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OFFSPRING SEX RATIO OF INTRODUCED RED DEER IN PATAGONIA, ARGENTINA AFTER AN INTENSIVE DROUGHT

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ABSTRACT. Red deer (*Cervus elaphus*) introduced to Patagonia have reached high densities in the forest-steppe ecotone. Drought conditions during 1998/99 were suspected to impact subsequent reproductive performance. Necropsies of 50 adult females during the 1999 winter revealed lowered pregnancy rates and lactation in 32% of non-pregnant as opposed to 0% among pregnant females. There were no signs of fetal resorptions or abortions. The fetal sex ratio (20m:8f) deviates significantly from unity, and mothers with female or male fetuses averaged 6.7 and 5.2 years, respectively (P=0.14). However, 90% of primiparous females (2.5 years old) had males, the following age class had all females, the middle age class (5-8 years old) had all males, and older females had equally male or female fetuses. These females were at borderline of body condition allowing conception and thus were at extremely low levels of condition during breeding. The male-biased fetal sex ratio contrasts reports of other studies that only females in best condition tend to have male-biased offspring. However, ambivalent results from other studies may stem from not having evaluated body fat reserves and reproductive tracts, or studies done during environmental conditions not extreme enough. The present results also indicate that red deer populations occur at densities where they can easily become food-limited through a singular environmental phenomenon such as a drought. Although recruitment rates would be drastically reduced through such temporary food shortage, red deer will recuperate rapidly and will continue to exert intensive pressure on the flora causing subsequent damage if population densities are not lowered through hunting.

RESUMEN. **La proporción de sexo fetal del ciervo colorado introducido en la Patagonia, Argentina después una sequía intensa.** El ciervo colorado (*Cervus elaphus*) introducido en Patagonia ha alcanzado densidades altas en el ecotono de bosque-estepa. Se sospecha que la sequía de 1998/99 tuvo un impacto sobre la reproducción. Las necropsias de 50 hembras adultas durante el invierno 1999 revelaron una tasa de preñez reducida y lactación en 32% de hembras no-preñadas versus 0% en las preñadas. No hubo indicaciones de reabsorciones o abortos. La proporción de sexo fetal (20m:8h) difirió significativamente de la unidad, pero la edad de las madres con fetos machos o hembras no difirió, con promedios de 6,7 y 5,2 años, respectivamente. Sin embargo, el 90% de hembras primíparas (de 2,5 años) tuvo machos, la siguiente clase de edad tuvo todas hembras, la clase mediana (de 5-8 años) tuvo todos machos, y las hembras de mayor edad tuvieron igualmente fetos de ambos sexos. Estas hembras tuvieron una condición física mínima que permitió la concepción y por lo tanto una condición extremamente baja durante la brama. La mayor proporción de fetos de sexo macho se opone a resultados de otros estudios en los cuales se concluyó que solamente las hembras de mejor condición física tienden a tener más crías machos. Sin embargo, conclusiones ambivalentes de otros estudios podrían ser resultado de la no evaluación de la condición física o el tracto reproductivo, o de estudios bajo condiciones ambientales no suficientemente extremas. El presente estudio muestra además que las poblaciones del ciervo colorado se encuentran en densidades tales que fácilmente pueden estar sujetas a una limitación nutricional por un fenómeno ambiental tan singular como el de una sequía puntual. Aunque

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la tasa de reclutamiento baja drásticamente por la escasez de comida, el ciervo colorado se recupera rápidamente y continúa ejerciendo presión intensiva sobre la flora si no es controlado a través de la caza.

Key words: *Cervus elaphus*, reproduction, fetal sex ratio, environmental conditions

Palabras clave: *Cervus elaphus*, reproducción, proporción de sexo fetal, condiciones ambientales

INTRODUCTION

Red deer (*Cervus elaphus*) were first introduced from Europe to central Argentina in 1906, and from there to the Andean cordillera by 1922. The population in this mountainous region of Patagonia has increased since that time both numerically and geographically. Even though red deer have invaded several national parks and have reached high densities in several locations, there have been few studies to date. Although the history of initial introductions of red deer in Patagonia is fairly well known (Flueck and Smith, 1993), little information is available on subsequent developments. In addition to some local introductions in Chile, deer have also invaded Chile from several Argentine populations (Ortiz, 1992) and thus red deer represent continuous populations across the Andes (Flueck et al., 1995a). Furthermore, the high-altitude Andean environment is considered to be prime habitat for the native deer huemul (*Hippocamelus bisulcus*), which is threatened with extinction (Smith and Flueck, 1997; Díaz and Smith-Flueck, 2000), raising the question of potential impact by red deer. In the southern cone of South America, red deer are able to survive in dense temperate rain forests, ecotones, but also the dry Patagonian steppe where they are sympatric with guanaco (*Lama guanicoe*) (Flueck, 1996). Within some habitats along this precipitation gradient, the negative impact of red deer on plant communities has been described (Veblen et al., 1989; 1992).

Precipitation during 1998/99 was far below average and the spring and summer were extremely dry and hot, resulting in the drought of the century for large areas of southern Argentina and Chile. During the breeding season (March 1999), a sample of collected females and interviews with landowners provided some indication of nutritional stress due to the prevailing drought. As body condition was already so low in autumn, when it usually reaches maximal levels, I studied reproductive aspects of these deer during the following winter.

The severity of the drought and its effect on body condition allowed to evaluate its influence on fetal sex ratio. Sex ratio theory is one of the more developed areas of evolutionary ecology, yet adaptive explanation for sex ratio variation among vertebrates are still the subject of much debate. Although there are alternative views like Local Resource Competition, sex ratio variation in red deer has often been discussed in view of the Maternal Condition hypothesis by Trivers and Willard (1973). It predicts that females in good condition should invest in male offspring because these would have higher mating success. Prior to this study there was no ecological information available on reproductive parameters of these introduced red deer to evaluate their invasive potential in the Patagonian environment, particularly in relation to unusual environmental conditions.

STUDY AREA

The study area is located in the Nahuel Huapi National Park reserve (40°58'S, 71°12'W), Argentina. The topography is primarily mountainous with most features formed by glacial processes. The majority of soils originated from volcanic processes and are young. Towards the east, the volcanic material has been modified by fluvial and cofluvial transportation of material. The dominant climate is temperate with main precipitation occurring between

April and September. There is an abrupt precipitation gradient from west to east due to the rain shadow effect of the Andes which results in a strongly defined vegetation structure and floristic composition. The study site is between 900 and 1200 m elevation and represents the ecotone between forests and steppe (Mermoz and Martin, 1986). Patches of forests are characterized by «ñire» *(Nothofagus antarctica*) and «ciprés» (*Austrocedrus chilensis*) at lower elevations and are replaced by «lenga» (*Nothofagus pumilio*) at higher elevations. Forest patches at lower elevations alternate with wet grasslands («mallines») with abundant growth of herbaceous plants whereas at high elevation they are replaced by grasslands dominated by «coirón amargo» (*Stipa speciosa* var. *major*) and «coirón dulce» (*Festuca pallescens*), with variable occurrence of brush species like «neneo» (*Mulinum spinosum*), «calafate» (*Berberis* spp.) and «espino negro» (*Colletia spinosissima*). Riparian areas also contain galleries of brush like «radal» (*Lomatia hirsuta*), «maitén» (*Maytenus boaria*) and «laura» (*Schinus patagonicus*).

CLIMATIC CONDITIONS

The prevailing climatic conditions represented an extremely punctual phenomenon and had such a profound effect on these herbivores that a detailed description of climatic circumstances is provided. The relative effect of the drought is presumed to have been similar within the surrounding area. Therefore, the weather station of INTA at latitude 41° 07'S and longitude 71° 15'W, at an elevation of 775 m, was considered representative for the historic climatic conditions for the area (C. Bustos, Meteorología, INTA Estación EEA, Bariloche), and data collected regularly since 1981 have been analyzed.

The period of summer through winter 1998 (January-August) was already substantially dry with only 319.5 mm of precipitation as compared to the averaged 663.2 mm received during 1981-1997. This drought continued through the following spring 1998 and summer-autumn of 1999, producing only 145 mm of precipitation as compared to the average of 454 mm for 1981-1996 (**Fig. 1a** and **1b**). Furthermore, the dry period from spring 1998 through the following autumn was accompanied by unusually low humidity (September 1998-April 1999 below 95% C.I. of average of previous 16 years) and very hot temperatures (**Fig. 1c** and **1d**). Hence, the pattern of the temperature-precipitation relationship was very different as compared to averages of the historic climatic conditions for the past two

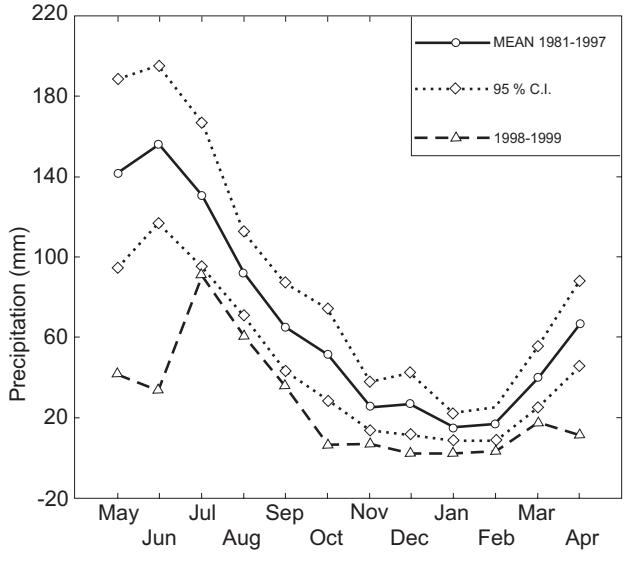

Fig. 1a. Mean monthly precipitation (mm) from 1981-1997 and during 1998-1999.

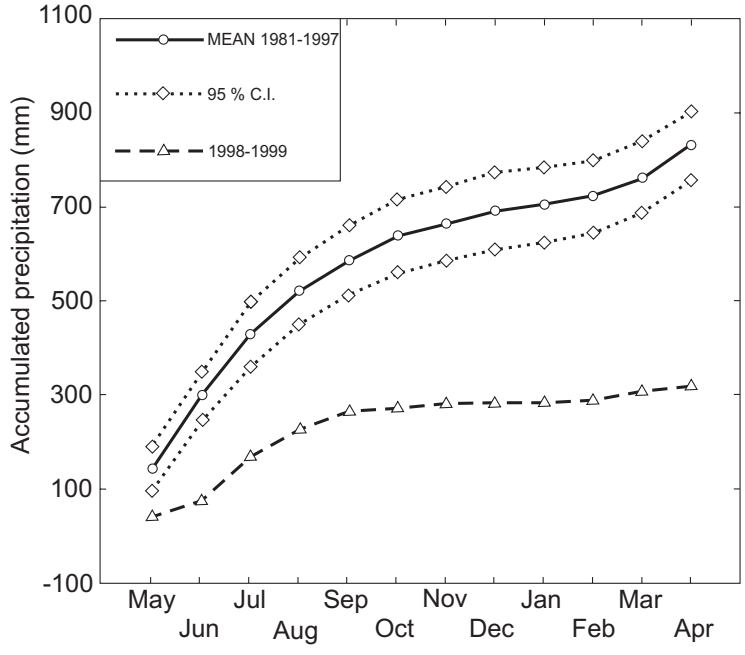

Fig. 1b. Mean accumulated precipitation (mm) from 1981-1997 and during 1998-1999.

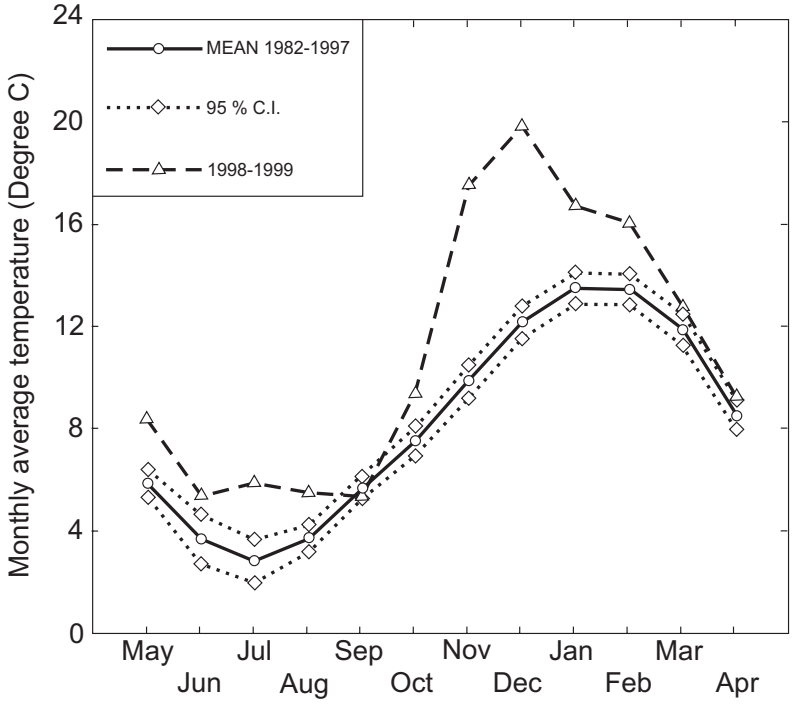

Fig. 1c. Mean monthly temperatures (°C) from 1982-1997 and during 1998-1999.

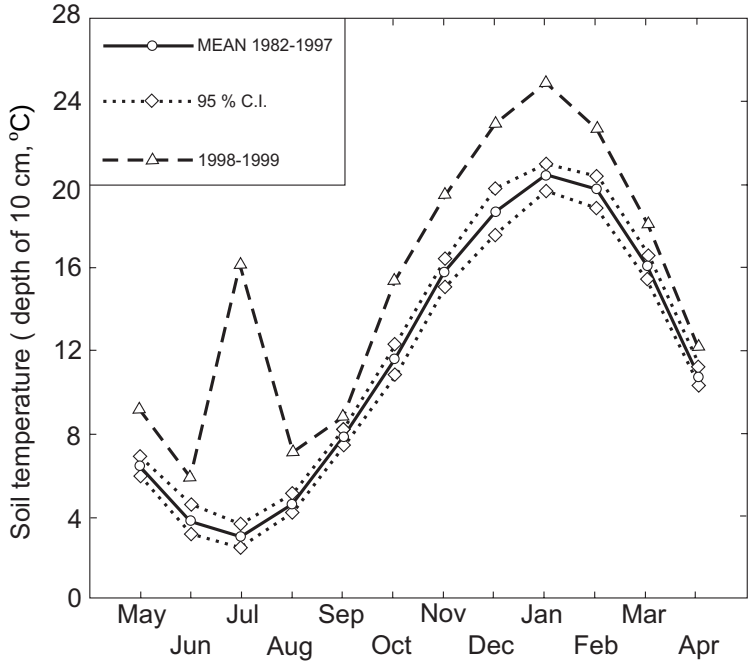

Fig. 1d. Mean soil temperature (°C) at 10 cm depth from 1982-1997 and during 1998-1999.

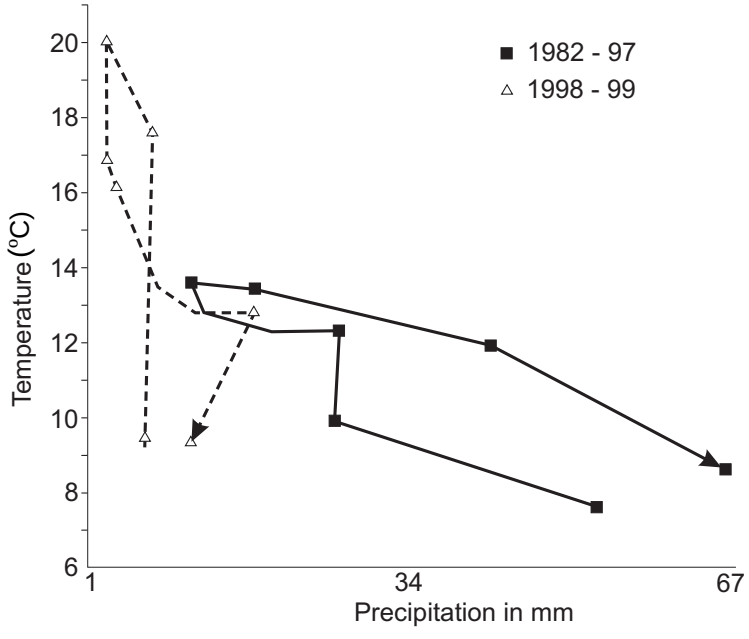

Fig. 2. Climograph for average October through April (spring-autumn) of 1982-97 and the drought season of 1998/99: monthly average temperature (°C) and monthly total precipitation (mm). The tail of the arrow represents October whereas the head represent April.

decades (**Fig. 2**). The substantially higher temperature in 1998-1999 resulted in an increased potential evapotranspiration rate (Ricklefs, 1979) and the water deficit was effectively higher than would be indicated by the amounts of precipitation. Thus, after correcting for these temperature differences, the period of October 1998 to April 1999 received only 17% of precipitation as compared to the average of 1982-1997. Water stress was so intense that there was a high mortality rate among evergreen conifers and broad-leafed trees of all age classes, including old growth trees like *Nothofagus dombeyi* (pers. obs.).

METHODS

Female red deer were examined during the last trimester of gestation, mainly during the months of October and November. Adult females (2 years or older) were approached by stalking and collected at first sight using a rifle without regard for age or size (n = 50). All females were part of social groups, the smallest groups consisting of a female with a yearling female and possibly a calf. Typically, group size was between 5 to 10 deer. The time and location were noted, several morphometric measurements (Mitchell et al., 1976) were taken and the animal was examined for lactational status. Chest girth was used as an index to body size (Millspaugh and Brundige, 1996).

Subsequently, a necropsy was performed to measure fat reserves and determine the reproductive status. Rump fat was measured as the deepest layer along an incision placed at a 45 degree angle, beginning at the base of the tail (Kistner et al., 1980); brisket fat was measured as the deepest layer along a midcentral incision over the sternum, beginning at the xyphoid process (Austin, 1984); omental fat was estimated as a percentage coverage by fat of the membrane (Dauphine, 1976); and the kidney fat index was calculated as fat mass divided by kidney mass times 100 (Anderson et al., 1990). Females without a fetus were examined carefully to determine if it was due to not being pregnant, due to parturition, or due to resorption or abortion. Fetal sex was evaluated with regard to age of females and the sex ratio was analyzed using the normal approximation of the binominal test (Zar, 1996).

Aging was done by comparing tooth eruption and tooth wear patterns to a reference set of known-aged jaws from 1 to 18 years obtained from deer of the same area. The set was prepared using cementum annuli analysis performed in Matson's laboratory (n = 99). This method has been shown to determine ages correctly (> 97%) in *C. elaphus* aged 2-15 years (Keiss, 1969; Hamlin et al., 2000). To circumvent potential sources of errors in this study, aging of jaws was performed in the laboratory after all jaws had been collected, using the known-aged set as a reference. Jaws were first grouped according to determined age and subsequently each group was reevaluated comparatively. Donnelly (1997) found that tooth wear is similar among red deer of the same age. Furthermore, the age classes up to 4,5 years old can readily be distinguished without error, particularly using comparative material.

RESULTS

Several biological parameters were similar in pregnant and non-pregnant females. Chest girths as an index to body size ranged from 108 to 136 cm (P = 0.31), and the median ages of 5.6 (SE = 0.61) years in pregnant (n = 28) and 7.6 (SE = 1.0) years in non-pregnant females (n = 22) were also similar (P = 0.08). Lactation on the other hand was significantly more prevalent in non-pregnant (32%) than pregnant females (0%) (Fisher's exact test, P = 0.005). There were no indications of reabsorption or abortion of fetuses in non-pregnant females. The sex ratio of 20 male and 8 female fetuses deviates significantly from unity (2-tailed normal approximation: $0.02 < P < 0.05$). Mothers with female or male fetuses averaged 6.7 and 5.2 years, respectively, which was not significantly different (2-tailed 2-sample test: P = 0.14). However, 90% of primiparous females (2.5 years old) had male fetuses (n = 10), the following age class had all female fetuses (n = 4), the middle age class (5-8 years old) had all males fetuses (n = 8), and older females had equally male or female fetuses (n = 6). The effect of body condition on fetal sex could not be evaluated in more detail due to near absence of fat reserves without variance. Body condition measurements indicated that the females were severely undernourished in 1999 as compared to previous years (Flueck, 2001). Of several fat reserves evaluated, they were very low for all females, reaching on average only 0,1 mm of rump fat, 0.44 mm of brisket fat, and 0.28

% of omental fat, irrespective of reproductive status.

DISCUSSION

Red deer have been shown earlier to occur at comparatively high densities in the region of this study area, reaching 100 deer/km² in ecotonal habitat and 50 deer/km² in open steppe (Flueck et al., 1995b). The severe drought of 1998/99 not only reduced the reproductive rate of adult deer substantially (Flueck, 2001), but skewed the sex ratio of fetuses heavily towards males. The factor determining conception most likely is body condition with respect to fat reserves during the rut (Flueck, 1994). The preponderance of primiparous females among pregnant animals can be explained by the fact that they had not been pregnant before and therefore, were in better condition allowing ovulation to occur even under these severe environmental conditions. Although the absence of variance in fat reserves during late pregnancy precluded a more detailed analysis of its effect on fetal sex, females which had the best body condition at conception certainly included 2 year old due to absence of previous pregnancies as well as females which would have lost their calves soon after birth during the previous spring. Prime aged females (9-12 years old) would have been least likely to have lost their calves which was reflected in the high proportion of this age class among females which did not conceive (Flueck, 2001). One could argue that primiparous and middle aged females had principally male offspring because they must have been in better condition to become pregnant as compared to nonpregnant females. As a group, they were on the borderline of body condition allowing ovulation and their actual reserves were completely depleted at necropsy. Therefore, these females represent animals of extremely low body condition. Contrary to several studies concluding that in this species females of better condition carry principally male fetuses (Kohlmann, 1999; Kruuk et al., 1999), the present study thus clearly shows the opposite.

The debate continues if mammals can actually control sex ratio adaptively (Hardy, 1997). There are ambivalent data on factors which influence the offspring sex ratio in red deer, and patterns of sex-ratio variation reported in the literature are often inconsistent (Hewison et al., 1999). Intuitively, environmental conditions favoring a numeric response of a population would be expected to result in more female offspring due to their direct contribution to the intrinsic growth rate of the population. Several cervid species have been shown to exhibit this response (Verme, 1983; 1985). In contrast, under overt environmental conditions it is advantageous to have more males because this lowers the intrinsic population growth rate and also reduces local competition by providing more dispersers, a common trait among cervid males. Moreover, for red deer the existence of local resource competition hypothesis has been shown among females (Clutton-Brock et al., 1982a).

Red deer were studied on the Scottish island Rhum which had experienced substantial overgrazing resulting in a population decline while at the same time female body weights continued to decline (Clutton-Brock and Albon, 1983). Later intensive studies since 1971 showed that 3 year old females rarely bred, and 4 year old were principally the first age class to recruit calves. However, mothers, especially with male calves, were substantially more likely to fail to breed in the following year (Clutton-Brock et al., 1982b; Clutton-Brock and Albon, 1985). Although these are all indications that females were limited by nutrition, no evidence was found that a good year resulted in more male calves, nor was there a relationship with age or lactation, and only the reproductive rate was affected (Clutton-Brock et al., 1982b; Clutton-Brock and Albon, 1985). Even in female groups of different sizes and, therefore, different intensity of competition, there was no significant difference in birth sex ratios which were slightly male-biased in both cases (56 versus 58% males) (Clutton-Brock et al., 1982a). One tendency found was that dominant females have more male calves.

The tendency of dominant females to have more male offspring was parallel to suffering

less from competition, they produce heavier calves and sons died less likely (Clutton-Brock et al., 1988). As dominance increases with age, older females tended thus to produce more males (Clutton-Brock et al., 1988). In contrast, Kruuk et al. (1999) found that this dominance effect on male-biased offspring disappeared as population density increased further, whereas an even birth sex ratio remained among subordinate females through the whole population density gradient. As birth rates decreased while density went up, they related this decreased fecundity to decreasing male birth rates. Their interpretations may not hold though, if assumptions are violated. For instance, they concluded that the declining fecundity measured across all females must have been due to male-biased fetal loss among the dominant females after the second trimester of gestation. However, it is exactly the dominant females which are in better conditions than subordinates, and hence would be expected to be less affected than subordinate females. Moreover, if fetal loss also occurred in subordinate females, which would be more likely than even in dominant females, then we would also expect a male-biased fetal loss for the same reasoning as applied to dominant females: yet the birth sex ratio among subordinate females remained the same through the whole gradient of densities (Kruuk et al., 1999). These inconsistencies likely stem from not having evaluated body condition nor reproductive tracts of individual females (Clutton-Brock et al., 1982b). Mitchell et al. (1986) for example studied a similar red deer population at a relatively high density and in poor habitat in Scotland, also with a low reproductive rate. This population apparently had adapted to these conditions and of 1471 females necropsied, there were no signs of resorption or abortion, yet only 773 were pregnant. Thus, females did either not conceive at all, or they carried a calf to term. In addition, fetal sex ratio was nearly 1:1 (n = 460) and there was no trend with age or lactational status.

The biased fetal sex ratio in the present study was not a result of potential sex-biased fetal mortality as suggested by Kruuk et al. (1999) because there were no signs of reabsorptions or abortions. Rather, the extreme climatic conditions of only one season precipitated an unusually strong response, but opposite to the predictions by Trivers and Willard (1973) that only females in good condition should produce more male offspring. A more plausible mechanism producing biased fetal sex ratios is the relative timing of insemination which is potentially under the control of the female (Krackow, 1997), or environmental cues which alter hormonal or behavioral aspects of the female. The present results also indicate that these red deer populations occur at densities where they become easily food-limited through singular climatic phenomenon such as a drought period. Although the recruitment rate, especially of female offspring, was drastically reduced through this temporary food shortage, the population will likely recuperate rapidly and red deer will continue to exert intensive pressure on the flora with associated damage to flora and fauna, unless population densities are lowered through hunting. The relationship between environmental conditions and possible effect on offspring ratio has important implication due to its strong effect on population dynamics and hence, management approaches.

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