

Maternal age is not a predominant determinant of progeny sex ratio variation in ungulates

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In a recent paper published in the Forum of Oikos, Saltz (2001) suggests that maternal age is the most common and predominant determinant of progeny sex ratio (PSR) among ungulates. He discusses this interpretation of the published data in the context of two hypotheses for adaptive variation in PSR, the Trivers and Willard model (Trivers and Willard 1973) and the local resource competition hypothesis (Clark 1978). He states that it is his “opinion that in many cases PSR is determined by the age of the mother” and that failure to account for maternal age may explain the notable and quite numerous inconsistencies in patterns of offspring sex ratios between studies of the same species (Festa-Bianchet 1996, Hewison et al. 1999, Saltz 2001). His central premise is that prime-age mothers produce predominantly male offspring while young and old mothers produce an excess of females and that this can be explained by a Trivers and Willard type effect.

Here we argue that this is not so, using three lines of reasoning. First, we show that there is no theoretical basis in the Trivers and Willard model for hypothesising that maternal age is a primary *determinant* (rather than simply a correlate) of PSR variation. Second, we review the literature on PSR of ungulates and show that patterns of age-related sex ratio variation do not agree with the central premise proposed by Saltz (2001) of a bell-shaped relationship between age and PSR. Finally, we question the logic of Saltz’s suggestion that age is a more reliable cue of a mother’s ability to provide care than environmental conditions at conception. We point out that it is not environmental conditions per se which are predicted to influence PSR under the Trivers and Willard model, but rather individual maternal condition *relative* to that of other mothers in the population (Trivers and Willard 1973).

The Trivers and Willard model does not predict a deterministic relationship between progeny sex ratios and maternal age

Trivers and Willard assumed that mothers in good condition produce offspring in good condition while mothers in poor condition produce poor quality offspring, and that differences in offspring condition at the end of the period of maternal care are maintained through to adulthood. Based on these assumptions, they predicted that mothers in good condition relative to other mothers in the population should produce (or invest more in) sons, because the lifetime reproductive success of sons increases with increasing condition much faster than that of females (assuming polygyny and an influence of male condition on the outcome of male-male competition for oestrous females). Conversely mothers in relatively poor condition should produce (or invest more in) females as “an adult female in poor condition who produces a daughter will leave more surviving grandchildren than a similar female who produces a son” (Trivers and Willard 1973). Two considerations are noteworthy with respect to this argument and in the light of the assertions of Saltz (2001).

First, the hypothesis is couched in terms of the individual and not, as Saltz often supposes in his review, the population. The strategy of an individual mother under the Trivers and Willard model can only be predicted when her condition, or more strictly her capacity to provide maternal care, is known *relative* to that of other mothers in the population. Hence, for a given population, there should be an equilibrium point for maternal condition above which mothers produce sons and below which they produce daughters (Clutton-

Brock et al. 1986). Therefore, male-biased sex ratios at the population level, as in the example of the Asiatic wild ass (Saltz 2001, pp. 377–79), cannot be linked to the predictions of the Trivers and Willard model, which makes no predictions about population sex ratio (see Frank 1990 for a more detailed treatment of this problem). Indeed, Saltz later recognises that to understand patterns of sex ratio variation, we need “... in-depth knowledge of individual animal characteristics, population status, and environmental conditions ...” (Saltz 2001, p. 382).

Second, the Trivers and Willard model makes predictions for an individual mother’s investment strategy as a function of her ability to provide maternal care. Trivers and Willard make no explicit mention and formulate no hypotheses concerning the potential *determining* influence of maternal age on the sex ratio of the progeny that she should produce. As such, we see no a priori justification for supposing a deterministic effect of maternal age on progeny sex ratios in ungulates. The assertion that “prime-age female Asiatic wild asses tend to produce male offspring in agreement with TWH (Trivers and Willard hypothesis)” (Saltz 2001, p. 379) is ill founded as maternal age is not a *determinant* of PSR under the Trivers and Willard model (although it may be a correlate) (Trivers and Willard 1973). While several authors have looked for a correlation between maternal age and PSR, they considered age as a proxy for a direct measure of maternal capacity to care (Burke and Birch 1995 “We analyzed the relationship of two indices of maternal condition with offspring sex: maternal age and mandibular fat” or Green and Rothstein 1991 “Measures of long term condition included age, birth date ...”). In some cases investigators used age in the absence of more direct measures of maternal condition (Saltz and Rubenstein 1995, Saltz 1996), assuming that primiparous mothers are in relatively poor body condition, as they have only reached around 80% of asymptotic body size (Georgiadis 1985), while old mothers are also in relatively poor condition due to the effects of senescence (Myserud et al. 2001), possibly as a result of pronounced tooth wear reducing digestion efficiency (Skogland 1988). Hence, a correlation between maternal age and PSR may be hypothesised under the Trivers and Willard model if age is somehow related to maternal body condition, but this does not constitute a direct determining influence of age on PSR.

Maternal age does not determine progeny sex ratios in ungulates

We surveyed the literature on the effects of maternal age on progeny sex ratio in ungulates, including those studies mentioned by Saltz (Saltz 2001, p. 378 Table 1) plus some additional studies that he overlooked (Table

1). We specifically examined the agreement of the literature with the central premise of Saltz (2001), that prime-age mothers produce an excess of male offspring while young and old mothers produce more females. Our literature search shows that there is no support for this premise (Table 1). Of the 28 studies that we found which explicitly tested for an effect of maternal age on progeny sex ratios, only one (Saltz and Rubenstein 1995) provided statistically significant support for such a “bell-shaped” pattern. One other study provided partial support but did not quantify the progeny sex ratio of old mothers (Wauters et al. 1995). We were unable to verify the conclusions of a further 2 studies in Table 1 of Saltz (2001) as we were unable to obtain the source references. Thus, in at least 24/28 (86%) of studies, there was no support for the “bell-shaped” pattern of age-related variation in progeny sex ratio described by Saltz (2001, p. 381).

In fact, there is little support in the literature for the suggestion that maternal age is a primary determinant of offspring sex ratios in ungulates—more than half the studies reviewed (16/28) that explicitly tested for maternal age effects on progeny sex ratio found none (Table 1). When patterns of age-related variation in PSR were detected, they were inconsistent. Among primiparous mothers, three studies described male-biased litters (Rutberg 1986, Owen Smith 1988, Green and Rothstein 1991) while three others noted female-biased litters (Thomas et al. 1989, Saltz and Rubenstein 1995, Wauters et al. 1995). Similarly, for old females, some studies found male-biased (Thomas et al. 1989, Côté and Festa-Bianchet 2001), others female-biased (Green and Rothstein 1991, Saltz and Rubenstein 1995) litters. Some authors described a general increase in PSR in the population with average maternal age (Alados and Escos 1994, Kent 1996), while others described a general decrease (Degayner and Jordan 1987). Interpreting these findings within the context of the Trivers and Willard model seems extremely difficult, almost certainly because age is an imperfect proxy for primary determinants of PSR in ungulates such as maternal condition or social rank. Indeed, as Saltz (2001, p. 379) himself points out, “maternal age is only weakly correlated with the mother’s present condition”.

Maternal condition is a reliable cue for investment capacity in most ungulates

In his recent paper, Saltz (2001) argues that maternal age is a primary determinant of ungulate progeny sex ratios because age is a reliable cue on which mothers can base their reproductive decisions at conception (i.e. sex ratio of the litter). He suggests that, in contrast, environmental conditions at conception do not provide a reliable cue for a mother’s capacity to provide care

Table 1. Relationship between maternal age and progeny sex ratios (PSR) in published studies of ungulate. We looked for support for the central premise of Saltz (2001), that prime-age mothers produce an excess of male offspring while young and old mothers produce more females (note that we include only those papers where the authors have specifically looked for maternal age effects on progeny sex ratios).

Species	Support for Saltz (2001)?	Relationship of maternal age and PSR	Reference	Notes and quotes
<i>Ovis aries</i>	No	Proportion of sons in population increases with average age	Kent 1992, 1995, 1996	Effect of average maternal age on population sex ratio; no test of individual maternal age effects
<i>Sus scrofa</i>	No	None (slope actually negative)	Meikle et al. 1996	“Our results do not support the hypothesis of an age-related increase in the proportion of investment in sons” (p. 976)
<i>Gazella gazella</i>	?	?	Baharav 1989 (in Saltz 2001)	No access to this publication
<i>Gazella cuvieri</i>	No	Mothers producing sons older than those producing daughters	Alados and Escos 1994	Does not indicate that this species fits the bell-shaped pattern described by Saltz (2001)
<i>Ovis canadensis</i>	No	Proportion of daughters increases with ewe age	Bérubé et al. 1996	
<i>Bison bison</i>	No	Primiparous mothers produce male-biased litters	Rutberg 1986	These results are a “... potential discrepancy with the Trivers-Willard prediction ...”
	No	No age-related variation in PSR	Wolff 1988	“The sex ratio of calves born to 3-year old (primiparous) cows ... was not male biased ...”
	No	Last calves of old mothers nearly always female, but mostly males born to 2 yr-old mothers	Green and Rothstein 1991	No consistent support for age-related variation in PSR
<i>Capreolus capreolus</i>	Partial	Adult mothers produced higher proportion of males (55%) than primiparous females (32%)	Wauters et al. 1995	No data on offspring sex ratios for old mothers
<i>Odocoileus virginianus</i>	No	No indication of differences in average age between mothers producing sons or daughters for a given litter size	Burke and Birch 1995	Not a good test of the Saltz bell-shaped model
	No	Percent males decreased with increasing age of the mother	Degayner and Jordan 1987	Relationship weaker when maternal body weight controlled for
<i>Odocoileus hemionus</i>	No	No relationship observed	Kucera 1991	Not a good test of the Saltz bell-shaped model
<i>Dama mesopotamica</i>	No	No significant relationship between PSR and maternal age ($P = 0.580$)	Saltz 1996	“Progeny sex ratio was not related to maternal age”
<i>Dama dama</i>	No	No effect of maternal age on PSR	Birgersson 1998	“... none of the observed birth sex ratios from different categories (ages) of mothers deviated from unity or from each other”
<i>Cervus elaphus</i>	No	No effect of age on PSR	Kohlmann 1999	“I did not detect significant effects of maternal age on fetal sex ratios ...”
	No	Maternal age not related to PSR	Kruuk et al. 1999	
<i>Rangifer tarandus</i>	No	No effect of age on PSR within any category of parity	Kojola and Eloranta 1989	“... effect of age and parity on sex ratio variation were rather inconclusive.” p. 1334
	No	No relation between PSR and maternal age	Reimers and Lenvik 1997	
	No	Young mothers 1.5–4 yrs produced excess of females, but old (> 10 yrs) mothers produced excess of males	Thomas et al. 1989	Age-related patterns of offspring sex ratio not consistent between subspecies (Peary caribou and Barren-ground caribou)
<i>Equus hemionus</i>	Yes	Young and old mothers produced more females, prime-age mothers more males	Saltz and Rubenstein 1995	No measure of maternal condition available
<i>Equus zebra</i>	No	No significant relationship between PSR and maternal age ($P > 0.3$)	Novellie et al. 1996	No relationship at all in a second population
<i>Equus grevyii</i>	?	?	Hayward 1987 (in Saltz 2001)	No access to this publication

Table 1. (Continued).

Species	Support for Saltz (2001)?	Relationship of maternal age and PSR	Reference	Notes and quotes
<i>Equus caballus</i>	No	No difference in PSR between primiparous and multiparous mothers No relationship between PSR and maternal age	Cameron et al. 1999 Monard et al. 1997	"... there was no suggestion that prime age females produced more males than young and old ones."
<i>Ceratotherium simum</i>	No	Young mothers produced an excess of males	Owen Smith 1988	Age correlated with social rank
<i>Oreannos americanus</i>	No	Mothers < 6 yrs produced 70% daughters, old mothers (> 10 yrs) produced 25% daughters	Côté and Festa-Bianchet 2001	"No clear relation was found between maternal age and the likelihood of different types (litter size and sex ratio) of birth."
<i>Ammotragus lervia</i>	No	No relation of maternal age and PSR	Cassinello and Gomendio 1996	"... the sex ratio did not depend on female age ..."
<i>Alces alcesers</i>	No	No relation of maternal age with PSR	Nygrén and Kojola 1997	

during peak reproductive effort, that is late gestation and early to mid-lactation (Oftedal 1985), and so do not provide information on which sex of offspring to conceive (Saltz 2001). As described above, however, the Trivers and Willard model predicts what sex of offspring individual mothers should conceive as a function of their capacity to provide care *relative* to other mothers in the population (Trivers and Willard 1973). Hence, for maternal condition at conception to be a reliable cue for ability to provide maternal care during late gestation and lactation, mothers in good condition at rut *relative to other mothers in the population* must remain in good condition *relative to other mothers* during peak maternal investment. That is, although mothers in seasonal environments lose some body condition during seasons when resources are scarce, good condition mothers at conception should not become poor condition mothers by parturition, and poor condition mothers should not become good condition mothers – *relative* phenotypic quality of individuals should remain more or less constant. For most ungulates, this assumption is met as most are considered capital breeders (sensu Jönsson 1997) where mothers rely on body reserves accumulated during periods of resource abundance to offset the costs of reproduction. Thus, the level of body reserves at conception should be a reliable cue of future condition and, hence, of ability to provide maternal care at and around birth. That progeny sex ratio has been reported to be related to previous reproductive success (Bérubé et al. 1996 on bighorn sheep, Rutberg 1986 on bison, Owen Smith 1988 on white rhino) while reproductive effort is known to influence maternal condition at conception in several species (Festa-Bianchet et al. 1998 on bighorn, Clutton-Brock et al. 1983 on red deer, Cameron et al. 1993 on caribou) supports the premise that female ungulates of capital breeder species may use body reserves at conception as a cue for future condition.

Absolute environmental conditions may have an influence on whether those mothers in relatively good condition reach a threshold level where they have sufficient "extra" investment capacity available to produce high quality offspring of the sex with more variable reproductive success (generally males for polygynous ungulates) (Byers and Moodie 1990, Pélabon et al. 1995). For example, dominant red deer mothers on the Isle of Rum were reported to produce more sons and subordinate mothers to produce more daughters (Clutton-Brock et al. 1986). Subsequent analysis revealed that this relationship holds during periods of favorable environmental conditions (low population density, low winter rainfall) only. During years of nutritional stress this pattern disappears, possibly due to sex-bias in fetal mortality (Kruuk et al. 1999). The authors concluded that adaptive bias in conception sex ratios related to variation in individual phenotypic quality may only occur under favorable environmental conditions. Thus,

environmental conditions do not constitute the actual mechanism determining ungulate progeny sex ratios, rather "... the action of these (sex ratio determining) mechanisms depends on environmental conditions." (Kruuk et al. 1999).

Conclusion

From both a theoretical and an empirical point of view, there is no support for the suggestion that maternal age is a primary determinant of offspring sex ratio in ungulates. Age may be in some cases a correlate of progeny sex ratio (although there are only a few documented cases where this is so, see Table 1), but only as a proxy for other maternal characteristics which do determine PSR, whether this be body condition and/or social rank. Finally, a Trivers-Willard type effect is only expected to occur when the three underlying assumptions of the model are fulfilled (Trivers and Willard 1973). Empirical evidence from ungulates shows that in several species at least one of these assumptions does not hold (Hewison and Gaillard 1999). Thus, the use of this model to test for patterns of adaptive variation in progeny sex ratios should probably be limited to those species of ungulates which are markedly polygynous.

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