

# Population density affects sex ratio variation in red deer

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Many mammal populations show significant deviations from an equal sex ratio at birth, but these effects are notoriously inconsistent<sup>1</sup>. This may be because more than one mechanism affects the sex ratio and the action of these mechanisms depends on environmental conditions. Here we show that the adaptive relationship between maternal dominance and offspring sex ratio previously demonstrated in red deer (*Cervus elaphus*)<sup>2,3</sup>, where dominant females produced more males, disappeared at high population density. The proportion of males born each year declined with increasing population density and with winter rainfall, both of which are environmental variables associated with nutritional stress during pregnancy. These changes in the sex ratio corresponded to reductions in fecundity, suggesting that they were caused by differential fetal loss. In contrast, the earlier association with maternal dominance is presumed to have been generated pre-implantation. The effects of one source of variation superseded the other within about two generations. Comparison with other ungulate studies indicates that positive associations between maternal quality and the proportion of male offspring born have only been documented in populations below carrying capacity.

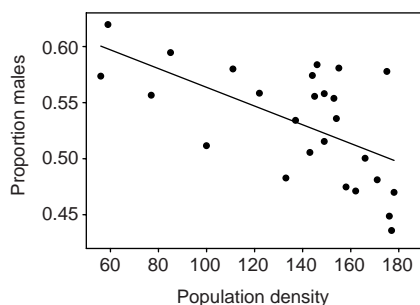
It has been argued that, if maternal condition affects the breeding success of male offspring more than that of female offspring, mothers in superior condition should produce more males, whereas those in poorer condition should produce more females<sup>4</sup>. Despite the intuitive appeal of this argument, few studies have provided unequivocal proof of such manipulation, and sex ratio trends in mammalian populations are disconcertingly variable<sup>1,5</sup>. For example, in ungulate populations, some studies have shown that females in good condition produce significantly greater proportions of sons<sup>6–11</sup>, whereas others found either no association between condition and offspring sex ratio<sup>12–14</sup> or a negative association<sup>15,16</sup>. One plausible explanation for the variation is that the mechanisms generating sex ratio variation are affected by environmental conditions.

Previous studies of the unmanaged red deer population on the Isle of Rum, Scotland, showed that dominant females were

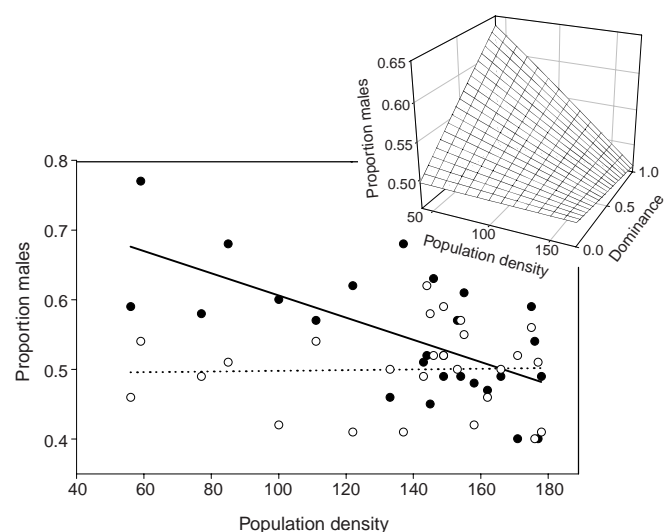
consistently more likely than subordinates to produce sons<sup>2,3</sup>. As maternal dominance affected the breeding success of male offspring more than that of females, this variation in offspring sex ratio was likely to increase a female's expected number of grandchildren<sup>4</sup>. However, rising population density in the study area has resulted in a significant decline in the proportion of males born each year (hereafter, the annual birth sex ratio)<sup>17</sup>, which has fallen by approximately 10% since the cessation of culling in 1973 (Fig. 1). This overall decline reflects a decline in the proportion of males born to dominant females (Fig. 2). Fitting individual calf sex as the response variable in a generalized linear mixed model (GLMM; see Methods) showed that there was a significant interaction between population density at the time, and maternal dominance rank: offspring sex ratio was associated with dominance at low but not at high density (Table 1; Fig. 2, inset). Furthermore, a positive association between a female's condition, assessed by kidney fat weight, and the probability of her carrying a male calf has been shown in adjoining areas of the same island, where culling has maintained density at levels equivalent to that at the start of this study<sup>11</sup>. Thus, the changes in our study population were not associated with a larger-scale temporal trend.

The sex ratio at birth was also correlated with the amount of rainfall between November and January (approximately the second to fourth months of gestation). On average, an extra 100 mm of winter rainfall reduced the annual birth sex ratio in the following spring by 1.3% (Fig. 3). In the GLMM of calf sex, winter rainfall was the only weather variable to have any significant explanatory power (Table 1; see Methods for details of other weather variables considered). If the GLMM was repeated separately for mothers suckling a calf from the previous year (and thus known to be in poorer condition<sup>18</sup>) and for those without a calf, winter rainfall was only significant in the former ( $\chi^2_{(1)} = 7.5, P = 0.006$ ) and not in the latter ( $\chi^2_{(1)} = 0.50, P = 0.480$ ).

As conception occurs in October, the correlation between November–January rainfall and annual birth sex ratio was presumably generated by post-implantation fetal mortality, occurring no earlier than the second month of gestation. This was confirmed by an analysis of female fecundity: the probability that a female calved in a given spring decreased with rainfall in the preceding



**Figure 1** Proportion of males born each year in relation to population density, after correcting for effect of winter rainfall. Regression coefficient:  $-0.080 (\pm 0.026 \text{ s.e.})$ ,  $t = -3.12$ , d.f. = 23,  $P = 0.005$ ;  $r = -0.552$ .



**Figure 2** Proportion of males born to dominant versus subordinate females in each year. Dominant females (filled circles and full line) are those with above-median dominance scores; subordinates (open circles and dotted line) are those with below-median scores. For each year, the average of the two values does not necessarily correspond to the population mean in Fig. 1, as dominance rank was not known for all females. Inset: Relation between sex ratio, dominance rank and population density as predicted by the generalized linear mixed model.

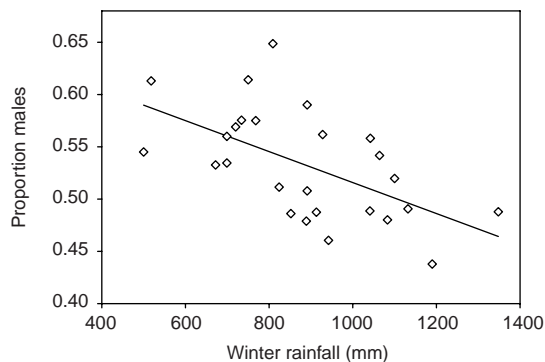
**Table 1 Generalized linear mixed model of calf sex**

Term	Wald statistic ( $\chi^2$ )	d.f.	P-value
Mother's age and age <sup>2</sup>	0.1	2	0.95
Previous calf	0.3	2	0.86
Mother's dominance	0.1	1	0.75
Winter rainfall	5.5	1	0.019
Population density	3.4	1	0.065
Dominance-density	4.5	1	0.034
Minimal model	Average effect	s.e.	
Mother's dominance	0.051	0.17	
Winter rainfall	-0.00061	0.00026	
Population density	-0.0026	0.0017	
Dominance-density	-0.012	0.0057	

GLMM of calf sex gives the probability that a calf is male;  $n = 1,587$ . Population density and winter rainfall are for the winter preceding a calf's birth. Wald statistics are from the full model when each term was fitted last in the model; average effects are from the minimal model comprising only the significant terms. Interactions are denoted by a dot between terms. d.f., Degrees of freedom; s.e., standard error.

winter (Table 2). Female fecundity also decreased with rising population density. Although it is impossible to separate the pre- and post-conception effects of population density, we suggest that the nutritional stress of high density, mediated through competitive interactions, is more likely to affect fetal mortality during the winter than female conception rates in the autumn, and thus that the effects of density were also generated by differential fetal mortality. Fecundity increased significantly with dominance ranking ( $P = 0.046$ ) (see also ref. 19). However, unlike the association between dominance and offspring sex ratio, this relationship was not affected by density (Table 2): dominant females were consistently more likely to calve in a given year than subordinates, but at low densities the sex ratio of their offspring differed. This supports previous suggestions that any relationship between dominance and offspring sex ratio was not generated by differential fetal mortality, but instead involved mechanisms acting before implantation: corpus luteum function is affected by social status in red deer<sup>20</sup>, and the observed difference in fecundity would have to more than double to account for the difference in sex ratios between dominants and subordinates<sup>2</sup>.

It is unclear whether the decline in sex ratio under poor winter conditions represents an adaptive maternal strategy. Both high population density and high November–January rainfall increase juvenile mortality in the population during the winter<sup>21,22</sup>, an indication that they are associated with nutritional stress. However, juvenile winter mortality occurs mainly in March and April<sup>18</sup>, indicating that the effects of the stress are not realized until slightly later, at a time corresponding to the later stages of gestation. It is



**Figure 3** Proportion of males born each year in relation to winter rainfall (November to January, in mm), after correcting for the effect of density. Regression coefficient:  $-0.0128$  ( $\pm 0.046$  s.e.),  $t = -3.03$ , d.f. = 23,  $P = 0.006$ ;  $r = -0.543$ .

**Table 2 Generalized linear mixed model of female fecundity**

Term	Wald statistic ( $\chi^2$ )	d.f.	P-value
Mother's age <sup>2</sup>	5.7	2	0.058
Previous calf	221.2	1	<0.001
Mother's dominance	4.0	1	0.046
Winter rainfall	13.2	1	<0.001
Population density	12.5	1	<0.001
Dominance-density	0.2	1	0.66
Previous calf-density	9.3	1	0.002
Previous calf-rainfall	7.4	1	0.007
Density-rainfall	4.6	1	0.032
Minimal model	Average effect	s.e.	
Previous calf	-2.43	0.16	
Mother's dominance	0.38	0.19	
Winter rainfall	-0.0011	0.001	
Density	-0.00031	0.0058	
Previous calf-rainfall	-0.0015	0.00062	
Previous calf-density	-0.015	0.0059	
Density-rainfall	-0.000040	0.000019	

GLMM of female fecundity gives the probability that a female gives birth in a given year;  $n = 2,269$ . See legend to Table 1 for details.

plausible that the resorption of male fetuses by mothers that are unable to invest enough resources to provide them with a reasonable chance of breeding successfully is selectively advantageous<sup>4</sup>. However, an alternative explanation is that the high mortality of male fetuses is a by-product of faster male growth rates, which have evolved under sexual selection: in dimorphic species, males require more food and so will be more adversely affected by food restrictions<sup>23</sup>. At least two lines of evidence support the latter suggestion for this population. Overall mortality rates are higher for juvenile males than females, and this differential in juvenile mortality increases with both population density<sup>23</sup> and winter rainfall<sup>22</sup>. It seems reasonable to suppose that male fetuses, like male calves, may be similarly more vulnerable than females.

As yet, no other study of wild mammals has allowed a comparison of both fecundity and offspring sex ratio between individuals under different environmental conditions. However, comparison with other ungulate studies indicates that there may be a link between resource availability and the tendency for females in good condition to produce male-biased sex ratios. In eight other ungulate studies, females in good condition produced a significantly higher proportion of male offspring than females in poorer condition in the same population. Of these populations, three were captive (pigs<sup>7</sup>, arrui<sup>6</sup>, sheep<sup>24</sup>); two were semi-domesticated (reindeer<sup>8</sup>, bison<sup>9</sup>); one was in a game-management area (roe deer<sup>10</sup>); one was subject to exceptionally high predation rates (pronghorns, with almost 90% mortality in fawns<sup>25</sup>); and the eighth involved red deer on Rum in the parts of the island where culling has been maintained<sup>11</sup>. In all cases, population density was presumably below carrying capacity, or not limited by resource availability: this may be a necessary criterion for such associations to be detectable. It is, however, far from sufficient: studies that have found no association or an association in the opposite direction include a wide range of conditions from captivity<sup>12,14</sup> and heavy culling<sup>13</sup> to minimal culling<sup>26</sup>, trophy hunting<sup>16</sup> and a wild population<sup>27</sup>.

The effect of population density on the sex ratio has implications for the management of red deer populations. Variation of up to 10% may seriously violate assumptions of equal birth rates employed in population dynamics models, and is likely to affect optimal harvesting rates and the growth rates of small populations. The result also highlights the need for adequate density control on sporting estates where red deer populations are managed to maximize the production of males.

The existence of more than one mechanism affecting birth sex ratios in a single population, and the dependence of these mechanisms on environmental conditions, could explain the inconsistency in sex-ratio deviations across mammalian populations. Adaptive

differences in the conception sex ratio related to individual phenotypic variation may require favourable environmental conditions, whereas differences in the susceptibility of male and female fetuses to nutritional stress may generate population-wide trends in annual birth sex ratios. In the Rum red deer population, the action of one mechanism swamped the other within about two generations. This may explain why general trends in sex-ratio variation have been so difficult to detect. □

**Methods**

Since 1971, life history data have been collected on individual red deer (*Cervus elaphus*) in the North Block of the Isle of Rum, Scotland, an area of about 12 km<sup>2</sup> (ref. 18). We take as our measure of density the number of females of more than one year old in the study area; since the cessation of culling in 1973, density has risen from 57 to 178. Females produce at most one calf per year throughout their breeding lifespan, whereas male reproductive success shows greater variance; adult male weight is 1.7 times that of females, and male calves are heavier at birth<sup>18</sup>. All animals in the study population are individually recognizable; daily monitoring of the population during the calving season shows whether or not each female calved in a given year, and, if so, the sex of her offspring. An age-corrected dominance rank for each female, ranging from 0 to 1, is calculated from observations of interactions between pairs of individuals, as described elsewhere.<sup>2</sup> Females are also classified as to whether or not they reared a calf the previous year that survived to six months. Average temperature and total rainfall in the following periods were considered: August to October, November to January, February to March. None of the weather variables showed consistent change over the study period.

We report two forms of statistical analysis. The proportion of males born each year (referred to as the annual birth sex ratio) was related to density and weather measures using simple linear regression (normality of errors was satisfied; 1973 was excluded owing to incomplete data collection). The probability that an individual calf was male and the probability that a female gave birth in a given year were analysed using generalized linear mixed models<sup>28</sup>, with restricted maximum likelihood estimation of variance components. Just as generalized linear models allow the extension of general linear models to data where the errors are not normally distributed, GLMMs allow similar extensions to the conventional mixed model case where the response variable is determined by both random and fixed effects. In this case, the random component arose because of repeated sampling within a year and repeated sampling of the same females across years. Year and female identity were therefore fitted as random effects. In both models, the response variables were binary (male, not male; had calf, did not have calf), necessitating the use of a logit link function. The significance of the explanatory terms, the fixed effects, was assessed by their Wald statistics (distributed as  $\chi^2$ ) for each term when fitted last in the model. All interaction terms were tested, but are not reported unless statistically significant. Analysis was performed in Genstat 5, version 3.2.

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## Multifractality in human heartbeat dynamics

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There is evidence that physiological signals under healthy conditions may have a fractal temporal structure<sup>1</sup>. Here we investigate the possibility that time series generated by certain physiological control systems may be members of a special class of complex processes, termed multifractal, which require a large number of exponents to characterize their scaling properties<sup>2–6</sup>. We report on evidence for multifractality in a biological dynamical system, the healthy human heartbeat, and show that the multifractal character and nonlinear properties of the healthy heart rate are encoded in the Fourier phases. We uncover a loss of multifractality for a life-threatening condition, congestive heart failure.

Biomedical signals are generated by complex self-regulating systems that process inputs with a broad range of characteristics<sup>7,8</sup>. Many physiological time series, such as the one shown in Fig. 1a, are extremely inhomogeneous and non-stationary, fluctuating in an irregular and complex manner. The analysis of the fractal properties of such fluctuations has been restricted to second-order linear characteristics such as the power spectrum and the two-point autocorrelation function. These analyses reveal that the fractal behaviour of healthy, free-running physiological systems is often