

## Timing of foetal growth spurts can explain sex ratio variation in polygynous mammals

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### Abstract

The prediction from sex ratio theory that natural selection on sexually dimorphic mammals should favour an excess of male offspring only when mothers are in good condition, has been tested extensively but with little consistency in results. Although recent studies have shown that environmental variations may cause some of the discrepancy, there have also been reports of contrasting sex ratios under similar environmental settings. Here it is suggested that variation in timing of environmental stress and sex-specific differences in foetal growth pattern in relation to maternal condition, may explain such seeming contradictions in sex ratio variation of polygynous mammals.

### Keywords

Environmental stress, maternal condition, polygynous mammals, sex-specific foetal growth rates, sex ratio variation

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In sexually dimorphic, polygynous mammals, sons are more costly to produce than daughters (Clutton-Brock *et al.* 1981), sons have more variable reproductive success than females and will experience higher lifetime reproductive success if born to mothers in better than average condition (Clutton-Brock *et al.* 1984). Consequently, sex ratio theory predicts that natural selection in such species should favour an excess of male offspring only when mothers are in good condition (Trivers & Willard 1973). Despite extensive empirical testing of this theory, results are still ambiguous (Clutton-Brock & Iason 1986; Hewison & Gaillard 1999). Recently, however, two papers (Kruuk *et al.* 1999; Post *et al.* 1999) have shed light on why this could be so. Both studies demonstrated that changes in winter density and climate in two red deer (*Cervus elaphus*) populations had confounding effects for the predicted relationship between maternal condition and offspring sex. Nevertheless, although both populations were exposed to similar environmental changes and both studies inferred foetal mortality as a mechanism, the reported changes in sex ratios were in opposite directions. Here I suggest that such conflicting results may be explained by considering interactions between the timing of sex-specific foetal growth spurts and environmental stress on maternal condition.

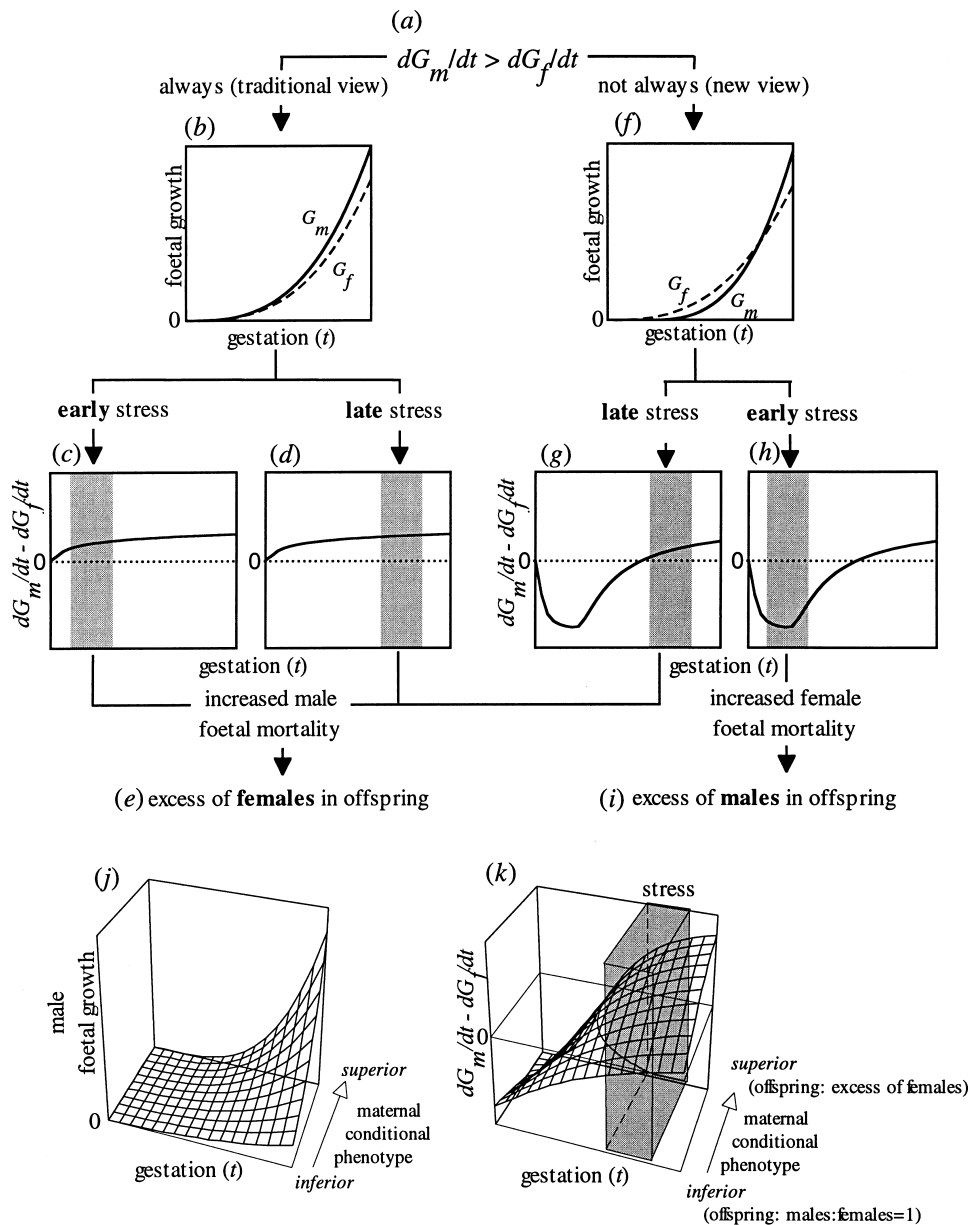
At any time  $t$  during gestation, the nonlinear growth of a foetus can be described by the general relationship:

$$G_s(t) = a_s(t - i_s)^{b_s} \quad (1)$$

where  $s$  specifies sex (m, male; f, female) and  $a_s$ ,  $b_s$  and  $i_s$  are sex- and species-specific constants (Robbins & Robbins 1979; Ricklefs 1987). By differentiating  $G_s(t)$ , we can evaluate the relative changes in foetal growth rates of males ( $dG_m/dt$ ) and females ( $dG_f/dt$ ) (Fig. 1a) throughout the gestation period.

The timing of environmental stress is known to vary over the gestation period and can exert its main impact either during early or later in gestation (Clutton-Brock & Iason 1986). For example, increased thermoregulatory and locomotory costs to pregnant females as a result of cold and snowy weather may severely affect their allocation of energy and nutrients to the foetus (Hobbs 1989). Furthermore, empirical, indirect evidence suggests that the sex growing fastest *in utero* will be the one most susceptible to foetal mortality when maternal condition is compromised (Robinette *et al.* 1957; Clutton-Brock *et al.* 1984). In sexually dimorphic, polygynous mammals, it is commonly assumed that this sex is the male sex because males are born heavier than females (Clutton-Brock & Iason 1986). Hence, under this traditional scenario (Fig. 1b), environmental stress exerted on maternal condition early (Fig. 1c) and/or later (Fig. 1d) in gestation will both result in an excess of female offspring (Fig. 1e).

Recently, however, it has been shown that red deer female foetuses grow faster than males in early gestation and males faster than females later in gestation (Post *et al.* 1999) (Fig. 1f). Here, environmental stress on maternal condition later in gestation (Fig. 1g) would, as in the



**Figure 1** Variation in sex ratios in relation to timing of sex-specific foetal growth spurts (males,  $G_m$ ; females,  $G_f$ ) and environmental stress (shaded bars). (a) The difference in foetal growth rates of males ( $dG_m/dt$ ) and females ( $dG_f/dt$ ) determines which sex suffers the highest foetal mortality when mothers condition is compromised. This assumption relies on indirect evidence, that is, the observation that a significant decrease of the fastest growing sex in respect to the other at birth imply differential prenatal mortality (Robinette *et al.* 1957). Foetal growth rates of males are higher than those of females when  $dG_m/dt - dG_f/dt > 0$ . (b–e) The traditional view is that the foetal growth rate of males is always greater than that of females (b) resulting in mothers producing, no matter the timing of environmental stress on maternal condition (c, d), an excess of female offspring (e). (f–i) The new view based on the hypothesis that  $dG_m/dt$  is not always larger than  $dG_f/dt$  as documented in red deer (Post *et al.* 1999) (f). Mothers compromised by environmental stress late in gestation (g) produce an excess of female offspring (e), but when compromised during early gestation (h) they produce an excess of male offspring (i). (j–k) Mothers vary in their ability to produce heavy sons (j), thereby creating differences in sex-specific growth rates across maternal condition phenotypes, where, for example, superior mothers may produce an excess of female offspring and inferior mothers an offspring sex ratio close to parity when stress occurs later in gestation (k). Model parameters (see equation 1) used in (b–d):  $a_m = a_f = 0.23$ ,  $b_m = 3$ ,  $b_f = 2.9$ ,  $i_m = i_f = 0$ ; (f–h)  $a_m = 0.23$ ,  $a_f = 0.20$ ,  $b_m = 3$ ,  $b_f = 2.75$ ,  $i_m = 13$ ,  $i_f = 0$ ; (j–k)  $a_m = 0.23$  for all males,  $b_m = [4; 4.8]$ , step = 0.08,  $i_m = [18; 28]$  step 1;  $dG_m/dt$  was calculated in relation to  $dG_f/dt$  with  $a_f = 0.23$ ,  $b_f = 2.9$ ,  $i_f = 0$ . These parameters lie within the range of previously reported values for mammals:  $a$ , 0.10–0.23;  $b$ , 2–5;  $i$ , 0–25 (Robbins & Robbins 1979; Post *et al.* 1999; V. Dantzer, personal communication).

traditional scenario, result in an excess of female offspring (Fig. 1e). In contrast, environmental stress during early gestation (Fig. 1h) would, due to relatively higher female foetal growth rate and, hence, higher mortality of female foetuses, result in an excess of male offspring (Fig. 1i). Thus, it follows that the interaction between environmental stress, maternal condition and foetal growth may result in opposite offspring sex ratio within a single species just by differential timing between populations.

The above mentioned argument can be developed considering variations in maternal condition among females of a single population. It is known that females in superior condition produce bigger sons than females in poor condition (Clutton-Brock *et al.* 1984). Then, with little variation in individual gestation lengths, heavier sons born to superior mothers would display faster foetal growth rates than lighter sons born to inferior mothers (Birgersson & Ekvall 1997), resulting in an across-individual variation in  $G_m$  (Fig. 1j). Since mothers, despite condition, invest more in sons than in daughters and lifetime reproductive success of daughters do not vary significantly across maternal condition phenotypes (Clutton-Brock *et al.* 1981, 1984), it may be reasonable to assume that  $G_f$  (and hence  $dG_f/dt$ ) is similar across mothers. Hence, the above-suggested individual variations in  $G_m$  could then produce marked variations in  $dG_m/dt - dG_f/dt$  and, consequently, birth sex ratios across mothers. For example, environmental stress concentrated later in the gestation period would result in superior females producing an excess of daughters but inferior females sex ratios close to parity, because in this period of gestation  $dG_m/dt > dG_f/dt$  for superior mothers but is equal for inferior mothers (Fig. 1k). Such a conditional variation in response to changes in environmental stress has been reported in a Scottish red deer population (Kruuk *et al.* 1999).

Skews in birth sex ratios may also be obtained without individual differences in male foetal growth patterns as outlined above, because mothers in good condition are less susceptible to stress than mothers in poor condition (Birgersson & Ekvall 1997). If, for example, female foetuses grow faster in early gestation and environmental stress occurs in this period (Fig. 1h), mothers in poor condition would produce more males than mothers in good condition, because female foetal mortality would be relatively higher in low-quality mothers. This is, indeed, what has been observed in roe deer (*Capreolus capreolus*) (Hewison & Gaillard 1996). A recent experimental study on a sexually dimorphic bird species further corroborates this relationship: a progressive decline in female condition resulted in progressively skewed offspring sex ratios (Nager *et al.* 1999).

Based on the observation that increased environmental stress through increased density during pregnancy leads to

increased number of stillbirths (Andersen & Linnell 1998), I have implicitly assumed that environmental stress on maternal condition leads to increased foetal mortality of the fastest growing sex throughout the gestation period. However, as previously reported for some cervids, heavy foetal mortality may occur mainly in the first two trimesters of gestation (Robinette *et al.* 1957), implying that compromised maternal condition through environmental stress during the end of gestation would lead to lower birth weight rather than increased foetal mortality. If so, then changes in  $dG_m/dt - dG_f/dt$  combined with environmental stress during the end of gestation could affect variations in sexual dimorphism rather than birth sex ratio per se. However, the novel view on foetal growth and environmental stress presented here (Fig. 1f–i) may, if widespread, add significantly to our understanding of the observed sex ratio variation in polygynous mammals, because environmental density-dependent and density-independent factors are known to vary between populations as well as between species (Sæther 1997). Furthermore, although explaining some of the inconsistencies in birth sex ratio observed across mammals, the nonadaptive mechanism presented here does not exclude adaptive mechanisms such as the developmental asynchrony hypothesis (Krackow 1995). Individual adaptive differences in sex ratios, as shown experimentally in sexually dimorphic birds (Nager *et al.* 1999), may be more important during favourable environmental conditions, whereas severe adverse environmental conditions may, through energetic and nutritional stress, cause across-individual variation in birth sex ratios beyond maternal control (Kruuk *et al.* 1999). Indeed, the developmental asynchrony hypothesis may also be viewed as a nonadaptive by-product of constrained selection (Krackow 1995).

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#### BIOSKETCH

Mads C. Forchhammer is engaged in research related to evolutionary ecology and population ecology. Recently, he has worked with life history strategies and analytic population dynamics of large mammals related to density-dependent as well as climatic processes.

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