Seasonal and interannual variations in the sex-ratio of Lesser Kestrel *Falco naumanni* broods

Sex allocation in avian broods has been examined to test the pre-
dictions of Fisher's (1930) theory of sex-ratios. Sex-ratios at birth
do not usually differ from parity in birds and mammals (Charnov
1982, Clutton-Brock 1986). In sexually dimorphic species, however,
an unequal parental investment in male and female offspring may
shift the sex-ratio after birth (secondary sex-ratio), usually in favour
of the sex which costs less to rear (Howe 1977, Roskaft & Slagsvold
1985).

Sex allocation may also become skewed under certain environ-
mental constraints or when the relative fitnesses of the sexes vary
(Trivers & Willard 1973, Myers 1978, Charnov 1982). Dijkstra *et al.*
(1990) reported that first clutches of the Kestrel *Falco tinnunculus*
contained more males but that the reverse was true for late clutches.
These authors explained the trend in terms of the different future
reproductive output of males and females. Other hypotheses posed
to explain adaptive sex allocation and which might be relevant to
birds of prey (Olsen & Cockburn 1991) are the "local resource com-
petition hypothesis" (Clark 1978), which suggests that parents should
invest more in the sex with which they compete less, and the hy-
pothesis of "antagonism in selection pressures on the sexes" (Olsen
& Cockburn 1991), according to which parents with small body-size
should tend to produce the smaller sex and *vice versa.*

The secondary sex-ratio has already been studied in a population
of Lesser Kestrels *Falco naumanni* in southern Spain (Negro & Hiraldo
1991). These authors found no seasonal or overall sex-ratio devia-

Table 1. *Number of female (♀), number of male (♂) and percentage of male (%♂) Lesser Kestrel fledglings according to population (Sevilla or Monegros), year and relative laying date (grouped into six 10-day periods). Significance levels (p) correspond to a two-tailed binomial test.*

	Periods (days of year)																		Total of year			Signifi-cance
	1 (91–100)			2 (101–110)			3 (111–120)			4 (121–130)			5 (131–140)			6 (141–150)						
	♀	♂	%♂	♀	♂	%♂	♀	♂	%♂	♀	♂	%♂	♀	♂	%♂	♀	♂	%♂	♀	♂	%♂	
Sevilla																						
1988							21	30	58.8	36	31	46.2	13	5	27.7	1	6	—	71	72	50.3	n.s.
1989										34	35	50.7	45	42	48.2	1	0	—	80	77	49.1	n.s.
1990							22	25	53.2	56	60	51.7	4	3	—				82	88	51.7	n.s.
1991							3	7	—	107	88	45.1	39	34	46.5	1	1	—	150	130	46.4	n.s.
1992							74	64	46.3	35	24	40.6	1	3	—				110	91	45.2	n.s.
1993	2	0	—	11	9	42.8	43	36	45.5	21	11	34.3	40	19	32.2	7	1	—	124	76	38.0	P < 0.001
Monegros																						
1993							29	45	60.8	124	125	50.2	68	53	43.6	8	4	33.3	229	227	49.8	n.s.

tion from parity. Since the future reproductive output of male and female lesser Kestrels can also be affected by ecological conditions (Village 1990), the study of possible sex-ratio variations between populations in different environments is of critical importance. In this paper, we re-examine the secondary sex-ratio of Lesser Kestrels by using a larger data set from southern Spain as well as data from an area in northern Spain where ecological constraints are different (Tella *et al.* in press). In addition, we examine the overall sex-ratio in each region.

STUDY AREA AND METHODS

The study was conducted in two areas. The first area, in Sevilla province (southern Spain), contained some 200 pairs in eight large colonies (20–50 pairs each). The second area, in Monegros (Aragon, northern Spain), contained approximately 230 pairs in 49 colonies of very different sizes (1–34 pairs each). These two areas are 700 km apart, and Lesser Kestrels are highly philopatric in both areas (J.L.T., J.A.D., J.J.N. & F.H., unpubl.). In consequence, they can be considered as separate populations.

Nestlings were sexed, following the method of Negro & Hiraldo (1991), using the colour of the rectrices and upper tail-coverts. In nestlings which are 3 weeks old or older, rectrices and upper tail-coverts are greyish or cinnamon in males and brown and more heavily streaked in females. In Sevilla, sexing was carried out in 1988–1993. The Monegros area was visited only in 1993 and the nestlings were sexed in nests which were monitored regularly, thus avoiding the inclusion of adopted chicks in the analysis (adoption is frequent in this study area; J.L. Tella, M.G. Forero, J.A. Donázar, J.J. Negro & F. Hiraldo, unpubl.).

Hatching dates were estimated according to the primary feather length of the largest chick in each brood (Donázar *et al.* 1991). We subtracted 32 days for incubation to estimate laying dates and grouped laying dates into 10-day intervals. We consider this grouping pro-

cedure more effective in detecting a seasonal trend than that of Negro & Hiraldo (1991), who used only three time periods.

The mean laying date in the Sevilla study area varied by up to 30 days between years (J.L.T., J.A.D., J.J.N. & F.H., unpubl.). In order to permit comparisons between populations, we used relative laying dates in the two areas by making the start the laying date of the first clutch each year.

The sex-ratio was expressed as the proportion of males in the sample of fledglings (secondary sex-ratio). To examine whether the sex-ratio differed from unity, we used a two-tailed binomial test (Zar 1984). The association of sex-ratio with laying date was analysed by a logistic regression and adjusted to a probability distribution (SX-software, NH Analytical Software Corp., USA; see Zijlstra *et al.* 1992 for more details).

RESULTS

Sex-ratios in the two populations are shown in Table 1. Overall, the sex-ratio in Monegros was balanced in 1993. On the other hand, in Sevilla we observed two patterns. In 1988–1992 the sex-ratio did not differ significantly from parity, but in 1993 the proportion of males was significantly lower. Data from 1993 showed the overall sex-ratio in Sevilla to be female biased (46.3% males, $n = 1151$, $P < 0.02$). Removing the 1993 data from the analysis, the sex-ratios for the period 1988–1992 were homogeneous ($X^2_4 = 2.533$, n.s.), and the sex-ratio did not differ from parity (48.1% males, $n = 951$, n.s.).

The analysis by 10-day periods revealed a significant seasonal decrease in the proportion of males in Monegros ($n = 128$ nests, FP $= 4.52$, $P < 0.04$), described by the following equation:

$$\ln(SR/[1 - SR]) = 0.719 - 0.338 \cdot d,$$

where SR is the sex ratio, d is the mean day of each laying-date period and FP is the function of probability.

The birds in Sevilla did not show a clear seasonal variation in the sex-ratio when each year was considered separately, although in 1988 and 1993 the proportion of males was lower at the end of the season. When the 6 years of study were pooled, there was a significant seasonal decline in the sex-ratio ($n = 495$ nests, FP = 5.68, $P < 0.002$), described by the following equation:

$$\ln(SR/[1 - SR]) = 0.169 - 0.164{\cdot}d.$$

The seasonal decline at Sevilla, nonetheless, was less pronounced than that observed in Monegros during 1993 (Fig. 1) and it is due to the contribution of a single year (1993). If the data from 1993 are eliminated, no seasonal changes or disparity from a 1:1 ratio were observed (first period: 49.4% males, $n = 425$; second period: 47.0% males, $n = 483$; third period: 48.8% males, $n = 43$; n.s. in all cases).

DISCUSSION

Lesser Kestrel females are larger than males (body-mass ratio 1.2: 1, $n = 341$ adults), and, according to Fisher's (1930) theory of sex-ratios, a bias in the secondary sex-ratio towards the smaller sex can be expected. However, overall sex-ratio did not differ from unity in Monegros nor, in most years, in Sevilla. These results might be due to sex-specific growth patterns, which have been invoked to explain balanced sex-ratios in dimorphic species (Richter 1983, Rofstad 1986, Teather & Weatherhead 1988, but see Fiala & Congdon 1983, Richner 1991).

Our results showed a female-biased sex-ratio in only 1 year in the Sevilla population. Food stress could induce biased sex allocations, but it is not clear which sex would be favoured (Trivers & Willard 1973, Clark 1978, Bortolotti 1986, Olsen & Cockburn 1991, Wiebe & Bortolotti 1992, Anderson et al. 1993). Our results did not show any clear relationship between food shortage and a biased sex-ratio. In the Sevilla area, food stress was apparent in several years (Donázar et al. 1993). However, the sex-ratios did not show a trend toward more females in years when productivity was lower (1989, 1991, and 1993). Moreover, of 68 chicks that died from starvation, 33 were males and 35 were females.

The seasonal variation in the sex-ratio at fledging is known in only four other avian species (Common Grackle Quiscalus quiscalus, Howe 1977; Kestrel, Dijkstra et al. 1990; Peregrine Falcon Falco peregrinus, Olsen & Cockburn 1991; and Marsh Harrier Circus aeruginosus, Zijlstra et al. 1992). We found a seasonal decline in the sex-ratio in the two Lesser Kestrel populations. In the Sevilla population, this trend was apparent only when the data from all years were pooled. Our results do not permit the identification of the factors which determine the observed seasonal variations. It is difficult however, to propose a single ecological factor to explain the trends observed in the two study areas. These two populations are subjected to very different selective pressures, e.g. habitat loss and predation, and show very different patterns in behavioural traits such as parental investment and the proportion of migrant birds (Negro et al. 1991, Tella et al. in press).

Our results demonstrate that, within a species, it is possible to find variations in the sex-ratio through the season, between years and between populations. Many studies of the adaptive significance
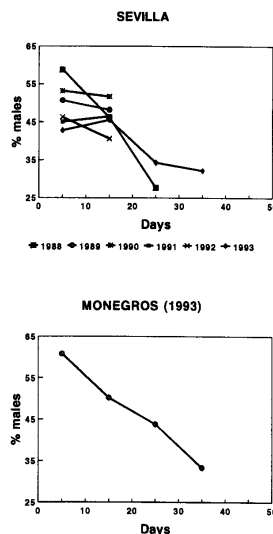

Figure 1. Seasonal changes in sex-ratio of broods of two populations of Lesser Kestrel after standardization of laying dates (day 0 = date first egg was laid).

of the variability of sex-ratios in birds and their evolution are based on pools of data from several years (e.g. Fiala 1981, Harmsen & Cooke 1983, Dijkstra et al. 1990, Olsen & Cockburn 1991), and these should be interpreted with care and caution.

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