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An evolutionary explanation for seasonal trends in avian sex ratios

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We present an extensive set of data for five species of raptorial birds to demonstrate that some raptor species produce an excess of daughters early in the season and an excess of sons in late nests, while others show the reverse. By means of a simulation model we investigate an evolutionary explanation for this phenomenon in terms of sex-specific differences in the relation between age at first breeding and date of birth. The model predicts that that gender should be produced first in the season whose age of first breeding is more strongly accelerated by an early birth date. We argue that this tends to be the male gender in raptor species, such as the common kestrel (*Falco tinnunculus*), which tend to breed early in life, while it is the female gender in larger species with later onset of breeding, such as the marsh harrier (*Circus aeruginosus*). The empirical evidence is qualitatively consistent with this hypothesis. Our model is quite general in that it makes no assumptions about the mechanism (primary sex-ratio bias at egg laying or secondary sex-differential mortality before fledging) by which the bias is generated. Yet it is able to create quantitative predictions for species where sufficient demographic and life-history data are available. From the available data set in the common kestrel we derive a quantitative prediction for the seasonal trend in brood sex ratio. The observed trend is in good agreement with this prediction. *Key words*: European kestrel, life history, population genetical model, raptors, seasonality, sex allocation. [*Behav Ecol* 7:426–430 (1996)]

Avian offspring sex ratios seldom deviate from parity (Clutton-Brock, 1986). Yet systematic seasonal changes in the sex ratio have been reported for several raptor species (Dijkstra et al., 1990; Olsen and Cockburn 1991; Zijlstra et al., 1992). Indeed, sex-ratio theory predicts intraspecific variation in the sex ratio when special environmental circumstances have different fitness consequences for male and female offspring (Bull, 1981; Charnov and Bull, 1977; Korpelainen, 1990; Trivers and Willard, 1973). In a particular environment, that gender should be produced in excess which profits most from the prevailing starting conditions. If different dates of laying reflect systematic differences in environmental circumstances, one might thus expect seasonal variations in offspring sex ratios. In two of the best documented cases, a seasonal decrease in the percentage of sons has been reported for the European kestrel (*Falco tinnunculus*; Dijkstra et al., 1990), while an increase in the percentage of sons was found in broods of the marsh harrier (*Circus aeruginosus*; Zijlstra et al., 1992). These data have recently been augmented by extensive data sets collected by R. Bijlsma, J. van Diermen, and W. van Maanen (unpublished data) in populations of the sparrowhawk (*Accipiter nisus*) and the goshawk (*Accipiter gentilis*) in the Netherlands (Figure 1). These species show a seasonal increase in the numbers of sons in their broods, in agreement with the situation in the peregrine, *Falco peregrinus* (Olsen and Cockburn, 1991). On the other hand, a recent study on the lesser kestrel (*Falco naumanni*) in Spain demonstrates a seasonal decrease in the proportion of sons (Tella et al., in press). Why do some raptor species produce an excess of daughters early in the season, whereas others produce an excess of sons?

Fisher (1930) predicted that the average sex ratio of a population reflects the relative parental investment required for raising a son or a daughter. Yet selection may lead to intra-specific variation in the sex ratio. Trivers and Willard (1973)

argued that, in species with parental care, parents in good condition should produce an excess of that gender which profits most from an increment in parental condition. In birds, early breeders are generally those in the best condition and habitat (Daan et al., 1989; Newton, 1979). Accordingly, when applied to the seasonal sex-ratio trends found in raptors (Figure 1), the Trivers and Willard (1973) hypothesis requires that sons profit more from good parental conditions in the common and lesser kestrel, while daughters profit more from good parental conditions in the other species. In view of the ecological similarity of raptor species, it is not obvious why this requirement should be met.

We propose an alternative explanation based not on parental conditions, but on size- and sex-specific differences in maturation time, where maturation time is operationally defined as the age at first breeding. In raptors, larger species have a longer maturation time (Newton, 1979) and in many species age of first breeding takes longer in males than in females. In fact, males often reach adult plumage at a later age than females and breed less frequently in subadult plumage (Newton, 1979). It is conceivable that individuals born early in the season have a higher chance to breed at an early age. Furthermore, the maturation time of males and females might be differently affected by birth date. In the kestrel, males born early in the season are overrepresented among yearling breeders in the study area (Dijkstra et al., 1990). No such tendency was found for females. Fitness, whether expressed as lifetime reproductive success (LRS) or as reproductive value, is positively affected by an early age of first breeding due to reproduction-independent mortality. In population studies LRS is empirically found to correlate negatively with age of first breeding (Newton, 1988). Thus it is likely that the expected rate of gene propagation is reduced in those individuals that have to skip their first breeding season. Accordingly, gender differences in the dependence of maturation time on birth date should have considerable consequences for optimal sex-ratio strategies. In this article we investigate the hypothesis that seasonally skewed sex ratios can be explained by gender differences in the relation between birth date and the age at

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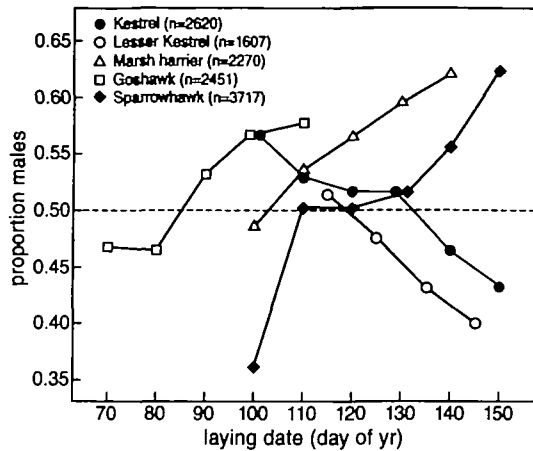


Figure 1
Seasonal changes in the brood sex ratios of four raptor species in the Netherlands. Symbols represent proportion of males in broods initiated within 10 day intervals: ● European kestrel, *Falco tinnunculus* (number of nestlings for consecutive data points: $n = 171, 754, 807, 588, 293, 67, p < .025$; Dijkstra et al., 1990); ◆ sparrowhawk, *Accipiter nisus* ($n = 25, 626, 2116, 749, 148, 53, p < .05$; unpublished data of J. van Diermen, R. Bijlsma, and W. van Maanen), □ goshawk, *Accipiter gentilis* ($n = 30, 463, 1286, 511, 161, p < .005$; unpublished data of R. Bijlsma and W. van Maanen), Δ marsh harrier, *Circus aeruginosus* ($n = 300, 909, 802, 188, 71, p < .005$; Zijlstra et al., 1992); ○ lesser kestrel, *Falco naumanni* ($n = 421, 787, 369, 30, p < .005$; Tella et al., in press). Significance levels of the deviation of the slope from zero tested by logistic regression.

first breeding. We expect that the gender whose maturation time is more strongly reduced by an early birth date should be produced first. This hypothesis is addressed by means of a simulation model. In this model, and indeed throughout this article, we assume that it is the (female) parent which determines gender of the offspring, and we are thus specifically concerned with the fitness consequences of the sex ratio for that parent. Results would not necessarily be the same if gender were determined by differential gene expression in the offspring.

Model structure

Our basic model considers a randomly mating, diploid population with overlapping generations and seasonal reproduction. Individuals are classified as males or females, and each gender is further subdivided into juveniles, immature (non-reproductive) adults, and mature (reproductive) adults. Mortality from one reproductive season to the next is independent of gender and was set to $\mu_0 = \frac{2}{3}$ for juveniles and $\mu_1 = \frac{1}{2}$ for adults. Each season is arbitrarily split into four quarters which are indicated by the "dates" $t = 0, \frac{1}{4}, \frac{2}{4},$ and 1 , respectively. Juveniles enter the adult population in the first season after their birth. Whether an individual enters the mature stage depends on its age, date of birth (t), and the sex-specific mean age at first breeding (A). We consider the values $A = 1, 1.5, 2,$ and 2.5 , which have the following interpretation: Independent of its birth date, an individual with $A = 1$ or $A = 2$ will enter the mature stage at age 1 or 2. For $A = 1.5$ or $A = 2.5$, the age at first breeding of an individual is affected by its birth date (t). For $A = 1.5$, there is a probability, $p(t) = 1 - t$, to enter the reproductive stage at age 1; otherwise, breeding starts at age 2. Similarly, for $A = 2.5$, maturation will occur with probability $p(t) = 1 - t$ at age 2 and with certainty at age 3. Hence, in both cases the probability of early maturation declines from 1 to 0 with progressive birth date. Reproduction

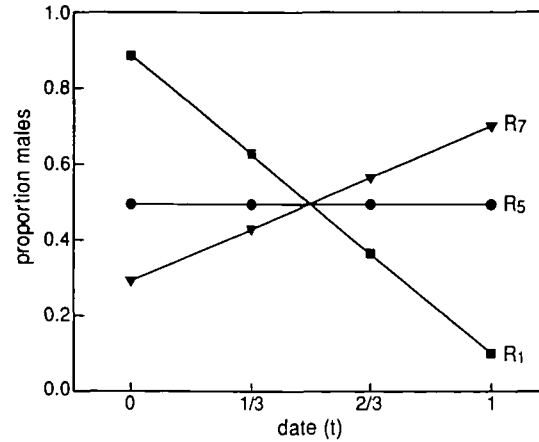


Figure 2
Illustration of 3 of the 11 linear seasonal sex-ratio trends (alleles $R_1 = -0.8, R_5 = 0.0,$ and $R_7 = 0.4$) used in the simulations.

is modeled as follows: In each quarter of the season 100 breeding pairs are drawn at random, without replacement, from the mature males and females. Each breeding pair produces five offspring. The gender of each offspring is randomly chosen from a distribution based on the birth date (t) and the mother's genotype at an autosomal locus R . We consider eleven alleles at this locus. Each allele is indicated by a real number R_i ($R_0 = -1.0, R_1 = -0.8, \dots, R_9 = +0.8, R_{10} = +1.0$) that corresponds to the tendency to produce a son with probability $0.5 + R_i(t - 0.5)$ at date t . Hence, R_i may be viewed as the slope of a linear seasonal sex-ratio trend that is symmetric around mid-season and always leads to a sex ratio of 0.5 when averaged over the whole season (Figure 2). Alleles interact additively, that is, mothers of genotype $R_i R_j$ produce a sex-ratio trend that is intermediate between the trends induced by R_i and R_j . In the simulations, the alleles R_0, \dots, R_{10} were initially present in equal frequencies. All simulations were run for 2000 seasons and replicated 50 times.

Model 1: Constant recruitment

In the basic version of the model (Model 1), recruitment of offspring is independent of the date of birth. The simulation results are summarized in Table 1 (upper rows) and Figure 3 (solid lines). When male and female age at first breeding were both independent of birth date, sex ratios remained constant over the season. The same was true when male and female age at first breeding were equally affected by birth date. In contrast, an extreme seasonal sex-ratio trend emerged whenever one gender had a constant maturation time, while the age at first breeding of the other gender was reduced by an early birth date. In these cases the gender profiting from an early birth date was always produced in excess at the start of the season. The small gene diversity in these cases (Table 1) indicates a tendency toward fixation of the most extreme alleles (R_0 or R_{10} , respectively).

Model 2: Decline in recruitment

Clearly such extreme sex-ratio trends are not found in nature. Extreme trends have several evolutionary disadvantages. One of the most obvious is related to seasonal variation in the total recruitment of offspring. Most avian species show a general seasonal decline in both clutch size and survival of the offspring (Daan et al., 1989). Faced with a seasonal decline in recruitment, an extreme seasonal sex-ratio trend leads to an

Table 1
Summary of the simulation results: sex-ratio trends evolved after 2000 seasons as a function of male and female maturation time

A_s	A_f			
	1	1.5	2	2.5
1	-.006(.056) .667	+.937(.009) .295	+.013(.050) .698	+.923(.010) .345
	+.005(.019) .646	+.479(.016) .634	-.013(.016) .714	+.424(.016) .754
1.5	-.936(.011) .257	+.020(.036) .739	-.904(.013) .399	+.042(.030) .772
	-.435(.017) .685	-.017(.013) .729	-.448(.015) .739	+.014(.013) .763
2	-.044(.047) .749	+.913(.011) .365	-.020(.050) .759	+.914(.012) .316
	-.006(.019) .725	+.450(.015) .685	+.006(.017) .745	+.458(.013) .758
2.5	-.921(.010) .364	+.016(.041) .760	-.900(.012) .389	-.033(.030) .805
	-.442(.016) .745	-.015(.013) .772	-.463(.016) .723	+.014(0.14) .786

The upper half of each cell corresponds to Model 1 (constant recruitment), the lower half to Model 2 (birth date dependent recruitment of juveniles). Sex-ratio trends are represented by the mean slope (over 50 replicates) of the linear regression of sex ratio on date, with the standard error of the mean given in parentheses. Numbers in bold type correspond to the mean gene diversity (Weir, 1990) after 2000 seasons. Gene diversity is a number between 0 (fixation of one allele) and 1 (all alleles present in equal frequency) and is defined by the ratio H_p/H_{max} between the Hardy-Weinberg heterozygosity realized after 2000 seasons ($H_p = 1 - \sum p_i^2$) and the maximal Hardy-Weinberg heterozygosity (here $H_{max} = 10/11$).

overrepresentation of the gender that is produced first. Accordingly, such a trend leads to a shift in the population sex ratio, thereby improving the prospects of those alleles that lead to overrepresentation of the opposite sex. To investigate the evolutionary consequences of these effects, we modified the model described above. In Model 2, a seasonal decline in recruitment was simulated by making juvenile mortality dependent on birth date: $\mu_0(t) = \frac{1}{2} + (t - 0.5)/3$. Simulations

based on Model 2 yielded seasonal sex-ratio trends (Table 1, lower rows; Figure 3, dotted lines) that were qualitatively similar, but less extreme, than those in Model 1. The higher gene diversity indicates that the intermediate sex-ratio trends were not attained by fixation of a single allele, but by a balanced polymorphism. In those cases where the sexes did not differ in the dependence on birth date of age at first breeding, there was now stabilizing selection for a seasonally constant sex ratio. This is indicated by the standard errors of the slopes of the regression lines of sex ratio on season, which were always smaller than in Model 1 (Table 1).

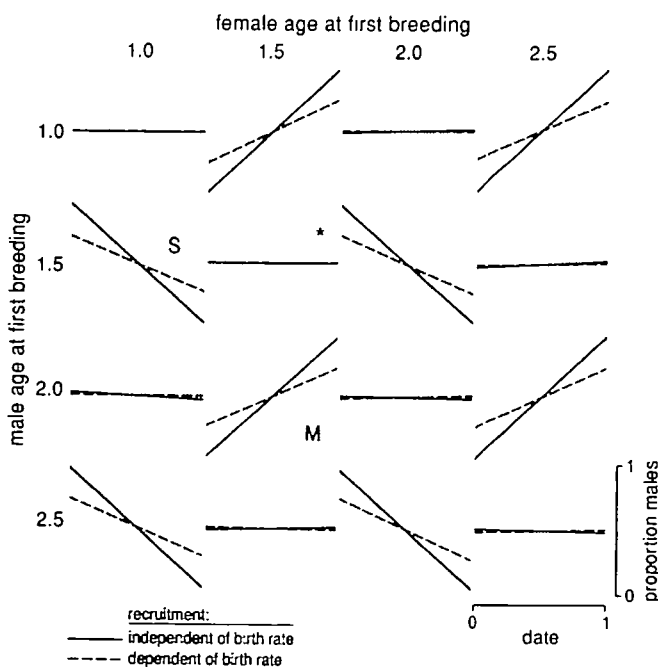


Figure 3
Graphical illustration of the simulation results summarized in Table 1. For a given combination of male and female maturation times (rows and columns, respectively), a cell shows the sex-ratio trend which had evolved after 2000 seasons (solid lines: recruitment independent of birth date; dotted lines: recruitment declining with birth date). Trends are represented by mean regression lines (over 50 replicates). Cell S: small raptors; cell M: medium-sized raptors; cell *: sparrowhawk.

Sex-specific recruitment in raptors

The relationship between birth date and age at first breeding in the above models is of course a caricature of the real world. Nonetheless, there is reason to suppose that the situation in small- and medium-sized raptor species approximately corresponds to the cells marked S and M in Figure 3. In the kestrel, the probability of breeding as a yearling is high and independent of birth date in females, while in males this probability declines with progressive birth date (Dijkstra et al., 1990). This corresponds with cell S, which predicts a seasonal decline in sex ratio, as is indeed observed (Figure 1). The seasonal change in sex ratio in lesser kestrel broods from Spain is similar to that of the common kestrel, with decreasing numbers of males in later broods. In this species males have a reduced chance to breed as yearlings compared to females (Tella J, personal communication). We predict that this probability varies with date of birth in males. Larger raptors have a higher age of first breeding, and the available evidence suggests that females have a higher probability to breed as yearlings than males: in peregrines and goshawks females more often breed in immature plumage than males (Newton, 1979). In the marsh harrier both sexes occasionally breed in immature plumage, and adult plumage is reached later in males (Newton, 1979). The probability of breeding as a yearling is likely to be negligible in males in these species, while at least some marsh harrier females will breed as yearlings (Dijkstra C, personal observation). Thus they would fall into the category of cell M in Figure 3. From the seasonally increasing sex ratios observed in cell M and in the data (Figure 1), we predict that

Table 2

Demographic data for the European kestrel (Dijkstra et al., 1990) used in Model 3, observed sex ratios in broods, and mean sex ratios in simulations

Part of breeding season	1	2	3	4
Date (t)	0	$\frac{1}{3}$	$\frac{2}{3}$	1
Clutch size	5.91	5.49	5.13	4.64
Survival from egg until age 1	0.273	0.169	0.175	0.115
Recruits per brood (clutch size * survival)	1.61	0.93	0.90	0.51
Male 1 year breeding probability	0.65	0.74	0.61	0.53
Female 1 year breeding probability	0.73	0.88	0.87	0.77
Brood sex ratio	0.536	0.517	0.515	0.457
SEM (number of nestlings)	0.016 (925)	0.018 (807)	0.017 (821)	0.029 (300)
Sex ratio in simulations	0.543	0.516	0.481	0.467
SEM (50 replicates)	0.014	0.010	0.009	0.015

Probabilities of breeding were derived from the fraction among nonmigrant birds known to be alive in their first year, which did actually breed.

the probability to breed as yearlings decreases in females of these species with progressive date of birth.

The sparrowhawk seems to be exceptional among raptors, in that females do not have an earlier age at first breeding than males. Both sexes breed occasionally as yearlings with similar frequency (Newton, 1986, Table 10). On the basis of mean age at first breeding alone, we would therefore not predict a seasonal sex-ratio trend (Figure 3, cell *). The positive sex-ratio trend found in the sparrowhawk (Figure 1) can, however, be explained on the basis of sex-specific differences in the relation between birth date and recruitment. In fact, an early birth date seems to have a stronger positive effect on juvenile survival in females than in males (Newton, 1986, Table 32). As a consequence, sparrowhawk females profit more from an early birth date than males, and should be produced first.

Model 3: Quantitative predictions for the kestrel

Qualitatively, our hypothesis can reasonably account for the seasonal sex-ratio trends found in raptors. It remains to be seen whether such a trend can be predicted quantitatively for

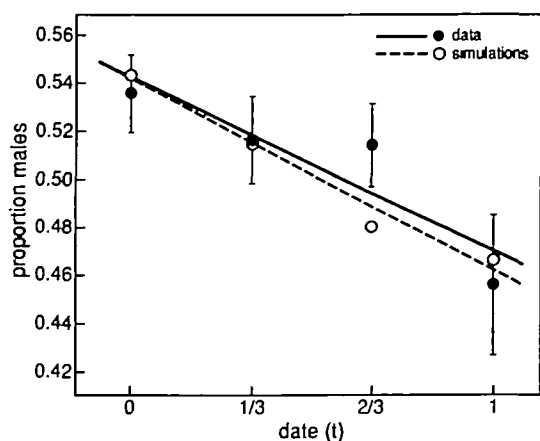


Figure 4
Seasonal variation in the sex ratio in the broods of the European kestrel: comparison between observations (Dijkstra et al., 1990; closed circles: mean \pm standard error of the mean, solid regression line) and simulation results (mean sex ratio over 50 replicates: open circles, dotted line).

any species. The required demographic data on seasonal variation in recruitment and age at first breeding of both sexes are only available for the kestrel (*Falco tinnunculus*). For our field studies (Daan et al., 1990; Dijkstra et al., 1990) in the Netherlands (1977–1992), we divided the reproductive season into four parts. This low resolution was chosen to keep Model 3 entirely identical with Model 2 except for the demographic parameters. Obviously the data were collected with higher date resolution, as can be found in the original publications. For each part we calculated average clutch size, survival until fledging, survival until age 1, and the proportion of breeders starting to breed at age 1 (Table 2). In Model 3, the basic model was modified to take account of these data (A values were based on first-year breeding probabilities and $1 - \mu_0$ was set equal to recruits per brood/5). There was considerable variation between the simulations, but averaged over all simulations a sex-ratio trend emerged that declines significantly with the progress of the season ($p < .005$) and is statistically indistinguishable from that observed in kestrel broods (Table 2 and Figure 4).

Conclusion

Seasonal sex-ratio shifts have also been described in another bird species (the common grackle; Howe, 1977), in some mammal species (Clutton-Brock and Jason, 1986), and in a fish species (silverside; Conover and Kynard, 1981). In all these species, the mechanism controlling the seasonal change in sex ratio is unknown. In the silverside, both genetic and environmental gender determination are involved (Conover et al., 1992). In birds and mammals, differential juvenile mortality of the sexes is certainly an important factor. For the grackle (Howe, 1977) and the kestrel (Dijkstra et al., 1990), there is evidence that the primary sex ratio before laying deviates from parity. Investigating the mechanisms responsible for a shift in primary sex ratio should shed some light on the intriguing question of why, in birds, the female is the heterogametic sex.

Superficially our model predictions seem to be in line with the Trivers and Willard (1973) hypothesis: Early breeders are usually in the best condition and habitat, and these birds produce in excess the gender which profits most from an early birth date. However, our explanation does not require differences in parental investment. One might argue that Model 2 includes a "parental" effect since the seasonal decline in recruitment incorporated in this model probably reflects the

better conditions for early breeders. Interestingly, the sex-ratio trends found in Model 1 were reduced rather than augmented by the inclusion of such an effect. Hence, the seasonal variation in the sex ratio is more readily explained by sex-specific differences in life-history characteristics of offspring than by differences in parental investment. In a more general sense, the results are in full support of a broader interpretation of the Trivers and Willard theory that parents should adjust the sex ratio of their offspring to their individual circumstances.

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