

REVIEW

Existing theories do not explain sex ratio variation at birth in monomorphic roe deer (*Capreolus capreolus*)

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Abstract

The phenomenon of skewed sex ratios at birth has been reported in many ungulate species. So far, no consistent trend has emerged for roe deer (*Capreolus capreolus*), because male-biased, female-biased and equal sex ratios at birth have all been found. Nevertheless, both the Trivers–Willard hypothesis and the theory of local resource competition have gained support. Despite the great number of studies carried out regarding the ecology of roe deer, too many aspects remain unclear, and contradictory results have been produced with respect to several crucial elements. Without further research, the discussion on which theory applies will therefore remain inconclusive. We put forward the argument that eventually the theories of Trivers–Willard and local resource competition can be considered as being not essentially different. After all, both theories explain the observed skewed sex ratios as being due to the effect of the progeny's sex on the mother's body condition and hence her reproductive success in subsequent years. Furthermore, neither theory is likely to prove to be suitable for roe deer, as several assumptions are unlikely to be met. In roe deer, skewed ratios probably only have a temporal character. As a matter of fact, several observations of skewed sex ratios in birds and mammals did not withstand the accumulation of further data, as sex ratios that were initially believed to be biased turned out to be equal in the long term. This is likely to be the case in roe deer as well. We hypothesize that roe deer, as r-strategists, will produce as many offspring as possible, regardless of sex.

Key words: roe deer, sex ratio theory.

INTRODUCTION

Darwin (1871) discussed the evolution of sex ratios in animals, although he was unable to propose a plausible explanation for his observations. Initially, the sex ratios of most species were believed to be equal. This was first explained by Fisher (1930) as being a consequence of the reproductive advantage of the rarer sex. As Fisher assumed this to be density dependent, sex ratios were expected to

stabilize near equality. However, over the following decades it became clear that for many species the sex ratio often deviates from one (see Frank 1990 and Hardy 1997 2002 for reviews).

Subsequently, several theories arose over the years in an attempt to explain these observed skewed sex ratios: the local mate competition theory (Hamilton 1967), the local resource competition theory (Clark 1978; Silk 1983), the local resource enhancement theory (e.g. Gowaty & Lennartz 1985; Lessels & Avery 1987), the Trivers–Willard theory (Trivers & Willard 1973; Carranza 2001), the advantaged daughters theory (Hiraiwa–Hasegawa 1993), and the first cohort advantage theory (Wright *et al.* 1995). The main question in this matter was: under high densities is it a

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better strategy to produce male or female offspring?

The phenomenon of skewed sex ratios at birth has been reported in many ungulate species (Kojola 1998; Hewison & Gaillard 1999). For some, the observed sex ratio skews could be explained by existing theories, such as the Trivers–Willard hypothesis in the case of red deer (*Cervus elaphus*; Clutton-Brock *et al.* 1986; Kohlmann 1999; Kruuk *et al.* 1999) and mountain goat (*Oreamnos americanus*; Côté & Festa-Bianchet 2001). So far, no consistent trend has emerged for roe deer (*Capreolus capreolus*), because male-biased, female-biased and equal sex ratios at birth have all been found (e.g. Danilkin & Hewison 1996; Hewison *et al.* 1999).

The theories of local mate competition, local resource enhancement, advantaged daughters and first cohort advantage need no further analysis in the case of roe deer, as the ecological characteristics of this species are clearly in contrast with those required to fit these theories. First, roe deer do not mate in discrete and momentary groups (e.g. Bramley 1970; Liberg *et al.* 1998), a condition of the local mate competition hypothesis. Second, being a solitary species (Dziociolowski 1979; Danilkin & Hewison 1996), roe deer are not markedly cooperative, a precondition needed for the theory of local resource enhancement. Third, roe deer do not display pronounced social ranking (Hewison *et al.* 1998), a condition required for the advantaged daughters hypothesis. Fourth, roe deer give birth to only one litter per year (e.g. Linnell *et al.* 1998), so no seasonal cohort effects will be present. The latter is an element of the first cohort advantage hypothesis. On the population level, cohort effects on birth weight and body development rates have been found between years, but no sex differences have been observed (Gaillard *et al.* 1993b; Andersen & Linnell 1997).

Thus, from the above-mentioned theories, only the local resource competition and the Trivers–Willard hypotheses might be applicable to roe deer. The local resource competition hypothesis has gained particular support (Hewison & Gaillard 1996; Hewison *et al.* 1999; Hewison *et al.* 2005), but evidence for the Trivers–Willard hypothesis has been presented also (e.g. Wauters *et al.* 1995). Hewison *et al.* (1999) have attempted to answer the question of which theory applies to roe deer. They concluded that it is unlikely that the Trivers–Willard hypothesis is appropriate for roe deer, and presented evidence in support of local resource competition (see also Hewison *et al.* 2005). However, they state that further studies are necessary to produce a final answer in this case.

Meanwhile, research on the ecology of roe deer has continued. By means of this review of the literature, a new

effort is made to distinguish between valid and invalid assumptions regarding sex ratio theories in the case of roe deer. Sex ratio theories are often applied to species that do not meet the original assumptions of the concerned theories (Frank 1990; Carranza 2001). With regard to roe deer, it seems appropriate to ask the question of whether either of the two theories for which indications have been put forward is supported by the current literature.

First, the general assumption on which all sex ratio theories are based, that females can affect the sex ratio of their offspring, will be discussed with respect to roe deer, followed by the assumptions specific for both the Trivers–Willard and the local resource competition hypotheses.

GENERAL ASSUMPTION: FEMALES AFFECT THE SEX RATIO

Prenatal

For at least three decades, it has been believed that in mammals, females might be able to adjust the sex ratio of their progeny in utero (Trivers & Willard 1973; Silk 1983; Hewison & Gaillard 1996; Johns 2004). It has been suggested that a sex ratio bias could already exist at the time of zygote formation, and would be based on parental hormone levels (Flint *et al.* 1997; James 1998) or glucose levels (Cameron 2004). Otherwise, adjustment of the sex ratio could also take place through selective abortion (Smith *et al.* 1996).

In roe deer, the latter idea seems to fit in with the delayed implantation of the fertilized blastocyst, which is a pronounced feature of the sexual cycle of female roe deer (Aitken 1974; Lengwinat & Meyer 1996). The actual implantation may only occur if conditions remain suitable during the critical season, being mid-winter. This delay may also facilitate sex-selective implantation subject to maternal condition at the time, prior to substantial parental investment (Hewison & Gaillard 1996).

However, convincing evidence for the actual existence of a physiological mechanism for sex ratio adjustment at conception has never been given, either for roe deer or for any other higher vertebrate (Krackow 1995, 2002). In higher vertebrates, sex-selective abortion is rather unlikely as the costs will usually be much higher than the expected benefits. This is particularly significant in roe deer, as fawn mortality is generally high (up to 90%) in both sexes as a result of external influences such as harsh weather conditions (Gaillard *et al.* 1993a) and predation (Aanes & Linnell *et al.* 1995; Andersen 1996; Jarnemo *et al.* 2004). Furthermore, parents are able to adjust their investment levels to their

offspring's sex, thereby minimizing any costs of an inability to control their offspring's sex ratio. Therefore, adjusting the level of investment after conception might be a more flexible strategy, especially when the ability to invest can vary over the maternal investment period (Hewison & Gaillard 1999).

Postnatal

The assumption that it is important to "choose" the sex of offspring might imply that there are metabolic costs involved resulting in differences in pre- and postnatal care. In sexually dimorphic cervid species such as red deer and fallow deer (*Dama dama*), the metabolic costs of rearing males are indeed significantly greater than those of rearing females, due to the demands of gestation and lactation (Clutton-Brock *et al.* 1981; Birgersson *et al.* 1998). Females may only do so when in good condition, to avoid a reduction of their own reproductive performance in subsequent years (Gomendio *et al.* 1990). However, roe deer are among the least dimorphic ungulate species (Niethammer & Krapp 1986; Hewison & Gaillard 1999; Mysterud *et al.* 2002). Moreover, timing and synchronicity of births are identical between the sexes (Gaillard *et al.* 1993c; Linnell & Andersen 1998), early growth rates do not differ according to sex (Gaillard *et al.* 1993b; Andersen & Linnell 1997), and both summer and winter survival rates of fawns are similar for males and females (Gaillard *et al.* 1993a; Wauters *et al.* 1995; Andersen & Linnell 1998). Hence, the direct metabolic costs to female roe deer of rearing either sex are expected to be similar. Nonetheless, no certainty can be given in this respect as several studies did find slightly higher birth weights for male roe deer fawns (Gaillard *et al.* 1996), although the results were non-significant in most studies (Gaillard *et al.* 1993b; Andersen & Linnell 1997). Non-significance might in this case not only involve statistics, but could also mean that if there is a difference at all, it is too small to be important in an ecological sense.

In ungulates, males do not contribute to parental care (Linnell *et al.* 1998). Consequently the number, size and growth of offspring are determined solely by the energy allocated by the mother, that is, the level of maternal care (Andersen *et al.* 2000). Compared with other ungulates, roe deer show high levels of maternal care (Andersen *et al.* 1998). The mean litter mass has been found to be 20% higher than would be expected from the allometric relationship between maternal body mass and litter size (Mauget *et al.* 1997). Increasing deer density has a negative effect on prenatal care only, leading to low weights of individual fawns at birth (Andersen *et al.* 2000). Density has no significant effect on postnatal care, and most females are able

to achieve high postnatal growth rates for their individual fawns (Andersen & Linnell 1997).

Conclusion

Several studies on maternal care in roe deer have produced contradictory results. On the one hand, it has been suggested that maternal investments are male-biased (Wauters *et al.* 1995), which is clearly in line with the Trivers–Willard hypothesis. On the other hand it has been shown that mothers provide similar levels of care to both sons and daughters. Apparently females with additional investment potential do not necessarily invest it in sons and might even invest more in daughters (Hewison *et al.* 1999, 2005). This contradicts the expectations arising from the Trivers–Willard hypothesis.

TRIVERS–WILLARD: THE SPECIES IS POLYGYNOUS

The Trivers–Willard hypothesis assumes a skewed reproductive success for the sexes, which depends on an individual's body condition, which in turn should be based on the amount of natal care by the mother. This seems especially the case in highly polygynous species.

The issue of the roe deer mating system being either polygynous or monogamous is still under debate. In general, roe deer are believed to be monogamous (e.g. Kurt 1968; Cederlund 1983; Bideau *et al.* 1993). Indeed, there is not much evidence to suggest that roe deer are markedly polygynous, since sexual dimorphism during adulthood is minimal (Niethammer & Krapp 1986; Hewison & Gaillard 1999; Mysterud *et al.* 2002). Furthermore, this species exhibits less well-developed sexual weaponry and smaller testes relative to red deer and other polygynous cervids (Hewison & Gaillard 1996). It has been put forward that roe deer become polygynous at high population densities (Cibien *et al.* 1989; Bideau *et al.* 1993; Wahlström & Liberg 1995b).

Liberg *et al.* (1998) postulated that male roe deer are only able to reproduce when they obtain a territory, since practically all matings take place on territories. Nevertheless, not a single study so far has revealed what proportion of all males actually acquires a territory. Liberg *et al.* (1998) found a large variation in mating success among territorial males. Additionally, some males might be more competitive than others, allowing them to obtain more matings than others. As male and female home ranges overlap, a larger male territory may provide more mating opportunities. Remarkably, up to 50% of females make mating excursions to territories other than those of the overlapping males

during the rut, suggesting a preference for specific males (Liberg *et al.* 1998).

Obviously, the degree of polygyny is determined by the number of matings per male. With increasing deer density, the territory size will reduce, but the core area remains of approximately the same size (Vincent *et al.* 1995; Danilkin & Hewison 1996). At high density levels, fewer males are expected to obtain a territory of their own and therefore are unable to take part in reproduction (Liberg *et al.* 1998). Since only young females seem to postpone their reproductive activity under high densities (Gaillard *et al.* 1992), the number of reproducing females will grow faster than the number of territorial, and thus reproducing (Liberg *et al.* 1998), males. Hence, a higher degree of polygyny under high densities seems plausible. In terms of actual matings, there is very little evidence for a high level of polygyny, as only some observations of one male mating with several females have been reported (Strandgaard 1972; Liberg *et al.* 1998).

Another important aspect is uncertain as well, as the number of females that can be fertilized by a single male during one rutting season is unknown. A major determinant in this respect is the variance in the duration of the receptive period (estrus) among female roe deer. Births are highly synchronized (Gaillard *et al.* 1993c; Linnell & Andersen 1998), but due to delayed implantation of the fertilized blastocyst (Aitken 1974; Lengwinat & Meyer 1996), some degree of variance in the timing of estrus is possible. However, the degree of this variance is unknown.

TRIVERS–WILLARD: VARIATION IN LIFETIME REPRODUCTIVE SUCCESS

Dependence on body condition and maternal care

An essential assumption arising from the Trivers–Willard hypothesis is that the lifetime reproductive success (LRS) differs for both sexes and that this difference is influenced by the level of maternal care. This seems not to be the case in roe deer. In general, the level of maternal investment affects the LRS, as body weight at birth influences life-expectancy, and hence the LRS. However, this applies to both sexes (Gaillard *et al.* 1993b; Andersen & Linnell 1997).

The LRS of male roe deer is determined by the number of matings. It is commonly believed that only territorial males mate (Liberg *et al.* 1998), but there is no evidence indicating that the physical condition of a buck determines

the probability of obtaining a territory. The competitive ability of territorial males is supposedly not determined by their body weight, as found in other cervid species like red deer (Clutton-Brock *et al.* 1988), but by other factors such as age-related aggression level (Strandgaard 1972; Hewison *et al.* 1999), which is not determined by the level of maternal care.

Paradoxically, the body weight of females does influence the reproductive output: a body weight threshold for successful reproduction has been found (Loudon 1987; Gaillard *et al.* 1992, Hewison & Gaillard 1996). As a result, not all 1-year-old females take part in reproduction. However, nearly all prime-aged females reproduce (>98%, Gaillard *et al.* 1992; >90%, Danilkin & Hewison 1996), independent of density (Gaillard *et al.* 1992). In senescence, there seems to be a decrease in the proportion taking part in reproduction, but not a decrease in litter size (Gaillard *et al.* 1998). In general, juveniles produce singletons and occasionally twins (Hewison 1996). The average litter size of adults can vary widely from 1.13 to 2.3 embryos per female, but is most commonly around two (Danilkin & Hewison 1996). There also seems to be a weight threshold above which either singletons (below threshold) or twins (above threshold) are born (Gaillard *et al.* 1998; Andersen & Linnell 2000). It is to be expected that maternal care only influences the LRS of females, expressed as the total number of litters. Determining factors are the probability of getting pregnant as a 1-year-old and life expectancy.

IS THERE ANY KNOWN VARIATION IN LRS?

There is a clear lack of data with regard to LRS. Although this feature is indispensable when testing the Trivers–Willard hypothesis, no studies concerning the LRS of roe deer have been published so far.

If roe deer were fully monogamous, the LRS of females would be expected to be slightly higher compared with males, as the female reproductive period is generally longer. Females often start reproduction at an earlier age and males die younger than females (Andersen *et al.* 1998; Liberg *et al.* 1998). The reproductive output per litter would be equal. Multiple matings in a particular season would increase the reproductive success of that year almost exponentially for males, depending on the litter size. One or more years with multiple matings would substantially increase the male's LRS, compared with females. This would also increase the variation in LRS among males. The degree of polygyny is the determining factor, regarding which insufficient data is available.

LOCAL RESOURCE COMPETITION: SEX-BIASED DISPERSAL

The theory of local resource competition assumes dispersal rates to be sex-biased and density-dependent. The dispersal rates of both sexes should be higher at high densities, in order to reduce the local competition for resources.

Sex bias in dispersal rates

Differential dispersal rates between the sexes have often been found in mammals, and are mainly a consequence of the type of mating system. In polygynous and promiscuous species, dispersal rates are expected to be biased towards males, due to competition for mating, whereas dispersal rates will be similar for both sexes in monogamous species (Dobson 1982). Generally, ungulate species are polygynous and display male-biased dispersal, like red deer (Coulson *et al.* 1997).

Contrasting results have been produced when it comes to dispersal rates in roe deer: male-biased dispersal rates have been found (Bideau *et al.* 1993; Vincent *et al.* 1995), but similar dispersal rates for both sexes have also been reported (Wahlström & Liberg 1995a,b; Pettorelli *et al.* 2003). Linnell *et al.* (1998) provided an overview of dispersal distances in roe deer. In most studies referred to, only minor sex differences were found, if any were found at all.

Do dispersal rates increase with density?

Linnell *et al.* (1998) concluded that dispersal of both sexes is high at very low density (which is remarkable for ungulates), high at intermediate density, and low at very high density. The latter phenomenon probably results from the individuals having low body weights, making the extra costs involved in dispersal insurmountable.

These results contradict the relevant assumption arising from the local resource competition theory in two ways. First, the sex bias in dispersal is unclear in roe deer, although evidence has been presented that dispersal rates are similar for both sexes. Second, this theory predicts higher dispersal rates in the case of an increased level of competition, while in roe deer, this appears not to be true when competition on resources is most severe, under high densities.

LOCAL RESOURCE COMPETITION: REDUCTION OF COMPETITION

The local resource competition hypothesis assumes that the competition level will decrease by means of dispersal

of individuals of a certain sex. Dispersal seems to be a relative notion in roe deer population dynamics, since the traveled distances are small in most parts of the roe deer's geographical range. Except for the boreal forest habitats in Scandinavia where distances greater than 10-20 km are usual, average dispersal distances range from approximately 1 to 3 km in both sexes in roe deer (see Linnell *et al.* 1998 for references). This means that although dispersal out of the mother's home range takes place, the dispersing individuals mostly remain within the same population. In a particular population, it has been shown that directional transition took place from poor to rich habitats, but there was no distinction between the sexes (Pettorelli *et al.* 2003). Dispersal is unlikely to be the major process limiting population growth and preventing populations from exceeding carrying capacity, but rather acts as a redistributing force on a local scale only (Wahlström & Liberg 1995b; Danilkin & Hewison 1996).

With regard to the theory of local resource competition, effects of dispersal on the individual level rather than the population level are of importance. Theoretically, when all individuals are evenly distributed over a populated area (in accordance with the theory of ideal free distribution; Wahlström & Kjellander 1995), dispersal by an individual from the natal home range is likely to be balanced by immigration by an individual from a neighbouring home range. In this way, competition will not be reduced for the philopatric individuals. Similar results have been found in other deer species (Clutton-Brock *et al.* 1985). However, increasing competition on resources might result in increased emigration to habitats that used to be less attractive. The overall performance of the population will decrease until an equilibrium has been reached, but on the individual level the emigration will be beneficial. At least temporally the competition on resources will be reduced, which means some subtle support for this assumption from the theory of local resource competition.

However, another mechanism other than dispersal might be more effective in reducing the local competition on resources. After all, lower recruitment rates at high deer densities (e.g. Kurt 1968; Vincent *et al.* 1995) following a decrease in maternal body weight (Loudon 1987; Hewison 1996), together with a smaller proportion of young females breeding at high densities (Gaillard *et al.* 1992), indicate that competition for resources does reduce the growth of social groups. Even though under these circumstances individual fawns might still be able to develop rapidly (Andersen & Linnell 1997), the number of offspring will reduce, as under high densities, and therefore poor body condition can be expected, and young females will pro-

duce smaller litters or even postpone the first reproduction (Andersen *et al.* 1998).

SYNTHESIS

Despite the great number of studies carried out regarding the ecology of roe deer, it is not possible to decide whether the assumptions from the potentially suitable theories of either Trivers–Willard or local resource competition are valid for this species. Too many aspects remain unclear, and contradictory results have been produced regarding several crucial elements. Therefore, without further research, the discussion will remain inconclusive. Unequivocal evidence should be presented with regard to the variance in LRS of both male and female roe deer, the degree of polygyny, and dispersal rates for both sexes.

However, we propose that ultimately the theories of Trivers–Willard and local resource competition can be considered to be not essentially different. In fact, as a supporter of the local resource competition theory, Silk (1983) has already implicitly stated that the two theories do not necessarily exclude each other; she explained that macaques (*Macaca spp.*) “adjust the sex ratio of their progeny in relation to the expected reproductive success of their sons and daughters.” Furthermore, both theories address the effect of the sex ratio on the offspring itself, via the variation in LRS and the level of competition among offspring. However, another perspective is probably more appropriate, as the sex ratio of the progeny will rather be determined by its effect on the *mother's* fitness (see also Cockburn *et al.* 2002). Both theories could explain the observed skewed sex ratios by the effect of the progeny's sex on the mother's body condition and hence her reproductive success in subsequent years.

What is more, neither theory will probably prove to be suitable for roe deer, as several assumptions are unlikely to be met, for example an incontrovertible polygynous mating system and differential maternal investment levels for male and female offspring. Furthermore, a physiological mechanism for sex ratio adjustment may not even exist in higher vertebrates (Krackow 1995, 2002). Since roe deer seem considerably vulnerable to predation (mainly by red fox; see Linnell *et al.* 1995; Jarnemo *et al.* 2004), it is possible to even assume co-evolution between roe deer and its predators, leading to a strategy of high reproduction. In this respect, selective abortion aimed at producing a certain sex seems too costly, and thus unlikely.

Andersen *et al.* (2000) showed that females in above-average body condition do not naturally invest in heavier, “high quality” offspring at all, but rather in a larger number

of offspring. Moreover, considering the roe deer's adaptation to early successional vegetation stages (Linnell *et al.* 1998), and the indication that the two sexes may have similar dispersal rates (Wahlström & Liberg 1995b; Petteorelli *et al.* 2003), it is possible that roe deer may not select for a certain sex at all, but rather for the number of offspring.

Roe deer can be regarded as an r-strategist (cf. Boyce 1984), which means that it is dependent on transitional and early-successional vegetation stages (Danilkin & Hewison 1996). Consequently, the reproductive effort of roe deer is expected to be directed towards populating a suitable area, instead of towards producing a specific sex at a certain quality of the mother. As a result, roe deer are predicted to produce as many offspring as possible, regardless of the sex. This view is supported by Andersen *et al.* (2000), who stated that in a polytocous species like roe deer, high-quality females should produce larger litters than poor quality females in response to the high variability of rearing success (Andersen & Linnell 1997; Gaillard *et al.* 1997). This also implies that it might be advantageous to have high dispersal rates in both sexes, which seems the case in roe deer (Wahlström & Liberg 1995b; Linnell *et al.* 1998).

Successful rearing of offspring will depend mostly on resource availability during lactation, for which females have no information during gestation. Additionally, fawn mortality rates are generally high (Gaillard *et al.* 1993a; Linnell *et al.* 1995; Aanes & Andersen 1996; Jarnemo *et al.* 2004). Roe deer mothers should thus be selected to maximize the number of offspring to produce according to their body weight, which appears to be the case in roe deer (Andersen *et al.* 1998, 2000). As roe deer depend on habitat types that come up irregularly in a temporal and spatial sense, both sexes are predicted to explore their surroundings for newly arisen suitable habitats. Indeed, the two sexes seem to display similar dispersal rates (Wahlström & Liberg 1995b). High dispersal rates of females have also been found in other cervid species that are adapted to exploit early successional stages, for example white-tailed deer (*Odocoileus virginianus*) and elk (*Alces alces*; Linnell *et al.* 1998).

How could the skewed sex ratios observed at birth be explained in roe deer, when the above hypothesis is correct? In this respect it should be noted that this hypothesis does not preclude any biased sex ratio, although such skewed ratios probably only have a temporal character, in line with the ideas of Fisher (1930). As a matter of fact, several skewed sex ratios initially observed in birds and mammals did not withstand the accumulation of further data, as sex ratios that were first believed to be biased later appeared to be equal over the long term (Palmer 2000). This is likely to

be the case in roe deer as well.

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