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Sex ratio variation and mixed pairs in roe deer: evidence for control of sex allocation?

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Abstract Sex allocation has provided rich ground for the development of evolutionary theory. The dominant models in vertebrates have provided predictions of sex ratio based on asymmetry in variance in breeding success between sexes in the breeding system, and the relative effect of local competition. In ungulates, empirical work has provided some support for these models, but has also generated apparently contradictory observations. Recent models have provided some predictions for both individual and population sex ratio, showing that the availability of high-quality habitat patches and dispersal rates can critically affect both population- and individual-level expectations. We explore patterns in offspring sex ratio among a large sample of roe deer, a species with some interesting aspects of the breeding system. We found that in singleton pregnancies (the minority) there was an excess of male embryos, which was more marked in does in good condition at most sites. While the sex ratio among twins was close to parity, and unaffected either by average condition among populations or by individual condition within populations, we observed a clear excess of mixed pregnancies (sub-binomial variance, SBV). The excess was greater where the average condition was high. Within sites, population changes in average condition were associated with changes in SBV: in populations declining in condition,

SBV also declined. There was no tendency for mixed twins to be more likely in individuals in better condition within a population. We conclude that condition-dependent allocation of sex does occur in roe deer. We suggest that in these “income breeders”, mixed pairs might offer the greatest opportunity to optimize maternal investment during lactation, when conditions will be unpredictable, and that this is increasingly the case when average condition is poor.

Keywords Sex ratio · Roe deer · Trivers–Willard · *Capreolus* · Sex ratio variance

Introduction

Variation in primary sex ratio in vertebrates is poorly understood compared with invertebrates, probably because of the relative complexity of sex allocation and life history in vertebrates (Pen and Weissing 2002). One of the most influential models of sex allocation in mammals is that of Trivers and Willard (1973). This holds that, where variance among males in reproductive success is high, a high-quality female should be more likely to produce sons than a female of poor quality, provided she can influence the fitness of her offspring. A poor-quality female, on the other hand, should favour daughters, as they will be more likely to produce offspring than would a poor-quality son. A female allocating the sex of offspring as envisaged by the Trivers and Willard hypothesis (TWH) would therefore maximise the number of her grand-offspring.

The model has received a great deal of attention from empiricists. Ungulates are particularly useful for testing the predictions of this model; the mating system is frequently polygynous, with male reproductive success determined by conflict among males (Sheldon and West 2004). The local

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resource competition hypothesis (LRC) has been considered as an alternative mechanism for determining optimal sex ratio. It emphasises the effect of dispersal (Clark 1978), proposing that mothers in poorer than average condition, and who cannot therefore afford the additional costs of sharing local resources with philopatric offspring, should produce more of the dispersing sex. Some ungulate studies have provided support for the TWH (e.g. Kruuk et al. 1999, for red deer at low density). Many have not, even when all of the assumptions of the TWH are met (e.g. Blanchard et al. 2005). There are numerous cases of apparent within-species contradictions; Saltz (2001) documents nine.

Recent theoretical work has shown that sex ratio skew in either direction can be consistent with TWH (Leimar 1996). This is possible if mothers transmit condition to their daughters in the form of rank or territory inheritance; in these circumstances, it may benefit a high-quality mother to produce a daughter, who will in turn produce high-quality daughters. Wild and West (2007) modelled the consequences of combining LRC with the predictions of TWH. They showed that LRC could greatly complicate predictions for sex ratio based on condition-dependent sex allocation, and that predicted offspring sex ratio was highly sensitive to the interplay of some crucial population characteristics, such as environmental patchiness and dispersal. The work of Wild and West (2007) exposes the limitations of empirical studies for interpreting patterns in sex ratio variation, and also draws attention to just what can be said of comparisons among populations. For example, population sex ratio is expected to vary as a function of relative density. For male-biased dispersal, which prevails among mammals (Greenwood 1980), greater male bias is expected at higher density and, importantly, that this holds even if TWH and LRC are operating.

Roe deer (*Capreolus capreolus*) have been the focus of a number of studies testing the predictions of hypotheses concerning sex ratio allocation (e.g. Hewison et al. 1999a, b; Hewison and Gaillard 1996; Wauters et al. 1995). Roe deer are an interesting example in that they are routinely polytocous: twins are the modal litter size. They can therefore potentially manipulate both the sex and number of offspring. This is potentially important because a female unable to invest in two offspring, but with ample resources available for a single offspring, might benefit from investing in the sex with the highest variance in reproductive success, providing the early advantage was maintained to adulthood [McGinley (1984) assumed variance in reproductive success was generally higher in males]. This perspective leads to the expectation of not only a sex bias depending on stress in females, but also that this bias will be more marked in low litter sizes (McGinley 1984). In a sample of Swedish roe deer found dead mainly from starvation, and therefore possibly unrepresentative, a

population-level increase in the proportion of males in response to a harsh winter has been reported (Borg 1970). The expected litter size effect has been observed in white-tailed deer; male bias is significantly higher in litters of size one compared with twins (Verme 1969).

The predominance of twins in roe deer also allows sex allocation to be quantified in terms of binomial variance. If sex allocation were random, the frequency of twins of different compositions (whether MM, FF, FM) should follow a Bernoulli process [i.e. from a statistical perspective, the sex of offspring can be considered as a sequence of independent coin tosses, where offspring sex depends on which side the “coin” falls (Krackow et al. 2002)]. Any deviation from this pattern is therefore evidence for some control of sex allocation. Williams (1979) pointed out that the TWH predicts a progeny sex ratio greater than binomial. This has not been explored previously in any polytocous ungulate. Hardy (1997) commented that sex ratio variance in vertebrates was generally neglected, and this continues to be the case (I. Hardy, personal communication).

Studies of roe deer sex allocation to date are one of the examples of apparently contradictory findings in ungulates identified by Saltz (2001). Wauters et al. (1995) reported support for the TWH; females in good condition [indexed by body mass, which is generally accepted to be a reliable index of condition in roe deer (Hewison et al. 2005)] produced a higher proportion of males. Wauters' work was based on a relatively small sample size ($n = 74$), and subsequent work has not confirmed this tendency. Hewison and Gaillard (1996) reported the opposite relationship; sex ratio decreased with maternal body mass, and this was consistent across 14 populations the UK in a variety of conditions. A further study by Hewison et al. (1999a, b) failed to find a relationship between maternal mass and sex ratio at two sites (in France and Norway), one high-density and one managed. In another study at one of these sites and an additional site in Sweden, Hewison et al. (2005) did demonstrate that heavier females produced a statistically significant excess of female offspring (provided a one-tail test was justified, which in the circumstances is debatable).

Hewison et al. (1999a, b) observed that heavier females tended to produce heavier female juveniles, but not heavier male juveniles. Sex differences in the slope of the relationship between mother and offspring mass were later demonstrated (Hewison et al. 2005): the slopes were steeper for female offspring than for males. This was interpreted to mean that higher quality females were investing relatively more in female offspring.

Hewison et al. (2005) speculated that a reversal of the sexes within the TWH framework was evident in roe deer. They attributed this partly to the observations that roe deer are not particularly polygynous, and that the sexes are only

weakly dimorphic (males are only ca. 10% heavier than females). They also hypothesised that variance in reproductive success was higher in females than males. Recent molecular work has not confirmed this. Vanpé et al. (2008) show that variance in breeding success was lower in female roe deer compared with males (in a single Swedish population under controlled hunting). However, the relatively low ratio (1.42) may indicate that the opportunity for sexual selection is low by comparison with more dimorphic ungulates (Vanpé et al. 2008). In the highly dimorphic Saiga antelope (*Saiga tatarica*), where twins also predominate, foetal mass strongly depends on both the mass of the mother and the sex of the offspring (Kuhl et al. 2007).

The mating system in roe deer is unusual among ungulates, and such that there is scope for variability in both sexes. In most locations, males are territorial in the breeding season, with nonoverlapping core ranges that are stable from year to year (Liberg et al. 1998). Male ranges can encompass several overlapping female ranges, and large variation among males in mating success has also been observed (Liberg et al. 1998). Moreover, vacant territories are readily taken up and occupied by the same male for up to seven years (Hewison et al. 1998). Recent radiotracking work suggests that does roam freely through several male ranges during the breeding season (Linnell 2006). Roe deer are also unusual for ungulates in that both sexes show high rates of dispersal (Linnell et al. 1998). Dispersal appears to be “voluntary” in females (Wahlstrom and Kjellander 1995), and provoked by the adult male territory holder for young males (Linnell et al. 1998; Wahlstrom 1994).

In females, body mass has been shown to be a useful predictor of reproductive performance; large females reproduce earlier (Gaillard et al. 1992), produce more twins (Hewison and Gaillard 2001) and live longer (Gaillard et al. 2000). Condition-dependent female choice is also a possibility; a single observation of aggression among females in territories where males attract large numbers of females has been observed (Liberg et al. 1998).

We test whether the patterns of sex ratio variation with condition are consistent with the predictions of different models by quantifying the effect of maternal quality on the number, sex ratio and sex ratio variance of offspring both within sites and among sites using a large sample of culled females in the UK.

Methods

Study sites and data used

Ministry of Defence (MOD) sites are scattered through England and Wales, though the majority are concentrated

in southern England. The MOD shoots deer at these sites for a variety of reasons, including damage to forestry and to agriculture adjoining their property (MOD 1993). The culling is carried out by personnel of the Services Branch of the British Deer Society (SB-BDS). Whenever a deer is culled on MOD property, a detailed cull card is filled out recording the age, sex, rumen contents, parasite burden, coat condition and reproductive state of the culled animal. These records are then lodged with the MOD Conservation Office. Between 1994 and 2005, 1,768 pregnant females were recorded, and 1,544 of these were culled between 15 January and the end of March when foetus sexing is reliable. Forty-one sites contributed records to the database during this period.

While analyses using individual does as replicates and site as a categorical predictor were most relevant for our purposes, we also looked at site-level effects. As the number of culls contributed by each site differed widely, for analyses where we compare patterns among populations, we used those sites contributing most records for analyses using individual carcasses. These sites also tended to have the greatest continuity in their contributions, minimizing confounding between location and temporal effects. While 41 sites contributed records of pregnant females, 18 sites contributed more than 90% of the records of pregnant females. Seven of the sites considered here were also included in the study of Hewison (1993), and we make some comparison of our data with the earlier records at these locations (Salisbury, Aldershot, Bramley, Kirkudbright, Spadeadam, Stanford, Lulworth).

Analyses were carried out using the SAS software (1997; SAS Institute, Cary, NC, USA). The SAS GENMOD procedure was used to fit models predicting sex ratio. Because predictor variables were inter-correlated we used sequential type (type 1) testing for GENMOD models. Hence, model outputs depend on the order of entry of predictor variables to the model. Likelihood ratio chi-squared values are quoted for significance testing. Because the models assume binomial errors, the presence of over- or underdispersion tends to cause type 1 and type 2 errors, respectively, in hypothesis testing. This was allowed for by introducing a dispersion parameter into the models for twins (with the GENMOD DSCALE option).

The following variables recorded by the MOD were among those that we used in this study.

Body weights

Body weights were as recorded by the MOD deer officers as “cleaned body weight”, i.e. the whole carcass with thoracic and abdominal contents removed, but with head, skin and legs retained (MOD 1993) (in the UK the carcass cannot be sold for venison if the skin is not on it). We use

body weight as an index of condition. There are circumstances where body mass might not be a reliable indicator of individual quality in ungulates (Sheldon and West 2004). These are not likely to be met in roe deer: Hewison et al. (2005) argue that for roe deer, body mass is a good long-term measure of phenotypic quality, as roe deer carry little fat reserves and among-year weight variation is low. At the population level, Hewison (1993) and Hewison and Gaillard (1996) treated low mean body mass as evidence that a population was resource-limited. We observed no tendency for carcasses culled later in the season to be larger, as was observed in two French populations (Hewison et al. 2002), so no correction for month was necessary.

Age

The age of each animal in years and months is estimated by the stalker immediately after death using dentition. Tooth wear is likely to be only an approximate guide to age in roe deer. Hewison et al. (1999a, b) showed that estimates of age varied with observer, and also that there was variation in the rate of tooth wear among and within populations. They concluded that only two age classes can be reliably identified: kids (<1 year at culling), and older individuals. (Kids were excluded from all analyses in our study.)

Reproductive condition

The number and sex of foetuses are recorded, as well as their length. Because roe deer exhibit embryonic diapause, pregnancy cannot be recognized early in the culling year. Hewison and Gaillard (1996) considered that only observations made after 1 January could be used to diagnose pregnancy. We follow the policy of Hewison and Gaillard (2001) and restrict our sample to culls made on or after the 15 January up to the end of March. Sex ratio is measured here as the proportion of males (as is conventional).

Testing for deviation from binomial expectation

If the probability of becoming male in any population is constant (this probability may be 0.5, but not necessarily), then it can be modelled as a Bernoulli process, i.e. as a series of “fair” coin tosses. If the population proportion of males is p , the expected mean in litters of size n is np with variance $np(1-p)$ (Krackow et al. 2002). We used the ratio R to describe the degree of deviation from the variance consistent with binomiality. This is simply the observed variance divided by the binomial expectation of variance. Hence, values that are greater than one indicate more variance than expected (super-binomial variance, SRBV), while values that are lower than 1 indicate sub-binomial variance (SBV, frequently referred to as

“precise” sex ratio allocation in insects; e.g. Hardy et al. (1998). Chi-squared likelihood ratio G tests were used to test the null hypothesis of binomiality. In the case where $n = 2$, which is predominant in roe deer, sub-binomiality implies an excess of “balanced” litters (FM), while super-binomiality implies an excess of the unbalanced litters (MM, FF). Such patterns can be recognised in the sign and magnitude of standardised residuals. We asked whether site R values were related to mean site body mass.

Results

Foetus number effects

The majority of pregnancies were twins (72%), with 26.6% singletons and 1.4% triplets. The tendency for pregnant females to bear twins varied among sites and increased with body mass ($\chi^2_{[17]} = 59.2$, $P < 0.001$ for site and $\chi^2_{[1]} = 14.4$, $P < 0.001$ for mass, logistic regression). The average number of foetuses for adults was 1.73 (SE = 0.01, $n = 1,536$), varying between 1.45 and 1.91 among sites (Table 1). The odds ratio for mass was 1.22 (CI 1.13–1.31). (This indicates that, for an increment of 1.0 kg in maternal mass, a twin pregnancy becomes 22% more likely.) There was no evidence of a difference among years ($\chi^2_{[13]} = 11.8$, $P = 0.60$). None of the two-way interaction terms was significant (χ^2 , $P > 0.05$).

The effect of body mass on foetus number was evident among, as well as within, sites—average foetus number was lower at sites where body mass was lower ($r = -0.59$, $P = 0.01$, $n = 18$ sites, Fig. 1). The mean number of foetuses per pregnant female observed at a site was not correlated with the overall sex ratio of foetuses at the site ($r = -0.35$, $P = 0.15$, $n = 18$ sites), nor was site sex ratio correlated with mean mass at the site ($r = -0.15$, $P = 0.55$, $n = 18$ sites).

Influence of condition on sex ratio

Overall, the sex ratio was very close to parity for twins (51.0% male, $n = 2,260$ foetuses), while for singletons, there was a clear male bias (60.0% male, $n = 416$ foetuses, $\chi^2_{[1]} = 22.4$, $P < 0.001$). In the small number of triplets observed, the ratio was exactly 0.5 ($n = 66$ foetuses). An initial analysis predicting foetus sex using site and litter size as predictors (omitting triplets) confirmed that litter size was a significant predictor of foetus sex ($\chi^2_{[1]} = 10.9$, $P = 0.0009$, odds ratio 0.67, CI 0.53–0.85, logistic regression).

In subsequent analyses, we treated singleton and twin pregnancies separately. Site and year were included as categorical predictors. Among the singleton pregnancies,

Table 1 Attributes of the pregnancies in the studied sample

Site	Mean foetus (SE, n)	Mean pregnant mass (SE)	n		n		n		n		Binomial test (twins)	Sex ratio (singletons)	Sex ratio (twins)	Sex ratio (all)	Mean mass: F	M	FF	FM	MM
			F	M	F	M	F	M	F	M									
Aldershot	1.67 (0.08, 43)	17.54 (0.32)	5	10	2	17	8	+	+	–	0.66	0.61	0.62	17.16 (1.20)	17.75 (0.72)	19.52 (1.36)	16.98 0.51	18.05 0.65	
Ash	1.91 (0.04, 47)	16.80 (0.26)	2	2	9	27	7	+	+	–	0.50	0.47	0.48	14.98 (1.20)	15.89 0.72	17.0 0 (0.65)	17.18 0.31	15.83 0.68	
Bordon/Longmoor	1.69 (0.06, 54)	17.58 (0.37)	9	8	3	31	3	+	–	****	0.47	0.50	0.49	17.03 (0.52)	16.6 (1.00)	18.46 (1.69)	17.59 0.50	19.98 1.05	
Bramley	1.73 (0.05, 67)	16.53 (0.20)	7	11	3	35	11	+	–	****	0.61	0.58	0.59	15.76 (0.04)	16.8 (0.52)	19.30 (2.50)	16.38 0.28	16.67 0.25	
Garelochhead	1.63 (0.09, 30)	14.28 (0.41)	5	6	3	10	6	+	+	–	0.55	0.58	0.57	13.92 (1.97)	14.0 (1.30)	13.77 (0.92)	14.66 0.51	14.38 0.89	
Glendouglas	1.42 (0.08, 38)	13.39 (0.27)	4	18	7	6	3	+	–	+	0.85*	0.38	0.57	12.83 (0.54)	12.50 (0.27)	14.07 (0.59)	15.06 0.46	14.23 1.58	
Hawley/Minley	1.90 (0.08, 29)	17.51 (0.46)	1	3	7	15	2	+	+	–	0.75	0.39	0.42	17.71 (–)	18.31 (0.15)	17.25 (0.34)	17.28 0.82	17.71 (–)	
Kirkcudbright	1.73 (0.07, 44)	15.76 (0.32)	5	7	8	15	9	+	+	–	0.58	0.51	0.53	16.16 (1.1)	14.14 (0.90)	15.38 (0.89)	16.34 0.48	16.14 0.39	
Lulworth	1.51 (0.09, 35)	16.31 (0.27)	7	10	2	13	2	+	–	*	0.59	0.50	0.53	16.73 (0.43)	15.66 (0.42)	15.74 (1.54)	16.94 0.47	14.76 0.68	
Otterburn	1.82 (0.09, 33)	15.97 (0.30)	4	4	6	14	3	+	+	–	0.50	0.43	0.44	15.66 (0.29)	17.37 (0.90)	16.50 (0.96)	15.70 0.40	15.28 1.75	
Pirbright	1.54 (0.09, 35)	16.91 (0.34)	5	11	2	14	3	+	–	*	0.69	0.53	0.57	16.53 (1.53)	17.42 (0.61)	16.80 (0)	16.86 0.42	16.04 1.35	
Porton	1.77 (0.04, 137)	16.78 (0.15)	17	15	23	67	14	+	–	**	0.47	0.46	0.46	16.02 (0.47)	17.16 (0.43)	16.40 (0.37)	16.96 0.19	17.06 0.54	
Sandhurst	1.45 (0.07, 47)	15.86 (0.30)	9	17	6	12	3	+	+	–	0.66	0.43	0.51	15.13 (0.75)	15.17 (0.41)	16.87 (0.60)	16.99 0.68	15.44 0.00	
Spadeadam	1.63 (0.08, 38)	14.96 (0.38)	7	7	4	13	7	+	+	–	0.50	0.56	0.54	13.77 (1.34)	14.85 (1.02)	16.12 (1.01)	15.47 0.53	14.46 0.65	
SPTAC	1.89 (0.03, 166)	17.29 (0.11)	8	14	27	72	42	+	+	–	0.64	0.55	0.56	16.99 (0.63)	16.57 (0.43)	17.25 (0.23)	17.30 0.16	17.48 0.18	
SPTAE	1.85 (0.04, 105)	17.92 (0.14)	10	8	18	46	21	+	+	–	0.44	0.52	0.51	17.07 (0.62)	18.27 (0.76)	18.41 (0.32)	17.92 0.20	17.66 0.24	
SPTAW	1.80 (0.02, 385)	16.96 (0.09)	26	60	52	165	72	+	–	**	0.69*	0.53	0.56	16.20 (0.23)	16.45 (0.27)	17.36 (0.25)	17.12 0.12	17.01 0.20	
Stanford	1.69 (0.06, 70)	15.87 (0.22)	12	12	12	23	7	+	+	–	0.50	0.44	0.45	14.57 (0.43)	16.50 (0.53)	15.81 (0.63)	15.95 0.30	16.15 0.69	
All of the above	1.75 (0.01, 1386)	16.71 (0.05)	144	223	194	595	223	+	–	****	0.60***	0.51	0.53	15.88 (0.18)	16.11(0.16)	16.92 (0.14)	16.96 0.07	16.86 0.12	
Minor sites	1.71 (0.04, 164)	16.46 (0.17)	22	26	29	60	23	+	+	–	0.54	0.48	0.49	15.79 (0.56)	16.10 (0.51)	16.63 (0.48)	16.94 0.22	15.87 0.35	
Total	1.75 (0.01, 1550)	16.68 (0.05)	166	250	223	654	248	+	–	****	0.60***	0.51	0.52	15.86 (0.17)	16.11 (0.15)	16.88 (0.14)	16.96 0.07	16.76 (0.12)	

The column "Binomial test" contains the signs of the residual numbers of MM, FM and MM observed by comparison with binomial expectation

*, **, *** Ho rejected at 0.05, 0.01, 0.001, respectively

The final five columns give the mean maternal mass for females bearing pregnancies of different types

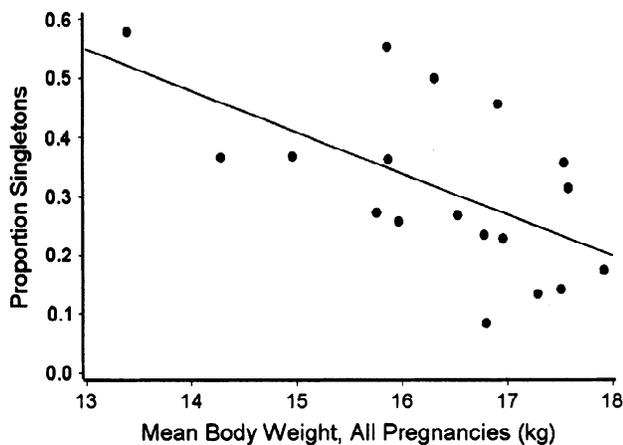


Fig. 1 The effect of body mass on the proportion of pregnant roe deer with single-foetus pregnancies. The least squares regression line is included

the probability of a foetus being male increased with female mass ($\chi^2_{[1]} = 3.1$, $P = 0.074$, parameter estimate = 0.196, SE = 0.07). There was, however, evidence that this effect differed among sites ($\chi^2_{[17]} = 40.6$ for the site \times mass interaction, $P = 0.001$). Sample sizes were inadequate for separate analyses of the data at each site (Table 1). However, we observed that females bearing single male foetuses were heavier than those bearing female foetuses at 13 of the sites, compared with five where the opposite was observed. To test for the possibility that the effect of maternal mass on sex ratio varied with the mean maternal mass at a site, we carried out a further model including a female mass \times mean site mass interaction. This was nonsignificant ($\chi^2_{[1]} = 2.54$, $P = 0.12$).

Among twin pregnancies, there was no evidence for any effect of body mass on the number of male foetuses ($\chi^2_{[1]} = 0.43$, $P = 0.51$). There was no evidence for a site sex ratio effect ($\chi^2_{[17]} = 20.8$, $P = 0.23$), but some evidence that sex ratio varied among years ($\chi^2_{[11]} = 18.5$, $P = 0.07$). There was no evidence that the year effect depended on site (site \times year interaction $\chi^2_{[144]} = 127.5$, $P = 0.84$). As for singletons, there was no evidence that the effect of individual body mass on sex ratio differed depending on mean body mass at the site ($\chi^2_{[1]} = 0.07$, $P = 0.78$).

A further analysis was carried out to test if the likelihood of a pregnancy being balanced (i.e. treating FM as “successes” and both MM and FF as “failures”) could be predicted using body mass. There was no evidence that this likelihood was related to body mass. The proportion of balanced pregnancies did, however, vary with both site and year ($\chi^2_{[17]} = 26.6$, $P = 0.06$ and $\chi^2_{[11]} = 25.8$, $P < 0.01$, respectively). Interaction terms were nonsignificant.

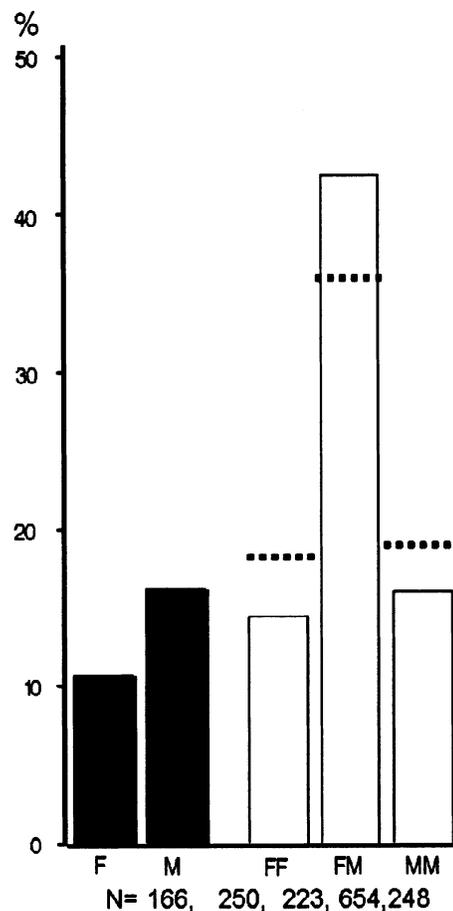


Fig. 2 Distribution of pregnancy types among does (singletons and twins). Dotted lines for twins denote % expected from the binomial distribution. The exact values are: FF, expected 17.4%, observed 14.4%; FM, expected 36.5%, observed 42.4%; MM, expected 18.4%, observed 16.1%. The 22 cases of triplets observed (not shown) were 2 \times FFF, 10 \times MFF, 8 \times MMF, 3 \times FFF

Variance of sex ratio

Among all twin pregnancies, there was strong evidence for deviation from binomiality ($\chi^2_{[1]} = 30.2$, $P < 0.0001$ for the goodness of fit test), with the pattern among standardised residuals showing the balanced pregnancies to be in excess compared with unbalanced (Fig. 2). The corresponding R value is 0.84. Most individual sites also showed this pattern (are below $R = 1$), and while a statistically significant deviation is observed for only six individual sites, the deviations are in the same direction for the majority (Table 1).

There was no evidence that the degree of departure of variance from binomial expectation for a population (indexed by the magnitude of R) was related to the average number of foetuses produced per pregnant female ($r = -0.08$, $P = 0.76$). Nor was it related to site sex ratio ($r = -0.19$, $P = 0.43$). There was evidence that it was

related to average female condition (Fig. 3). Sites with females in good condition deviated to a greater degree (i.e. tended to have relatively more balanced pregnancies than expected; GLM, $F_{(1,16)} = 7.7$, $P = 0.014$; slope = -0.13 , $SD = 0.04$).

The variability in sample size complicates the interpretation of this pattern, as points based on more carcasses will have higher precision, violating the GLM assumption of homogeneity of variance. A solution is to weight observations in the GLM in proportion to the sample size they are based on. For these data, however, the data-rich points near the centre of the range of x dominate those with most leverage on the slope at the extremes of x . Instead, we explored the sensitivity of the unweighted model by randomly selecting a maximum of 20 data points from each site and repeating the GLM. The slope was negative in all of 100 such random samples and, on average, close to that in the unweighted GLM (mean = -0.11 , $SD = 0.03$). Hence, the negative slope in Fig. 3 is robust to concerns about sample size variation.

Seven of the sites contributing to our sample were also studied by Hewison using data collected before that used in this study (Hewison 1993). Hewison did not comment on SBV, and we re-examined his data. There was no overall deviation in Hewison’s sample ($\chi^2_{(1)} = 0.09$, $P = 0.96$). There was, however, evidence for SBV at two of the sites he studied [Bramley ($P = 0.0007$) and Kirkcudbright ($P = 0.015$)]. Furthermore, when we compare changes in weight between the does culled in Hewison’s sample and those in ours, we find they are correlated with changes in SBV, and that the pattern is the same as that in our comparison among sites. Where average condition has been

declining, SBV has also declined (Fig. 4). At the two sites where average condition increased, SBV also increased.

Discussion

We find evidence for control of sex allocation in both twin litters and singletons. In twin pregnancies, there was general tendency for mixed litters (MF) to be in excess compared with random sex allocation. This was more marked in populations where average condition was higher, but was not observed at the individual level. Singleton litters were male-biased and, for most populations, more so when an individual female was in better condition. Change in sex ratio with litter size has not often been observed for large mammals. Servanty et al. (2007) have recently observed male bias in small litters of wild boar (*Sus scrofa scrofa*) and female bias in larger litters. The only ungulate example known to us is the study of Verme (1969) on white-tailed deer.

How do these observations fit in with those of previous studies in roe deer? The absence of an effect of body mass on sex ratio for twin pregnancies, and the weak tendency for male offspring to be more frequent with mothers in better condition for singleton pregnancies (at most sites), contrasts with the studies of Hewison et al. (1999a, b, 2005) and Hewison and Gaillard 1996, who observed more female offspring for heavier mothers. Our observations also differ from those of Wauters et al. (1995), who observed more male offspring for heavier females for both singletons and twins, which is as predicted for “classic” TWH. The pattern of offspring sex ratio with increasing

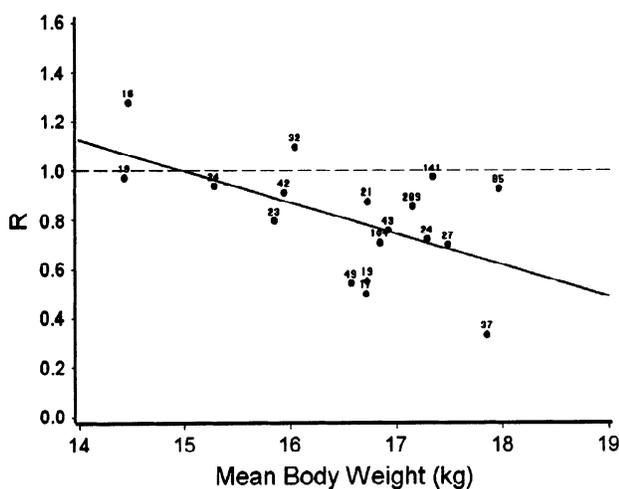


Fig. 3 Deviation from binomial variance expectation in twin pregnancies and mean female body mass across sites ($r = -0.57$, $P = 0.014$). Dotted reference line indicates agreement with binomial variance, $R = 1.0$. Numbers next to points are sample sizes (number of does culled bearing twins at each site)

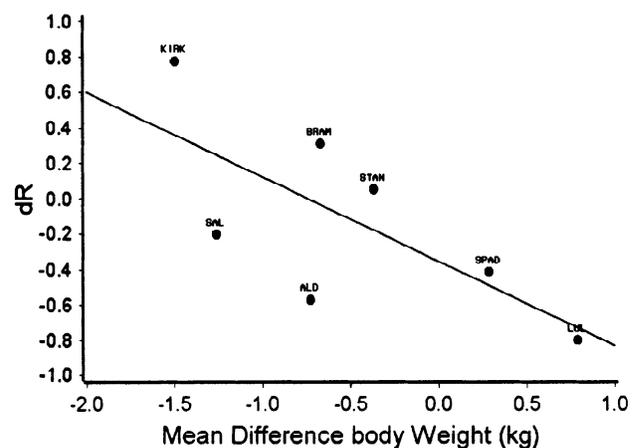


Fig. 4 The relationship between change in R values and change in mean body mass (does pregnant with twins only), comparing culls at the seven sites observed both by Hewison (1993) and in this study (slope -0.48 ; CI -1.16 – 0.10 ; $F_{(1,5)} = 5.14$, $P = 0.072$). Site labels: ALD Aldershot, BRAM Bramley, KIRK Kirkcudbright, LUL Lulworth, SAL Salisbury (combined SPTAC, SPTAE, SPTAW), SPAD Spadeadam, STAN Stanford

maternal mass in our study (Table 1) is clearly not consistent with the F, M, FF, FM, MM expected under TWH (Williams 1979), or with the reversal of that order suggested for this species by Hewison et al. (2005).

The male bias among singleton pregnancies and the absence of this bias in the larger litter size does, however, accord with the idea that, where an individual is too stressed to produce a litter of more than one, a sex bias toward the more valuable sex should result (McGinley 1984). This explanation for the observed bias holds only if males are most often the more valuable sex. The recent genetic work of Vanpé et al. (2008), showing that male breeding success is more variable than female, is consistent with this view. Moreover, the fact that the difference between males and females is relatively small in comparison with other well-studied ungulates might also suggest that we should not expect the effect to be either consistent or strong. Hence, the variation among studies with respect to the TWH is less surprising. As Servanty et al. (2007) point out, the predictions of simple models are much less clear where more than one offspring is produced, as there are potential tradeoffs between size, number and sex of the offspring.

The SBV in twin pregnancies is a previously unconsidered complication, and has not hitherto been commented on for roe deer. Our re-analysis of Hewison's (1993) data does, however, reveal this phenomenon at some of his sites. Further, the French and Swedish populations studied by Hewison et al. (1999a, b) also show a (statistically insignificant) tendency in the same direction. The females pregnant with twins in the sample studied by Borg (1970) conform closely to binomial expectation; as these died largely from starvation, it is unclear how they represent the population, but we would clearly expect such individuals to be inferior competitors.

In our study, differences in SBV were associated with variation in average condition across sites, rather than with individual deer condition as such. We explored whether there was a temporal effect as well by comparing our observations with those of Hewison (1993) where we studied the same sites. We observed a significant decline in female mass (pregnant with twins) at several sites: declines at five out of seven, statistically significantly so at three [Bramley ($t_{75} = 2.6$, $P = 0.01$), Kirkcudbright ($t_{50} = 2.4$, $P = 0.02$), Salisbury ($t_{563} = 5.1$, $P < 0.001$)]. Hewison and Gaillard (1996) observed cohort jaw length decreases—also evidence for increasing density. Reduced mean body size, possibly linked to increased density, appears to be associated with litters showing no excess of mixed pairs (and also with a tendency for singleton births). While the comparison of sites for this effect depends on rather few observations at the extremes of mean condition (Fig. 3), the same effect is observed over time within sites (Fig. 4).

A comparable pattern has been observed in Townsend's voles (Lambin 1994), where SBV was more marked in low-density years. The modelling work of Wild and West (2007) generates the prediction that as density increases, and with it the relative importance of LRC, shifts in sex ratio adjustment should be observed, both among and within populations. While we do not observe a simple sex ratio shift with density, the tendency for SBV to diminish at supposed high density may indicate a similar association with the relative importance of LRC.

Density is known to be influential in red deer; support for the TWH largely disappeared when the population approached carrying capacity (Kruuk et al. 1999). These authors pointed out that no evidence of support for TWH had ever arisen from a study of a high-density ungulate population, and hypothesised that increased mortality at high density obscured the effect. Roe deer are increasing in numbers in the UK (Newson et al. 2006), and density effects are a possible explanation for some of the apparent discrepancies among studies.

We propose that mixed pregnancies may, in some circumstances, be advantageous for roe deer. Under what conditions might a mixed strategy be optimal? Where fat reserves are not carried, as they are not by roe deer, conditions during lactation are unpredictable, as they will be a function of the environment at that time. A tendency for mixed pairs might allow greater flexibility to optimise investment during lactation. The unusual pattern of dispersal in roe deer may be relevant; unlike most ungulates, a high degree of dispersal is observed in both sexes (apparently "voluntary" in females, but provoked by aggression from the territory holder in males (Linnell et al. 1998)). The expected reproductive value of sons and daughters might vary depending on an interaction between resource availability in a season, and the availability of vacant territories for sons. Our observations on the relationship between SBV and average condition lead to the expectation that the mixed strategy is, on average, more advantageous when intra-specific competition is higher. It would be informative to extend the work of Hewison et al. (2005) across a range of contrasting sites to establish whether the tendency for sex allocation is consistently in the direction they observed, or whether there was also a density effect. The likelihood of a mixed pregnancy varied with both site and year in our study, suggesting a link with resource availability.

A mechanism for control of sex allocation has not been established, but the physiology of this species is such that maternal control of offspring sex is a possibility. Roe deer are the only members of the deer family to exhibit a period of embryonic diapause. For approximately 150 days, between fertilisation and implantation, the blastocyst persists at around 100 cells. A hormone produced by the

blastocyst triggers the maternal response (Lambert 2004). The number of corpora lutea is, in most populations, higher than the number of subsequent fetuses (Hewison 1993, p. 51), and implantation failure can be as high as 60% (Hewison and Gaillard 1996). This raises the possibility that individual variation in nutritional stress might affect within-site implantation, and that implantation could be sex-selective (Hewison and Gaillard 2001). Among populations, implantation failure rates vary with climatic severity (Hewison and Gaillard 2001). An effect of male condition on offspring sex cannot be ruled out; Gomendio et al. (2006) have shown experimentally that more fertile red deer males produce more sons.

Environmental factors are known to affect the relative reproductive value of male and female offspring (West and Sheldon 2002). An effect of environmental patchiness, and temporal variation, could affect the relative value of male and female offspring, and could also at least partly explain the discrepancies among studies. Julliard (2000) showed how environmental patchiness could affect optimal sex ratio where dispersal tendency differs between the sexes, and Wild and West (2007) have shown that dispersal and habitat patchiness are crucial parameters in models of sex ratio determination. However, the effect of female condition on sex ratio and its variance in roe deer can probably be most effectively addressed only by experimentally manipulating the condition of wild or captive females. This has proved productive in other mammals (Austad and Sunquist 1986).

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