

Offspring sex ratio in Eurasian Kestrel (*Falco tinnunculus*) with reversed sexual size dimorphism

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Abstract Fisher's theory predicts equal sex ratios at the end of parental care if the cost associated with raising offspring of each sex is equal. However, sex ratios have important evolutionary consequences and are often biased for many factors. Reported sex ratios are often biased in raptors, which display various degrees of reversed sexual dimorphism, but there seems no consistent pattern in their offspring sex ratios. In this study, we investigated the offspring sex ratio of the Eurasian Kestrel (*Falco tinnunculus*) and tested whether the patterns of biased sex ratios were related to laying order, egg mass, hatching order, laying date or clutch size. The brood sex ratio of the Eurasian Kestrel (male) in eggs was 47.0%, not statistically biased from 0.5, but in fledglings it was 40.8%, significantly biased from 0.5 ($p = 0.029$). At population level, both primary and secondary sex ratios did not depart from parity. We found that clutch size and egg mass affected the secondary brood sex ratio, i.e., the larger the clutch size, the larger the number of males and eggs producing sons were heavier than eggs producing daughters. Laying date affected both the primary and secondary sex ratios, and laying earlier is associated with a greater proportion of males.

Keywords Eurasian Kestrel, primary sex ratio, secondary sex ratio, sex dimorphism.

Introduction

Over the past 40 years there have been intensive theoretical and experimental investigations of how natural selection moulds the sex ratio. Fisher's (1930) classic frequency-dependent model of sex allocation predicts that the offspring sex ratio should not deviate from parity as long as the costs of producing

males and females are equal. Modern empirical sex ratio research began when Hamilton (1967) observed that many insects and mites have highly female-biased sex ratios and that this trait is associated with high levels of brother-sister mating. Hamilton explained this result by his theory of local mate competition, which has been extended to other cases of interactions between siblings. Briefly, if one sex suffers a greater reduction in fitness through competition with siblings of the same sex, the mother is programmed in her selection of the sex ratio to favor the sex that suffers less competition. Fisher's frequency-dependent argument is thus modified in populations where relatives compete. A second major development was by Trivers and Willard (1973) who originally proposed that maternal quality should

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affect the direction of this investment for species, exhibiting high variation in male reproductive success. Modern classic sex allocation theory predicts that selection should act on parents to sex-specifically vary the level of investment in offspring when the fitness returns differ for the two sexes (Charnov, 1982; Frank, 1990; Hardy, 2002).

Birds have long been considered incapable of facultatively shifting their primary sex ratio because their sex determination is chromosomal (Clutton-Brock, 1986). However, recent studies have suggested that sex ratio adjustment in birds is not as constrained as thought earlier (West and Sheldon, 2002). In birds, the sex-ratio adjustment can occur at laying period (primary sex-ratio adjustment) and during the period of provisioning for the young (secondary sex-ratio adjustment) (Ellegren and Sheldon, 1997; Kilner, 1998).

An increasing number of studies have provided strong evidence that female birds can adjust the primary sex-ratio of their offspring by laying sex-biased clutches (Dijkstra et al., 1990; Heinsohn et al., 1997; Komdeur et al., 1997, 2002; Kilner, 1998; Nager et al., 1999; Kalmbach et al., 2001; Rutstein et al., 2004; Korsten et al., 2006). These studies have shown that females adjust the sex ratio of their clutches in relation to potential future fitness gains (Komdeur et al., 1997; Kalmbach et al., 2001; Rutstein et al., 2004), to female body condition (Pike and Petrie, 2005; Rutkowska and Cichoń, 2006), attractiveness (Burley, 1981; Ellegren et al., 1996; West and Sheldon, 2002; Griffith et al., 2003; Cassey et al., 2006; Korsten et al., 2006; Ferree, 2007) or quality of their mates (Kölliker et al., 1999; Oddie and Reim, 2002). Also, sex-biased mortality between hatchings and fledgings has been shown to further bias towards secondary sex ratios (Torres and Drummond, 1997; Kilner, 1998; Legge et al., 2001; Bize et al., 2005; Fargallo et al., 2006).

Mechanisms for both primary and secondary sex-ratio adjustment in birds remain largely unknown (Emlen, 1997; Sheldon, 1998; Krackow, 1999; Martins, 2004), but preovulatory mechanisms have been suggested as the most efficient means of primary sex-ratio adjustment for some species (Komdeur et al., 2002). Pike and Petrie (2003) presented an excellent review of the potential mechanisms of avian sex manipulation, such as steroid hormones, paternal attractiveness, maternal condition, photoperiod and phenotypic sex and others. In addition, much new experimental and relevant evidence have appeared

since then, providing new and interesting perspectives (Pike and Petrie, 2006; Rutkowska and Badyaev, 2008).

Sex allocation patterns among raptor populations have attracted considerable research attention because most raptorial birds exhibit reversed sexual size dimorphism (females are the larger sex) (Newton and Marquiss, 1979; Olsen and Cockburn, 1991; Appleby et al., 1997; Brommer et al., 2003; McDonald et al., 2005). One consequence of this size difference is a disparity in food requirements: daughters require more food than sons do during the nestling period (Anderson et al., 1993a; Krijgsveld et al., 1998; Riedstra et al., 1998; Laaksonen et al., 2004). Rearing larger daughters is more costly since they require more parental investment in the form of food requirements as opposed to sons. Theoretically, the offspring sex ratio in raptors should be male-biased. However, there seems no consistent pattern in the offspring sex ratios of raptors; the proportion of males is either increasing (Newton and Marquiss, 1979; Olsen and Cockburn, 1991; Korpimäki et al., 2000) or decreasing (Tella et al., 1996) and no clear adaptive explanations for these trends have been found so far.

The Eurasian Kestrel (*Falco tinnunculus*), a sexually size-dimorphic raptor (females ca. 20% heavier than males; Village, 1990), widespread in open country throughout the Palearctic, Afrotropical and Oriental regions (Cramp and Simmons, 1980). A total of 12 subspecies have been identified (Dickinson, 2003). The subspecies in our study is *F. tinnunculus interstinctus*. The female Eurasian Kestrel might be able to adjust her reproductive effort by promoting sex differences in the mass of first-laid eggs (Blanco et al., 2003), where sexual differences in the size of first-laid eggs defines the pattern of within-brood mass hierarchies of fledglings. In addition, some researchers have documented that females have the potential ability to adjust resources allocated to different-sex eggs laid in varying order (Anderson et al., 1997; Blanco et al., 2003; Martínez-Padilla and Fargallo, 2007).

We investigated the primary and secondary offspring sex ratio of the Eurasian Kestrel at the Zuojia Nature Reserve in northeastern China. Our objectives were: 1) to test whether its offspring sex ratio demonstrates a general deviation from a balanced sex ratio and 2) whether a pattern of biased sex ratio exists in relation to laying order, egg mass, hatching order, laying date and clutch size.

Study area and methods

Study area

We conducted the study in the Zuojia Nature Reserve in Jilin Province, northeastern China during the breeding seasons (from late March to late July) in 2007 and 2008. The Zuojia Nature Reserve stretches from the eastern Changbai mountains to the western plains (126°1′–127°2′N, 44°6′–45°5′E), where the elevation ranges from 200 m to 530 m. The region is subject to an eastern monsoon climate, characterized by hot, dry summers and cold, snowy winters; the area is covered by approximately 35% open habitat and 65% forests. Vegetation in the area is diverse and the existing forests are secondary.

Data collection

The Eurasian Kestrels do not build their own nests, but rely mainly on the stick nests of the Magpie (*Pica pica*) in our study area (Xiang et al., 1991; Deng et al., 2006; Zhou et al., 2009). Most magpie nests used by the kestrels were inaccessible. We therefore installed nest boxes to develop the study and most kestrels then shifted to breed in these boxes.

The nest boxes we used in the study were constructed from rough-cut boards and put together with exterior nails or deck screws. The internal dimensions of the boxes were all the same: 50 cm deep, a 35 cm × 35 cm bottom area and with a 12.5 cm or 15 cm diameter entrance hole near the top. These nest boxes were placed randomly about 8–13 m above ground in various tree species with distances ranging from 50 m to 150 m between the nearest two boxes. The number of boxes monitored was 68 in 2007 and 77 in 2008.

We monitored nest boxes used by the Eurasian Kestrels every day to record the laying date and marked the laying sequence of each egg accurately during the egg laying period. We used an electronic balance to weigh eggs to the nearest 0.01 g on the day of being laid. In order to assign all marked eggs to their corresponding nestlings, and record the hatching order, we checked nests hourly (between 08:00 and 19:00 hours) on the days of expected hatching. We distinguished nestlings by drawing some simple symbols on their head with indelible ink. We removed unhatched eggs from the nest after several days when the rest of the clutch had hatched. We discarded eggs containing no visible embryos, and stored dead em-

bryos in 100% ethanol. After hatching, we visited nests at an interval of two days to collect body tissues of the dead nestlings as a source of DNA and to monitor fledging success. We collected a blood sample of each nestling (20–50 µL) from brachial veins with a sterilized hypodermic needle, 9 to 11 days after hatching. We stored blood samples in EDTA for determination of sex in the laboratory.

Sex determination

We sexed the nestlings using a polymerase chain reaction (PCR) amplification based on the technique used by Fridolfsson and Ellegren (1999). We isolated DNA from the red blood cells using proteinase K digestion and phenol-chloroform extraction. We ran PCR amplification using a particular set of primers (2550F and 2718R), as suggested by Fridolfsson and Ellegren (1999). The temperature profile in PCR was as follows: hotstart at 94°C, initial denaturation at 94°C for 5 min, followed by a “touch-down” scheme (Don et al., 1991) where the annealing temperature was lowered 1°C per cycle, starting from 58°C, until a temperature of 48°C was reached. Then 25–35 additional cycles were run at a constant annealing temperature of 48°C. Denaturation was at 94°C for 30 s, annealing for 45 s and extension at 72°C for 1 min. A final extension step of 5 min was added after the last cycle. PCR products, separated by electrophoresis on 2% agarose gels containing ethidium bromide, were visualized under UV light. We assigned the sex of individuals from five adult pairs correctly using this technique, so we could be confident the method worked successfully in this species.

Statistics analysis

We used two data sets to analyze the offspring sex ratio. The data set for analyzing the primary sex ratio included broods that all laid eggs had hatched successfully, including dead embryos. We sampled all nestlings (both blood and tissue samples) for a total of 81 nestlings in 15 broods. The data set for analyzing the secondary sex ratio included 105 nestlings in 23 successfully fledged broods. We examined the brood sex ratio (hereafter referred to as the proportion of males) using the binomial test (Zar, 1984). We used the Wilcoxon signed rank test in S-PLUS 6.0 to test the primary and secondary sex ratios at population level. In order to study the rela-

relationship between primary sex ratio, laying order, clutch size and egg mass, we performed linear mixed model (LMM) in SPSS 14.0 (SPSS Inc., Chicago, Illinois, USA). In this model, we entered the sex ratio as the response variable, clutch size and laying order as fixed factors. The kestrel hatches asynchronously with a hatching spread of 3–5 days and therefore we divided the laying order into three categories: initial, middle and last. The initial category corresponded to the first eggs and the last category to the last eggs. The other eggs were defined as the middle category (Hardy, 2002). Thus, the sex ratio used in the model stood for the sex ratio of each category. Moreover, egg mass in the model also represented the egg mass of each category. We encoded the laying dates into five stages: March, early April (April I), middle April (April II), late April (April III) and May and introduced it as a random factor, with egg mass as covariate. By introducing the laying date as a higher level random effect in addition to the residual error term, our LMM permitted an estimation of the fixed effects and interaction parameters while accounting for random variation in the sex ratio between broods. We analyzed the relationship between secondary sex ratio, laying order, clutch size, hatching order and egg mass using the same model. For all statistical tests, we used a significance level of 0.05. We presented values as means \pm SD.

Results

Sex ratio at brood and population level

The brood sex ratio of the Eurasian Kestrel in eggs was $47.0 \pm 4.3\%$, not statistically biased from 0.5 (Wilcoxon signed rank test, $Z_{15} = -0.402$, $p = 0.342$). However, the brood sex ratio in fledglings was $40.8 \pm 4.5\%$, significantly different from 0.5 (Wilcoxon signed rank test, $Z_{23} = -1.882$, $p = 0.029$).

The primary sex ratio at population level was 48.2%, which did not depart from parity (binomial test, $n = 81$, $p = 0.824$). The sex ratio in eggs for the two study years showed a similar pattern (binomial test, 48.9%, $n = 45$, $p = 1.000$ in 2007; 47.2%, $n = 36$, $p = 0.868$ in 2008). The secondary sex ratio at population level was 42.9%, which did not depart significantly from parity (binomial test, $n = 105$, $p = 0.172$). Moreover, we detected the same tendency in nestlings (binomial test, 41.9%, $n = 62$, $p = 0.253$ in 2007; 44.2%, $n = 43$, $p = 0.542$ in 2008).

Effect of laying order, egg mass, clutch size on primary brood sex ratio

The sex ratio of eggs for different categories of laying order did not differ from parity (binomial tests: initial, 40.0%, $n = 15$, $p = 0.607$; middle, 43.1%, $n = 51$, $p = 0.401$; last, 73.3%, $n = 15$, $p = 0.118$). Results of LMM showed that the sex ratio in eggs was not associated with laying order, clutch size and their interaction (Table 1). Our results indicate that the laying date had a significant impact on primary offspring sex (Table 1), but there was no significant correlation ($r = -0.025$, $p = 0.929$) (Fig. 1a). Egg mass did not have a significant effect on primary sex ratio, but the egg mass of males (23.15 ± 1.36 , $n = 42$) was slightly heavier than that of females (22.89 ± 1.28 , $n = 38$), although the difference was not statistically significant (Mann-Whitney test $U = 712$, $p = 0.407$). In addition, egg mass was not associated linearly with laying order; the eggs in the middle position in the laying order were the heaviest (Fig. 2).

Effects of laying order, egg mass, clutch size and hatching order on secondary brood sex ratio

The secondary brood sex ratio was significantly related to clutch size ($F = 5.297$, $p = 0.017$) and egg mass ($F = 8.099$, $p = 0.016$). With increasing clutch size and egg mass, the proportion of males became gradually higher, but there were no significantly positive correlations (Figs. 3 and 4). Laying order

Table 1 LMM analyses of the effects of clutch size and laying order on the sex of the eggs in Eurasian Kestrels

| Source | NDF | DDF | $F_{\text{NDF, DDF}}$ | p |
|-----------------------------------|----------|-------|-----------------------|-------|
| Clutch size | 3 | 8 | 1.570 | 0.271 |
| Laying order | 1 | 8 | 0.004 | 0.951 |
| Egg mass | 1 | 8 | 1.796 | 0.217 |
| Clutch size \times Laying order | 1 | 8 | 0.000 | 0.983 |
| Covariance parameter estimates: | | | | |
| | Estimate | SE | Z | p |
| Laying date | 0.262 | 0.130 | 2.000 | 0.046 |

The model accounts for random variation between laying date. NDF represents the degrees of freedom of the numerator and DDF that of the denominator. $F_{\text{NDF, DDF}}$ stands for Fisher's test statistics, p represents the significance level, "estimate" represents the estimated covariance parameters, SE stands for standard error, Z represents Z statistic value of the Wald test.

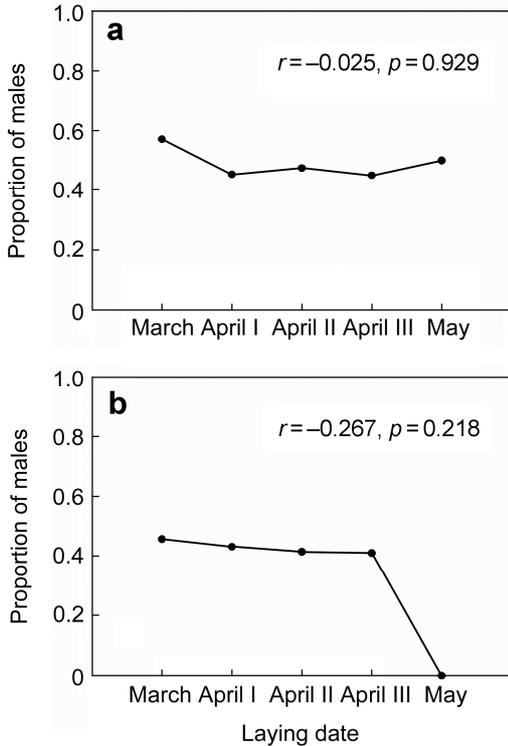


Fig. 1 Primary sex ratio (a) and secondary sex ratio (b) of Eurasian Kestrel in relation to laying date

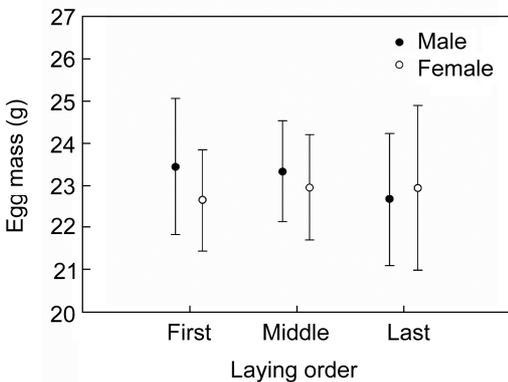


Fig. 2 Relationship between eggs mass and laying order in Eurasian Kestrel in northeastern China

and hatching order did not have a significant effect on the proportion of males in fledglings; however, when they interacted with clutch size, both factors had a significant effect on the secondary brood sex ratio (Table 2). In addition, the LMM showed that laying date had a significant effect on secondary offspring sex (Table 1), but there was no significant correlation ($r = -0.267, p = 0.218$) (Fig. 1b).

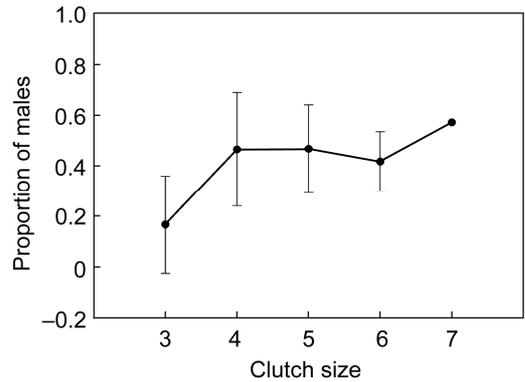


Fig. 3 Relationship between secondary brood sex ratio and clutch size in Eurasian Kestrel in northeastern China

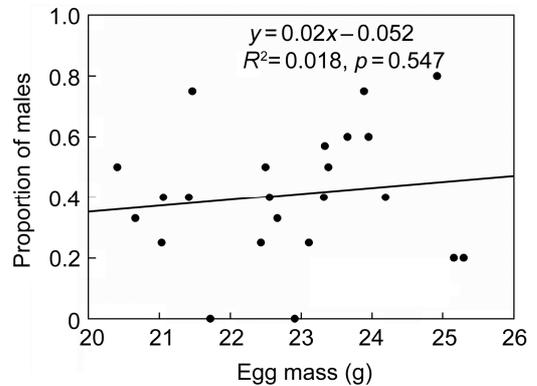


Fig. 4 Correlations between secondary brood sex ratio and egg mass in Eurasian Kestrel in northeastern China

Discussion

In this study, the sex ratio at population level and the primary brood sex ratio did not depart from parity, which was similar to the result obtained by Ankney (1982). We found that the secondary brood sex ratio of Eurasian Kestrels was consistently female-biased across the two-year study. A number of studies have shown that females can adjust sex ratio of their offspring by adjusting the laying and hatching orders (Ankney, 1982; Kilner, 1998; Cichoń et al., 2003; Ležalová et al., 2005). However, our results, as another study (Martínez-Padilla and Fargallo, 2007) on the species, indicated that the laying order did not affect the sex ratio of Eurasian Kestrels. Interestingly, our results showed that clutch size and egg mass only affected secondary brood sex ratio, while the laying date affected both primary and secondary sex ratios.

For many bird species, there is no a consistent re-

Table 2 LMM analyses of the effects of clutch size, laying order and hatching order on the sex of the fledglings in Eurasian Kestrel

| Source | NDF | DDF | $F_{NDF, DDF}$ | p |
|---------------------------------|----------|-------|----------------|-------|
| Clutch size | 3 | 11 | 5.297 | 0.017 |
| Laying order | 1 | 11 | 0.851 | 0.376 |
| Hatching order | 1 | 11 | 0.128 | 0.728 |
| Egg mass | 1 | 11 | 8.099 | 0.016 |
| Clutch size × Laying order | 1 | 11 | 6.447 | 0.028 |
| Clutch size × Hatching order | 1 | 11 | 5.508 | 0.039 |
| Covariance parameter estimates: | | | | |
| | Estimate | SE | Z | p |
| Laying date | 0.194 | 0.008 | 2.345 | 0.019 |

The model accounts for random variation between laying date. NDF is the degree of freedom of the numerator and DDF of the denominator, $F_{NDF, DDF}$ is Fisher's test statistic, p represents significance level, "estimate" represents the estimated covariance parameters, SE stands for standard error, and Z represents the Z statistic value of the Wald test.

relationship between egg mass and sex ratio, because females might adjust egg mass either positively or negatively to correlate with the laying order in assigning resources to different sexual offspring (Fiala, 1981; Ankney, 1982; Bancroft, 1984). Anderson et al. (1997) suggested that the sex ratio of offspring was significantly associated with the laying order and that male eggs were significantly larger than female eggs in the American Kestrel (*F. sparverius*). In our study, egg mass had a significant effect on the secondary brood sex ratio and showed the same pattern as the American Kestrel in spite of a lack of significant difference between female and male eggs. Therefore, we speculate that the sexually size-dimorphic Eurasian Kestrel was able to adjust the sex ratio of its offspring by adopting different strategies of egg mass provisioning according to egg sex and laying order.

Some studies showed that the fledgling sex ratios of several raptor species are skewed toward males early in the season while late broods had an excess of females (Dijkstra et al., 1990; Daan et al., 1996; Tella et al., 1996; Griggio et al., 2002). In our study, the laying date had a significant effect on the primary and secondary brood sex ratios. Moreover, both sex ratios showed a slightly decreasing trend as

the season progressed in spite of a lack of significant shift. Eurasian Kestrel nestlings are sexually dimorphic, with daughters larger than sons. The larger daughters may need more foods and have an advantage during sibling competition for food (Anderson et al., 1993a, 1993b). Sex-specific characteristics of nestlings may affect the reproductive biology of the species, while nestling mortality should fall more heavily on sons than on daughters. We suggest that the seasonal variation in the sex ratio of the Eurasian Kestrel might be associated with favouritism for the male function on the part of the parents, both to counter the risk of excess mortality of sons and because sons require less parental care per capita during earlier breeding seasons.

A large number of studies show that clutch size does not affect the sex ratio of birds, except for the study by Wegge (1980), who indicated that in a declining population of Capercaillie (*Tetrao urogallus*), the sex ratio of fledglings declined with clutch size, but that this was probably a consequence of differential mortality between hatchings and fledglings. In our study, clutch size had a significant effect on the secondary sex ratio in spite of a lack of significant correlation. The highest male proportion occurred with a clutch size of seven, with the highest probability of mortality of hatchings from the seventh egg. Two potential reasons may explain this conclusion. First, we found that the Eurasian Kestrel, bred in an artificial nest box, had a larger clutch size than kestrels bred in natural nests (5.77 ± 0.15 vs 4.86 ± 0.26), where clutch size of the species was not more than 6 in natural nests (W. Gao unpublished data). As a result, it was difficult for the parents to rear all the nestlings in this condition. We therefore considered that the kestrel may adopt a "brood reduction strategy" in order to adjust the secondary brood sex ratio (Slagsvold et al., 1984). Secondly, food availability might also constrain the survival rate of nestlings. Kestrels feed mainly on small mammals, especially voles, but birds, frogs and insects also form part of their diet during the nestling period, which might reflect a reduced availability of rodents due to their being preyed upon continuously by the kestrels and several other raptor species in the study area (Geng et al., 2009).

Our results revealed relatively complex patterns of sex allocation in the Eurasian Kestrel that appears to be associated with both maternal ability to modify the sex of the progeny by adapting to its environment. Future work on the kestrel should include ex-

periments that evaluate the ultimate mechanism of sex ratio allocation and parental provisioning patterns to different sex eggs with egg mass, adjusting for reproductive efforts.

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两性异型红隼的子代性比研究

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摘要: Fisher经典的性比分配理论预测: 如果双亲繁殖雄性和雌性子代的代价相同, 那么子代的性比应趋于平衡。然而, 性比组成是长期进化的结果, 常因不同因素的影响而出现偏离。文献报道猛禽由于存在不同形式的两性异型现象而导致子代性比常出现偏离, 但子代性比偏离方向因种而异。本研究中我们对红隼 (*Falco tinnunculus*) 子代的性比组成进行了调查, 目的是检验红隼子代性比是否受产卵日期、产卵顺序、卵重、出雏顺序或窝卵数影响。在窝水平上, 红隼 (雄性) 的初级性比为47.0%, 没有偏离0.5, 但次级性比为40.8%, 显著偏离0.5 ($p = 0.029$)。在种群水平上, 初级性比和次级性比都没有出现偏离。窝卵数和卵重影响红隼的次级性比组成, 窝卵数越大, 雄性后代数量越多, 且发育为雄性后代的卵重较发育为雌性后代的重。初级性比和次级性比都受到产卵日期的影响, 产卵越早, 雄性后代比例越高。

关键词: 红隼, 初级性比, 次级性比, 两性异型