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Sex ratios of Sparrowhawk (*Accipiter nisus*) broods: the importance of age in males

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Evolutionary theory predicts that variation in parental quality in sexually dimorphic species may lead to biased brood sex ratios, because of differences in the costs and benefits of raising male or female offspring with resource availability. We analysed the secondary brood sex ratio in Sparrowhawks, a raptor species showing extreme sexual dimorphism, with females being nearly twice the size of males. Brood sex ratios were analysed in relation to laying date, brood size and parental age, an indicator for parental quality. Female age did not affect brood size and offspring sex ratio, but yearling females started egg-laying later than older females. Broods of first-year males hatched later and produced fewer fledglings than those of older males. The brood sex ratio was balanced in older males, but male-biased in yearling males. Inter-annual variation in the seasonal sex ratio trends correlated with variation in the local age distribution of breeding males. Our finding, that females of first-year males produce relatively late and small broods of the cheaper sex, may be indicative of a relatively low paternal quality, since males provide most of the food for the female and the brood during the reproductive period. We propose that future theoretical models for seasonal trends in brood sex ratio in sexually dimorphic species should also consider variation in parental quality with breeding date.

1. Introduction

Fisher (1930) predicted that equal investment in male and female offspring was likely to be an evolutionary stable strategy. In accordance with his equilibrium theory, offspring sex ratios (proportion of males) in bird populations seldom deviate from parity (Clutton-Brock 1986). Modification of Fisher's assumptions revealed that it is adaptive for parents to bias investment in favour of one or the other sex under certain circumstances (Hamilton 1967, Charnov 1982). For instance, if the relative fitness of sons and daughters differs, depending on some feature of the circumstances in which they are born, parents should produce the gender which profits most from the prevailing conditions (Trivers & Willard 1973). An often-cited example is the European kestrel (*Falco tinnunculus*; Dijkstra *et al.* 1990). The seasonal decrease in the proportion of male offspring in the population was functionally explained by the finding that early born males had a higher chance to breed in their first year of life, whereas no such tendency was found for females (Dijkstra *et al.* 1990).

Seasonal variation in brood sex ratio is indeed common in raptors, with some species producing an excess of daughters early in the season and an excess of sons in late nests, while others show the reverse (reviewed by Daan *et al.* 1996). Daan *et al.* (1996) further present a general model to give an evolutionary explanation for this phenomenon in terms of sex-specific differences in the relation between age of first breeding and date of birth. Their model fitted the empirical data of four out of five species (including the Kestrel). The sparrowhawk (*Accipiter nisus*), however, showed an overall seasonal increase in the percentage of sons (Fig. 1 in Daan *et al.* 1996) despite similar maturation rates for males and females (Newton 1986).

One factor, which the maturation model of Daan *et al.* (1996) does not take into account, is that one or the other sex may receive fitness benefits, in addition to an early birth date, from being sired by high-quality parents. Early hatched young are often larger and heavier than late hatched ones, and a cross-foster experiment in European coots (*Fulica atra*) has shown that this was essentially due to the high quality rearing environment offered by early breeding pairs (Brinkhof 1997). Further, in sexual dimorphic species the relative effect of good nutrition during rearing on juvenile growth might differ between the sexes. Female offspring in Japanese Quail (*Coturnix coturnix japonica*) grew considerably larger than male offspring under good feeding conditions, but not under restricted feeding (Gebhardt-Henrich & Marks 1993). Such sex specific differences in juvenile growth might be important in the Sparrowhawk, which shows an extreme reversed sexual size dimorphism among raptors, with females being nearly twice as heavy as males (Glutz von Blotzheim *et al.* 1971).

The maturation model of Daan *et al.* (1996) does not include differential costs for raising male and female offspring. Myers (1978) proposed that parents with little resources for raising young may bias the brood sex ratio towards the cheaper sex, as to allow for maximisation of the total number of young produced. This hypothesis was supported by some studies in raptors, which found a higher proportion of males among first-hatched offspring (Dzus *et al.* 1996) or overall within a brood under conditions of low food abundance (Wiebe & Bortolotti 1992). In Sparrowhawks the investment required to raise female offspring will considerably exceed that of male offspring (Richner 1991) and the total investment for the current brood may thus strongly depend on the sex ratio as well as on brood size. Given the trade-off between current and future reproduction (Williams 1966, Lessells 1991), variation in resources may then lead to variation in brood size and brood sex ratio between pairs differing in quality.

Similar to other bird species (Sæther 1990, Perdeck & Cavé 1992) age can be used as an indication of parental quality in Sparrowhawks. In general, second year and older Sparrowhawks start breeding earlier and produce larger clutch and brood sizes than first-year breeders, whereas pairs with mixed age composition perform intermediately (Newton *et al.* 1981, Bijlsma 1993). To our knowledge, however, brood sex ratios in Sparrowhawks have so far not been investigated in relation to laying date, brood size and parental age. The aim of the present study was to perform such an analysis and to assess the role of parental age differences in the occurrence of annual and seasonal variation in brood sex ratios.

2. Material and methods

2.1. Study area, study species and standard procedures

The study was carried out from 1992 to 1996 in Greater Hamburg and adjacent parts of Schleswig-Holstein in northern Germany (53°50′N, 10°00′E). The study area extended over approximately 1000 km^2 and consists of urban (15%), suburban (23%), agricultural (52%, including forestry) landscapes. The Sparrowhawk is especially common in the urban area, with up to 13 pairs per 100 km^2 breeding annually in public parks and gardens within the city of Hamburg (Risch *et al.* 1996).

Female Sparrowhawks are up to twice as heavy as males, weighing about 250–300g, while males rarely exceed 150g (Glutz von Blotzheim *et al.* 1971, Newton 1986). Fledglings resemble their parents of the same sex in weight (Moss 1979). Both sexes become sexually mature in their first year of life and thus are able to breed as yearlings. During the breeding season Sparrowhawks show a strict task-differentiation between the sexes. Males compete for territories, while females compete for males with an established territory (Newton 1979). Further, males provide all food for female and brood, from well before egg-laying until the nestlings are about half-grown, while the female is responsible for incubation and feeding of nestlings.

Throughout the breeding season of each year potential nesting sites were checked weekly to locate nests. During nest observations, the age of the parents was estimated on basis of moulted feathers found near the nest and direct observations as described in Newton *et al.* (1981). Birds older than 2 years could not be aged precisely. We therefore expressed age categorically, i.e., as first-year (juvenile plumage) or adult (second-year-and-more (adult plumage). Since all breeding Sparrowhawks are sexually mature, we reserved the term adult for birds in adult plumage in order to distinguish them from first-year birds in juvenile plumage. Female age was more often determined than male age due to their higher attendance rate at nests. Brood size was determined and young were sexed and aged in 162 successful nests (i.e., nests in which at least one chick survived up till ringing). Brood size ranged between one and six nestlings, and was on average 4.2 (SE = 0.10) young. The age of the oldest nestling was estimated using the length of the outer primaries following the standard growth curves given by Moss (1979) and Bijlsma (1993). Using this method nesting age was reliably predicted in our population, as the estimated age was always within two days from the exact age found in broods of known hatching date (n = 26). The mean nestling age at which brood size and brood sex ratio were determined was 16.9 (SE = 0.27) days. The sex of the nestlings was determined using the size of the feet and the width of the tarsal joint. From the 10th day of life onwards females are unmistakably discriminated from males by their larger feet (Moss 1979).

Incubation usually starts about two days after laying of the first egg and the chicks hatch about 35 days later (Newton 1986, pers. obs.). Laying date of the first egg was then calculated by back-dating as follows: Laying date = ringing date – (nestling age + 37). Laying dates are presented as the day of the year (i.e., day 121 = 1 May in normal years, 30 April in leap years).

We understand the term sex ratio as proportion of males. All sex ratio data presented in this study are secondary sex ratios that were obtained at banding. The term "secondary" indicates that those sex ratios can theoretically be biased by non-random mortality of eggs and nestlings, as opposed to primary sex ratios existing at ovulation.

2.2. Data analysis

The analysis was performed using the statistical software package Statistix 4.0 (Analytical Software 1992). Modelling was performed by fitting generalised linear models using a stepwise backward procedure (McCullagh & Nelder 1989). Thus modelling was hierarchical, which implies that a minimal adequate model, i.e., a model in which the highest-order terms are significant, was achieved by the successive removal of non-significant terms, starting from the maximal model considered. These models include multiple regression models with continuous explanatory variables (variates), analysis of variance (ANOVA) with categorical variables (factors), as well as models with any mixture of factors and covariates (ANCOVA), and their interactions. Linear regression (normal error) with F-tests was used for the analysis of laying date and brood size. Logistic regression (binomial error) with chi-square-tests was used when analysing proportions. These analyses include the annual fraction of first-year breeders in the population and the fraction of male offspring in the broods (brood sex ratio; i.e., the number of male offspring was taken as response variable, the total number of offspring in the brood as denominator). The predictor variables considered in each of the analyses are given in the Results. All statistical tests were two-tailed.

3. Results

3.1. Age structure of the breeding population

The analysis of the annual variation in the age structure of the breeding population was restricted to successful nests, as we intended to use this information to investigate differences in brood size and brood sex ratio between years. The age of the female parent was known for 153 successful nests. In 102 cases the age of the male was known as well. The proportion of first-year females was not significantly different among years (logistic regression; $\chi^2_4 = 4.48$, $P = 0.34$), whereas the difference in the proportion of first-year males among breeders was near significance ($\chi^2_4 = 9.44$, $P = 0.051$). We further tested whether the age structure of the breeding population showed systematic changes over successive years. While the proportion of first-year females among breeders did not show a trend ($\chi^2_1 = 1.11$, $P = 0.29$), the proportion of first-year males in the breeding population significantly declined from 1992 to 1996 ($\chi^2_1 = 7.72$, $P = 0.005$). Starting with 1992 the proportion of first-year breeders was 0.40, 0.18, 0.23, 0.14 and 0.04 respectively.

Among the 102 breeding pairs for which the age of male and female was known, in 80 cases the breeding partners were of the same age category, i.e., in 64 cases both were older than first-year and in 16 both were first-year breeders. Of the remaining 22 pairs of unequal age, the combination 'adult male–first-year female' and 'first-year male–adult female' occurred in 20 and 2 cases respectively. The distribution of the female age-classes over the male age-classes was highly skewed ($\chi^2_1 = 27.49$, $P < 0.0001$). Breeding partners were more frequently of similar age than expected on the basis of random mating.

3.2. Laying date in relation to year and parental age

The mean laying date of successful broods (n = 153) differed significantly between years (ANOVA, $F_{4,148} = 2.75$, $P = 0.03$). The mean laying date in the earliest two years, i.e., day 119 in 1993 and 1996, was 5 days earlier than in the year with the latest average laying date, i.e., day 124 in 1992. The difference in timing between years remained significant when restricting the analysis to the nests for which the age of both parents was known (n = 102; $F_{4,97} = 4.26$, $P = 0.003$). We therefore considered the latter representative and suitable for an analysis of the role of parental age differences in explaining the inter-annual variation in laying date.

Laying date was related to year, male age and female age (Table 1). The interaction between the age of male and female was not investigated, as the combination 'first-year male–adult female' was too rare in our data set (n = 2, see Fig. 1). The result implies that the difference in the timing of breeding between years could not be attributed to differences in the age structure of the male breeding population alone. Independent of the difference in timing between years, laying date was negatively related to age of both the male and female parent. The effect was larger for male than female age. Given the age of the female, the laying date of an adult male's clutch was on average 8.3 days earlier than that of a first-year male. The mean laying date of adult females was, given the

Table 1. Multiple regression analysis of the relationship of laying date with the age of the female and male parent. The null model gives the constant fitted only. The change in the sum of squares (deviance) and d.f. for accepted parameters were obtained by removing (d.f. = +) each term, in turn, from the minimal adequate model. For 'year' the mean constant over the 5 years is given. The age of the male and female was tested as factor; first-year = 0, older than first-year = 1.

	(Increase in)			Estimates of coefficients
Parameter	Sum of squares	d.f.	P	
Null model	6810.82	101		
Minimal adequate model	3524.92	95		
Constant		+1		
Year	473.82	+4	0.017	132.1
Female age	392.40	+1	0.002	–5.03
Male age	666.21	+1	< 0.001	–8.34

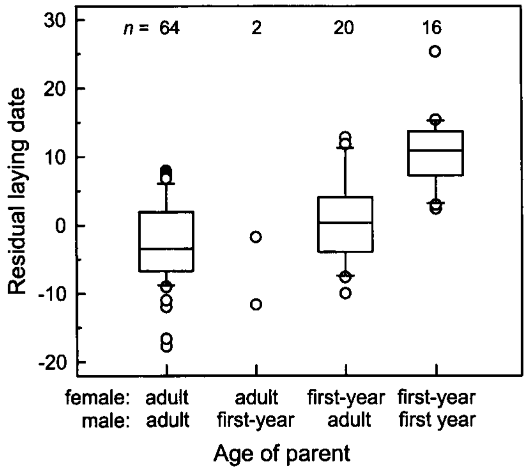

Figure 1. Box plot of residual laying date in relation to different combinations of age of female and male parent. The term adult indicates birds in adult plumage (2nd year and older). To control for variation in timing between years (see Table 1) residuals from a regression of laying date on year (i.e., standardised laying dates) were used for presentation. The extents of the box indicate the 25th and 75th percentiles, the line inside the box the 50th percentile, and the capped bars the 10th and 90th percentile of the data. The open circles represent all data outside the 10th and 90th percentile points.

age of the male, on average 5 days earlier than that of first-year females (see coefficients in Table 1). As a result, females of both age-classes that bred with adult males started egg laying earlier than females breeding with first-year males (Fig. 1).

3.3. Brood size in successful nests

The variation in the brood size at ringing was analysed using multiple regression. Brood size was significantly related to laying date ($F_{1,151} = 21.80$, $P < 0.0001$; $R^2 = 0.13$), whereas the age of the brood at ringing did not contribute significantly to the variance explained ($F_{1,150} = 2.38$, $P = 0.12$). In addition, year ($F_{4,147} = 0.39$, $P = 0.82$) and the interaction between year and laying date ($F_{4,143} = 0.84$, $P = 0.50$) were not significant, indicating that the level and slope of the seasonal variation in brood size was similar among years. In all years brood size declined progressively with laying date (Fig. 2a).

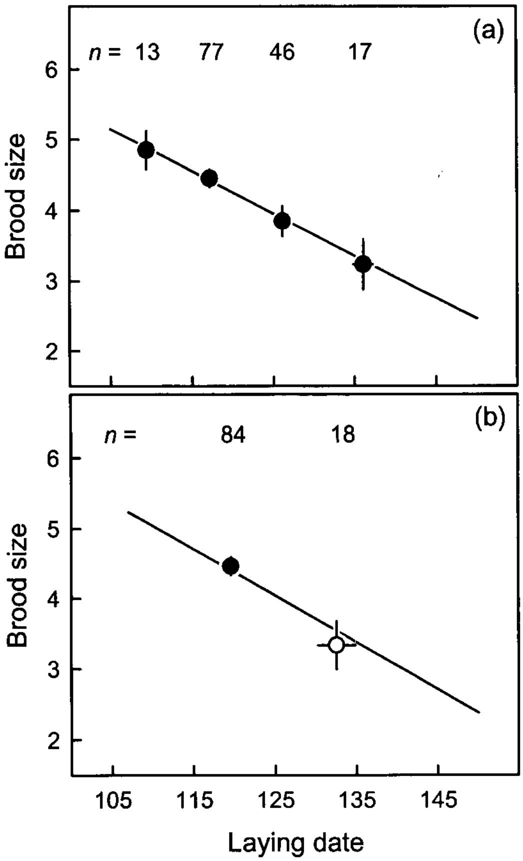

Figure 2. (a) Seasonal variation in brood size (1992–1996). The dots give the mean brood size (± 1 SE) over 10-days laying periods. Sample sizes of groups are given at the top of the graph. The regression line (equation: brood size = 11.34–0.059 x laying date) is based on the analysis of ungrouped data. (b) Mean brood size (± 1 SE) in relation to laying date for first-year males (open circle) and older males (solid circle).

Brood size also declined with laying date among the selection of nests in which the age of both parents was known (n = 102), and the slope of the decline was similar to the one found among broods were the age of the male was unknown (n = 51; for the interaction between laying date and the factor male age known (known = 1, unknown = 0): $F_{1,149} = 0.023$, $P = 0.89$). Disregarding the effect of season, brood size was significantly related to the age of the male parent ($F_{1,100} = 11.93$, $P = 0.0008$), whereas the age of the female parent was not significant ($F_{1,99} = 0.07$, $P = 0.79$). On average pairs with an adult male

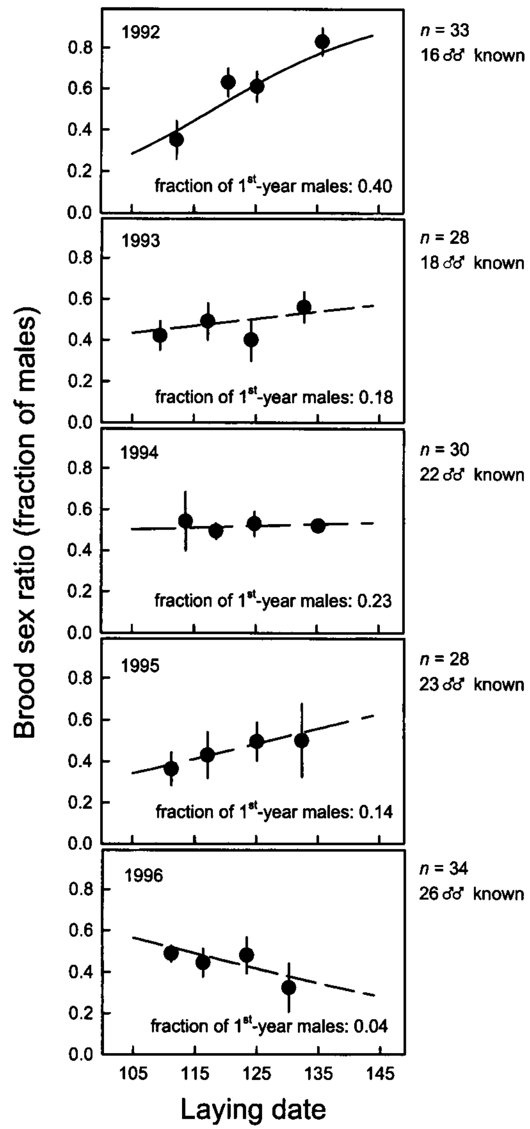

Figure 3. Seasonal variation in brood sex ratio over the years 1992–1996. Symbols give the mean (± 1 SE) sex ratio over a range of nests grouped according to laying date. The lines give the best fit for the seasonal trend in the brood sex ratio in each year. A significant relationship is marked with a solid line, a non-significant trend with a broken line. The fraction of first-year males among breeders was assessed in a selection of broods with a male parent of known age.

raised 1.13 more young than pairs with a first-year male. The effect of male age was, however, no longer significant ($F_{1,99} = 1.67$, $P = 0.20$) when the effect of laying date was taken into account. Thus the higher breeding success of pairs with an adult male was associated with their earlier laying date (Fig. 2b).

3.4. Brood sex ratio

Over the years 1992–1996 a total of 638 young were banded and sexed; 318 and 320 were identified as male or female respectively. Thus the overall nestling sex ratio was 0.50. Over the successive years 1992–1996 the annual mean sex ratio was 0.57 (n = 33), 0.47 (n = 28), 0.52 (n = 30), 0.46 (n = 28) and 0.47 (n = 34) respectively.

We considered individual broods as a unit in the analysis, and investigated the variation in the brood sex ratio with logistic regression. The mean brood sex ratio was independent of year (tested as factor; $\chi^2_4 = 4.56$, $P = 0.34$), age at ringing ($\chi^2_1 = 0.34$, $P = 0.56$) and brood size ($\chi^2_1 = 0.72$, $P = 0.40$). Within years, the brood sex ratio increased significantly with laying date in 1992 ($\chi^2_1 = 7.49$, $P = 0.006$), whereas in the four remaining years no significant seasonal trend was detected (all P-values > 0.25, Fig. 3). However, a combined analysis showed that the difference in slope of the seasonal brood sex ratio trend among years was not significant (for the interaction year x laying date: $\chi^2_4 = 8.24$, $P = 0.08$). Overall, there was a tendency for the brood sex ratio to increase with laying date, but the increase was not significant ($\chi^2_1 = 3.01$, $P = 0.08$).

The mean sex ratio in broods of first-year (n = 42) and adult females (n = 111) was 0.53 (95% confidence interval: 0.45–0.61) and 0.49 (95% c.i.: 0.44–0.53) respectively (Fig. 4). The difference in brood sex ratio between the female age-classes was not significant ($\chi^2_1 = 1.10$, $P = 0.29$). In the dataset where the age of both parents was known (n = 102), the brood sex ratio was significantly related to male age, whereas female age was again not significant (Table 2a). The mean sex ratio in brood of first-year and adult males was 0.60 (95% c.i.: 0.47–0.72) and 0.46 (95% c.i.: 0.41–0.51) respectively. Thus broods of first-year males produced a higher proportion of male offspring than those of adult males (Fig. 4).

Given that first-year males produced smaller broods we further investigated whether their higher brood sex ratio was due to the production of extra male or to the reduction of female offspring. The number of male offspring per nest did not differ significantly between first-year (mean ± SE = 2.00 ± 0.23) and adult males (2.05 ± 0.12; Poisson-regression: $\chi^2_1 = 0.02$, P = 0.89). However, broods of first-year males produced significantly less female offspring (first-year: 1.33 ± 0.23, adult: 2.42 ± 0.12; $\chi^2_1 = 8.86$, P = 0.003). Thus essentially the smaller size and higher sex ratio of first-year male broods was a result of producing fewer females.

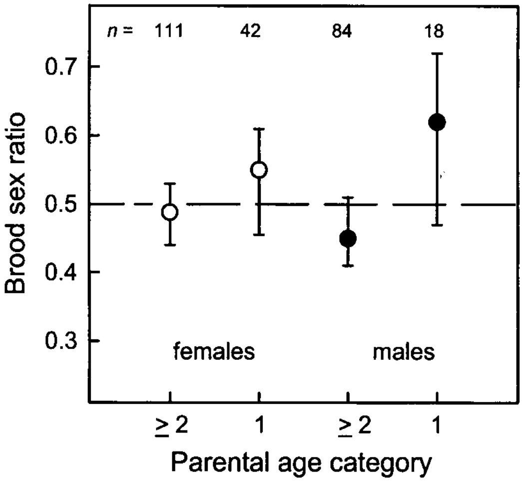

Figure 4. Brood sex ratio in relation to the age of the female and male parent. The symbols indicate the mean value (± 1 SE) per age-class. Sample sizes are given at the top of the graph.

3.5. Age structure of the breeding population and seasonal variation in brood sex ratio

In testing the sequence of years (i.e., year as a ordered variable with the values 1 to 5 for the years 1992 up to and including 1996), the brood sex ratio was significantly related to year, laying date, and the interaction year x laying date (Table 2b). The significance of the interaction-term indicates that the slope of the seasonal trend in the brood sex ratio varied systematically in the course of the years studied. In the first year (1992) the brood sex ratio increased with season (i.e., year = 0, slope = 0.052) and in the years thereafter the slope gradually decreased, reaching about zero-values

Table 2. Logistic regression analysis of the proportion of males among banded young (i.e., brood sex ratio). In (a) the analysis was restricted to broods of which the age of both parents was known. In (b) and (c) all brood were included in the analyses. For further explanation see Table 1 and text. † = rejected term.

	Parameter	(Increase in) Deviance	d.f.	P	Estimates of coefficients
a	Null model	94.64	101		
	Minimal adequate model	90.50	100		
	Constant		+1		0.405
	Male age	4.15	+1	0.042	–0.571
	Female age †	0.14	–1	0.708	
b,c	Minimal adequate model	147.43	152		
b	Full model	136.97	149		
	Constant		+1		–6.115
	Laying date	7.80	+1	0.005	0.0519
	Year (sequential, 1-5)	5.16	+1	0.023	2.130
	Year × Laying date	5.55	+1	0.018	–0.0184
c	Minimal adequate model	134.78	149		
	Constant		+1		3.707
	Laying date	2.30	+1	0.129	–0.0328
	FM1 (Fraction first-year males)	6.19	+1	0.013	–28.619
	FM1 × Laying date	6.69	+1	0.010	0.246
	Year + Year × Laying date †	0.02	+2	0.990	

in 1996 (i.e., year = 4, slope = 0.052 + (4 × –0.015) = –0.008; see coefficients in Table 2b).

Next we added for each year an estimate for the age structure of the male population, expressed as the fraction of first-year males among breeders. Note that this fraction was determined among male breeders of known age and we assumed that this fraction was representative for the total population in a given year. The brood sex ratio was significantly related to laying date, the annual fraction of first-year males (*FM1*), and the interaction between laying date and *FM1*. In particular, year and the interaction year x laying date (see Table 2b) were no longer significant (Table 2c). This implies that the gradual decrease in the annual fraction of first-year males in the course of the study explained the gradual decline in the slope of the seasonal trend in sex ratio over successive years.

4. Discussion

Our study has shown that the major reproductive traits in the observed Sparrowhawk population were correlated with the age of the male parent. Females paired with an adult male started egg laying earlier and produced more fledglings. In particular, broods of first-year males produced less female offspring than those of adult males. However, the influence of female age was slight. In addition to the effect of male age, female age was correlated with laying date only.

The predominant role of male age is most likely related to the specific breeding biology of Sparrowhawks. The male is the main food provider for both the female and the brood from well before egg laying until the young are half-grown (Newton 1986). Age does not reflect individual quality *per se*, but in many bird species as well as in the Sparrowhawk annual reproductive success is often found to correlate positively with age (Newton *et al.* 1981, Sæther 1990). Thus age may roughly reflect individual quality variations. Better food conditions at nests of adult males may arise both from the occupancy of a higher quality territory (Cavé *et al.* 1989) and improved foraging skills (Newton 1989, Forslund & Pärt 1995). Moreover reproductive effort might increase with age (Pianka & Parker 1975, Charlesworth 1980). All three factors may play a role in enhancing food conditions at nests of adult male Sparrowhawks and may explain why their females started egg laying earlier and produced more offspring than those paired with first-year males. The seasonal decline in brood size was similar to that found in other Sparrowhawk populations (Newton & Marquiss 1984, Bijlsma 1993). The larger brood size of early nests appeared essentially due to the earlier laying date, as we could not detect an additional effect of male age, given the effect of season. Finally, as the recruitment of independent offspring usually declines with season (Daan *et al.* 1989, Rohwer 1992, Spear & Nur 1994, Brinkhof *et al.* 1997) being mated with an adult male thus enabled the female to achieve a higher fitness.

Similar to most bird species (Clutton-Brock 1986) the secondary offspring sex ratio in Sparrowhawk populations does not deviate from parity (Newton 1979, present study). However, in our study broods of first-year males had a higher sex ratio than those of adult males. Such variation might be adaptive and fit the Trivers-Willard hypothesis (Trivers & Willard 1973), if female offspring would suffer relatively more from poor rearing conditions at nest of first-year males than male offspring. This has been shown in Japanese Quail, where poor nutrition affected juvenile growth of the larger female relatively more than of the smaller male (Gebhardt-Henrich & Marks 1993). Poor juvenile growth may diminish the reproductive value of offspring by reducing post-fledging survival (Tinbergen & Boerlijst 1990, Brinkhof *et al.* 1997) and through lasting effects on adult body size (Würdinger 1975, Larsson & Forslund 1991, Brinkhof 1997). Newton (1985) indeed showed that small female Sparrowhawks had a lower lifetime reproductive success than large females. We are aware that only experiments can reveal whether female Sparrowhawks adjust the brood sex ratio to the prospected level of food provisioning by the male during the nestling period, for instance by supplemental feeding prior to egg laying. Further, the brood sex ratio of first-year males could be biased experimentally, as to investigate whether such males are indeed unable to meet the supposed higher food demands of female-biased broods.

Variation in secondary brood sex ratio may result from differences in primary sex ratio at laying, in embryo mortality or in nestling mortality. Sex ratio variation in relation to the laying sequence, such as found in other studies (Fiala 1981, Dijkstra *et al.* 1990, Bednarz & Hayden 1991, Zijlstra & Bruinenberg-Rinsma 1992) might also play a role. The few nestlings which die usually do so within the first days after hatching, when differences in competitive ability between young are probably more determined by hatching order than by sex (Newton & Marquiss 1979, but see Mock & Parker 1997). A correlation between food supply and offspring sex ratios has been shown in the American kestrel (*Falco sparverius*; Wiebe & Bortolotti 1992). Also in Bald Eagles (*Haliaetus leucocephalus*) sex ratio variations were correlated with the local food situation (Dzus *et al.* 1996), which in dimorphic species may affect the sexes differently.

One method to investigate the mechanism through which broods of first-year male Sparrowhawks become male-biased would be to determine the primary sex ratio at hatching by means of molecular techniques (Griffith & Tiwari 1993, Lessells *et al.* 1996). Van den Burg *et al.* (2002) examined dead Sparrowhawk embryos from unhatched eggs and did not find evidence for sex-specific variation in mortality prior to fledging. Further, most hatched eggs produce a fledgling (own data 1996, Bijlsma 1993).

We thus assume that the secondary brood sex ratio mainly reflects the primary sex ratio. However, we could not entirely exclude whether or not our results are biased by sex-specific variations in egg or nestling mortality.

Daan *et al.* (1996) proposed sex specific differences in maturation rate as a general explanation for seasonal trends in brood sex ratios in avian raptors. The prediction of their sex ratio model fitted the empirical data of four species, whereas the seasonal increase in the overall proportion of male offspring found in Sparrowhawks was not predicted. We also found an overall tendency for the brood sex ratio to increase with laying date, which was indeed significant in one out of five years. However, the seasonal increase was statistically more readily explained by the age of the male parent than by laying date, as first-year males bred late and produced male-biased brood sex ratios. Given that age is an appropriate predictor of parental quality this might indicate that differences in parental quality between early and late breeders were more important than birth date of the young. Moreover, taking the effect of male age for granted, annual variation in the age composition of the male breeding population explained the annual variation in seasonal brood sex ratio trends in our population. Annual variation in brood sex ratios trends is not covered by the model of Daan *et al.* (1996), which considers sex specific differences in the age at first breeding as an absolute function of birth date. The empirical population sex ratio data used to test the maturation-model were pooled over years, although at least in the Lesser Kestrel the overall seasonal decline in sex ratio (Daan *et al.* 1996) was not found in each year (original data in Tella *et al.* 1996). Annual variation in seasonal brood sex ratio trends are probably common (see also Picozzi 1984; present study) and also need a general explanation, which might be related to age effects of the parent providing most of the food during reproduction.

Summarising, extreme sexual size dimorphism of Sparrowhawks is the most likely explanation for our present finding that brood sex ratio's vary between first-year and adult males. The Sparrowhawk could thereby be on the far end of a continuum, in which parental quality increasingly affects the relative fitness benefits (Trivers & Willard 1973) or fitness costs (Williams 1966) of raising male or female offspring, and ultimately the optimal brood sex ratio.

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Selostus: **Varpushaukkakoiraan iän vaikutus rengastusikäisten poikasten sukupuolijakaumaan**

Lintuemojen oletetaan panostavan koirasjälkeläiseensä yhtä paljon kuin naarasjälkeläiseensä.

Poikasten sukupuolijakauman tulisi olla tasainen eli pesyeissä olisi yhtä paljon koiraspoikasia ja naaraspoikasia. Tietyissä tilanteissa emojen on kuitenkin edullisempaa pyrkiä suosimaan toista sukupuolta. Petolinnuilla vuosien välinen vaihtelu pesyeiden sukupuolijakaumassa on yleistä. Varpushaukkakoiras ja -naaras ovat huomattavan erikokoisia. Naaras on liki kaksi kertaa painavampi kuin koiras. Naaraspoikasen hoito vaatii varpushaukkaemoilta noin kaksinkertaisen panostuksen koiraspoikasen hoidon vaatimaan panostukseen verrattuna. Nämä tekijät voivat johtaa epätasapainoon pesäpoikasten sukupuolijakaumassa. On oletettavaa, että varpushaukkaparin lisääntymismenestys riippuu osaltaan poikasiin investoidun hoidon määrästä. Varpushaukalla koirasemot kilpailevat keskenään reviireistä ja vastaavasti naaraat kilpailevat koiraiden valtaamista reviireistä. Emojen ikä indikoi emojen laatua. Varpushaukalla vanhojen yksilöiden oletetaan olevan laadultaan parempia emoja kuin nuorten yksilöiden. Kirjoittajat tutkivat vuosina 1992–1996 varpushaukkapesyeiden sukupuolijakaumaa Hampurin alueella. Kaikkiaan 162 varpushaukkapesyeestä määritettiin sukupuolijakauma. Yhteensä 638 poikasen sukupuoli määritettiin jaloista otettujen mittojen avulla. Koiraspoikasia oli 318 ja naaraspoikasia 320. Poikasten ikä oli keskimäärin 17 vuorokautta pesyekoon tutkimushetkellä. Varpushaukkakoiraat ja -naaraat ovat lisääntymiskykyisiä syntymäänsä seuraavana pesimäkautena eli yksivuotiaina. Emot luokiteltiin yksinkertaistamisen vuoksi yksivuotiaisiin (nuoruuspukuiset) ja aikuisiin (≥ 2 vuotiaat) pesien lähistöltä tai pesistä löytyneiden sulkien perusteella. Naaraan ikä ei vaikuttanut poikuekokoon tai poikasten sukupuolijakaumaan. Yksivuotiaat naaraat aloittivat muninnan myöhemmin kuin vanhemmat naaraat. Yksivuotiaiden koiraiden pesyeet kuoriutuivat myöhemmin ja pesyeet tuottivat vähemmän lentopoikasia kuin vanhempien koiraiden pesyeet. Vanhojen koiraiden poikasten sukupuolijakauma oli tasainen; yksivuotiaiden koiraiden poikueissa puolestaan oli enemmän koiraspoikasia kuin naaraspoikasia. Tutkijoiden mukaan vuosien välinen vaihtelu poikasten sukupuolijakaumassa selittyi alueella pesivien koiraiden ikäjakaumalla. Koirasvarpushaukka tuo pesälle pääosan naaraan ja poikasten käyttämästä ravinnosta. Vanhat koiraat voivat valita reviirikseen eniten ravintoa tarjoavat alueet. Lisäksi vanhat varpushaukkakoiraat voivat olla taitavampia saalistajia kuin nuoremmat koiraat. Tutkijat päättelevät, että nuori varpushaukkakoiras on laadultaan huonompi kuin vanha koiras. Pariutumalla vanhan koiraan kanssa naaras voi parantaa samalla omaa kelpoisuuttaan. Emojen laadulliset erot tulisi kirjoittajien mukaan huomioida tutkittaessa poikasten sukupuolijakauman vuosien välisiin eroihin vaikuttavia tekijöitä. Erityisen tärkeää tämä on niiden lintulajien kohdalla, joiden koiraat ja naaraat ovat huomattavan erikokoisia.

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