

Nonlinear and population-specific offspring sex ratios in relation to high variation in prey abundance

Alexandre Millon and Vincent Bretagnolle

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Montagu's harrier (*Circus pygargus*), a specialist raptor in western France, faces huge variations in the abundance of its main prey, the common vole (*Microtus arvalis*). This simple predator–prey system provides fine-tuned data for investigating patterns of sex allocation under environmental variability. We analysed variations in brood sex ratio at fledging (1364 chicks from 451 broods) in two adjacent harrier populations for respectively 16- and 8-year surveys of both the predator and its prey. Overall sex ratio (number of males/total number of offspring) was close to parity (0.513) but this apparent equilibrium resulted in fact from opposite skews in the two populations which differed by almost 10% (0.561 vs 0.464). Brood reduction only is unlikely to produce such a difference in average brood sex ratios. Brood sex ratio of the predator was affected by prey abundance. Contrary to expectations and whatever the population, relatively more offspring of the smaller sex were produced during peak years of the vole cycle but also during poor years, thus providing the first evidence for a nonlinear influence of environmental quality (prey abundance) on sex ratio. Assuming that observed sex ratios in both populations are the result of an adaptive strategy that maximizes harrier reproductive output, we discuss possible origins of the bias and why nonlinearity may be involved in sex ratio adjustment. These results further point out that sex ratio analyses should take into account population characteristics, and more generally, environmental variations both in space and time.

A. Millon, and V. Bretagnolle, Centre d'Études Biologiques de Chizé, CNRS UPR 1934, FR-79360 Villiers-en-bois, France (millon@cebc.cnrs.fr).

Fisher (1930) was the first to identify frequency-dependent selection pressures that maintain population sex ratio close to parity (i.e. producing the rarer sex is an evolutionarily stable strategy). According to his theory, parents should invest equally in male and female and as a consequence, sex ratio at the population level is expected to be biased in favour to the cheaper sex. Additionally, sex ratio adjustments at the litter level are expected when fitness returns for parents differ between a son and a daughter. Then natural selection should favour individuals investing in the sex which maximizes their fitness (Hamilton 1967, Trivers and Willard 1973, Charnov 1982, Frank 1990, Leimar 1996).

Results of studies on parasitoid wasps have confirmed the predictions of sex ratio theory (West et al. 2000). In contrast, studies on vertebrates and especially birds and mammals (Williams 1979, Clutton-Brock 1986), and possibly also reptiles (Shine 1999), led to contradictory results that tarnished what is usually considered as one the greatest successes of evolutionary biology (Cockburn et al. 2002). Non equivocal evidences of bias in primary sex ratio in birds are now well established (Komdeur et al. 1997), even if in some cases evidence for adaptive significance is still lacking (Heinsohn et al. 1997). Moreover, recent studies provided experimental support for the ability of birds to adjust egg sex ratio (Nager

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et al. 1999, Kalmbach et al. 2001). But the adaptive value of sex ratio manipulations in birds is still debated in view of the apparent heterogeneity of results between or even within species, and of the poor knowledge of mechanisms that could allow sex ratio manipulation due to chromosomal sex determination (Krackow 1999). This confusion is well emphasized by the opposite conclusions that emerge from two recent meta-analyses (West and Sheldon 2002, Ewen et al. 2004).

Many factors may actually interact in determining the sex ratio of the progeny, and the net result of antagonistic selection pressures seldom leads to strong biases (Cockburn et al. 2002). For example, effect of maternal dominance on sex ratio in red deer is concealed by increasing population density and high winter rainfall, two external variables affecting mother condition (Kruuk et al. 1999). Spatial heterogeneity in habitat quality may also influence sex allocation pattern in species with sex-biased dispersal (Julliard 2000). However, spatial component in sex allocation theory has received only recent theoretical attention (Ranta et al. 2000), and empirical support is rarely available (but see Byholm et al. 2002). Brood sex ratios are lastly expected to vary with food availability especially in dimorphic bird species, where cost for producing a son might differ from that of a daughter. However, difficulties in evaluating accurately effective costs for parents to raise a particular sex may have led to apparent contradictory findings (Torres and Drummond 1999a, Arroyo 2002a, Hipkiss et al. 2002). When food abundance varies, individual-level sex allocation theory (sensu Trivers and Willard 1973) predicts a linear relationship between food availability and proportion of the larger sex (Wiebe and Bortolotti 1992, Torres and Drummond 1999b, Arroyo 2002b). The more energetically expensive sex is thus expected to be favoured as food abundance increases.

Here we report variations in brood sex ratio at fledging from long term surveys of two populations (8 and 16 years) of Montagu's harrier (*Circus pygargus*), a raptor. In this species, sexual size dimorphism is reversed (female ca 19% heavier than male). Fisher's arguments predict therefore a small bias towards male at the specific level, which has been detected in some populations (Leroux and Bretagnolle 1996) but not in others (Arroyo 2002b). These contradictory results suggest that other factors may affect sex ratio in this species, at the individual-level for example, such as breeding timing or brood size. Moreover, in western France, Montagu's harrier is highly specialised on common vole (*Microtus arvalis*), which abundance strongly affects reproductive output of its predator (Salamolard et al. 2000). The population dynamic of this rodent is cyclic, showing two orders of magnitude variations between peak and crash years over a 3-yr period, and is relatively predictable within the breeding season. This predator-prey model thus provides ideal

conditions to test the effect of food availability on sex ratio in a size-dimorphic species. To evaluate the level of spatial heterogeneity, and determine if sex ratio adjustment is sensitive to population specific demographic traits, analyses were conducted separately for the two study populations.

Methods

Study species and areas

Montagu's harrier is an opportunistic raptor which specialises locally on particular prey with high abundance, especially small rodents like voles. In the study areas common voles represent 64% (range 34–87%) of diet composition in biomass according to the phase of the cycle (Salamolard et al. 2000). Vole abundance strongly affects life history traits of Montagu's harrier, such as clutch size or age at first reproduction (Salamolard et al. 2000). Parental care is highly asymmetric, with females incubating and brooding whereas males provide almost all food to the family from pre-laying to postfledging periods. Age at first breeding is earlier in females than in males, as one-year-old females but not males, are able to mate and breed successfully. Sexual size dimorphism in chicks, calculated as the asymptotic mass difference at the end of the nesting period between female and male (Møller 1994), is 0.049 (\log_{10} -transformed values; t-test, $t = 44.2$, $df = 178$, $p < 0.0001$).

The two study sites are located in central-western France (Région Poitou-Charentes). Rochefort (182 km², 46.03°N, 0.97°W, hereafter RO) is part of a large wetland increasingly converted from wet meadows to cereal fields, surveyed between 1987 and 2002. The second study site, southern Deux-Sèvres (1995–2002, 46.24°N, 0.41°W, hereafter DS) ca 50 km from RO, covers 340 km² of an intensive agricultural landscape. Breeding pair density did not differ between the two study sites and is significantly correlated to spring vole abundance (ANCOVA, site: $F_{1,18} = 0.005$, $p = 0.95$, vole: $F_{1,18} = 6.8$, $p = 0.018$, interaction: $F_{1,536} = 0.03$, $p = 0.87$). Clutch size was however significantly higher in DS than in RO even when taking into account spring vole abundance (mean \pm sd: DS = 4.23 ± 0.99 , RO = 3.90 ± 0.97 ; ANCOVA, site: $F_{1,536} = 12.6$, $p = 0.0004$, vole: $F_{1,536} = 55.7$, $p < 0.0001$, interaction: $F_{1,536} = 0.009$, $p = 0.92$), suggesting that DS might represent a higher quality habitat for harriers than RO. Several parameters covaried between the two study populations over the common period of survey (1995–2002, $n = 8$): summer vole abundance ($r_s = 0.88$, $p = 0.02$), breeding pairs density ($r_s = 0.76$, $p = 0.044$), median laying date ($r_s = 0.76$, $p = 0.044$) and clutch size ($r_s = 0.755$, $p = 0.046$). Harrier populations breeding in these two study sites do not however represent strictly isolated populations, since at least two birds born in RO have been found as breeder in

DS. Furthermore some pairs are located between the two sites.

Broods where not all fledglings have been sexed were excluded from the analyses (52 chicks in 36 broods), leaving 1364 chicks from 451 broods that have been sexed. Offspring were sexed using iris colour, a reliable dimorphic character in Montagu's harrier (Leroux and Bretagnolle 1996). Cumulated data from several studies in France and Spain showed that all birds sexed as nestling and later resighted as adults or recovered, were correctly sexed ($n = 102$).

Vole abundance

Abundance of common vole was assessed yearly by two trapping sessions, since the study started. The first session occurred in spring (end of April) to estimate prey availability for harriers during the pre-laying period. The second took place in summer (end of June) during the brooding period. A trap line consists in sampling a 100 m-transect with 51 live traps without bait spaced every 2 m for 24 hours. For each session a total of 24 to 36 lines in RO and 80 to 96 lines in DS were deposited. The variation in average vole density in study sites ranged from 3 to 215 individuals ha^{-1} (Salamolard et al. 2000). The two study sites displayed higher between-year variability in vole abundance in summer (log-transformed values, mean \pm sd, RO: 0.17 ± 0.60 ; DS: 0.04 ± 0.62) than in spring (mean \pm sd, RO: -0.22 ± 0.46 ; DS: -0.16 ± 0.50). However, they did not differ in abundance level, neither in spring ($t = -0.13$, $df = 12.9$, $p = 0.90$) nor in summer ($t = -0.007$, $df = 14$, $p = 0.99$). Spring and summer sessions were highly correlated between the study areas (RO: $r = 0.80$, $n = 14$, $p < 0.001$; DS: $r = 0.90$, $n = 8$, $p = 0.002$, Fig. 1b), and consequently only summer vole abundance was used in statistical analyses. Common voles in central-western France experience fluctuations of high amplitude (S-index varying from 0.51 to 0.61). Oscillations appear to be extremely regular at exactly 3-yr intervals using three different long term data sets in both study areas (respectively, 10, 15 and 22 years). Auto-regressive models of first and second order on population growth rate show that second order models AR(2) were selected for all common vole time series (Bretagnolle et al., unpubl.).

Vole sampling was designed according to habitat types (i.e. crops). In RO, following Salamolard et al. (2000), three main habitats (cereal, pasture and fallow/waste land) were used, weighting took into account changes in land management over the study period. In DS, land use was determined yearly and mapped onto a GIS at the parcel level, according to 8 different categories (cereal, maize/sunflower, rye-grass, alfalfa, pasture, pea, colza and others). Vole abundance was not defined at the level

of a pair home range but rather at the population level. On each site vole abundance was weighted according to relative area of each habitat, and was \log_{10} -transformed.

Simulations and statistical analysis

Unless otherwise stated, sex ratios have been calculated within the brood (number of males/brood size) because sex of siblings cannot be considered as independent samples (Krackow and Tkadlec 2001). In order to establish statistically whether a bias for a given year and study population was significant, we used a simulation approach (Wilson and Hardy 2002) and performed 10 000 runs of simulated data under the binomial distribution. This allows us to incorporate actual brood size distribution for a given year and population within the simulation program (Lambin 1994), as brood size acts as a statistical constraint on sex ratio values. We choose overall mean sex ratio for each population since use of 1:1 sex ratio could have led to an overestimation of the occurrence of adjustments (Wilson and Hardy 2002).

Pseudoreplication may arise since an unknown proportion of the harrier population is breeding in subsequent years, thus yearly sex ratios cannot a priori be considered as statistically totally independent. We first checked if multiple brood sex ratios from the same individual could be treated as independent units. Repeatability in brood sex ratio conducted on wingtagged adults was low (♀ : 0.05, F-ratio (29,48 df) = 1.15, $p = 0.33$; ♂ : 0.24, F-ratio (21,31 df) = 1.75, $p = 0.08$; see Lessells and Boag 1987 for methods). Additionally, mean variance of randomly selected individuals did not differ from those of repeated broods of males or females and two-tailed resampling test led to identical p-values (10 000 iterations, male: $p = 0.07$; female: $p = 0.33$; see Ewen et al. 2003 for methods). We are therefore confident that the level of pseudo-replication remains weak and did not affect the results.

We used logistic regressions with binomial error and logit link to deal with dependent variable such as brood sex ratio constrained between 0 and 1. We always checked for the heterogeneity factor (HF), and F-tests were applied to correct for dispersion (Krackow and Tkadlec 2001), that appeared always to be slight. Explanatory variables included relative laying date (calculated as the difference from the yearly mean laying date for each population), brood size, and reproductive success (number of fledglings/clutch size). We chose to build models separately for the two populations because of the consistent difference in mean sex ratio. Analyses incorporating population as a factor were nevertheless conducted and led to identical results.

The influence of vole abundance on sex ratios was tested using yearly sex ratio, rather than brood sex ratio,

as the statistical unit. This variable was normally distributed Kolmogorov–Smirnov test, $D=0.11$, $p=0.94$) and thus analysed using a general linear model and regressions coefficients were weighted by the inverse standard error. The main reason for doing this was that vole abundance was not available at the harrier's nest scale, but was estimated at the level of the entire study site. Moreover, Montagu's harriers are not territorial raptors, foraging on average over 2500 ha (up to 6000 ha), with overlap between neighbouring pairs and within-season variability (unpubl.). Assessing vole abundance within harrier individual home ranges is therefore unrealistic.

Sex ratio is expressed as mean \pm se. Statistical analyses and simulations were performed on R 1.4.1 (Ihaka and Gentleman 1996).

Results

Population-specific sex ratio

Cumulating all broods irrespective of study sites, fledging sex ratio of Montagu's harrier was very close to parity (0.513 ± 0.01 , $n=451$). However, this apparent equilibrium resulted from opposite skews between the two study sites. Brood sex ratio was 0.561 ± 0.02 ($n=229$) for RO, and 0.464 ± 0.02 ($n=222$) for DS. Using year as the sample unit, mean sex ratios were 0.556 ± 0.02 ($n=16$) and 0.447 ± 0.02 ($n=8$) for RO and DS respectively. With chicks as the statistical unit, numbers of males and females did not differ from parity when both studies sites were combined (0.508 , binomial test, $n=1364$, $p=0.57$). However, RO showed a significant bias toward male (0.561 , binomial test, $n=618$, $p=0.0025$) whereas in DS, harriers tended to produce more females, though marginally significantly (0.464 , binomial test, $n=746$, $p=0.052$). Fledgling sex ratios statistically differed between the two populations during the common study period (1995–2002; G-test, $G=8.3$,

$p=0.004$) but did not covary ($r_s=0.38$, $p=0.36$, $n=8$; Fig. 1a). During the 16 years of survey in RO, there was no evidence for correlation between average brood sex ratio in year t and year $t+1$ ($r=-0.07$, $p=0.82$).

Does a sex suffer more brood reduction?

Brood reduction showed a higher rate in RO than in DS: 23.6% of hatchlings died in the first site vs 12.1% in the second site (G-test, $G=27.2$, $p<0.0001$). Such a difference in mortality could account for the sex ratio difference between the two populations. Sex ratio analysis including only broods where no mortality of eggs or chicks occurred is suspected to be biased in favour of the sex the more susceptible to mortality (Fiala 1980). The skew was in both cases accentuated in the initial way (RO: 0.589 ± 0.05 , $n=28$; DS: 0.449 ± 0.03 , $n=82$) suggesting that if differential mortality occurred, the more susceptible sex differed between the two populations: males in DS and females in RO. Neither brood size nor relative laying date significantly affected sex ratio (either linearly or quadratically, Table 1). Moreover sex ratio varied independently of reproductive success (Table 1).

Vole abundance and sex ratio variation

Both populations underwent strong year-to-year sex ratio variations (Fig. 1a). Simulation results indicated that such variations resulted from actual adjustments and were not simply a byproduct of binomial variance (Fig. 2). Moreover, there was no correlation between deviation from the average sex ratio and the sample size ($r=0.18$, $n=24$, $p=0.39$). Overall 10 out of 24 years showed significant departure from binomial distribution: five out of 16 in RO and five out of eight in DS (Fig. 2).

Vole abundance significantly affected average brood sex ratio, with the quadratic term of summer abundance

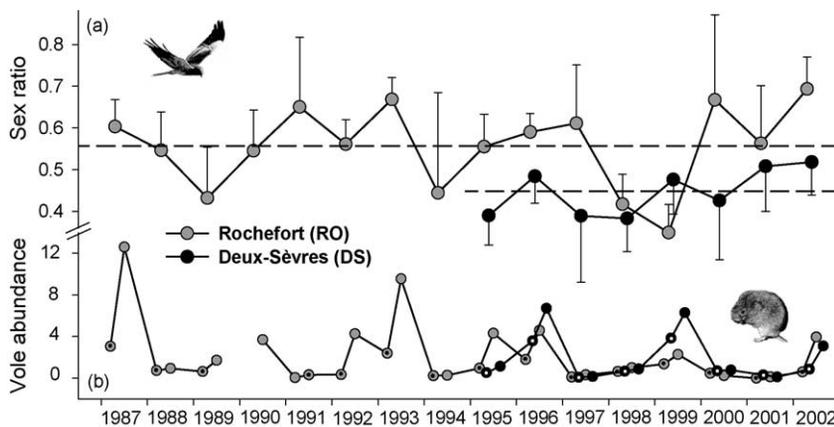


Fig. 1. (a) Brood sex ratios (proportion of males \pm SE) of the two study populations of Montagu's harrier. Dots represent mean population sex ratio (see methods for calculation), and dashed line mean sex ratio for each population. (b) Time series of the vole abundance index (number of capture/trapline/24 h weighted by area of main habitats, see methods) for RO and DS in spring (dotted circle) and summer (filled circle). Missing value for spring 1990 in RO.

Table 1. Models of logistic regression incorporating brood size, breeding success and relative laying date for explaining brood sex ratio. HF represents the heterogeneity factor. Reproductive success is measured as the number of fledglings/clutch size. (-)² indicates incorporation of the quadratic term into the model.

	Deux-Sèvres (DS)				Rochefort (RO)			
	deviance	HF	df	p-value (F-test)	deviance	HF	df	p-value (F-test)
Null model	269.9	0.96	221		282.1	0.96	228	
brood size	0.37		1	0.55	0.11		1	0.74
(brood size) ²	2.64		1	0.11	1.97		1	0.16
Null model	269.9	0.96	221		168.4	0.90	146	
relative laying date	0.47		1	0.49	0.22		1	0.64
(relative laying date) ²	1.79		1	0.18	0.56		1	0.46
Null model	208.9	0.90	185		171.0	0.96	137	
reproductive success	0.18		1	0.67	0.68		1	0.41

being significant ($p = 0.012$, Table 2) while all interaction terms were not significant and thus removed from the model (all $p > 0.22$). A higher proportion of males was produced in low and high food years as compared to intermediate food years. Conversely more females were produced during intermediate phases of the vole cycle (Fig. 3). The direction of adjustments revealed by simulation analysis was consistent in both populations: offspring sex ratio in peak (four) as well as crash vole

years (one) were relatively male-biased, whereas intermediate years (five) of the vole cycle were relatively female-biased (Fig. 2).

Discussion

Considering both populations together, no bias was detected in offspring sex ratio. However, the two study

Fig. 2. Frequency distribution of 10 000 brood sex ratios at the population level simulated under a binomial distribution. Solid line indicates mean brood sex ratio value calculated with year as sample unit (RO: 0.556; DS: 0.447). Actual brood size distribution for a given year and population is incorporated inside computation. Tick interval on y-axis represents 100 replicates. Triangle indicates actual yearly average of brood sex ratio. Within population, graphs are arranged according to increasing vole abundance from left to right and downward. Years where mean brood sex ratio was outside the 95% range of the binomial distribution are pointed out with an asterisk.

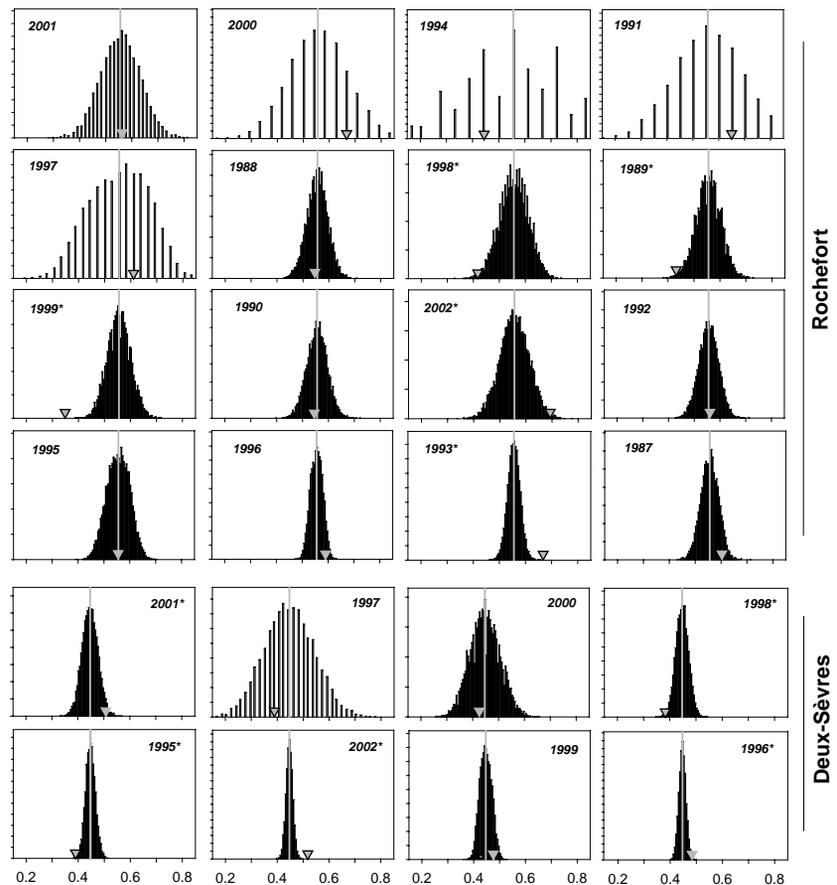


Table 2. Regression analyses of relative sex ratio (yearly average) according to vole abundance at the population level. Regressions coefficients were weighted by the inverse standard error.

	Parameter estimate	Adjusted R-squared	df	p-value (F-test)
Model		0.426	20	0.003
Intercept	0.403			
Site	0.097			0.007
Vole	0.009			0.77
(Vole) ²	0.128			0.012

populations showed opposite skews in sex ratio, with one population producing on average 10% more males than the other. Despite this difference, the two populations did not differ in their reaction to high variations in food abundance, brood sex ratios following a quadratic relationship (U-shaped). Our results raise three important issues that we successively discuss below.

The origin of the bias

In both populations, observed fledgling sex ratios (which are secondary sex ratios) could have resulted from nestling sex-biased mortality. Our long term data on sex ratio (since 1987) necessarily deals with secondary sex ratio since molecular sexing techniques were available only recently (Griffiths and Tiwari 1993). Brood reduction may result in sex-biased mortality if cost to produce a son or a daughter differs. However, sexual size dimorphism in mass in favour of female chicks is discernible only during the second half of the rearing period, whereas mortality mainly occurs at hatching (unpubl.). Moreover, there is controversy about whether

the larger sex is effectively more costly to produce. In some cases, the larger sex was found to require more energy during growth (Riedstra et al. 1998), but not in others (Newton and Marquiss 1979). In a Spanish population of Montagu's harrier, Arroyo (2002a) found that males were more sensitive to starvation than females, probably because larger size confers an advantage in sibling competition. Such a pattern of brood reduction could apply to DS but would fail to explain the bias towards males in RO.

Alternatively, Dijkstra et al. (1998) proposed a U-shaped relationship between sex ratio and brood size in dimorphic species, assuming that the larger sex requires more food and that brood reduction is influenced by sex composition within the brood. From an even sex ratio at hatching, their model predicts that a bias towards males, the smaller sex in raptors, should be expected in smaller as well as in larger broods. However, neither brood size nor reproductive success were related to the sex ratio in RO and DS. Lastly, it would remain difficult to account for reversed offspring production costs according to sex between two populations. Analyses of sex ratio from complete clutches only, suggest however such a reversed pattern between the two populations (males more likely to die in DS and females more likely to die in RO). To our knowledge, such a result would constitute the first example of population-specific post-natal mortality.

It therefore seems unlikely that brood reduction is the single process involved in the observed pattern, and future molecular sexing will allow to check if sex ratio is biased at conception in our study populations.

Nonlinear relationship between sex ratio and food abundance

We found that sex ratio varied significantly with vole abundance within the two study areas. Abundance of common vole in spring (i.e. during pre-laying) is a reliable estimator of food availability during chick rearing since food supply increased over the course of the breeding season in 22 out of 24 years, in contrast with voles cycle in Fennoscandia (Norrdahl 1995). Additionally, Montagu's harriers may be able to refer to other cues than overall abundance to obtain information early on vole density they will experience during chick rearing. Korpimäki and Hakkarainen (1991) suggested vole mass as a possible cue, but increase capture rate during the prelaying period or vole spatial distribution could also be involved.

There is a clear-cut pattern of sex ratio variation in our two populations of Montagu's harrier with a relative higher production of males in vole peaks and of females in intermediate years (Fig. 3). This trend in sex ratio according to food availability is however no longer

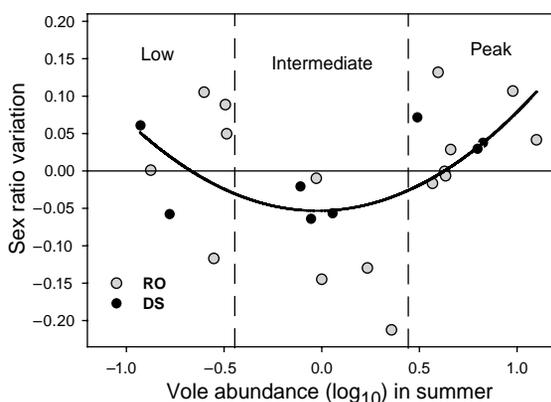


Fig. 3. Relative sex ratio in relation to \log_{10} -transformed vole abundance. The relative sex ratio was calculated as the difference between yearly mean sex ratio and overall mean for each population. The three different phases of the vole cycle are separated by vertical dashed lines (crash [< -0.45], intermediate [from -0.45 to 0.45] and peak [> 0.45]). -0.45 and 0.45 values correspond respectively to 0.355 and 2.82 captures/trapline/24 h. Fitted line calculated for pooled data (DS+RO).

observed since during vole crashes, population sex ratios appear to be more variable. As a general rule, sex ratio in dimorphic species has been found to be linearly affected by food supply and biased towards the smaller sex when prey is scarce, either the male (Wiebe and Bortolotti 1992, Dzus et al. 1996, Appleby et al. 1997, Torres and Drummond 1999b, Korpimäki et al. 2000, Arroyo 2002b in a Spanish Montagu's harrier population) or the female (Paterson and Emlen 1980). Such results have been regarded as an extension of Trivers and Willard model. But Sheldon et al. (1998) pointed out that sex difference in post-natal mortality may produce sex ratio biases that match those predicted under an adaptive scenario. Experimental field manipulations of parental effort provided nevertheless similar results: more individuals of the cheaper sex are produced when energy expenditure increases (Nager et al. 1999, Kalmbach et al. 2001). In contrast, Byholm et al. (2002) found that in northern goshawk (*Accipiter gentilis*) more males (the less expensive sex) were produced in years when grouses were more abundant. Additionally, we did not find evidence for the homeostasis hypothesis since no negative correlation was detected between sex ratios of successive years (Fisher 1930).

In this study, more males were produced both during peak and crash vole years, providing the first evidence for a nonlinear influence of environmental quality on sex ratio, and suggesting that the benefits of sex ratio adjustment may differ according to food abundance. Several explanations can be put forward to explain such a pattern. First, producing more males (in this case, the sex requiring less energy) when food availability is low, may allow adults to maximise their residual reproductive value. Additionally, offspring future reproduction probability could also be important (Appleby et al. 1997, Arroyo 2002b). In Montagu's harrier, there is indeed correlational evidence that one-year-old females enter the breeding population almost exclusively during the peak phase of the vole cycle (Salamolard et al. 2000). Consequently, parents raising females during the intermediate year of the cycle may benefit from an increase in recruitment probability of their yearling daughters. Contrary to cycles of other rodent species in Fennoscandia (Norrdahl 1995), common voles in our two study areas experience a cycle displaying very regular succession of the three distinct phases. Such a regular pattern may allow Montagu's harrier to adjust breeding parameters accordingly. Otherwise, it could be advantageous for parents to produce more males under good food conditions because it may enhance more male than female reproductive value. Trivers and Willard (1973) predicted that the favoured sex under good conditions is the sex with the higher variance in reproductive success, usually the male. However for species with reversed size dimorphism like raptors, females and not males are suspected to experience higher variance in reproductive

success (Olsen and Olsen 1987) and this is effectively the case for Montagu's harrier (unpubl.). Lastly, the ultimate way to analyse the adaptive value of observed sex ratio variation would obviously be the knowledge of recruitment pattern of males and females. However, we believe that it implies a perfect understanding of dispersal pattern, and notably its sex-specific variation according to vole abundance during the birth year. We are unfortunately currently unable to provide such information in our Montagu's harrier populations.

A U-shaped relationship was described between sex ratio and male ornament in the lesser kestrel (*Falco naumanni*) (Aparicio and Cordero 2001). These authors argued that sex-specific reproduction costs due to anisogamy should modify the predictions of the condition-dependence model of Trivers and Willard (1973) in a nonlinear manner. More recently in wandering albatross (*Diomedea exulans*), it has been described that very young and old parents tend to produce an excess of female offspring whereas intermediate-aged birds produce more males (Weimerskirch et al. in press). Occurrence of nonlinear pattern in sex ratio variation may therefore be more common than previously thought. Individuals face a tradeoff when breeding: they can maximize their fitness in preserving their own residual reproductive value, or adversely, reproductive values of their offspring. The result of this tradeoff may vary according to environmental conditions such as food availability and may lead to nonlinear adjustments. This phenomenon could possibly generate the still confused pattern of sex ratio variation in birds.

Opposite bias in sex ratio of adjacent populations

The two study populations probably share similar genotypes, since dispersal between the two sites has been documented and thus genetic drift is unlikely to be involved. The opposite bias observed is thus intriguing. Interestingly, the two study sites were found to differ in global quality for harriers, with DS having overall higher clutch size than RO even after correction by vole abundance. This could offer plausible explanation to the fact that harriers from RO significantly produce more sons than in DS. Parents breeding in less rich habitat would raise more of the smaller sex to fledging. But pattern of sex-biased mortality within populations as well as variation according to food abundance do not support this hypothesis. In addition, as parents are expected to maximize the establishment of their offspring in high quality habitat, sex-specific dispersal could lead to biased sex ratios (Julliard 2000). In western France, females Montagu's harrier is the more dispersing sex, as juvenile or adult (A. Leroux and V. Bretagnolle, unpubl.). Following predictions based on simulated data

(Julliard 2000), it would be adaptive therefore to produce more of the dispersing sex in the poorer habitat (RO) and more of the philopatric sex in the better habitat (DS). However, conversely to this expectation, the observed pattern is reversed, and would rather match predictions from the local resource competition hypothesis (Clark 1978).

To conclude, if factors influencing sex ratio often vary according to year within a population (Radford and Blakey 2000, Griffith et al. 2003), our results further point out that populations characteristics are also of biological relevance in sex ratio studies. Our puzzling results emphasize that sex ratio variation is influenced by several factors varying in space and time and the net balance resulting from different selection pressures is then expected to vary. Evaluating costs and benefits probably represents the best way to understand sex ratio variations in depth (West and Sheldon 2002).

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