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Sex ratios in broods of the Lesser Kestrel *Falco naumanni*

Sex ratio theory (Fisher 1930) holds that the ratio of male and female offspring should equal the inverse ratio of the cost of rearing them. Many raptorial birds show some degree of reversed size dimorphism and have provided interesting subjects for testing Fisher's predictions. Data from most falconiforms suggest, however, that fledging sex ratios do not deviate from unity in that group (see review in Newton 1979). Exceptions seem to be the Hen Harrier *Circus cyaneus* where females, the larger sex, outnumber males (Picozzi 1980), and

some populations of the Golden Eagle *Aquila chrysaetos* (Edwards *et al.* 1988). Sex-specific growth patterns have been proposed by Richter (1983) as a mechanism to balance sex ratios in species showing a pronounced sexual dimorphism, the smaller sex developing more quickly to reduce mortality in the presence of large siblings. In that manner, Fisher's theory would be still valid in raptors.

On the other hand, a seasonal variation in the primary sex ratio has been reported in broods of Common Kestrels *Falco tinnunculus* (Dijkstra *et al.* 1990). Early clutches contained more males but the reverse was true for late clutches, so the overall sex-ratio was unity. Such a sex ratio bias implies a non-random segregation at meiosis. Village (1990) suggested that this phenomenon should be examined in other kestrel populations, or in raptors where sexing of nestlings was more certain.

Adult Lesser Kestrels *Falco naumanni* exhibit a strong dichromatism (Village 1990), although most body measurements overlap between the sexes (Cramp & Simmons 1980). According to Bijlsma *et al.* (1988), the wing-length ratio in adults (female/male) is 1:1, and the weight ratio 1.1:1. The juvenile plumage of both sexes resembles that of adult females. The first objective of this study was to find a way of sexing Lesser Kestrels by their juvenile plumage. This has been previously suggested (Cramp & Simmons 1980, Bijlsma *et al.* 1988), but never demonstrated with any marking scheme or laboratory technique. Once we had established a reliable sexing method, our aims were, first, to estimate overall sex ratio among nestling Lesser Kestrels and, second, to find out whether there are intra- or interannual variations in the sex ratio.

During 1988–90 we sexed nestling Lesser Kestrels from eight colonies located in the southern Spanish provinces of Sevilla (7) and Cádiz (1). Males and females were distinguished by the colour of their rectrices and upper-tail coverts (greyish or cinnamon in males; brown and more heavily streaked in females), recorded when the young were ringed at 2–4 weeks after hatching. We were unable to distinguish between complete broods and depleted broods because clutch-size was unknown for most of the nests.

To test whether the nestling sex ratio changed during the breeding season, we divided every breeding season into three periods, defined by the dates when one-third, two-thirds, and all of the clutches had been laid. Mean laying dates varied significantly from year to year (Kruskal–Wallis test, $\chi^2 = 62.94$, $P < 0.001$, $n = 310$; unpubl. data).

Forty-five Lesser Kestrels born in 1988 and 1989 were subsequently seen after their first moult, when the sexes become dichromatic (Cramp & Simmons 1980). All of them had been correctly sexed, indicating that our sexing procedure is reliable.

During the study period we sexed 246 males (50.3%) and 243 females (49.7%). There was no significant difference from a nestling population sex ratio of 1:1, either in different years (1988: $\chi^2 = 0.025$, $P = 0.87$; 1989: $\chi^2 = 0.006$, $P = 0.93$; 1990: $\chi^2 = 0.147$, $P = 0.70$) or overall ($\chi^2 = 0.08$, $P = 0.92$). Broods contained 1–5 nestlings. The comparison of the observed frequencies of broods of different sex composition with those expected from the binomial expansion again showed no significant difference from an equal sex ratio (Table 1). To perform the latter analysis we assumed that the sex of any young was independent of that of all others. We excluded broods of five because of the small sample size. There was no evidence of a change in sex ratio during the season, either within years or for the three years combined (Table 2).

Brood size	Number of broods of each sex composition					Difference from 1:1
1	M 18 (18)	F 18 (18)				$\chi^2_1 = 0.028$, $P = 0.86$
2	MM 12 (19.5)	MF 45 (39)	FF 21 (19.5)			$\chi^2_2 = 3.340$, $P = 0.06$
3	MMM 7 (7.3)	MMF 24 (22.1)	MFF 22 (22.1)	FFF 6 (7.3)		$\chi^2_3 = 0.435$, $P = 0.80$
4	MMMM 1 (1.4)	MMMF 7 (5.7)	MMFF 11 (8.6)	MFFF 3 (5.7)	FFFF 1 (1.4)	$\chi^2_4 = 2.507$, $P = 0.47$

Table 1. Frequency distribution of Lesser Kestrel broods of different sex composition. In parentheses, frequencies expected from the binomial expansion assuming a sex ratio of unity. M = male, F = female.

Period	1988		1989		1990		All years	
	Males	Females	Males	Females	Males	Females	Males	Females
1	34 (50.7)	33	34 (50.0)	34	42 (50.0)	42	110 (50.2)	109
2	28 (45.9)	33	32 (50.7)	31	32 (54.2)	27	92 (50.3)	91
3	16 (51.6)	15	14 (48.2)	15	14 (51.8)	13	44 (50.6)	43
	$\chi^2_2 = 0.40$, $P = 0.8$		$\chi^2_2 = 0.05$, $P = 0.9$		$\chi^2_2 = 0.24$, $P = 0.8$		$\chi^2_2 = 0.003$, $P = 0.9$	

Table 2. Number of nestling Lesser Kestrels of each sex in three consecutive periods of the breeding season. The periods are defined by the dates each year when one-third, two-thirds and all clutches were laid. In parentheses, percentage of males

Because we first visited many of the nests when the nestlings were well-grown, we could not tell if the sex ratio among fledglings reflected that at hatching. Newton & Marquiss (1979) found that the sex ratio among nestling Sparrowhawks *Accipiter nisus* was unity in both complete and depleted nests. We could not distinguish depleted and complete broods in every case. However, the dead nestlings we found showed no biased sex ratios (23 males and 24 females sexed by their plumage). Reversed size dimorphism, a possible distorting factor regarding Fisher's predictions, is very slight in Lesser Kestrels. On the other hand, Lesser Kestrels are basically monogamous, and both sexes have a similar interannual adult survival (unpubl. data). Therefore, in terms of fitness, the parental generation would have similar expectations by producing male or female descendants.

Skewed sex ratios among nestlings have been reported in the Hen Harrier, which is often polygynous (Picozzi 1980), and the Golden Eagle, in which siblicide is not uncommon (Edwards *et al* 1988). But limited sample size and inaccuracy in sex determination may have biased those results (see Bortolotti 1989 and Arnold 1989).

A change in sex ratio at fledging across the breeding season is not evident in the Lesser Kestrel, and mechanisms of prenatal sex-selection suggested in the closely related Common Kestrel (Dijkstra *et al.* 1990) do not seem to be operating in this case.

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