Offspring sex ratio and male quality in Goshawk Accipiter gentilis

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Abstract -

In some bird species, brood sex ratios have been shown to vary with male quality and time of season. Sex ratio adjustment in favour of males would be adaptive if sons inherit their fathers characters that increased their attractiveness to females. In species without obvious sexual ornaments, as in Goshawks, female choice must be based on other characters. One possible male quality character is his ability to defend and protect a good territory. Brood sex ratios skewed towards males have been reported in Goshawks, but only in broods of four young did the male / female ratio differ significantly. In the present study of Goshawks in Sweden I registered a total number of 953 females and 1054 males (=52.5% males) in 745 broods, which is significantly different from parity. However, in the 116 broods with four young I did not find any evidence for my hypothesis about different sex ratio among clutches or territories.

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Introduction

Sex ratios deviating from unity are commonly reported in humans. No proved explanation has been given for the discrepancies between the proportions of females and males at the time of birth. In the last decades evidence has accumulated that animals with a chromosomal sex determination system are capable of adjusting the sex ratio of their offspring (for examples Clutton-Brock et al. 1984, Bortolotti 1986, Madsen & Shine 1992). In some bird species the brood sex ratio has been shown to vary with male quality and time of season (Svensson & Nilsson 1996, Ellegren et al. 1996, Dijkstra et al. 1990, Olsen & Cockburn 1991, Zijlstra et al. 1992). The Goshawk seems to adjust its sex ratio to more males later in season (in Daan et al. 1996).

In birds the female has the possibility to determine the sex of young. Sex ratio adjustment in favour of males would be adaptive if sons inherit their fathers characters and thus increased their attractiveness to females. In many species of birds males have conspicuous sexual ornament. Males with sexual ornaments attract more females, breed earlier or are able to attain extra pair copulations (EPC) (Andersson 1994, Möller 1994, Ellegren et al. 1996). In species without obvious sexual ornaments, such as in the Goshawk, female choice must be based on other characters. One possible male quality character is his ability to defend and protect a good territory. In species with large size dimorphism, as in Goshawks, brood sex ratios may be adjusted relative to the size of the parents. This has been observed in Peregrine Falcons *Falco peregrinus* where large females are early breeders and also produce more daughters (Olsen & Cockburn 1991). In American Kestrel *Falco sparverius* small females have been observed to produce sons (Wiebe and Bortolotti 1992).

In Finland, the clutch size in the Goshawk is related to annual variation in the density of prey (Sulkava 1964, Wikman 1977). Thus, I predict that a male with high fitness ought to defend a territory with abundant prey, and it would be advantageous and attractive to a female to mate with such a male as more progeny would be produced. As the success of a breeding attempt depends on the male's ability to provide food, the female might increase her fitness by adjusting her brood sex ratio in favour of males if her sons inherit the characters necessary for occupying and defending a superior territory and in that way attract females. Wikman (1976) reported a

	Brood size Kullstorlek						
	1	2	3	4	5		
No. females honor	24	227	477	218	7		
No. males hanar	36	233	531	246	8		
% males hanar	60.0	50.6	52.7	53.0	53.3		
% of broods kullar	8.0	30.9	45.1	15.6	0.4		

Table 1. Sex ratio of nestling Goshawks relative brood size. *Könsfördelningen hos duvhök i olika kullstorlekar*

sex ratio skewed towards males in Goshawks, but only in broods of four did the male / female ratio differ significantly. Kenward et al. (1993) reported 60% males in broods of four but in a small sample (n=5). In this paper I test the hypothesis that Goshawks skew the sex ratio towards males in territories where at least one four brood was laid.

Material and methods

A large number of broods of Goshawks have been sexed in Sweden in known territories. It is therefore possible to test if the brood sex ratio is skewed towards males in broods with four young or if there is a surplus of males in territories where at least one brood of four have been reared. I received information on sex ratios in 745 broods collected by 11 ringers (see acknowledgements) between 1975 and 1999 from both the northern to the southern part of Sweden (Table 1).

Results

The mean number (\pm SE) of young in these broods was 2.69 \pm 0.016 which is nearly equal to Wikman's (1976) value (2.62 \pm 0.03). The total number of females was 953 and that of males 1054 (=52.5% males), which is significantly different form parity (χ 2 = 5.08, df=1, P< 0.05). In my sample of 116 broods with four nestling, 53.0% were males which was not significantly different from an equal sex ratio (χ 2=1.69, df=1, P>0.10). There was not endency of more males in broods of four young compared to smaller broods (χ 2=6.09, df=4, P>0.10) (Table 2).

The ringers visited the territories in several years and found most territories occupied in many years, but with interruptions. It is impossible to detect if a territory is occupied by the same or a different pair nor to conclude why a territory was not occupied in certain years. In 68 territories where at least one brood of four young was raised, 457 males and 432 females were ringed in 297 broods. This sex ratio was not significantly different from 1:1 ($\chi^2 = 0.7$, df=1, P>0.3).

Discussion

Wikman (1976) reported 52.3% males in his sample of 429 sexed broods but could not detect a statistical significant departure from parity, because of too small sample size. In contrast, I found a similar estimate (52.5% males) to be significantly different from parity. However, Rosenfield et al. (1993) found a significantly skewed sex ratio (54% males) in the Cooper's Hawk Accipiter cooperi first after they had collected a large sample (n = 372). Wikman (1976) and Kenward et al. (1993) found a non-significantly reduced proportion of males in smaller broods. There was no evidence of such a pattern in my data set (Table 1). Wikman (1976) reported 56.7% males in his 78 broods with four nestlings, which is significantly different from an equal sex ratio and not in agreement with my material.

The significant differences of higher proportion of males than females at the time of ringing seem to diminish or being eliminated later in life since males have a lower average lifespan than females (males 435 days, n=284; females 548 days, n=223; P<0.05, see Ryttman 1993).

Sexing of nestling Goshawks at the time of ringing seems to be rather accurate. Of 202 ringed nestlings later found dead or controlled in traps for game bird protection, eight (4%) had been incorrectly sexed. Four females had been sexed as males and four males as females. In the following I only discuss the sex ratio in broods containing four young. In brood sizes of four the sex ratio mostly reflects that at hatching because clutches of five eggs are rare. For example, Wikman (1976) reported that 5% of 259 clutches contained 5 eggs. It is common that broods of Goshawks are reduced by chick mortality. Kenward et al. (1993) found that females tended to predominate Table 2. The distribution of sexes in broods of four young and the expected number with the hypothesis of equal sex ratio within broods ($\chi 2 = 6.09$, df = 4, P > 0.10).

No. of females in brood antal honor i kull	No. of males in brood <i>antal hanar i kull</i>	Observed no. of broods observerat antal kullar	Expected no. of broods förväntat antal kullar	
0	4	5	7.25	
1	3	36	29.0	
2	2	49	43.5	
3	1	20	29	
4	0	6	7.25	

Könsfördelningen i kullar om fyra ungar och förväntat antal om könskvoten följer en binomialfördelning om 1:1

in nests that had lost most offspring, but when the loss was only one nestling the trend was not significant. However, Kenward et al. (1993) had no clutches of five in their sample. As clutches of five are rare, few broods of four are the result of egg loss or nestling mortality. Where one chick has died or an egg failed to hatch the sex ratio is not significantly influenced.

To conclude, I could not find any evidence for my hypothesis about different sex ratios among clutches of four young or in territories where broods of four had occurred. In a species like the Goshawk, a female should benefit from breeding with a male, which has the ability to defend a good territory and to provide food. These qualities influence the female's clutch size (Sulkava 1964) and chances of successful reproduction. Male quality is certainly partly inherited. If superior males also are more successful in attracting females, one would expect females mated to such males to adjust sex ratios in favour of sons. But it seems as if female Goshawks defer or lack the possibility to adjust their sex ratios.

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Sammanfattning

Könskvoter i kullar och hanars kvalitet hos duvhök Accipiter gentilis

Flera fågelarter tycks ha möjligheten att påverka könet på sina avkommor. Då det är honorna hos fåglar, som bestämmer könet på avkomman, kan det vara fördelaktigt att styra könen så att honan sprider sina gener på det mest fördelaktiga sättet. Finner t.ex. honan en attraktiv hane och dennes attraktiva karaktär är ärftlig (ofta s.k. ornament) kan det vara fördelaktigt att producera fler hanar än genomsnittet.

För fågelarter där uppenbara ornament inte finns kan andra fitnesskaraktärer kanske vara avgörande för valet av hane från honans sida. En möjlighet skulle kunna vara, att honan väljer hane beroende på det revir, som hanen försvarar. Ett bra revir innebär att honan kan erhålla föda så att hon kan producera många ägg. Att hanen försvarar ett bra revir med mycket föda kan honan mycket lätt bedöma, då hon kommer till reviret.

Jag studerar i denna uppsats duvhökshonans möjlighet att påverka könet i kullar om fyra ungar och i revir där fyra ungar någon gång har fötts upp. I Finland har Wikman (1976) visat att det just i fyraungskullar fanns ett signifikant överskott av hanar. I mitt material om 745 kullar där könen har bestämts fanns det ett signifikant överskott av hanar i förhållande till honor (1054 resp. 953). Men just i de 116 fyra-ungskullar, som finns i materialet, finns inget signifikant överskott av hanar. Hanarna utgjorde där 53% eller 246 av 464 ungar. Inte heller i de revir där fyra ungar producerats vid någon tidpunkt fanns det ett signifikant överskott på hanar (457 hanar respektive 432 honor). Det verkar därför inte som om honorna hos duvhöken, om de väljer hanar med goda revir, försöker eller har förmåga att ändra könssammansättningen i sin kull till förmån för hanar.