Fledgling sex ratios in relation to brood size in size-dimorphic altricial birds

Cor Dijkstra,[a,b] **Serge Daan,**[a] **and Ido Pen**[a,c]
[a]Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands, [b]Ministry of Transport and Public Works, Institute for Inland Water Management and Waste Water Treatment (RIZA), PO Box 17, 8200 AA Lelystad, The Netherlands, and [c]Department of Genetics, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands

In six species of dimorphic raptors (females larger than males) and one passerine (males larger than females), the sex ratio at fledging varied systematically with brood size at fledging. In all species the strongest bias toward the smaller sex was established in the largest as well as the smallest broods; a more even distribution of males and females was observed in broods of intermediate size. We explored a specific differential mortality explanation for this sex ratio variation. Our hypothesis postulates that variation in mortality is caused by differences in food demand between broods of the same size, due to their sex composition. Data from the marsh harrier *Circus aeruginosus* on gender-related food demand and overall nestling mortality were used to predict the frequency of surviving males and females at fledging, assuming an even sex ratio at hatching and random mortality with respect to both sexes within broods. The model quantitatively fits the marsh harrier data well, especially in broods originating from large clutches. Although we anticipate that other mechanisms are also involved, the results support the hypothesis of sex-ratio–dependent mortality, differential between broods, as the process generating the observed brood-size dependence of fledgling sex ratios in sexually dimorphic birds. *Key words:* brood size, marsh harrier, sex ratio, sex specific mortality, sexual dimorphism. *[Behav Ecol 9:287–296 (1998)]*

Mechanisms causing biased sex ratios in avian broods may either concern the primary sex ratio—for instance, by nonrandom meiosis (Howe, 1977)—or sex-dependent mortality during development (Krackow, 1995). Evidence for skewed overall population sex ratios at hatching is limited (Clutton-Brock, 1986; Slagsvold et al., 1986), although deviations from parity have been observed, varying with laying date, maternal age, and territory quality (Blank and Nolan, 1983; Howe, 1977; Komdeur et al., 1997). Indirect evidence, where nestling mortality was insufficient to account for skewed fledgling sex ratios, indicates that a bias may already be present at hatching (Bednarz and Hayden, 1991; Dijkstra et al., 1990b; Wiebe and Bortolotti, 1992). Evidence for sex-dependent nestling mortality is available for several size-dimorphic species (Blank and Nolan, 1983; Clutton-Brock et al., 1985; Griffiths, 1992; Howe, 1977; Røskaft and Slagsvold, 1985; Sayce and Hunt, 1987; Teather and Weatherhead, 1989). In all these cases mortality was higher in the larger sex (males). Both descriptive as well as experimental data have shown that males in these species were more susceptible to food stress in terms of growth and survival (Røskaft and Slagsvold, 1985; Teather and Weatherhead, 1989). The increased mortality of the larger sex has been attributed to sex-dependent food demands in combination with hatching asynchrony. These factors would result in enhanced chances of the last hatchling starving, if it belongs to the larger sex with the higher food demand (Slagsvold, 1990). This would in turn result in a shift in sex ratio of the survivors toward the smaller sex in broods that suffered mortality. This hypothesis assumes the relatively minor gender differences in food demand of the youngest and smallest nestling to be decisive for its survival, but it does not take possible effects of sex-dependent food demand of the older and larger siblings on the last hatchling into account.

We therefore explored the possibility that the size and sex composition of the whole brood affects the chances of a nestling dying as a consequence of food requirements of the brood. Our approach was first to extract from the literature available information on sex ratios in relation to brood size, shortly before fledging, in sexually dimorphic species. This yielded an interestingly consistent pattern among species. The largest bias toward the "cheaper" sex is generally found both in the largest and in the smallest brood sizes. Using new data on brood-size-dependent sex ratio in the marsh harrier, we subsequently explored the hypothesis that the general pattern of brood-size variation in sex ratio is the result of differential energy requirements of the brood. This hypothesis yields some nonintuitive predictions on the dependence of sex ratio on brood size at fledging. These predictions fit well with the data, especially for broods originating from large clutches. We surmise that secondary processes, such as food-related mortality, are part of the mechanism by which the fledgling sex-ratio bias is generated.

Brood size and sex ratio in sexually dimorphic birds

A literature survey on fledgling sex ratios as a function of brood size revealed data on five species of raptors. These data are summarized in Table 1, which also includes unpublished data on the goshawk *Accipiter gentilis*, the European kestrel *Falco tinnunculus*, and the marsh harrier *Circus aeruginosus*. In addition, we have included data on the red-winged blackbird, *Agelaius phoeniceus*, in which the male is the larger sex. This is the only dimorphic passerine for which brood-size dependence of the sex ratio was published. It is necessary to provide some background information with respect to the methods of sex identification of the species.

Table 1

Sex ratio, expressed as the percentage of males among nestlings shortly before fledging, in broods of different size (number of young)

Species	Reference/ source of data	Brood size						
		1	2	3	4	5	6	7
European kestrel	Dijkstra et al. (1990b)	63.6 (22)	46.9 (64)	51.4 (321)	48.6 (584)	50.6 (810)	53.9 (438)	65.7 (35)
American kestrel	Anderson et al. (1993)[a]	83.3 (6)	— (0)	36.1 (36)	46.8 (88)	59.0 (100)		
Lesser kestrel	Negro and Hiraldo (1992)	50.0 (36)	44.2 (156)	51.4 (177)	54.3 (92)			
Marsh harrier	Zijlstra et al. (1992)	60.7 (67)	52.3 (328)	53.2 (825)	54.7 (828)	58.9 (385)	60.0 (30)	
European goshawk	Wickman (1975)	60.8 (51)	47.1 (240)	51.2 (537)	56.7 (312)	60.0 (5)		
European goshawk	Kenward et al. (1993)	52.6 (19)	45.6 (114)	55.1 (147)	60.0 (20)			
European goshawk	Bijlsma (1993)	54.1 (74)	54.1 (518)	52.0 (1209)	53.6 (776)	57.5 (40)		
Goshawk total		56.3 (144)	51.0 (872)	52.0 (1893)	54.6 (1108)	57.8 (45)		
European sparrowhawk	Newton and Marquiss (1979)	54.7 (75)	48.5 (198)	50.1 (483)	51.5 (736)	50.6 (605)	57.6 (66)	
Cooper's hawk	Rosenfield et al. (1996)	58.3 (24)	48.6 (74)	54.7 (258)	53.2 (588)	56.5 (375)	50.0 (18)	
Red-winged blackbird	Fiala (1981)	43.8 (16)	50.0 (86)	49.3 (450)	46.3 (784)	47.5 (40)		

Data from seven raptor species showing reversed sexual size dimorphism (females larger than males), and one dimorphic passerine (males larger than females).
Only data from five-egg clutches.

Falco tinnunculus, *European kestrel*
The data on the European kestrel were collected from, 1980 until, 1986 throughout the Netherlands. In total, 2274 nestlings from 547 broods with known clutch size were sexed shortly before fledging, using body mass in combination with plumage characteristics (upper tail coverts) to distinguish between males and females. The validity of the method was checked by retrapping individuals after they had attained adult plumage (Dijkstra et al., 1990b).

Falco sparverius, *American kestrel*
Sex ratios of American kestrel nestlings in broods of different size were presented by Anderson et al. (1993). This publica-
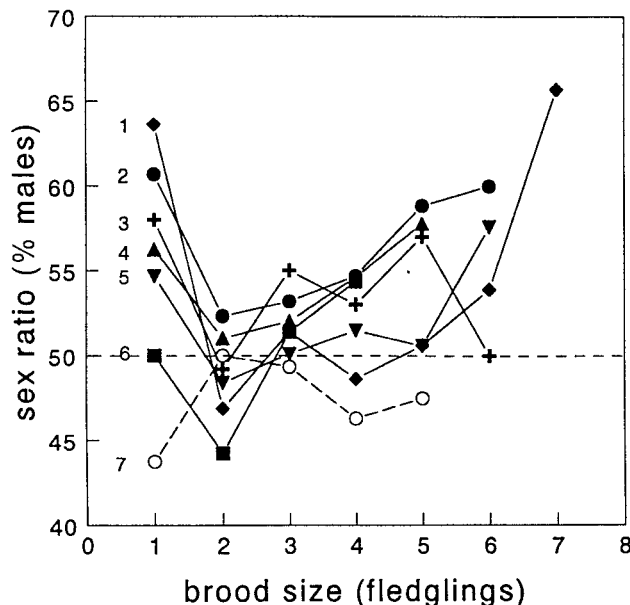

Figure 1
Nestling sex ratios shortly before fledging as a function of brood size, for seven sexually size-dimorphic species: six raptors (females larger than males, closed symbols); 1, European kestrel; 2, marsh harrier; 3, Cooper's hawk; 4, European goshawk; 5, European sparrowhawk; 6, lesser kestrel, and one passerine (males larger than females, open symbols); 7, the red-winged blackbird. For references, see Table 1.

tion gives data only for broods resulting from clutches of five eggs (Table 1). Nestlings were sexed reliably on highly sex-specific plumage characteristics during the last 25% of the nestling period (Anderson et al., 1993).

Falco naumanni, *lesser kestrel*
Lesser kestrel nestling sex ratios for different brood sizes were reported by Negro and Hiraldo (1992; $n = 461$ nestlings). Their method of sexing was the same as mentioned for the European kestrel, and all recaptures ($n = 45$) of birds with adult plumage were correctly sexed as nestlings.

Circus aeruginosus, *marsh harrier*
From, 1975 until, 1994, 3866 young were sexed at the end of the nestling period in the Lauwersmeer and Flevoland polders in The Netherlands. In a sample of 2463 young from 795 broods, the original clutch size was also known. Part of these data have been used in an earlier publication, without reference to brood size (Zijlstra et al., 1992). Sexing made use of toe-pad length, which in this population is a highly reliable sex characteristic from 20 days of age onwards (Zijlstra et al., 1992). All identified adult individuals had been sexed correctly as nestlings ($n = 65$).

Accipiter gentilis, *goshawk*
The data on goshawk sex ratios were collected in the Veluwe and the province Drenthe, The Netherlands. In these areas 2617 nestlings from 938 broods were sexed using toe-pad length and the profound sexual difference in body mass to discriminate between males and females (Bijlsma, 1993). Two earlier studies on this species reported sex ratios as a function of brood size using the same method of sexing. A Finnish population was studied by Wikman (1976; $n = 429$ broods, 1145 nestlings). Kenward et al. (1993) reported on a Swedish population ($n = 130$ nests, 300 nestlings). All three studies showed similar trends in the sex ratio for different brood sizes (Table 1), and they have been pooled in Figure 1.

Accipiter nisus, *sparrowhawk*
The data for the sparrowhawk were derived from Newton and Marquiss (1979; $n = 651$ broods, 2163 nestlings). They used the marked difference in body mass in this species to establish the gender of the nestlings shortly before fledging. No error of sexing was found upon recapturing the birds as adults (Newton and Marquiss, 1979).

Accipiter cooperii, *Cooper's hawk*
A total of 1337 Cooper's Hawk nestlings from 372 broods were sexed in the second half of the nestling period (Rosenfield et al., 1996). Again, apparent morphometric differences (after age 12 days) were used to discriminate between males and females in this strongly size-dimorphic raptor species.

Agelaius phoeniceus, *red-winged blackbird*
The red-winged blackbird appears to be the only sexually dimorphic (males larger than females) passerine species for which sex ratios for different brood sizes have been published. The data in Table 1 were derived from Fiala (1981: Table 3; $n = 1376$). Birds were sexed by weight on day 8 after hatching or later. Similar weight criteria have been reported as reliable in other studies (Holcomb and Twiest, 1970). In addition, gonadal inspection was used (Fiala, 1981).

Data on brood size dependence of the sex ratio in hen harriers, *Circus cyaneus*, were reported by Picozzi (1980). This study presented data from different observers working in different time periods on the Orkney islands. Picozzi presented convincing evidence for the validity of his method of sexing (using difference in size and iris color), by recapturing adults which were sexed as nestlings; 74 out of 75 recaptures were correctly sexed in the nest. Male nestlings outnumbered females in 7 out of the 8 years of this study (Picozzi, 1984). In contrast with this result, Balfour and Cadbury (1979) reported a female bias in this species during their study period (1953–1974). However, no quantitative evidence was presented on the accuracy of their method of sexing (iris color; Balfour, 1970), which makes it difficult to interpret these data. Because sex ratios for different brood sizes were published only for the pooled data of both studies (Picozzi, 1980), we omitted them from our analysis.

All species show a consistent pattern of brood-size dependence of the sex ratio (Figure 1). There is a substantial bias in favor of the smaller sex in the largest broods. This bias decreases toward smaller broods, and at brood size 2 the sex ratio is essentially 50%. At brood size 1, there is again a relative increase in numbers of the smaller sex. It is of special significance that the general pattern among raptors, with reversed sex-size dimorphism, is reversed in the data for the only species in which the male is the larger sex, the red-winged blackbird. We have tested the significance of brood-size dependence by logistic regression of sex ratio on log-transformed brood size and its quadratic term (dependent variable: number of the smaller sex in the sample per species; trials variable: number of young in the sample per species). The seven species were included in the model as dummy variables, as well as their interaction terms with both of the other predictor variables. Including the interaction terms did not lead to a significant reduction of the deviance, and they were dropped from the model (Table 2). This means that the species did not differ with respect to the shape of the curves presented in Figure 1. A statistically significant effect of "species" on sex ratio remained present in the final model. In other words, there were species differences in overall sex ratio. Both "log brood size" and its quadratic term caused a highly significant reduction of the deviance in the model (Table 2).

Potential role of differential mortality

The data presented above indicate a general curvilinear relationship between the number of surviving nestlings and the proportion of the smaller sex among the survivors in sexually dimorphic birds. Any theory explaining biased sex ratios either on functional grounds, or from a proximate point of view focusing on the mechanism, should be able to account for

Table 2

Logistic regression of the fraction of the smaller sex (males in the six raptor species, females in the red-winged blackbird) on log-transformed brood size and its quadratic term

Parameter		(Δ) Deviance	(Δ) df	p	Coefficient
Null model		37.48	38		
Final model		11.93	30		
Constant			1		
B = log brood size	χ^2_1:	6.91	1	<.01	−1.099
B^2	χ^2_1:	10.91	1	<.001	1.522
Species (S)	χ^2_6:	18.51	6	<.01	[a]
SB	χ^2_6:	3.80	6	ns	
SB^2	χ^2_6:	1.43	6	ns	

Species were used in the model as dummy variables (0,1). Data from the European kestrel, lesser kestrel, marsh harrier, goshawk, sparrowhawk, Cooper's hawk, and the red-winged blackbird (see Table 1). The analysis presented here does not include the American kestrel because in this species sex ratios for different brood sizes were only published for broods originating from clutches of five eggs. Including this species did not change the result.

[a] Coefficients for species: marsh harrier, 0.313; goshawk, −0.049; lesser kestrel, −0.179; European kestrel, −0.217; sparrowhawk, −0.175; red-winged blackbird, −0.08; Cooper's hawk, −0.044.

this general pattern. We attempted to obtain quantitative predictions on this brood-size dependence.

The model
The model we developed is based on the idea that, given a certain brood size, the probability that one of the nestlings dies is slightly increased when the food demand of the brood is high due to a high proportion of the larger sex. Similarly, it is reduced when there are many of the smaller sex present. The following assumptions were made: (1) The frequency of different combinations of males and females at hatching is binomially distributed, and gender is not related to hatching sequence within broods. This is a null hypothesis. It does not imply that we do not take existing strong evidence (e.g., Komdeur et al., 1997) for primary sex ratio bias seriously. (2) Mortality within broods is random with respect to sex. Hence there are no differences in competitiveness between males and females with respect to food. (3) For any given clutch size and within the resulting (temporary) brood sizes, variation around the observed average probability to lose a nestling is caused by varying food demands between the remaining broods in the sample due to their sex composition.

The initial condition is a clutch of c eggs. The primary sex ratio at hatching (proportion of sons) is given by σ_k. The number of sons is assumed to be binomially distributed, hence the probability that exactly n out of k hatchlings are sons is given by

$$q_k(n) = \binom{k}{n}\sigma_k^n(1 - \sigma_k)^{k-n}. \tag{1}$$

Denote the food demand of a son by m and the food demand of a daughter by $f = zm$. The average demand per chick in a brood with k chicks and average sex ratio of σ_k is then given by

$$E(D) = \sigma_k m + (1 - \sigma_k)zm, \tag{2}$$

and the relative demand $d_{k,n}$ with respect to the average brood, of a brood containing n sons equals

$$d_{k,n} = \frac{\frac{n}{k}m + \left(1 - \frac{n}{k}\right)zm}{E(D)} = \frac{\frac{n}{k}\frac{1}{z} + 1 - \frac{n}{k}}{\sigma_k\frac{1}{z} + 1 - \sigma_k}. \qquad (3)$$

Note that we only need to know the relative demand of sons versus daughters, not the absolute sex-specific demands.

As we shall see (Figure 2), the proportion, $\overline{m}_k$, of all pairs with clutch size c raising less than k ($\leq c$) fledglings obeys the empirical relationship

$$\overline{m}_k = \frac{1}{1 + \exp[-(r + tk^2)]}. \qquad (4)$$

Let $\overline{p}_k$ represent the observed average probability that at least one chick will die within the subsets of nests which have $0 < k \leq c$ chicks at some point between hatching and fledging. Then, $\overline{p}_k = \overline{m}_k/\overline{m}_{k+1}$. Note that for $k=c$, $\overline{m}_{k+1} = 1$, and therefore $\overline{p}_c = \overline{m}_c$. For a given brood size, k, there will be variation in food demand resulting from variation in sex composition of the brood. For $k = c$ (i.e., before any mortality occurred), we assume that the resulting variation in the proportion of nests losing at least one chick ($\overline{p}_c = m_c$) is described by Equation 4. For smaller brood sizes, i.e., when $k<c$, this is not correct because in those cases $\overline{p}_k \neq \overline{m}_k$. This implies that either t or r or both must change with the number of chicks left in the brood (k). As a consequence of our assumption 3 above, we assume that only t, the parameter which proportionally weights the effect of brood size and hence food demand, varies with changing k. Given the value of t, valid before any mortality occurred ($k=c$), we can calculate t_k for the subsets of nests that at any time during the nestling stage had smaller brood sizes ($0<k<c$) from the equation

$$\overline{p}_k = \frac{1}{1 + \exp[-(r + t_k k^2)]} \qquad (5)$$

or

$$t_k = \sqrt{\frac{\ln\left(\frac{\overline{p}_k}{1 - \overline{p}_k}\right) - r}{k}}. \qquad (6)$$

Denote by $p_{k,n}$ the probability that at least one chick dies in a brood of size k which contains n sons. This probability is estimated as

$$p_{k,n} = \frac{1}{1 + \exp\{-[r + t_k(d_{k,n}k)^2]\}}. \qquad (7)$$

The probability that in a brood with size k and n sons all chicks fledge is given by $(1 - p_{k,n})$. The sex ratio at fledging of a brood without any mortality must then equal

$$\sigma'_k = \frac{\sum_{n=0}^{k} \frac{n}{k}q_k(n)[1 - p_{k,n}]}{\sum_{n=0}^{k} q_k(n)[1 - p_{k,n}]}. \qquad (8)$$

Now suppose mortality reduces a complete brood of size $k = c$ to size ($k - 1$), and suppose such a reduced brood contains exactly n sons. There are two routes by which such a brood could arise. Either the original unreduced brood contained n sons and a daughter died, or the original brood contained ($n + 1$) sons and a son died. The probability of the first scenario must equal the probability, $q_k(n)$, that the original brood contained n sons, times the probability, $p_{k,n}$, that mortality occurred in such a brood, times the probability that a random member of such a brood was a daughter, ($1 - n/k$). Similarly,

the probability of the second scenario is the product of the probability $q_k(n+1)$ that the original brood contained ($n+1$) sons, the probability $p_{k,n-1}$, that mortality struck, and the probability ($n+1$)/k that the victim was a son. The total probability is then the sum of the probabilities of these two scenarios

$$q_{k-1}(n) = q_k(n)p_{k,n}\left(1 - \frac{n}{k}\right) + q_k(n + 1)p_{k,n}\left(\frac{n + 1}{k}\right). \qquad (9)$$

The sex ratios of such broods before any additional mortality is then given by the sum over n of the sex ratios of broods with n sons, times the probability of broods with n sons

$$\sigma_{k-1} = \frac{\sum_{n=0}^{k} \frac{n}{k - 1}q_{k-1}(n)}{\sum_{n=0}^{k} q_{k-1}(n)}. \qquad (10)$$

The sex ratio at fledging of broods where no further mortality occurs can then be computed as

$$\sigma'_{k-1} = \frac{\sum_{n=0}^{k-1} \frac{n}{k - 1}q_{k-1}(n)[1 - p_{k-1,n}]}{\sum_{n=0}^{k-1} q_{k-1}(n)[1 - p_{k-1,n}]}. \qquad (11)$$

If an additional round of mortality happens, we can calculate $q_{k-2}(n)$, σ_{k-2}, and σ'_{k-2} in a similar fashion, and we can work our way down until the number of young still alive, k, $= c - (c - 1) = 1$. Given the primary sex ratio, σ_k, the relative food demand, z, of daughters compared to sons, and the parameters r and t_k in the relationship between brood size and the probability that mortality occurs, the sex ratio at fledging as a function of the number of survivors in the brood can be calculated.

Application of the model in the marsh harrier
We used data for the marsh harrier to evaluate this model of differential mortality between broods. In this species, the energy requirements of male and female nestlings were assessed (Krijgsveld K, et al., in preparation; Riedstra et al., in press), and an extensive data set was available on nestling mortality as a function of brood size at hatching, as well as the resulting fledgling sex ratios (Zijlstra et al., 1992; this study). From these data we derived estimates of z, r, and t. Furthermore, as a null hypothesis, we assumed $\sigma_k = 0.5$ (the sex ratio at hatching) and calculated the model's predictions on the fledgling sex ratios for this species.

Sex-specific food demand: assessment of z. In captivity, total food consumption of marsh harrier hatchlings till the age of independence (about 70 days for both sexes) was on average 7252 g±428 (SD) for males ($n = 7$), and 9136 g±619 for females ($n = 6$) and the difference between the sexes was statistically significant (Mann-Whitney U test, $p < .001$; Krijgsveld K, et al., in preparation). Consequently, the relative food consumption (z) of females compared to males was 1.26 under ad libitum food conditions. A similar ratio ($z = 1.25$) was found in the natural situation, where metabolizable energy intake (M) of both sexes was estimated at 22–26 days of age using doubly labeled water dilution: $M_{male}=655.3\pm213$ kJ/days, and $M_{female}=820.7\pm158$ kJ/day ($n = 8$ matched pairs of a male and a female from the same nest; Riedstra et al., in press). Using these figures, we substituted $z=1.26$ for the relative food demand of females compared to males in the marsh harrier and calculated the demand of all brood compositions relative to the average brood in the sample (Equation 3).

Variation of nestling mortality in the population: assessment of r *and* t. To obtain estimates of r and t in Equation 4, we fitted functions to the observed population data on the prob-
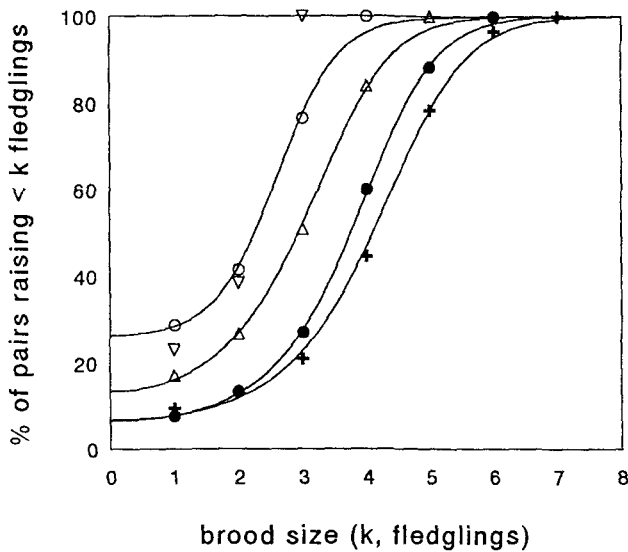
Figure 2
The observed proportion (m_k) of marsh harrier pairs raising fewer than k young, presented separately per clutch size (c): (✚) six or seven eggs ($n = 150$ nests), (●) five eggs ($n = 418$), (△) four eggs ($n = 269$), (○) three eggs ($n = 81$), (▽) two eggs ($n = 13$). Curves fitted by quadratic logistic regression: $\ln[m_k/(1 - m_k)] = r + tk^2$.

ability, m_k, that a nest (with original clutch size c) of brood size k loses at least one young. This probability is estimated by the fraction of all pairs with clutch c, which raised fewer then k fledglings (or the cumulative fraction of pairs raising up to $k - 1$ fledglings; see Figure 2). Logistic curve fitting was done on 931 broods, for different clutch sizes (six to seven eggs; five eggs; four eggs, and two to three eggs) separately. To these data reasonable fits were obtained by quadratic logistic regression (Equation 4):

6–7 eggs: $\ln[\overline{m}_k/(1 - \overline{m}_k)] = -2.615 + 0.156 * k^2$

5 eggs: $\ln[\overline{m}_k/(1 - \overline{m}_k)] = -2.652 + 0.189 * k^2$

4 eggs: $\ln[\overline{m}_k/(1 - \overline{m}_k)] = -1.856 + 0.216 * k^2$

2–3 eggs: $\ln[\overline{m}_k/(1 - \overline{m}_k)] = -1.169 + 0.235 * k^2$.

The coefficients of 1 and k^2 are unbiased estimates of r and t, respectively. The cumulative curves may be interpreted as the proportion of all pairs with clutch size c, unable to raise k or more young. For a given brood size k, there will be variation in food demand resulting from variation in sex composition of the brood. We assume that, when no mortality has occurred yet (i.e., when $k = c$), the resulting variation between broods in the probability that at least one chick dies is described by the relationships described here (Equation 4 in the model).

Average probability of mortality ($\overline{p}_k$): *assessment of* t_k. The proportions ($\overline{p}_k$) of Marsh Harrier nests which lost a young as a function of (temporary) brood size ($k = c, c - 1, c - 2$, etc.) are shown in Figure 3 for all clutch sizes (c) separately. As explained in the model, $\overline{p}_k$ is identical to m_k when $k = c$ (i.e., before any mortality occurred). The value of $\overline{p}_k$ initially dropped with decreasing brood size. For five-egg clutches, for instance, the fraction that lost at least one young was 369 out of 418, or 88.3% of all pairs. Of these 369 broods of 4 nestlings, 251, or 68.0%, lost another nestling, and so on. For all clutch sizes, the nests that were reduced to one nestling suffered again a higher chance of mortality, resulting in complete failure of the brood (Figure 3). These observed values
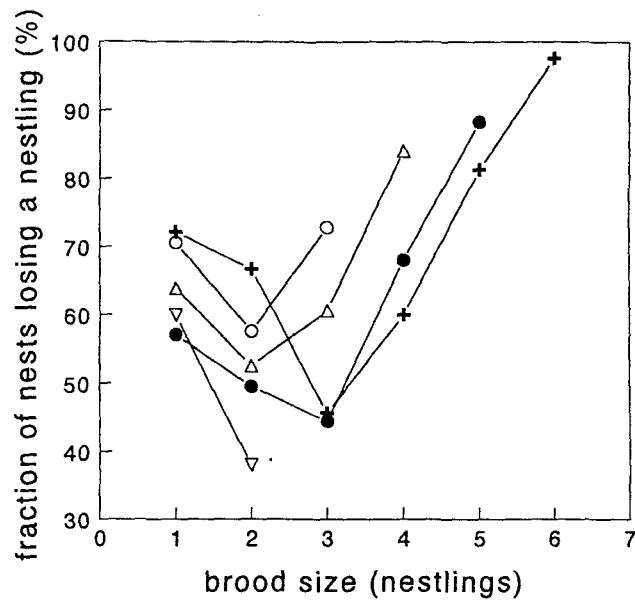

Figure 3
Observed proportions of Marsh Harrier broods losing a nestling ($\overline{p}_k$) as a function of the number of young surviving till then (k). The data are presented separately for broods resulting from different clutch sizes (c): (✚) six or seven eggs ($n = 150$); (●) five eggs ($n = 418$); (△) four eggs ($n = 269$); (○) three eggs ($n = 81$); (▽) two eggs ($n = 13$).

of $\overline{p}_k$ were substituted in Equation 6 to calculate the coefficients t_k for the subsets of nests where $k = c - 1, c - 2$, etc. The estimated probabilities that a chick will die as a function of sex composition of the brood ($\overline{p}_{k,n}$), were assessed using Equation 7.

Variation in mortality in relation to sex composition of the brood. The predicted variation of mortality due to sex composition of the brood is graphically explained in Figure 4 for clutches of five eggs. The five graphs (Figure 4A–E) represent situations with $k = 5, 4, 3, 2$, and 1 remaining young in the nest, respectively. The logistic regressions for clutches of five eggs (Equation 5), are included in all graphs. The field data from Figure 3, on the fractions of remaining broods losing another nestling ($\overline{p}_k$), are indicated on the curve by open symbols (Figure 4A–E). Before mortality has occurred (Figure 4A), this value is valid for broods with, on average, an even sex ratio because we assumed no sex ratio bias at hatching ($\sigma_k = 0.5$). This figure also shows the initial binomial frequency distribution of all combinations of males and females (Figure 4A, bars; Equation 1) positioned on the abcissa according to their food demand: If all nestlings in the brood are males ($n = 5$), brood size $k=5$ is scaled down by a factor $d_{k,n} = 0.885$ (Equation 3). If all nestlings are females, it is increased by a factor 1.115, and all mixed broods have intermediate values of d. Applying Equation 7, the expected probabilities to lose a nestling were calculated for all brood compositions. These values ($\overline{p}_{k,n}$) are indicated for any combination of males and females in the initial brood of five as closed symbols on the curve in Figure 4A. Using these estimates, we calculated for each gender combination the probability that all chicks fledged ($1 - \overline{p}_{k,n}$) and thereby derived the predicted fledgling sex ratios for complete broods of five (Equation 8).

For the nests entering the next rounds of mortality ($k = 4→1$), the frequency of each gender combination was computed, assuming random mortality with respect to sex within broods (Figure 4, bars; Equation 9). Because, in the model, female-biased broods have an enhanced probability of mor-
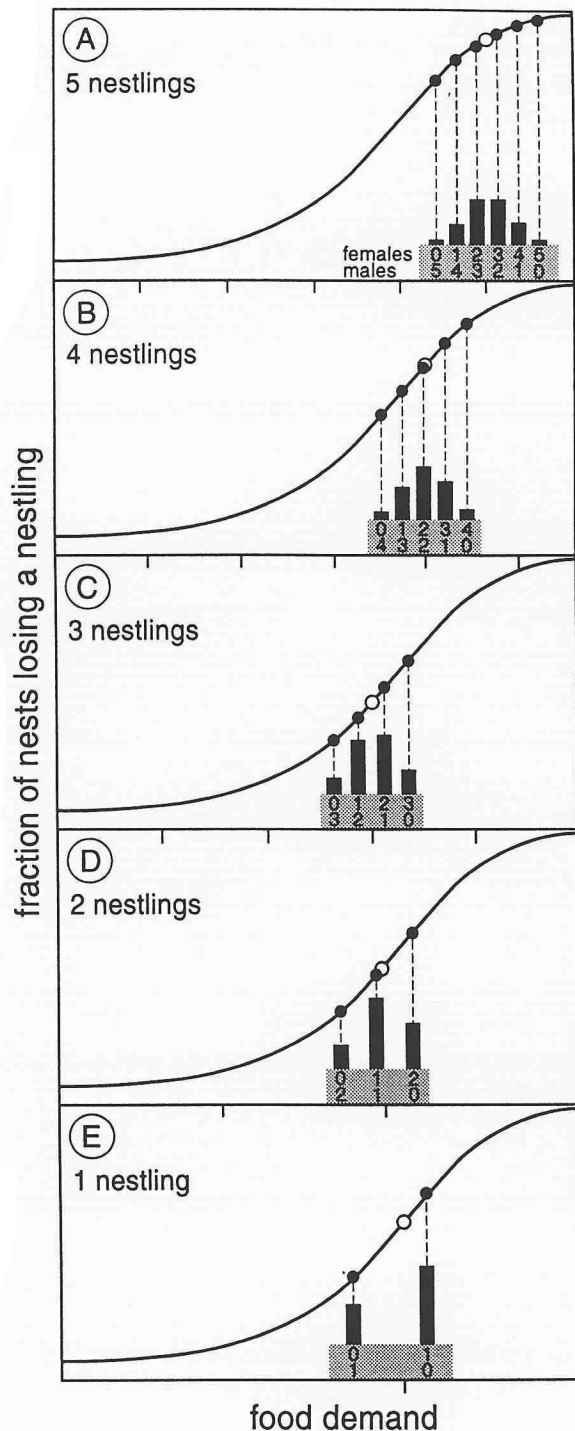
Figure 4
The estimated probabilities, for marsh harrier broods originating from a clutch of five eggs, to lose a nestling (●), depending on variation in food demand of the brood, which is determined by the number of males and females. The five graphs, from top to bottom, are for situations with, respectively, five, four, three, two, and one remaining young in the nest. The logistic regressions from Equation 5 for five-egg clutches are included in all graphs. The field data on the fractions of broods losing another young (from Figure 3) are indicated on the curves by open symbols (○). The binomial frequency distributions of all male–female combinations are also shown, assuming a sex ratio of 50% males at hatching (graph A), as well as the resulting skewed distributions in nests having lost one or more young (graphs B–E). Because of enhanced mortality rates among female-biased nests at every level of temporary brood size, these nests become ever more frequent in the remaining sample of broods, as more young have died (graphs B–E, bars).
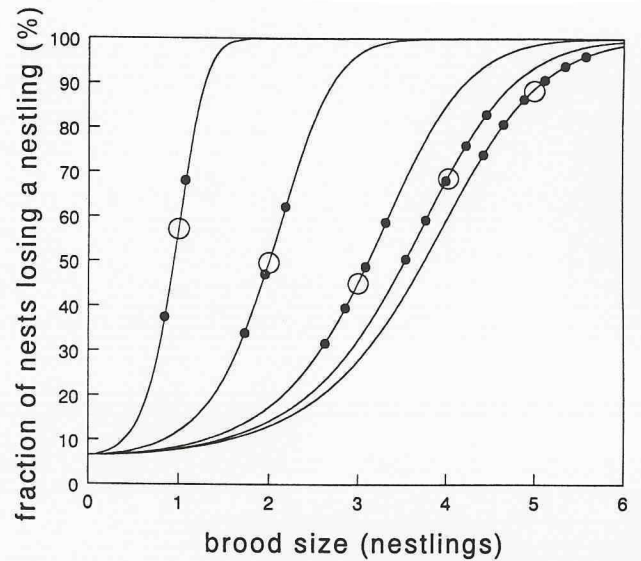

Figure 5
The same curves as presented in Figure 4: estimated mortality rates (●) around the observed overall values (○) for a decreasing number of remaining nestlings originating from five-egg clutches, but now plotted on the same abscissa scale.

tality, their frequency among the remaining nests increased with every additional round of mortality (Figure 4A–E, bars). Consequently, the average sex ratio of remaining broods (σ_5 σ_4 ... σ_1) was increasingly female biased as brood size declined (Equation 10). For this reason the relative food demand of different gender compositions ($d_{k,n}$; Equation 3) was increasingly asymmetrical around the average, with decreasing brood size (Figure 4A–E), thereby also skewing the predicted probability of losing another nestling for all brood compositions (closed symbols) relative to the observed average probabilities (open symbols). A summary of these results for clutches of five eggs is shown in Figure 5, but now plotted on the same x-axis scale (i.e., the number of young present in the nest). This presentation clearly illustrates that the variation in "feeding potential" among the remaining pairs in the subsamples necessarily becomes ever smaller as brood size declines.

Sex ratio and brood size at fledging. Using the estimates derived in Figures 4 and 5 for the probabilities of losing a nestling, we calculated, again illustrated for five-egg clutches, the sex ratio at fledging of broods where five, four, three, two, or one nestlings survived (σ'_5 σ'_4 ... σ'_1; Equations 8, 11, etc.). The predicted sex-ratio dependence of brood size at fledging is shown in Figure 6. Starting from a 50% sex ratio of the five hatchlings ($\sigma_5 = 0.5$), the small fraction of "complete" broods with five fledglings shows a strong male bias in the model. This is due to heavy mortality at this stage, which must be aggravated in female-biased nests. The large fraction of broods losing the first nestling is on average slightly female biased (σ_4), even though mortality does not specifically affect the females in each nest: mortality in this group of nests does not change their overall sex ratio (Figure 6). This female bias in combination with the observed relaxed mortality of the second young (Figure 3) results in a less extreme male bias in nests where four out of five young survive (Figure 6). By this process, there is a gradual reduction in the percentage males at fledging as broods become smaller. There is, however, another process counteracting this mechanism, which becomes more and more important at smaller brood sizes (still within the group of five-egg clutches). This is due to the
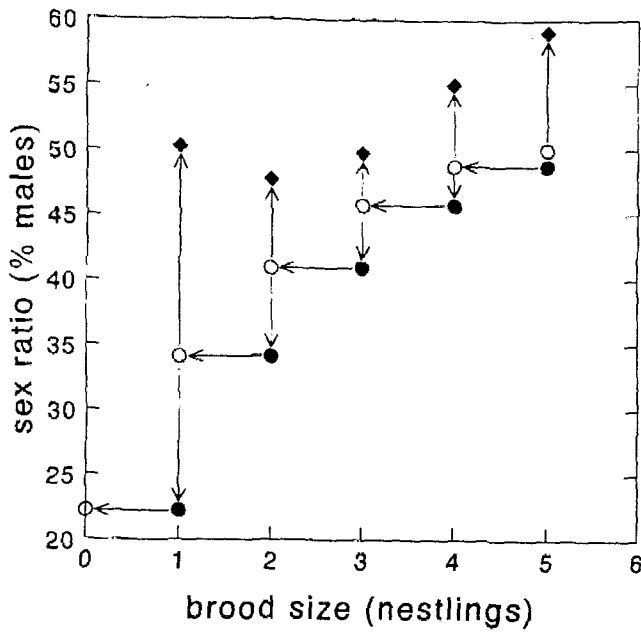
Figure 6
The predicted fledgling sex ratios (% males) for different final brood sizes (♦), originating from clutches of five eggs. Note that the sex ratio of those nests losing a young (●) does not change the actual mortality, which we assumed to be random with respect to gender within broods. Instead, female-biased nests have an increased chance of losing a young of any sex compared with the male-biased broods. Therefore the female bias is increasing in the remaining nests as brood size decreases through mortality.

binomial distribution: In broods of five, the unisexual broods, representing the extremes in terms of relative food demand, are a small minority (6.25%). The fraction of unisexual broods gradually increases as brood size declines. Hence the effect of gender-related differences in food demand on the probability of losing a nestling are most extreme here, as illustrated in Figure 4. Combined with a slightly increased observed probability of losing the last young (Figure 3), this causes a large difference in the sex ratio between those pairs raising their last nestling and those which do not. This counteracts the general decrease in fledgling sex ratio with declining brood size to such an extent that broods with one survivor again are slightly male biased (Figure 6). The model thus predicts a general curvilinear relationship between sex ratio and final brood size within clutches of five eggs.

We applied the same calculation also to the other clutch sizes. All predictions as well as the observed sex ratios, are presented in Figure 7. For large clutch sizes (five to seven eggs), the field data and the model show a similar curvilinear sex-ratio dependence on final brood size (Figure 7 A,B). A U-shaped curve is also predicted for small clutch sizes (two to four eggs), but here the data show a consistent increase in the percentage of males with decreasing brood size (Figure 7 C,D). In Figure 8, observed sex ratios for any combination of clutch and brood size are plotted against the predicted sex ratios. There is a reasonably close association with the model, explaining 41% of the observed variation. Also, the model predicted an overall sex ratio in the population of 53.7%, which is matched closely by the observed 54.7% males in the sample of 2463 marsh harrier fledglings. If we pool the broods stemming from different clutch sizes, again model predictions and observations fit reasonably well (Figure 9) and both show the U-shaped curve, which is typical for the sexually dimorphic species depicted in Figure 1.
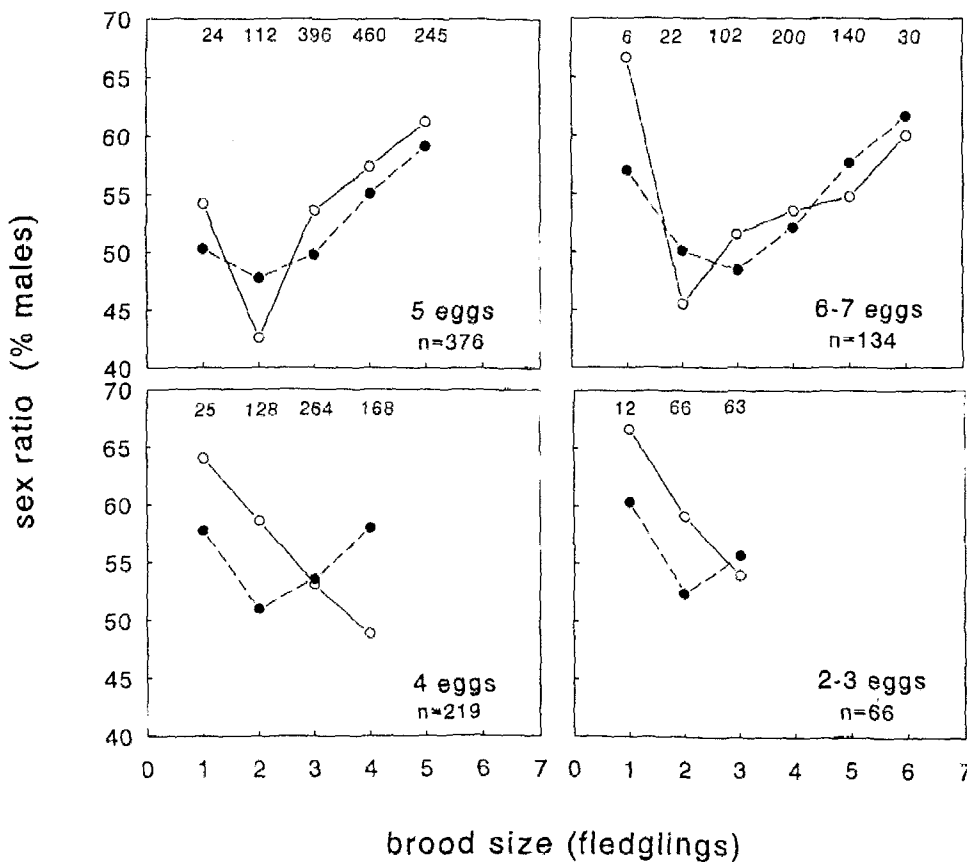

Figure 7
Observed (○) and predicted (●) fledgling sex ratios per final brood size in broods originating from clutches of different numbers of eggs. The lowest sex ratios are predicted for broods that experienced intermediate mortality. The highest sex ratio is predicted for complete broods and nests where only one young survived. The numbers along the top of each graph refer to the number of fledglings. (n = number of broods).
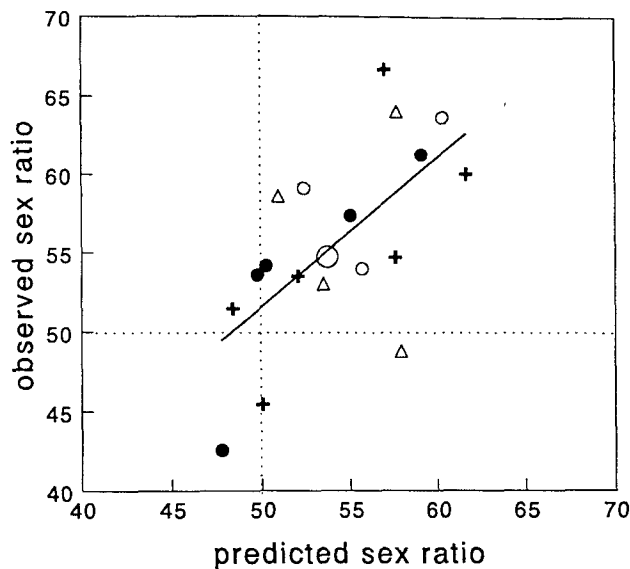
Figure 8
The observed fledgling sex ratios in marsh harrier broods of different size and originating from different clutch sizes as a function of predicted sex ratios from the model (data points from Figure 7). (✛) six or seven eggs; (●) five eggs; (△) four eggs; (○) two or three eggs. Linear regression: $y = 0.95x + 4.35$; $n = 18$, $r^2 = .41$, $p < .01$; (Ⓞ) overall average value.

Figure 9
Observed (○) and predicted (●) fledgling sex ratios in marsh harrier broods of varying final size, all clutch sizes pooled. The numbers across the top of the graph refer to the number of fledglings.

Based on these findings we hypothesize that the curvilinear relationship between brood size at fledging and the proportion of the smaller sex in sexually dimorphic altricial birds, as demonstrated in this study, may result from increased (random) mortality within female-biased broods, and relaxed (random) mortality within male-dominated nests, as a consequence of gender-specific food demand.

DISCUSSION

The theories of Fisher (1930) on optimal mean sex ratio and of Trivers and Willard (1973) on intraspecific sex ratio variation do not specify which mechanisms should operate to achieve the solutions. There is some evidence for primary sex-ratio control in several bird species (Dijkstra et al., 1990b; Howe, 1977; Komdeur et al., 1997). Here we have explored the possibility of secondary adjustment by differential mortality. The model developed assumes that the (estimated) variance around the (observed) probability that at least one of the offspring in a brood dies is related to the food demand of the brood, itself dependent on the gender composition of the brood. This model readily predicts for broods stemming from large clutches that the highest sex ratios occur at the largest and smallest final brood sizes (Figures 7, 9), even when the average sex ratio at hatching was assumed to be 0.5. Complete broods (without mortality) will have strongly male biased sex ratios because the majority of all nests loses at least one nestling. The observed fraction of nests losing a young as a function of the number of nestlings surviving till then is typically U-shaped in the marsh harrier (Figure 3). In other words, breeding pairs have a high probability of losing at least one young; those that do so show a relaxed mortality of the second nestling, etc. The small number of broods that at any time has one nestling left again shows an increased probability of losing their last young too. This varying mortality rate with reducing brood size, as established in the field, is decisive for the predicted fledgling sex ratios: the observed U-shaped mortality curve in the marsh harrier as a function of the number
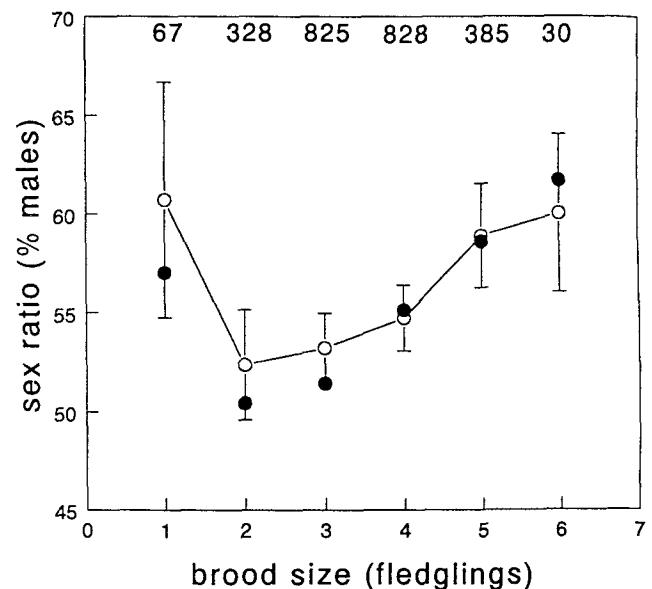
of nestlings left (Figure 3) results in a similar figure for the predicted fledgling sex ratio in broods of different final size (Figure 7). This nonintuitive prediction matches what is found as a significant, common pattern in fledgling sex ratios among all seven dimorphic species (Figure 1). We anticipate that the mortality pattern found in the marsh marrier also holds for the other species.

For the marsh harrier where sufficient energetic and demographic data are available to derive quantitative predictions, the predictions reasonably matched the observed sex ratios in all broods stemming from (the most common) large clutches (five to seven eggs; Figure 7). The model's performance was not as good for the smaller clutches (two to four eggs; Figure 7). There are several reasons the model may yield less precise predictions for the smallest clutch and brood sizes. First, the transition to zero nestlings probably includes cases of desertion by the parents and predation of complete nests, which were not identified as such. It is likely that such cases are not always related to food requirements and that nest desertion, in particular, is more frequent in smaller broods. Second, smaller clutches are typically produced late in the season (Zijlstra et al., 1992), and it is not excluded that a seasonal change in conditions or in strategy would add further complexity to the model (Daan et al., 1996b). Furthermore, the smaller broods occur less frequently, with broods of one nestling especially rare, and the sex-ratio database thereby is less powerful than for large broods.

Nonetheless, the model explains 41% of the variance in sex ratio among different brood-size/clutch-size combinations (Figure 8). This is surprising when we realize that a substantial portion of raptor nestlings die before having reached half their fledging age (Newton, 1979), when secondary sex characteristics and sex-specific energy demands are not yet fully developed (Krijgsveld K et al., submitted). However, due to pronounced hatching asynchrony in the marsh harrier, age differences of about 10 days between the first and last hatchling are common in large broods (Witkowski, 1989). This implies that many nestlings die when at least their older siblings have fully developed sex-specific food requirements. If sex-

ratio–dependent differential mortality also takes place during the early stages of development, this may mean that the parents adjust their rate of provisioning during that stage to the ratio of sons and daughters in the brood, thereby generating sex-ratio–dependent mortality. Obviously, if the parents could regulate mortality early on, they would save several weeks of lost energy investment in some of the offspring, at costs paid both by the surviving siblings and the parents (Daan et al., 1996a; Dijkstra et al., 1990a). An even more economic solution would be for parents to control sex ratio during egg formation (Krackow, 1995), and use situation-dependent and sex-ratio–dependent control via mortality only for fine tuning at a later stage. Because data on raptor primary sex ratios (at hatching) are lacking, we cannot be conclusive about these possibilities.

The available evidence for the marsh harrier is largely consistent with the hypothesis of differential mortality, dependent on sex-ratio–linked differences in food requirements between broods. We did not incorporate effects of age differences between siblings in the model as presented here (i.e., all siblings contributed equally to the total food demand of the brood). In interspecific comparisons, a positive relationship between the degree of sexual size dimorphism and hatching asynchrony has been found (Slagsvold, 1990). We surmise that in species showing both extreme size dimorphism and pronounced hatching asynchrony, the sex-linked food demand of the first-born nestlings within the brood is particularly decisive for the survival prospects of the last born. In these cases the primary sex ratio of the whole brood would be a less accurate predictor of nestling survival. In our model the sex of the potential victim—i.e., the youngest nestling in asynchronously hatching species, is of minor importance for its chances to survive. This is in contrast with earlier hypotheses that considered this to be the crucial factor explaining enhanced mortality of the most food-demanding sex (Slagsvold, 1990; Slagsvold et al., 1986; Teather and Weatherhead, 1989). To discriminate between these views and to establish the precise role of mortality in shaping fledgling sex ratios demands techniques to establish offspring sex at hatching. These techniques are already available for certain species (Griffiths, 1992; Griffiths and Tiwari, 1995; Griffiths et al., 1992; Komdeur et al., 1997; Lessells et al., 1996) or applicable to a wide range of avian species (Ellegren, 1996; Griffiths et al., 1996). Their application to problems of optimization and physiological control of sex ratio will open fascinating areas of research.

REFERENCES

Anderson DJ, Budde C, Apanius V, Martinez Gomez JE, Bird D, Weathers WW, 1993. Prey size influences female competitive dominance in nestling American kestrels *Falco sparverius*. Ecology 74: 367–376.

Balfour E, 1970. Iris colour in the hen harrier. Bird Study 17:47.

Balfour E, Cadbury CJ, 1979. Polygyny, spacing and sex ratio among hen harriers *Circus cyaneus* in Orkney, Scotland. Ornis Scand 10: 133–141.

Bednarz JC, Hayden TJ, 1991. Skewed brood sex ratio and sex-biased hatching sequence in Harris's hawks. Am Nat 137:116–132.

Bijlsma RG, 1993. Ecologische Atlas van de Nederlandse Roofvogels. Haarlem: Schuyt and Co.

Blank JL, Nolan V, 1983. Offspring sex ratio in red-winged blackbirds is dependent on maternal age. Proc Natl Acad Sci USA 80:6141–6145.

Clutton-Brock TH, 1986. Sex ratio variation in birds. Ibis 128:317–329.

Clutton-Brock TH, Albon SD, Guiness FE, 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313:131–133.

Daan S, Deerenberg C, Dijkstra C, 1996a. Increased daily work precipitates natural death in the Kestrel *Falco tinnunculus*. J Anim Ecol 65:539–544.

Daan S, Dijkstra C, Weissing FJ, 1996b. An evolutionary explanation for seasonal trends in avian sex ratios. Behav Ecol 7:426–430.

Dijkstra C, Bult A, Bijlsma S, Daan S, Meijer T, Zijlstra M, 1990a. Brood size manipulations in the kestrel *Falco tinnunculus*. Effects on offspring and adult survival. J Anim Ecol 59:269–285.

Dijkstra C, Daan S, Buker JB, 1990b. Adaptive seasonal variation in the sex ratio of kestrel broods. Funct Ecol 4:143–147.

Ellegren H, 1996. First gene on the avian W chromosome (CHD) provides a tag for universal sexing of non-ratite birds. Proc R Soc Lond B 263:1635–1641.

Fiala KL, 1981. Sex ratio constancy in the red-winged blackbird. Evolution 35:898–910.

Fisher RA, 1930. The genetical theory of natural selection. Oxford: Clarendon Press.

Griffiths R, 1992. Sex-biased mortality in the lesser black-backed bull *Larus fuscus* during the nestling stage. Ibis 134:237–244.

Griffiths R, Tiwari B, Becher SA, 1992. The identification of sex in the starling *Sturnus vulgaris* using a molecular DNA technique. Mole Ecol 1:191–194.

Griffiths R, Tiwari B, 1995. Sex of the last wild Spix's macaw. Nature 375:454.

Griffiths R, Daan S, Dijkstra C, 1996. Sex identification in birds using two CHD genes. Proc R Soc Lond B 263:1251–1256.

Holcomb LC, Twiest G, 1970. Growth rates and sex ratios of red-winged blackbird nestlings. Wilson Bull 82:294–303.

Howe HF, 1977. Sex-ratio adjustment in the common grackle. Science 198:744–746.

Kenward RE, Marcström V, Karlblom M, 1993. Post-nestling behaviour in goshawks, *Accipiter gentilis*. II. Sex differences in sociality and nest-switching. Anim Behav 46:371–378.

Komdeur J, Daan S, Tinbergen J, Mateman C, 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525.

Krackow S, 1995. Potential mechanisms for sex ratio adjustment in mammals and birds. Biol Rev 70:225–241.

Lessells CM, Mateman AC, Visser J, 1996. Great tit hatchling sex ratios. J Avian Biol 27:135–142.

Negro JJ, Hiraldo F, 1992. Sex ratios in broods of the lesser kestrel *Falco naumanni*. Ibis 134:190–191.

Newton I, 1979. Population ecology of raptors. Berkhamsted: T and AD Poyser.

Newton I, Marquiss M, 1979. Sex ratio among nestlings of the European sparrowhawk. Am Nat 113:309–315.

Picozzi N, 1980. Food, growth, survival and sex ratio of nestling hen harriers *Circus c. cyaneus* in Orkney. Ornis Scand 11:1–11.

Picozzi N, 1984. Sex ratio, survival and terrritorial behaviour of polygynous hen harriers *Circus c. cyaneus* in Orkney. Ibis 126:356–365.

Riedstra B, Dijkstra C, Daan S, in press. Daily energy expenditure of male and female marsh harrier nestlings *Circus aeruginosus*. Auk 115.

Rosenfield RN, Bielefeldt J, Vos SM, 1996. Skewed sex ratios in Cooper's hawk offspring. Auk 113:957–960.

Røskaft E, Slagsvold T, 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the rook. J Anim Ecol 54:261–266.

Sayce JR, Hunt GL, 1987. Sex ratios of prefledging western gulls. Auk 104:33–37.

Slagsvold T, 1990. Fisher's sex ratio theory may explain hatching patterns in birds. Evolution 44:1009–1017.

Slagsvold T, Røskaft E, Engen S, 1986. Sex ratio, differential cost of rearing young, and differential mortality between the sexes during the period of parental care: Fisher's theory applied to birds. Ornis Scand 17:117–125.

Teather KL, Weatherhead PJ, 1989. Sex-specific mortality in nestling great-tailed grackles. Ecology 70:1485–1493.

Trivers RL, Willard DE, 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92.

Wiebe KL, Bortolotti GR, 1992. Facultative sex ratio manipulation in American kestrels. Behav Ecol Sociobiol 30:379–386.

Wikman M, 1976. Sex ratio of finnish nestling Goshawks *Accipiter gentilis* (L.). Congress of the International Union of Game Biologists XII. Washington, DC: Wildlife Management Institute.

Witkowski J, 1989. Breeding biology and ecology of the marsh harrier *Circus aeruginosus* in the Barycz valley, Poland. Acta Ornithol 25:223–320.

Zijlstra M, Daan S, Bruinenberg-Rinsma J, 1992. Seasonal variation in the sex ratio of marsh harrier *Circus aeruginosus* broods. Funct Ecol 6:553–559.