex ratios of unity during years of high prey abundance, and ratios of 0.75:1 in years of low prey abundance (assuming that clutch size is two, sex determination is random, all males in F-M broods are siblicide victims, and all other mortality is random with respect to sex). Because all significant deviations involved sex ratios greater than unity, Edwards et al.'s data indicate nonrandom primary sex ratios, greater nestling mortality among females, and/or inaccurate sex determination.

I suspect that inaccurate sex determination may have contributed to the highly male-biased sex ratios. Edwards et al. sexed nestlings using a discriminant function derived from body mass and foot pad measurements of 49 (adult and subadult?) eagles found dead on or near their study area (Edwards and Kochert 1986). Discriminant functions are often less accurate when applied to new data sets; this seems especially likely when an equation from dead adults is used to sex pre-fledglings. Moreover, because their sexing criteria relied on body mass (which is not independent of nutritional status, digestive tract contents, or stage of development), accuracy of sex determination may have varied annually with food (jackrabbit) abundance. Bortolotti (1984b, see also 1984a) observed non-overlapping distributions of foot pad measurements for nestling male and female Bald Eagles (*Haliaeetus leucocephalus*) beginning at 45 days of age, but these birds were not under severe nutritional stress (Bortolotti 1984b). However, if growth rates of nestling Golden Eagles were substantially retarded by insufficient food, some females could have been improperly identified as males. I maintain that the sexing criteria used by Edwards et al. requires critical verification before it can be used on pre-fledgling Golden Eagles.

If their indirect method of sex determination was accurate, then Edwards et al. have certainly demonstrated nonrandom sex ratios among fledgling Golden Eagles. As in most cases of biased sex-ratios, however, explaining the phenomena (both proximately and ultimately) is decidedly more difficult than demonstrating it. Critical testing of the sex-biased siblicide hypothesis will require an examination of sex ratios within broods, rather than among broods. Presumably the authors have the necessary data to do this (i.e. sex ratios should be lower in one- vs. two-chick broods during years of jackrabbit scarcity). However, if sex allocation is nonrandom with respect to clutch size, laying order, parental quality, or local resource competition (e.g. Clark 1978, Verme 1983, Weatherhead 1985, Bortolotti 1986, Clutton-Brock 1986), even this could be an ambiguous test unless the sex of hatchlings was also recorded.

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