Offspring sex ratio in domestic goats: Trivers-Willard out of natural selection

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ABSTRACT: The Trivers-Willard hypothesis (TWH) predicts the ability of mothers to adaptively adjust offspring sex ratio through differential maternal investment based on their relative body condition. In the present study we have analyzed an extensive data set on the secondary sex ratio (SSR) including 59 335 goat kids born in 30 633 litters to 11 644 mothers on farms all over the Czech Republic during the years 1992–2004. We found a male-biased SSR 0.568, which significantly deviates from the predicted balanced Fisherian equilibrium 1 : 1 ($P < 0.0001$). A generalized estimating equation model controlled for mother's identity revealed a significant effect of maternal age and season of conception ($P < 0.001$). Conversely, neither paternal age, gestation length, nor litter size were found to explain the sex ratio variation. We also failed to prove any effect of variables associated with maternal condition, particularly her body weight, breed, arbitrary ranking of genetic quality, and hornedness that were available in a data subset. Thus, unlike in some other ungulate species, our findings do not support the TWH in the domestic goat despite the tendency for male-biased litters and we discuss some alternative adaptive and proximate mechanism of the mammalian SSR.

Keywords: maternal age; parental investment; sex allocation; sex ratio manipulation; Trivers-Willard hypothesis; ungulates

INTRODUCTION

Shifts in secondary sex ratio (SSR) and more generally patterns of sex allocation among different animal species/populations represent a classic and already extensively researched phenomenon of behavioural ecology. Since first mentioned by Darwin (1871), investigating variations in SSR and their possible ultimate mechanisms have already received enormous attention across the animal kingdom, mostly in the last three decades (for review see Clutton-Brock and Iason 1986; Sheldon and West 2004). However, despite this enormous effort the outcomes are often inconsistent or even contradictory when conducted on the same species (Festa-Bianchet 1996; Hewison and Gaillard 1999).

Different and mutually competing hypotheses explaining the adaptive value of maternal ability to influence the sex of her newborns have already been proposed (for review see Frank 1990). One of the most popular ones, the Trivers-Willard hypothesis (TWH), presumes that in a population of animals in which one sex benefits considerably more from an extra maternal investment in terms of higher lifetime reproductive success, natural selection should favour maternal ability to adaptively manipulate sex composition of litters based on her current body condition in relation to other females within the population. Since allocation of additional resources in weaning the sex with a higher reproductive potential is costly for mothers, only prime females in the best body condition could afford producing litters biased towards the sex with higher investment demands (Trivers and Willard 1973).

Trivers and Willard (1973) stated three necessary presumptions that must be met when applying the hypothesis in order to explain the patterns of SSR variation. First, maternal and young's body condi-

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tion at the end of parental investment period tends to be correlated, i.e. high quality mothers wean better offspring. Second, differences in offspring body condition at weaning persist into adulthood. Third and finally, adult males and females differ in the extent to which variability in phenotypic quality affects their reproductive success. Thus, slight advantages in body condition of one sex during parental investment period will help its future fitness more compared to the other sex.

It was not by chance that Trivers and Willard (1973) used the caribou (*Rangifer tarandus*) as a model to present their hypothesis. Soon it became obvious that TWH is especially suitable for sexually highly dimorphic, preferably monotocous species (but see Williams 1979 for its adaptation to polytocous animals), with a polygynous mating system where big dominant males in good body condition monopolize access to estrous females and thus outreproduce their sisters (Clutton-Brock et al. 1984). In other words, reproductive success of males with the above stated social organization and consequent life-history traits is much more variable compared to the females' one, thus, only a small proportion of males in the population sires most of the offspring. At the same time, there is a difference between reproductive cost of male and female offspring (Berube et al. 1996) with sons being more demanding of maternal investment (the amount of resources transferred) and therefore, only high-quality females can afford to successfully rear sons to weaning (Cameron et al. 1999; Cote and Festa-Bianchet 2001a).

Hewison and Gaillard (1999) argue that only a few ungulate species satisfy all the three presumptions of the TWH, specifically the red deer (*Cervus elaphus*), bighorn sheep (*Ovis canadensis*), reindeer (*Rangifer tarandus*), and bison (*Bison bison*) which could partly explain great inconsistencies in results of numerous studies. Moreover, as already mentioned by Trivers and Willard (1973), another problem represents the capacity of many species of ungulates for compensatory growth that would violate the second presumption. The ability to accelerate body growth or its externities (particularly horns) after a period of deceleration has been found in the bighorn sheep (Festa-Bianchet et al. 2004).

This study was aimed to investigate SSR variations and test predictions of the TWH in the domestic goat. Should the adaptive maternal control of SSR be present, following outcomes would be expected: (1) SSR variance greater (overdispersion) than would correspond to the binomial distribution based on the random Mendelian X- and Y- sex chromosome segregation (Williams 1979; Wilson and Hardy 2002); (2) negative correlation between litter size and sex ratio either because the benefit of having bigger litters tends to outweigh the adaptive value of SSR manipulation or due to limited parental investment resources in bigger litters (McGinley 1984); (3) significant effect of maternal quality characteristics on the SSR, i.e. male-biased litters in older, more experienced, dominant, heavier mothers and *vice versa*; and finally (4) effect of temporal variables correlated with current maternal body condition (such as gestation length or a season of conception) on the SSR.

The domestic goat's reproductive system and some life-history characteristics make this species a good study model for testing predictions of the TWH. It has been experimentally proven that heavier mothers on average deliver bigger litters of heavier kids (Alley et al. 1995). Although sex specific variations in reproductive success have never been directly tested, it is reasonable to suppose that lifetime reproductive success of a big dominant male in good body condition is much higher than that achievable by any female. In the current husbandry system, high-quality males can sire litters of 25–30 females, thus producing on average 50–60 offspring every breeding season, while those in poorer body condition are usually culled (Fantova 2000). Only the second condition of the TWH remains unclear as we are not aware of any study that would focus on correlations between the youth and adult body size but those have been reported for a close wild relative, the bighorn sheep (Festa-Bianchet et al. 1996). Finally, having lived with humans for the past 10 000 years (Zeder and Hesse 2000), the domestic goat provides a unique opportunity to test validity of the TWH under artificial selection pressures.

MATERIAL AND METHODS

Study model. Despite hundreds of different breeds with various morphological and ecological characteristics, the domestic goat is a polytocous, seasonally breeding ungulate with pronounced sexual size dimorphism (Polak and Frynta 2009) and a promiscuous mating system (Dunbar et al. 1990), while reproduction and mate selection is usually fully under the breeder's control. Females living in the northern hemisphere come synchroni-

cally into oestrus at the beginning of autumn when days get shorter and after five months of gestation goats deliver one to three kids, thus few enough for litter sex ratio to be important for litter cost (Williams 1979).

All our study animals were bred according to the standards of goat husbandry set and monitored by both the State Veterinary Administration and the Union of Sheep and Goat Breeders. Typically, the goats are kept in mixed-sex herds throughout the year apart from the rutting season when males are segregated. The minimum stabling area per animal is 1.5 m² and from April to October herds graze on pasture (J. Poláková, personal communication). Recommended daily feed intake for lactating females is 6–8 kg of hay, grain mixture, beet and/or carrot (Fantova 2000).

Data description. Having access to a large database of the Union of Sheep and Goat Breeders, an institution monitoring both quantitative and qualitative data on individual male and female goats from the majority of farms in the Czech Republic, we could gather records on goat kids born from 1992 to 2004. For each litter that entered our analysis as a separate unit, we had data on the total number of male and female kids (sexed within the first day after birth), exclusive ear tag number of both parents, and date of insemination and parturition. Consequently, based on these information we were able to derive the following principal variables associated with maternal condition and life-history characteristics: (1) maternal age calculated as a number of years since the first reproduction (supposing that primiparous females are typically one-year old; as our data set starts in 1992, the age was not reflected for females reproducing during that year); (2) litter size; (3) length of gestation; (4) season of conception reflecting a female's ability to come into oestrus (categorized as either 1 for goats that could not ovulate in autumn and winter during the main rutting period, thus were inseminated from January to July, and 2 for those that conceived in the principal reproduction season from August to December). All those variables can be reasonably considered as good predictors of relative maternal body condition in ungulates (Sheldon and West 2004). Finally, we included (5) sire's age determined as a number of years since the first reproduction. Initially, our data set also contained information on parity and number of progeny a given female had already delivered/weaned. Since those variables

were too closely correlated with maternal age, which was found to be a better predictor of SSR variation, they have been omitted from further analyses.

Moreover, for a limited subset of litters we had information on other maternal condition traits, such as (6) body weight and (7) hornedness, which are both good determinants of dominance rank (Gorecki 2004); (8) breed (specifically the White Shorthaired, Brown Shorthaired, and Boer goat, while the majority belonged to the former one); (9) breeder's arbitrary ranking of female's genetic quality, and (10) home farm identity. Due to frequently missing values, variables 6–10 were included in a separate analysis to avoid a substantial reduction of the sample size while testing the principle variables effects.

Statistical analysis. Considering the amount of available data collected throughout the 13-year period, we first removed corrupted or inaccurate records. Litters of more than four kids were automatically excluded from subsequent analyses as these are very rare and likely to be erroneous (V. Mátlová, personal communication). We then estimated statistical models in which the litter sex ratio was treated as a dependent variable with a binomial distribution; the logit link function was adopted. As the models require complete sets of explanatory variables, records with missing data were omitted ($n = 7024$).

Subsequently, we tested main effects of the principle explanatory variables (1–5) for all four litter size categories pooled together. In order to avoid pseudo replications resulted from inclusion of multiple litters of the same mother, we adopted a generalized estimating equation (GEE) model incorporating mother's identity. Initially, we also performed generalized linear mixed effects models (GLMM) enabling to control for both parents' identity, but we left this approach as the results were almost identical as those obtained by the simpler GEE procedure.

Next, although the litter size was not a significant factor influencing the SSR, we decided to perform the same analyses separately for each litter size category due to the fact that the sample size has been sufficient. Finally, we incorporated all the remaining explanatory variables (6–10) into main effects GLMs computed for pooled litter size categories data. Full models were then reduced to variables with $P < 0.05$.

All the calculations were performed using the R statistical package geepack (R development core team 2005). In addition, a *G*-test was performed to test deviations of the observed SSR from the expected equality 1 : 1 and we also used a binomial

test to count the 95% confidence intervals (CI) for the SSR value. Mean deviance of the data (residual deviance/residual degrees of freedom) was calculated to check for a dispersion parameter. In the following text, according to Wilson and Hardy (2002) the SSR is expressed as a proportion of males in the litter (SSR = males/litter size).

RESULTS

In total, we gathered records on the sex of 59 335 kids born to 11 644 mothers in 30 633 litters (the average litter size = 1.94). There were 33 685 males and 25 650 females, thus the overall sex ratio was 0.568 (95% CI = 0.564–0.572). This is significantly different from the even sex ratio 0.50 (G = 1091.43, P < 0.0001), although a separate analysis for each of the four litter size categories did not reveal significant deviations from the binomial distribution. Our data did not tend to be over- nor under- dispersed (dispersion parameter τ = 1.358), hence no need for rescaling. We were also able to quantify mean female's reproductive success as 5.10 newborns in 2.63 litters (Table 1).

Marginal GEE models. The initial GEE model revealed that a variable with the most significant effect on the SSR was maternal age ($\chi^2_{(1)}$ = 15.38, P < 0.0001). It was positively correlated with the proportion of sons (Figure 1), but its effect size was rather low (cf. bivariate correlation r = 0.018, P = 0.0003). We also succeeded to prove a statistically significant effect of conception season on the SSR variation as females that came into heat during the main breeding period subsequently delivered litters with a higher proportion of sons than those that conceived during the adjacent
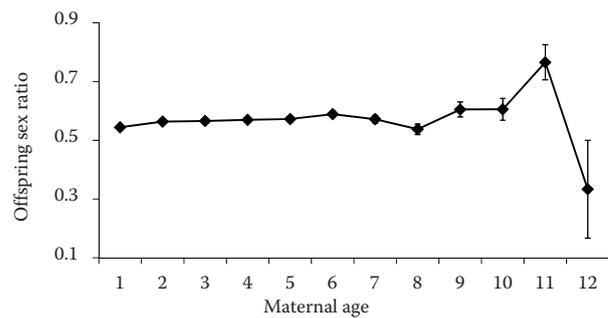

Figure 1. Secondary sex ratio in relation to maternal age in studied herds of domestic goats in years 1992–2004 analyzed by the Generalized estimating equation (GEE) marginal model. Age classes over 11 years old were pooled together due to insufficient sample sizes. Bars indicate standard error of mean

rutting season (0.566 vs. 0.524, $\chi^2_{(1)}$ = 9.92, P = 0.0016) (Figure 2). Conversely, other principle variables from our analysis were found to be below the selected level of statistical significance: paternal age ($\chi^2_{(1)}$ = 2.05, P = 0.1522), gestation length ($\chi^2_{(1)}$ = 0.60, P = 0.4385), or litter size ($\chi^2_{(3)}$ = 4.80, P = 0.1870), even though the latter one inclined to be positively correlated with the SSR (Table 1). After excluding the non-significant variables (with P > 0.05) in order to obtain an adequate minimal model, the effect of maternal age and season of conception remained unchanged (for statistics of the initial model see Table 2).

GEE models for each litter size category. When each litter size category was analyzed separately, we found that maternal age had a significant effect only in litters of 1 or 2 kids (singletons: $\chi^2_{(1)}$ = 9.49, P = 0.0021; twins: $\chi^2_{(1)}$ = 4.12, P = 0.0423) but not in bigger litters (triplets: $\chi^2_{(1)}$ = 3.82, P = 0.0505;

Table 1. Secondary sex ratio in studied goat herds categorized by litter size

Litter size	Litters	Kids	Males	Males/litter	Females	Females/litter	Sex ratio
1	8 515	8 515	4 700	0.552	3 815	0.448	0.552
2	16 174	32 348	18 359	1.135	13 989	0.865	0.568
3	5 304	15 912	9 160	1.727	6 752	1.273	0.576
4	640	2 560	1 466	2.291	1 094	1.709	0.573
All groups	30 633	59 335	33 685	1.426	25 650	1.074	0.568

Litter size	Number of males in a litter				
	0	1	2	3	4
1	3815	4700	–	–	–
2	3046	7897	5231	–	–
3	407	1644	2243	1010	–
4	29	78	285	174	74

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Table 2. Coefficient estimates as predicted by the initial Generalized estimating equation model testing effects of selected variables on the secondary sex ratio in domestic goats

Variable	Estimate	Standard error	Wald statistics	P
Intercept	−0.444	0.540	0.68	0.411
Maternal age	0.014	0.005	7.34	0.007*
Season of conception	0.181	0.061	8.81	0.003*
Paternal age	0.011	0.008	2.20	0.138
Litter size 2	0.042	0.027	2.43	0.119
Litter size 3	0.052	0.032	2.75	0.098
Litter size 4	0.115	0.062	3.44	0.064
Gestation length	0.003	0.004	0.60	0.440

*$P < 0.01$

quadruplets: $\chi^2_{(1)} = 0.22$, $P = 0.6374$). Interestingly, a season of conception was statistically significant only when a single kid was born ($\chi^2_{(1)} = 5.10$, $P = 0.0239$; twins: $\chi^2_{(1)} = 2.67$, $P = 0.1020$; triplets: $\chi^2_{(1)} = 2.61$, $P = 0.1065$; quadruplets: $\chi^2_{(1)} = 0.75$, $P = 0.3853$) which might be explained by selective mortality of male foetuses.

In any size category, we again could not prove significance of either sire's age (singleton: $\chi^2_{(1)} = 0.27$, $P = 0.6067$; twins: $\chi^2_{(1)} = 2.54$, $P = 0.1113$; triplets: $\chi^2_{(1)} = 0.08$, $P = 0.7783$; quadruplets: $\chi^2_{(1)} = 0.04$, $P = 0.8376$) or gestation length (singleton: $\chi^2_{(1)} = 0.84$, $P = 0.3605$; twins: $\chi^2_{(1)} = 0.79$, $P = 0.3755$; triplets: $\chi^2_{(1)} = 0.54$, $P = 0.4627$; quadruplets: $\chi^2_{(1)} = 1.60$, $P = 0.2062$).

GLM for selected maternal condition variables. We also analyzed the main effects of other

maternal body condition related variables that were available in a data subset of 4347 litters comprising 8019 newborns (4657 males and 3321 females). Even though a lot of values were missing and those records had to be omitted, the sample size still remained high (e.g. for body weight it shrank to 900 cases). Surprisingly, we did not find a significant effect of maternal body weight ($\chi^2_{(1)} = 0.09$, $P = 0.7626$), breed ($\chi^2_{(3)} = 5.56$, $P = 0.1351$), or arbitrary ranking of mother's genetic quality assigned by breeders ($\chi^2_{(5)} = 7.90$, $P = 0.1617$). Neither was the SSR affected by the mother's horn status (horned vs hornless) ($\chi^2_{(1)} < 0.01$, $P = 0.9849$). It was only the effect of home farm that nearly reached the selected level of statistical significance ($\chi^2_{(94)} = 113.92$, $P = 0.0794$).

DISCUSSION

Most of the attempts to study patterns in the ungulate SSR and to test putative adaptive value of differential resource allocation to male and female offspring have concentrated on wild living or semi-domestic/feral populations (Sheldon and West 2004). After many years of extensive research, offspring sex ratio has been found to be influenced by a complex interaction of biological, social, and environmental variables (Clutton-Brock and Iason 1986). Hence, it seems appropriate to conduct experiments on species living in their natural environment where different factors involved could be fully expressed.

On the other hand, having lived for the past thousands of years out of natural selection pressures, domestic animals represent an excellent control group for testing universal validity of various evolutionary hypotheses. Clutton-Brock
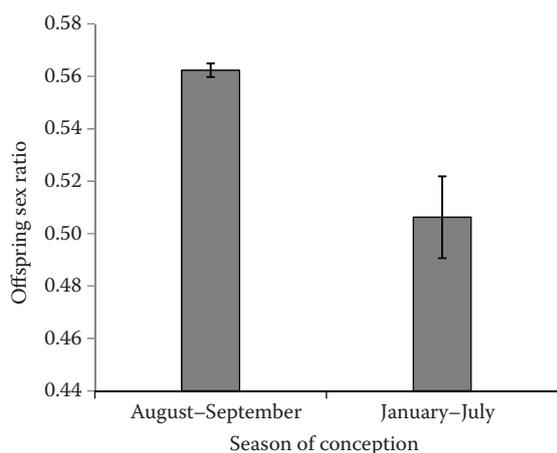

Figure 2. Comparison of secondary sex ratio according to a season of conception. Most of the female goats conceived during the main rut from August to December, while the rest of them delayed reproduction to the adjacent (less advantageous) breeding period from January to July. Bars indicate standard error of mean

and Iason (1986) suggest that being exposed to different selection pressures over many generations could moderate sex ratio variation in domestic species compared to wild mammals due to either an intense long-term artificial selection for fecundity or generally higher nutritional levels the domestic animals are maintained at. In either case, discovering specific mechanisms of sex ratio variation operating among livestock and conditions that could lead to sex-biased litters is not only of scientific interest but also huge economic importance. Males of domestic goats are usually less valued by farmers as only the highest quality bucks are kept for breeding while the rest is slaughtered. Contrary to that, females with reproductive (i.e. milking) potential of several years are much preferred. Hence, it is rather surprising, that despite relatively easy access to large sample sizes and prospective promising results with a great applicability potential, domestic species have been only occasionally used as a model to study offspring sex ratio variation (cattle: Foote 1977; goat: Gorecki and Koscinski 2003, Tolu et al. 2007; pig: Meikle et al. 1993).

We found that domestic goats delivered litters with a significantly higher proportion of males representing nearly 57% of all kids born over the period of 12 years, which is very close to the ratio of male to female kids 54 : 46 reported by Tolu et al. (2007), but precisely the opposite to the results of Gorecki and Koscinski (2003). Thus, considering higher average birth weight of males compared to females (Polak and Frynta, unpublished results), the male-biased sex ratio reported by this study contradicts the Fisher's equal allocation theory (Fisher 1930). Despite its general popularity, further mathematical models of the Fisher's theory revealed that establishing sex ratio equilibrium through individual selection would be overly slow and therefore, other mechanisms might play the role (James 1995).

It is hard to imagine any adaptive explanation for male-biased progeny on a population level within the studied herds. McGinley (1984) proposed an adaptive mechanism in accordance with the TWH hypothesizing that excess of male offspring in smaller litters can be explained by limited reproductive expenditure of nutritionally stressed does. Malnourished females could choose to reduce litter size and invest extra resources into a single offspring (which is in fact just a variation of Williams' (1979) predictions). Interestingly, this trend had been previously found in domestic goats by Sachdeva et al.

(1973). However, due to a contemporary management style of domestic goats focused on high milk yield, nutritional stress seems improbable, thus contradicting McGinley's (1984) assumption. The higher SSR can neither be considered as a result of artificial selection pressures as male kids are usually slaughtered at the age of 3 to 4 months when all maternal resources have already been invested. Actually, the higher proportion of male offspring despite farmers' opposing attempts to produce female-biased litters would suggest that adaptive sex ratio manipulation is difficult.

Thus, one has to look for physiological explanations of the observed SSR deviation from the evolutionary equilibrium. The proximate factors most frequently reported to affect the mammalian SSR are levels of steroid hormones (James 1996) and glucose (Cameron et al. 2008) in circulating blood of the mother at the time of conception. As biochemical clinical values of the examined goats were not available, we may only speculate that the elevated SSR found in our material are consistent with the fact that the studied herds were kept under fairly good nutritional and housing conditions (as supervised by the respective veterinary authorities).

Our study has been based on one of the largest sample sizes among SSR research ever conducted, similar to those investigated in cattle (Foote 1977). In a data set of nearly 60 000 goat kids, statistical support for small effect sizes should be favoured. Surprisingly, further analyses revealed that the SSR fits binomial distribution in any given litter size category. This may suggest that the effect of putative maternal ability to adjust the SSR was only limited or even absent.

There was a significant effect of maternal age on the SSR but the relationship was not straightforward. Based on the TWH we would have expected prime age mothers in the best body condition to produce higher SSR. However, the results show that primiparous females of domestic goats sometimes breeding even before reaching the age of 1 year already produce significantly male-biased litters. The proportion of male newborns then tends to increase only very slightly with age, but it is not the prime age group of three- to six-year-old mothers (Fantova 2000) where the SSR reaches its peak. Surprisingly, we found that litters with the highest SSR were delivered by eleven-year-old females, nearly the oldest age class in our sample. Although the confidence intervals of this peak value

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are wide due to small sample size, a tendency to produce litters with a high proportion of males in the upper age classes is obvious. In a pooled sample of mothers aged 10 years and older the SSR was 0.613 (n = 347 litters, 422 males and 266 females).

There are two possible explanations for such results. First, breeding in polygynous ungulates is very costly and requires a lot of energy in the form of resources invested into reproduction. As quality of parental investment can be improved by experience, one would expect that old, experienced mothers have optimized the use of available resources and thus can afford to produce more males. Or second, it could be suggested that survival to older ages is affected by the breeder's selection keeping the best quality mothers longer while inferior females are selected out as soon as their production drops. Interestingly, there is a slight, although not significant (P = 0.1066), tendency for increasing lifetime SSR according to the female's age at slaughter/death.

Other studies on the domestic goat failed to find any relationship between maternal age and offspring sex ratio (Gorecki and Koscinski 2003; Tolu et al. 2007), although positive correlation has been reported in the mountain goat (Cote and Festa-Bianchet 2001a). Saltz (2001) suggests that maternal age is the most common determinant of SSR that can actually explain seeming extrinsic effects of ecological variables (e.g. environmental and population dynamics fluctuations) when it is accounted for. Variations in the SSR are then merely reflections of demographic (age structure) trajectories. He argues that due to long gestation and weaning in polygynous ungulates, females need a reliable cue on which they could base predictions about their body condition during the most demanding period (which is lactation) and age is probably the best predictor of female's future status (but see Hewison et al. 2002 criticizing this opinion).

The only other independent variable proving to significantly influence offspring sex ratio was a season of conception. Female goats that came into oestrus and conceived during the main rutting period from late summer to the end of autumn delivered considerably higher proportion of sons compared to those that postponed their reproduction to the less favourable season from January to July. Alvarez et al. (2003) suggest that delayed reproduction is a common strategy among low quality, subordinate females. As a capital breeder, inferior females prioritize their own body growth and survival if energy resources are scarce

(Cote and Festa-Bianchet 2001b). Thus, such results may provide some support to the TWH.

CONCLUSION

Our analysis demonstrated that offspring sex ratio in the studied herds of domestic goats is considerably male-biased and only slightly but highly significantly affected by maternal age and season of conception. However, the explanatory power of evolutionary hypotheses of sex ratio variation seems to be in the case of our dataset only low. The results are more consistent with systematic deviation from the balanced sex ratio and with nearly binomial distribution of the sexes within litters. Thus, we share the scepticism of Festa-Bianchet (1996) that putative parental ability to manipulate offspring sex ratio might have been overestimated in literature due to higher publication success of positive results.

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