

Parity in Fledging Sex Ratios in a Dimorphic Raptor, Montagu's Harrier *Circus pygargus*

Meritxell Genovart^{1,*}, Martín Surroca², Alejandro Martínez-Abraín¹, and Juan Jiménez³

¹Population Ecology Group, Institut Mediterrani d'Estudis Avançats IMEDEA (CSIC-UIB), Miquel Marquès 21, 07190 Esporles, Balearic Islands, Spain

²Centro de Recuperacion de Fauna "Forn del Vidre", Carretera La Sènia-Fredes (Generalitat Valenciana), Castellón, Spain

³Servicio de Conservación de la Biodiversidad, Conselleria de Territori i Habitatge, Generalitat Valenciana, C/ Francisco Cubells, 7, 46011 Valencia, Spain

(Accepted July 10, 2007)

Meritxell Genovart, Martín Surroca, Alejandro Martínez-Abraín, and Juan Jiménez (2008) Parity in fledging sex ratios in a dimorphic raptor, Montagu's Harrier *Circus pygargus*. *Zoological Studies* 47(1): 11-16. We analyzed sex ratios of 809 fledglings from 285 broods of Montagu's Harrier (*Circus pygargus*) in a population located in Castellon (on the northeastern Iberian Peninsula) in the period 1996-2005. Montagu's Harrier females are about 15% larger than males, and according to Fisher's theory, a bias in the secondary sex ratio towards the cheaper (smaller) sex should be expected. This was previously found in another population of the same species. However, overall brood sex ratios in the present population did not depart from parity during the study. Additionally we analyzed offspring sex ratio variations among different years and 4 breeding areas, and although the sex ratios did not show the same trends, differences were not statistically significant. Results suggest 2 non-mutually exclusive explanations: 1) the growth of females (the larger sex) might not necessary imply greater energy requirements and 2) environmental (e.g., food availability) and demographic variables (e.g., age of recruitment) may vary among populations and differentially affect offspring sex ratios. Nevertheless, although the sample size for the overall sex ratio was large enough in our study, it was reduced when analyzing this parameter in different years and breeding areas, and such power constraints may have precluded detecting sex ratio deviations from parity in space and time. <http://zoolstud.sinica.edu.tw/Journals/47.1/11.pdf>

Key words: Fisher's theory, Sex allocation, Avian.

Fisher (1930) argued that the offspring sex ratio is the result of natural selection for equal investments in male and female offspring. If no other forces are acting, the overall offspring sex ratio in a population should be 1:1. Although the extraordinary sex ratios noted mainly in invertebrates appear to be rare in birds (Krackow 1995), several evidences of sex ratio biases have been recorded during the past decade or so (Wiebe and Bortolotti 1992, Komdeur et al 1997, Torres and Drummond 1999). Biased sex ratios may be favored in species where the reproductive costs or fitness benefits vary between sons and daughters (Clutton-Brock et al. 1985, Weatherhead and

Teather 1991, Post et al. 1999). Consequently sex ratios have been widely studied in sexually dimorphic birds; the greater food requirements of the larger sex makes it more costly for parents to raise and could also render it more susceptible to food shortages, leading to increased mortality of chicks of the larger sex during periods of environmental stress (Clutton-Brock et al. 1985, Weatherhead and Teather 1991). Additionally circumstances at the time of breeding may affect the parental condition, and parents might manipulate the sex of the progeny to lessen the risk of failure or maximize fitness gains (Trivers and Willard 1973, Charnov 1982, Wiebe and Bortolotti 1992, Hardy 2002,

*To whom correspondence and reprint requests should be addressed. Tel: 34-971-611756. Fax: 34-971-611761. E-mail: m.genovart@uib.es

Genovart et al. 2003). Several studies have analyzed offspring sex ratios in raptors, and also in Montagu's Harrier *Circus pygargus*, and results were not consistent, since some species showed a male-biased sex ratio, in accordance with Fisher's theory (Bednarz and Hayden 1991, Zijlstra et al. 1992), whereas others showed parity in the fledging sex ratio (Dijkstra et al 1990, Burnham et al 2003, Millon and Bretagnolle 2005). Moreover, other species and populations showed the faculty of biasing the progeny sex ratio to increase fitness benefits (Smallwood and Smallwood 1998, Arroyo 2002, Millon and Bretagnolle 2005).

We studied Montagu's Harrier, a medium-sized raptor species (280-340 g), with sexual size dimorphism, the females of which are about 15% heavier than the males (Leroux and Bretagnolle 1996). The study population is one of the few populations that mainly breed in natural habitats, and one of the few in Europe which have shown a population expansion during the last few years. This is probably due to high prey availability and suitable habitat for nesting, and the productivity observed is among the highest recorded for the

species (Jiménez and Surroca 1995, Arroyo et al. 2004, Limiñana et al. 2006).

Our objective was to assess the overall sex ratio in a population of Montagu's Harrier to test 1) whether dimorphism in this species is causing biased fledging sex ratios, as predicted by Fisher (1930); and 2) if different fitness levels between sexes during years or breeding areas translate into differences in fledging sex ratios.

MATERIALS AND METHODS

A population of Montagu's Harrier nesting in the province of Castellón (on the northeastern Iberian Peninsula) was monitored annually between 1996 and 2005. The study area covered approximately 1050 km², and nests were clustered following geographical information into 4 breeding areas (Fig. 1). Fledglings in 285 broods were sexed by iris color, which is gray in males and brown in females (Hammerstrom 1969, Scharff and Balfour 1971, Picozzi 1980, Schipper 1978). The sex ratio was expressed as the proportion of



Fig. 1. Breeding areas for Montagu's Harrier in the interior of Castellon Province.

males in a brood. Predation is not very important in this population, and we detected only 21 predated or plundered nests from the 409 total nests examined during the study. We also controlled for clutch size, as it may be an indicator of parental condition at the time of breeding (Bolton 1991, Clifford and Anderson 2001), and for the number of chicks fledged per nest. Since 43 nests were visited when chicks had already hatched and we failed to control for clutch size, hereafter we refer to clutch size as the minimum clutch size: the maximum number of eggs or chicks found in a nest. To test for differences in breeding parameters, we built a contingency table and applied a Chi-squared test. To avoid cells with low frequencies, we grouped values from each variable into 3 classes: lower than the mean value, equal to the mean value, and higher than the mean value. The mean minimum clutch size was 4.16 ± 0.05 eggs per nest, and the mean number of chicks fledged per nest was 3.20 ± 0.06 .

Sex ratios were analyzed with Generalized linear models (GLMs), modeled by logistic regression with a binomial error distribution and logit link function, using the GENMOD procedure implemented in SAS 9.0 (Cary, NC); the response variable was the number of males out of the total number of chicks fledged in a brood, and each brood was treated independently. If the sex ratio data conform to a binomial distribution, then the null model in a GLM with binomial errors should provide a good fit to the data (no statistically significant departures from the 1:1 ratio). We therefore compared the deviance of the null model against an χ^2 distribution, with the same degrees of freedom, to test for deviations from parity in our data. We defined “parity” in the sex ratio as departures of a very small magnitude (lower than 0.1) from the 1:1 sex ratio. Then a prospective power test was performed to determine the sample size necessary to detect this small effect size in the overall sex ratio with a power of 0.8 at $\alpha = 0.05$. Explanatory variables tested were year, breeding area, and minimum clutch size. Model selection was made based on Akaike’s information criterion (AIC), selecting the model with the smallest AIC as the most parsimonious (Burnham et al. 1994 1995).

RESULTS

From 285 broods analyzed over the 10 yr of this study, 809 fledglings were sexed by iris color, detecting 404 males and 405 females with an

overall sex ratio of 0.50 (males/chicks fledged). Accordingly, the null model distribution of the logistic regression provided a good fit to the data indicating that brood sex ratios did not depart from parity. The total sample size required to be capable of correctly accepting the null hypothesis of “parity” in the sex ratio was 785 fledglings.

The minimum clutch size and number of chicks fledged per brood showed variations between years and areas (Figs. 2, 3), although only the minimum clutch size exhibited a significant difference among years ($\chi^2 = 37.51$, $p < 0.01$), probably reflecting differences in breeding conditions among years. Offspring sex ratios did not show the same trend in different years or breeding areas (Fig. 4). However, none of the variables of interest had a statistically significant effect on brood sex ratio determination, and the most parsimonious model that better fit our data was the null model (Table 1). The model that included the breeding area had a rather similar AIC value to that of the null model, so we could not exclude the possibility that different breeding areas actually played a role in the resulting offspring sex ratios. There was no extra-binomial dispersion in the model.

DISCUSSION

According to Fisher’s theory (1930), a bias in the secondary sex ratio towards the cheaper (smaller) sex should be expected, i.e., that Montagu’s Harrier should produce more males than females (which are 15% larger in size). However the overall brood sex ratios in the study population did not deviate from parity, and males were not found to be in excess. This result differs from the male-biased offspring sex ratio previously

Table 1. Model selection for analyzing the relationship of offspring sex and year with breeding area and minimum clutch size. The deviance, number of parameters (k), and Akaike’s information criterion (AIC) of each model are also shown. The additive model is indicated by a plus sign (+)

Model	Deviance	k	AIC
Null	403.59	1	405.59
Breeding area	399.22	2	407.22
Year	395.39	10	415.38
Year + breeding area	390.18	13	416.18
Minimum clutch size	400.56	7	414.55

found in the same species (Leroux and Bretagnolle 1996) or in similar species such as Harris's Hawk *Parabuteo unicinctus* and the Marsh Harrier *Circus aeruginosus* (Bednarz and Hayden 1991, Zijlstra et al. 1992), all of which support Fisher's theory. However, parity in fledging sex ratios was also previously detected in other raptor species with sexual dimorphism (Burnham et al. 2003 in the Peregrine Falcon *F. peregrinus*, and Dijkstra et al. 1990 in

the Kestrel *F. tinunculus*). This inconsistency among results may have resulted from different non-mutually exclusive explanations: a) the growth of greater females might not necessary imply greater energy requirements locally (Newton 1979, Richter 1983) so deviations from parity may be due to other differential future reproductive values between sexes; and b) environmental and demographic variables, such as food availability or age

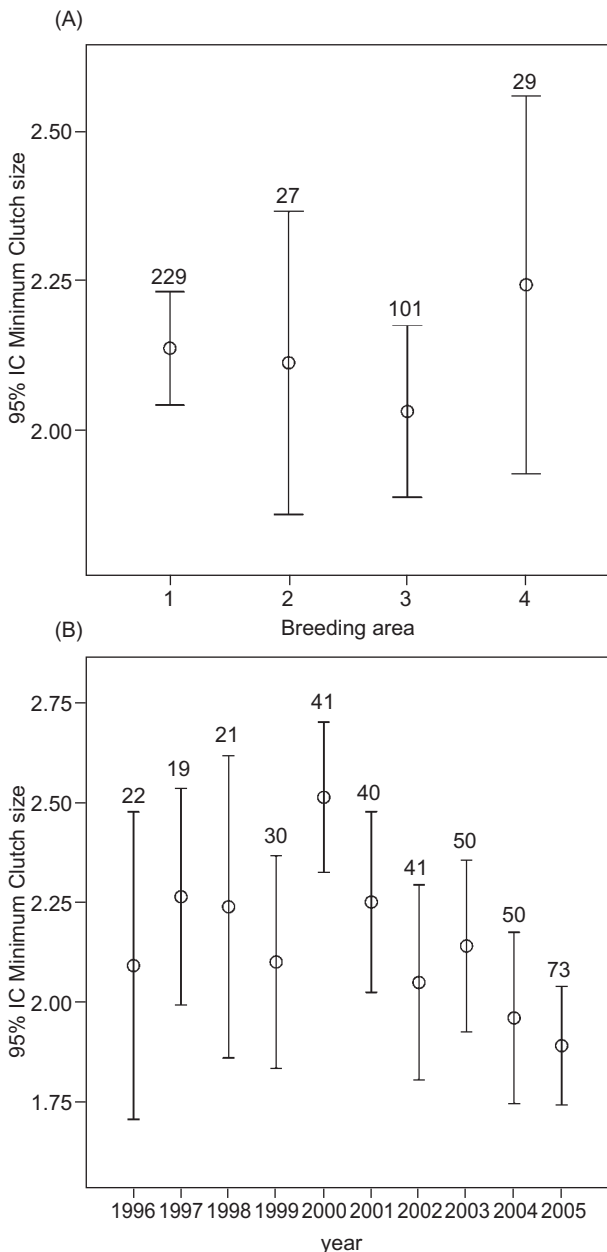


Fig. 2. Minimum clutch size per brood of Montagu's Harrier depending on the (A) breeding area and (B) year. Sample sizes are shown above the 95% confidence interval (CI) bars.

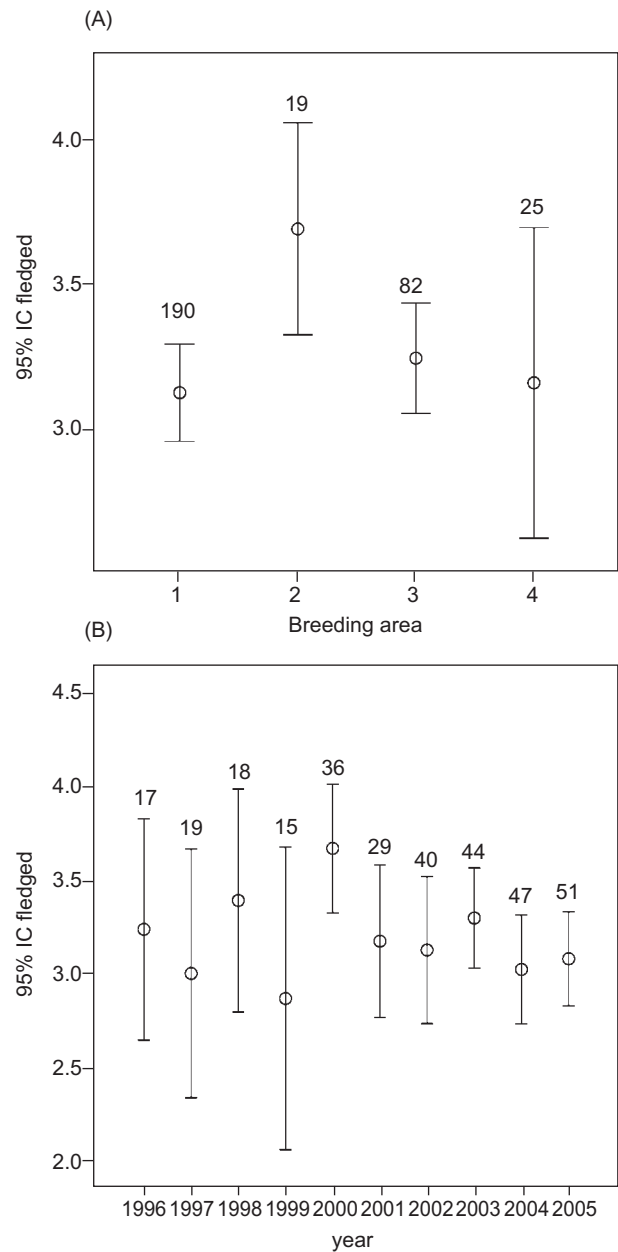


Fig. 3. Number of chicks fledged per brood of Montagu's Harrier depending on the (A) breeding area and (B) year. Sample sizes are shown above the 95% confidence interval (CI) bars.

at first reproduction, may differ among local populations. Thus geographical variations in sex ratios within species may occur as previously found for other raptors such as the Sparrowhawk *Accipiter nissus* (Newton and Marquis 1979, Daan et al. 1996), Harris's Hawk (Mader 1975, Bednarz and Hayden 1991, Dean et al. 1996), Lesser Kestrel (Tella et al. 1996) and also Montagu's Harrier

(Millon and Bretagnolle 2005).

Additionally, different costs and future fitness gains between sexes could lead to parental manipulation of offspring sex ratios (Charnov 1982, Trivers and Willard 1973, but see Ewen et al. 2004). Arroyo (2002) found that the fledging sex ratio of Montagu's Harrier was related to food availability during the pre-laying period, as more females were produced in years with higher food availability (but see Leroux and Bretagnolle 1996). Nager et al. (1999), working with gulls which also show sexual dimorphism, found that females in good condition produced progeny with a non-biased sex ratio, whereas those in a lower condition produced offspring with a skewed sex ratio towards the less-expensive sex. Our results actually show that although not all years or breeding areas showed the same trend in fledging sex ratios, differences were not statistically significant. As the species seems capable of manipulating the offspring sex ratio (Leroux and Bretagnolle 1996, Arroyo 2002), this parity in offspring sex ratio might be explained by an absence of pressures in this environment that overcomes the costs of manipulation. Nevertheless, although the sample size in the overall sex ratio was large enough in our study, it was reduced when analyzing this parameter in different years or breeding areas, and such power constraints may possibly have precluded detection of sex ratio deviations from parity in space and time (Hardy 2002, see example in Rosenfield et al. 1996), and larger sample sizes are required to confirm that no biased sex ratio occurs with different breeding conditions in this population.

Acknowledgments: G. Urios kindly provided the figure of the breeding areas. D. Oro, V. Bretagnolle, and an anonymous referee improved previous versions of the manuscript. This study was a part of the Program of Conservation of the Montagu's Harrier in the Comunitat Valenciana, carried out by the Generalitat Valenciana. MGM was supported by an I3P contract from the Spanish Ministry of Education and Science.

REFERENCES

Arroyo BE. 2002. Fledging sex ratio variation and future reproductive probability in Montagu's Harrier, *Circus pygargus*. *Behav. Ecol. Sociobiol.* **52**: 109-116.
 Arroyo BE, JT Garcia, V Bretagnolle. 2004. Montagu's Harrier. *BWP Update* **6**: 41-55.
 Bednarz JC, TJ Hayden. 1991. Skewed brood sex ratio and sex-biased hatching sequence in Harris's Hawks. *Am.*

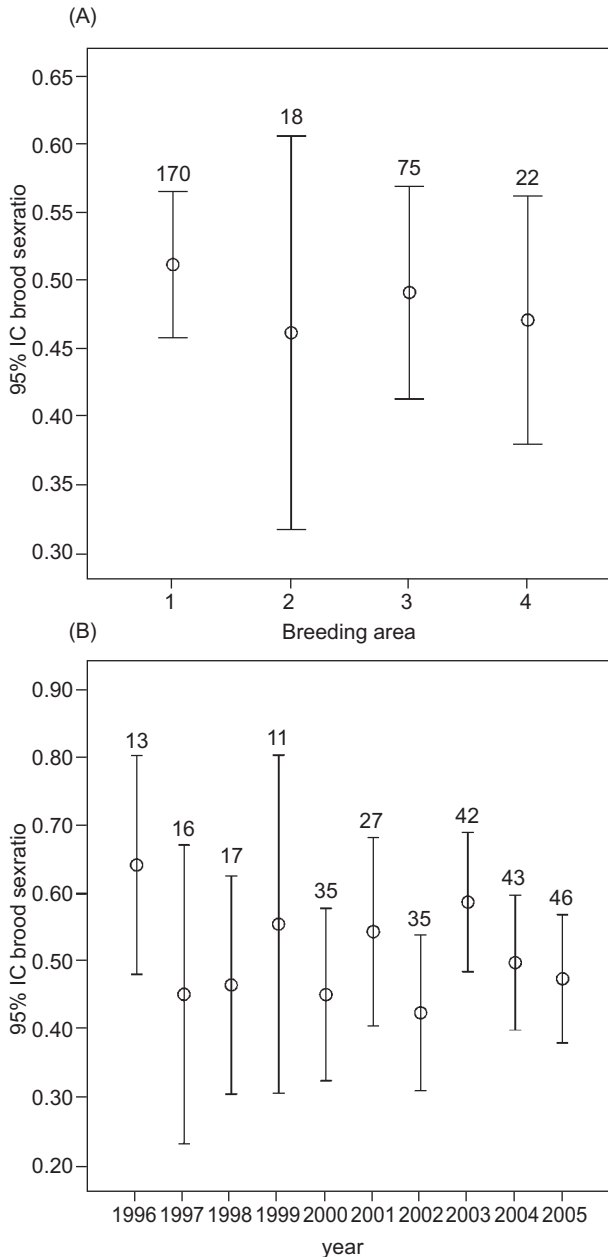


Fig. 4. Brood sex ratios of a Montagu's Harrier population in inland Castellon in different breeding areas (A) and years (B). Sex ratios are expressed as a percentage of males in a brood. Sample sizes are shown above the 95% confidence interval (CI) bars.

- Nat. **137**: 116-132.
- Bolton M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: relative contributions of egg size and parental quality. *J. Anim. Ecol.* **60**: 949-960.
- Burnham KP, DR Anderson, GC White. 1994. Evaluation of the Kullback-Leibler discrepancy for model selection in open population capture-recapture models. *Biometrical J.* **36**: 299-315.
- Burnham KP, DR Anderson, GC White. 1995. Selection among open population capture-recapture models when capture probabilities are heterogeneous. *J. Appl. Stat.* **22**: 611-624.
- Burnham W, C Sandfort, J Belthoff. 2003. Peregrine falcons eggs: egg size, hatchling sex, and clutch sex ratio. *Condor* **105**: 327-335.
- Charnov E. 1982. *The theory of sex allocation*. Princeton, NJ: Princeton Univ. Press.
- Clifford LD, DJ Anderson. 2001. Food limitation explains most clutch size variation in the Nazca Booby. *J. Anim. Ecol.* **70**: 539-545.
- Clutton-Brock TH, SD Albon, FE Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. *Nature* **313**: 131-133.
- Daan S, C Dijkstra, FJ Weissing. 1996. An evolutionary explanation for seasonal trends in avian sex ratios. *Behav. Ecol.* **7**: 426-430.
- Dijkstra C, S Daan, JB Buker. 1990. Adaptive seasonal variation in the sex ratio of Kestrel broods. *Funct. Ecol.* **4**: 143-147.
- Ewen JG, P Cassey, P Moller. 2004. Facultative primary sex ratio variation: a lack of evidence in birds? *Proc. R. Soc. Lond. B* **271**: 1277-1282.
- Fisher RA. 1930. *The genetical theory of natural selection*. Oxford, UK: Oxford Univ. Press.
- Genovart M, D Oro, X Ruiz, R Griffiths, P Monaghan, R Nager. 2003. Seasonal changes in brood sex composition in Audouin's Gull. *Condor* **105**: 783-790.
- Hammerstrom F. 1969. A harrier population study. *In* Peregrine Falcon populations: their biology and decline. Wisconsin Univ. Press, pp. 367-383.
- Hardy ICW. 2002. *Sex ratio: concepts and research methods*. Cambridge, UK: Cambridge Univ. Press.
- Jiménez J, M Surroca. 1995. Evolución poblacional y reproducción del Aguilucho cenizo *Circus pygargus* en la provincial de Castellón. *Alytes* **7**: 287-296.
- Komdeur J, S Daan, J Tinbergen, C Matemans. 1997. Extreme adaptive modification in sex ratio of 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.
- Leroux A, V Bretagnolle. 1996. Sex ratio variations in broods of Montagu's Harriers *Circus pygargus*. *J. Avian Biol.* **27**: 63-69.
- Limiñana R, M Surroca, S Miralles, V Urios, J Jiménez. 2006. Twenty three-year population trend and breeding biology of Montagu's Harrier *Circus pygargus* in a natural vegetation site in Northeast Spain. *Bird Study* **53**: 126-131
- Mader WJ. 1975. Biology of the Harris Hawk in southern Arizona. *Living Bird* **14**: 59-85.
- Millon A, B Bretagnolle. 2005. Nonlinear and population-specific offspring sex ratios in relation to high variation in prey abundance. *Oikos* **108**: 535-543.
- Nager RG, P Monaghan, R Griffiths, DC Houston, and R Dawson. 1999. Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Sciences of the United States of America* **96**: 570-573.
- Newton I. 1979. *Population ecology of raptors*. Berkhamsted, UK: T. and A. D. Poyser.
- Newton I, M Marquis. 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 cyaneus* in Orkney. *Ornis Scand.* **11**: 1-11.
- Post E, MC Forchhammer, NC Stenseth, R Langvatn. 1999. Extrinsic modification of vertebrate sex ratios by climatic variation. *Am. Nat.* **154**: 194-204.
- Richter W. 1983. Balanced sex ratios in dimorphic altricial birds: the contribution of sex-specific growth dynamics. *Am. Nat.* **121**: 158-171.
- Rosenfield RN, J Bielefeldt, SM Vos. 1996. Skewed sex ratios in Cooper's Hawk offspring. *Auk* **113**: 957-960.
- SAS Institute Inc. 1999. *SAS/STAT™*. SAS Institute Inc., Cary, N.C.
- Scharff WC, E Balfour. 1971. Growth and development of Hen Harriers. *Ibis* **113**: 323-329.
- Schipper WAJ. 1978. A comparison of breeding ecology in three European harriers (*Circus*). *Ardea* **66**: 77-102.
- Smallwood PD, JA Smallwood. 1998. Seasonal shifts in sex ratios of fledging American Kestrels (*Falco sparverius paulus*): the early bird hypothesis. *Evol. Biol.* **12**: 839-853.
- Tella JL, JA Donazar, JJ Negro, F Hiraldo. 1996. Seasonal and interannual variations in the sex-ratio of Lesser Kestrel *Falco naumanni* broods. *Ibis* **138**: 342-345.
- Torres R, H Drummond 1999. Variably male-biased sex ratio in a marine bird with females larger than males. *Oecologia* **118**: 16-22.
- Trivers RL, DE Willard. 1973. Natural selection of parental ability to vary the sex ratio offspring. *Science* **179**: 90-92.
- Weatherhead P, KL Teather. 1991. Are skewed fledging sex ratios in sexually dimorphic birds adaptive? *Am. Nat.* **138**: 1159-1172.
- Wiebe KL, GR Bortolotti. 1992. Facultative sex ratio manipulation in American Kestrels. *Behav. Ecol. Sociobiol.* **30**: 379-386.
- Zijlstra M, S Daan, J Rinsma. 1992. Seasonal variation in the sex ratio of Marsh Harrier *Circus aeruginosus* broods. *Funct. Ecol.* **6**: 553-559.