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Offspring sex ratio in relation to body reserves in red deer (*Cervus elaphus*)

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1 Introduction

The debate continues; can mammals actually control sex ratio adaptively (Hardy, 1997)? There are ambivalent data on factors that influence the offspring sex ratio in red deer (*Cervus elaphus*), 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 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. Red deer were introduced to Patagonia in the 1920s and have reached high densities in areas of the forest-steppe ecotone. This study is based on a singular extreme climatic event that occurred in Patagonia during the spring to autumn of 1998/99 and resulted in a natural experiment. Some important attributes of this study include the absence of possible medium and long term adaptive phenomena due to the punctual event and the temporal proximity of average, overt and favorable environmental conditions.

2 Study Area

The study area is located in the Nahuel Huapi National Reserve (40°58′ S, 71°12′ W), Argentina. The topography is primarily mountainous with most features formed by glacial processes. The dominant climate is temperate with most 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 sites are between 900 and 1,200 m elevation and represent the ecotone between forests and steppe. Patches of forests are characterized by false beech (*Nothofagus antarctica*) and cypress (*Austrocedrus chilensis*) at lower elevations and are replaced by deciduous lenga (*Nothofagus pumilio*) at higher elevations. Forest patches at lower elevations alternate with wet grasslands with abundant growth of herbaceous plants whereas at high elevation they are replaced by grass-dominated steppe containing *Stipa speciosa* var. *major* and *Festuca pallescens*, with variable occurrence of brush species like *Mulinum spinosum*, *Berberis* spp. and *Colletia spinosissima*. Riparian areas also contain galleries of *Lomatia hirsuta*, *Maytenus boaria* and *Schinus patagonicus* trees.

3 Climatic Conditions

The extremely dry and hot spring/summer 1998-1999 has been referred to as the drought of

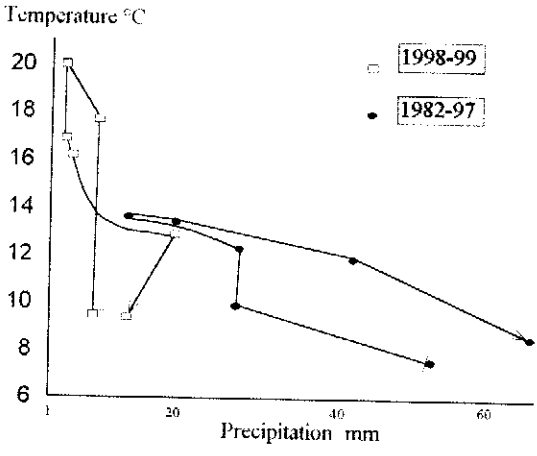

Fig. 1. Climograph for October through April (spring-autumn) of 1982-97 and the drought season of 1998/99: monthly average temperature [°C] and monthly total precipitation [mm]. The tail of the arrow represents October whereas the head represent April. Nahuel Huapi National Reserve (40°58′ S, 71°12′ W), Argentina

the century in much of Patagonia, including Chile. A weather station at 41° 07′ S, 71° 15′ W, at an elevation of 775 m, is considered representative of the historic climatic conditions for the area (Meteorologia, INTA Estación EEA, Bariloche), and data collected regularly since 1981 were analyzed.

Summer through winter 1998 was already substantially dry with only 320 mm of precipitation compared to the average of 663 mm received during 1981-1997. This drought continued through the following spring to autumn 1999, producing only 145 mm of precipitation as compared to the average of 454 mm for 1981-1996. Furthermore, this dry period was accompanied by below average humidity and very hot temperatures. Hence, the pattern of the temperature-precipitation relationship was very different as compared to averages of the historic climatic conditions for the past two decades (Fig.1). The substantially higher temperature in 1998-1999 resulted in an increased potential evapotranspiration rate 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 (*Nothofagus dombeyi*).

The year following the drought conditions provided excellent conditions for primary production. The total amount of precipitation conformed to the 1981-1997 average, however, the summer of 2000 received 11% more precipitation than the average of previous years. In addition, spring and summer monthly average temperatures in 2000 were 1°C higher than the 1981-1997 average and together with good summer rains resulted in high primary productivity.

4 Materials and Methods

I approached adult females by stalking and collected specimens at first sight without regard for age or size (females >2 years old) using a rifle. I noted the time, location and morphometric measurements (head, tail and total length; shoulder height; hind foot length; girth; diastema) (MITCHEL et al., 1976), and determined the state of lactation. To measure fat reserves

and determine the reproductive and health status, I performed standard necropsies (WOBESER and SPRAKER, 1980). I considered a female primiparous according to the physiognomy of the uterus and udder. The former are smaller, with a smoother surface, less vascularized, a thinner uterine wall and pinkish white color; the latter exhibit non-wrinkled smooth skin and smaller teats. I measured rump fat, brisket fat, omental fat and kidney fat (DAUPHINE, 1976; KISTNER et al., 1980; AUSTIN, 1984; ANDERSON et al., 1990) and examined females without a fetus carefully to determine its cause. Parturition as a cause was readily indicated by the date of collection, the physiognomy and absence of gross pathology of uteri, and the state of the udder. I determined the occurrence of abortions based on the enlarged size of uteri in pregnant females (LANGVATN, 1992a), the presence of placentitis (e.g. seropurulent exudate, separation of chorion from endometrium, edematous chorion, necrosis), endometritis, or retained fetal membranes (JONES and HUNT, 1983). Abortions resulting from infections delay the involution of the uterus, sometimes indefinitely, and thus are readily detected at a later time. Resorption was defined as the occurrence of a dead embryo or fetus without indications of infectious disease. I determined the lack of pregnancy based on the size and absence of pathology of the uterus, the date of collection, and the absence of a *corpus luteum verum* (CLV) (LANGVATN, 1992b). Ovulation without conception results in *corpus luteum spurium* (CLS), however macroscopically, it disappears within 30- 45 days (LANGVATN, 1992b). The pregnancy rates were compared among years in the same study area: 1992-98 (n = 88), 1999 (n = 50) and 2000 (n = 70).

Herd composition counts throughout the study area were conducted during summer-autumn from vantage points using 20-40x spotting scopes to classify animals as either adult female, calf or male. Population density was estimated from pellet groups along two permanent transects 5 and 2.5 km long installed in 1994 in the study (circular plots, r = 2.5 m). The centers of each plot were spaced at 50 m and permanently marked. After each reading, fecal pellets were removed from all plots. Plots were evaluated twice per year in 1994 and 1995, and twice per year since 1999. I aged deer comparing tooth eruption and tooth wear patterns to a reference set of known-aged jaws from 1 to 18 years obtained from deer from the same area. The set was prepared using *cementum annuli* analysis (n = 99).

I analyzed the sex ratio using the normal approximation of the binominal test (Zar 1996), I compared means using the 2-sample T-test and analyzed frequencies using the Fisher's exact test (at $\alpha = 0.05$).

5 Results

Population density

The standing crop of fecal pellet groups was 0.61 groups/m^2 (SE = 0.05) in 1994 and 0.63 groups/m^2 (SE = 0.05) in 1999. This implies that the deer density in 1994 remained essentially the same up to 1999 (or possibly increased slightly). However, whereas the deposition rate for spring to autumn in 1994/95 was 0.96 groups/m^2/year (SE = 0.009), it dropped to 0.74 groups/m^2/year (SE 0.009) from spring to autumn 1999/00. This indicates an overall population reduction of 23%. It supports frequent field observations of dead females during the winter after the drought as well as during the following parturition period. For instance, on several occasions dead females were found within a few meters of newborn calves.

Reproductive rates

The pregnancy rate of adult females was 98% in 1992-98 (n 88), then dropped to 56% following the drought (n = 50), and rebounded to 100% in 2000 (n = 70). There were no cases of

reabsorption, abortions, CLV or CLS in non-pregnant females following the drought. Also, no yearlings were found pregnant, only 77% (n = 13) of 2 year-olds conceived, and females older than 3 years conceived at a rate of merely 51% in 1999 (n = 35) (FLUECK, 2001a).

Relative foraging pressure

During the summer-autumn of 1992, 58 calves per 100 females (n = 1,242) were counted. As the pregnancy rate among adult females was nearly 100%, and assuming that 15% of the females were subadults (yearlings) with a low probability of having been pregnant, this indicates a loss of about 33% calves during the neonatal period. Lactating females have a 2-3 times higher forage consumption rate as compared to barren females. Thus, in terms of forage consumption, a 1992 summer population of 100 females can be described as consisting of 13 barren yearlings, 29 barren adult females and 58 x 2.5 = 145 'barren' adult females, making a total of 187 barren female equivalents. In contrast, the summer population following the drought had a very distinct composition and only 30 calves per 100 female (n = 472) were counted, corroborating the preceding pregnancy rate of only 56% among adult females. Thus, in terms of forage consumption, the 1999 summer population of 100 females can be described as 13 barren yearlings, 53 barren adult females and 34 x 2.5 = 85 'barren' adult females, making a total of 151 barren female equivalents. However, as about 23% of the females died during the winter and parturition period following the drought, this summer population consisted of about 116 barren female equivalents. Therefore, the pressure on the summer range in 2000 with above-average primary productivity was only about 62% as compared to previous years.

Body condition

Females were severely undernourished after the drought. Of several fat reserves evaluated, they were very low for all females (n = 52), reaching on average only 0.1 mm of rump fat, 0.44 mm of brisket fax, and 0.28% of omental fat, irrespective of reproductive status. The kidney fat index (fat mass/kidney mass) in autumn/winter 1992-1997 (n = 33) was 58.7 (SE = 0.4), whereas in autumn/winter after the drought (n = 52) it was 0.1 (SE = 0.06). In contrast, in autumn/winter of 2000 (n = 48) the index was 80.3 (SE = 0.5) (Fig. 2).

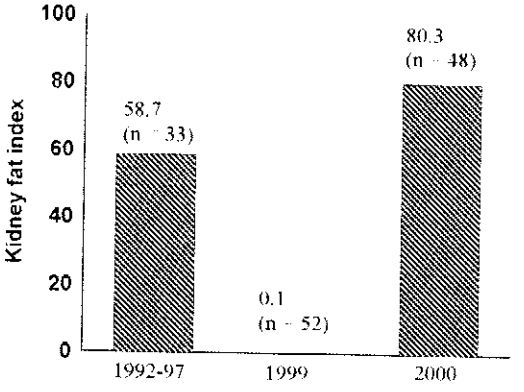

Fig. 2. Body fat reserves in 1992-97, 1999 and 2000 in female red deer, Argentina.

Several biological parameters measured after the drought 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 ($P = 0.08$).

Fetal sex ratio

After the drought, females were at extremely low levels of body condition during breeding and at the borderline where conception can still occur (FLUECK, 2001a). The fetal sex ratio ($n = 69$) was 46% males during 1992-98, whereas after the drought it was 71% males ($n = 28$) (2-tailed normal approximation: $0.02 < P < 0.05$). Mothers with female or male fetuses averaged 6.7 and 5.2 years, respectively ($P = 0.14$). Of the primiparous females (2.5 years old), 90% had male fetuses, the following age class had all female fetuses, the middle age class (4-8 years old) had all males, and older females had equally male or female fetuses. The extremely good conditions during spring/summer of 1999/00 resulted in a subsequent fetal sex ratio of 39% males ($n = 70$). However, primiparous females had all female fetuses, the following age class had equally male and female fetuses, the middle age class had 62% females, and older females had 86% female fetuses.

6 Discussion

The interplay of the environmental conditions with the population and reproductive dynamics of red deer resulted in 3 very distinct settings separated by only one year each. Specifically, a well-performing population experienced a period of years with average climatic conditions which was followed by a severe drought. Deer were not able to build up body reserves before rutting and the pregnancy rate was reduced by nearly 50%. This was likely due to failure of ovulation because there were no signs *corpus luteum verum* nor *spurium*. Due to the extremely low body reserves, an estimated 23% of the female population subsumed during the following winter and parturition periods. The following spring and summer conditions were above normal in terms of precipitation and temperature resulting in high primary productivity. However, there were less deer due to the drought-related increase in mortality, and there were also 55% less lactating females, and hence, the browsing pressure was reduced by about 62%. Consequently, body conditions measured in the following autumn were the highest on record since monitoring began in 1992.

The severe drought of 1998/99 reduced the reproductive rate of adult deer substantially (FLUECK, 2001a), and skewed the sex ratio of fetuses heavily towards males (FLUECK, 2001b). 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 after the drought can be explained because they had not been pregnant before and therefore, were in better condition allowing ovulation to occur even under these severe environmental conditions. As they were on the borderline of body condition allowing ovulation and their actual reserves were completely depleted at necropsy, these females represent animals of extremely low body condition. Contrary to several studies concluding that red deer females of better condition carry principally male fetuses (CLUTTON-BROCK et al., 1986; KOHLMANN, 1999; KRUUK et al., 1999), I show the opposite. The biased fetal sex ratio due to overt environmental conditions reported here 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. Significantly, the superb conditions in the following year resulted in a distinctly female biased sex ratio, also in contrast to predictions by TRIVERS and WILLARD (1973). As the pregnancy rate was 100%, differential fetal mortality as an adaptive mechanism (KRUUK et al., 1999) can be excluded.

The temporal proximity of several average years and a severe drought followed by an above-average year shows clearly that the effect on the population with respect to changes in offspring sex ratios was immediate and contrary to several other reports. In particular, due to the imminent chronology of events, the observed changes were unlikely related to changes within the female population, such as changes in age structure or dominance relationships. Rather, a conclusive relationship to energy reserves during breeding emerged as the underlying principle affecting the offspring sex ratios.

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Summary

Red deer (*Cervus elaphus*) introduced to Patagonia have reached high densities in forest-steppe ecotones and have been monitored since 1992. Severe drought conditions prevailed during spring to autumn of 1998/99, followed by a spring-summer (2000) with above average moisture and temperatures, resulting in high primary productivity. At the same time and due to the previous drought, there were less deer and fewer females with calves, resulting in the highest recorded level of physical condition of females. I compared offspring sex ratios of red deer during an average period (1992-98), a drought year (1999), and an above-average year (2000).

Adult females collected and examined during winter 1999 (n = 50) revealed a pregnancy rate of 56% as compared to 98% in 1992-98 (n = 88), or 100% in 2000 (n = 70). Body fat reserves in 1999 were severely depleted in most animals, irrespective of reproductive status; there were no signs of resorptions or abortions. The fetal sex ratio (n = 69) was 46% males during 1992-98, 71% males after the drought, and 39% males in 2000. Primiparous 2-year old females had 90% male and 100% female fetuses in 1999 and 2000, respectively. Mothers with female or male fetuses averaged 6.7 and 5.2 years, respectively (P = 0.14).

The male-biased and female-biased offspring ratios in 1999 and 2000 contrast other reports that only females in best condition tend to have male-biased offspring. The temporal proximity of average years, a drought followed by an above-average year shows that changes in offspring sex ratios were immediate. In particular, due to the imminent chronology of events, the observed changes were unlikely related to changes within the female population, such as changes in age structure or dominance relationships. Rather, a conclusive relationship to energy reserves during breeding emerged as the underlying principle affecting the offspring sex ratios.

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

Zusammenfassung

Geschlechterverhältnis der Nachkommen im Verhältnis zu den Körperreserven beim Rothirsch (Cervus elaphus)

Die in Patagonien eingebürgerten Rothirsche haben im Wald/Steppe-Ökoton hohe Dichten erreicht und werden seit 1992 untersucht. Von Frühjahr bis Herbst 1998/99 herrschte eine schwere Dürre, gefolgt von überdurchschnittlich hohen Niederschlägen und Temperaturen im Frühjahr und Sommer 2000, die zu einer hohen Primärproduktion führten. Gleichzeitig und bedingt durch die voraus gegangene Dürre gab es weniger Individuen und weniger Weibchen mit Kälbern. In der Folge wurde die höchste Körperkondition der weiblichen Tiere festgestellt. Verglichen wurde das Geschlechterverhältnis der Nachkommen während eines durchschnittlichen Zeitraums (1992-98), eines Dürrejahres (1999) und eines überdurchschnittlichen Jahres (2000).

Die im Winter 1999 gesammelten und untersuchten adulten Weibchen (n = 50) wiesen eine Trächtigkeitsrate von 56% auf, verglichen mit 98% im Zeitraum 1992-98 (n = 88) und 100% im Jahr 2000 (n = 70). Im Jahre 1999 waren, unabhängig vom Reproduktionsstatus, die Körperfett-Reserven der meisten Tiere stark verringert; es fanden sich keine Anzeichen für Fetenresorptionen oder Aborte. Im Zeitraum 1992-98 waren 46% der Feten (n = 69) männlichen Geschlechts, nach der Dürre 71% (n = 28) und im Jahr 2000 39% (n = 70). Erstgebärende 2jährige Weibchen hatten 1999 zu 90% männliche Feten, im Jahre 2000 zu 100% weibliche Feten. Das Durchschnittsalter der Mütter mit weiblichen Feten betrug 6,7, dasjenige der Weibchen mit männlichen Feten 5,2 Jahre (P = 0.14).

Die zum männlichen bzw. zum weiblichen Geschlecht verschobenen Geschlechterverhältnisse der Nachkommen in den Jahren 1999 bzw. 2000 stehen im Gegensatz zu Berichten, nach denen nur Weibchen in bester körperlicher Verfassung mehr männlichen Nachwuchs produzieren. Die zeitliche Nähe von durchschnittlichen Jahren, einem Dürrejahr und einem überdurchschnittlichen Jahr belegen, dass die Veränderungen im Geschlechterverhältnis der Nachkommen unmittelbar erfolgten. Wegen der Chronologie der Ereignisse ist es unwahrscheinlich, dass die festgestellten Änderungen im Geschlechterverhältnis zu Veränderungen im Weibchenbestand, wie zum Beispiel veränderter Altersstruktur oder geänderten Dominanzverhältnissen, in Beziehung gesetzt werden können. Vielmehr ergab sich eine schlüssige Beziehung zu den Energiereserven während der Fortpflanzung als bestimmender Faktor für das Geschlechterverhältnis der Nachkommen.

Schlüsselwörter: Körperkondition, *Cervus elaphus*, Umweltbedingungen, fetales Geschlechterverhältnis, Reproduktion

References

ANDERSON, A.E., BOWDEN, D.C., MEDIN, D.E., 1990: Indexing the annual fat cycle in a mule deer population. J. Wildl. Manage. **54**, 550-556.

AUSTIN, D.D., 1984: Fat depth at the xiphoid process-a rapid index to deer condition. Great Basin Naturalist **44**, 178-181.

CLUTTON-BROCK, T.H., ALBON, S.D., GUINNESS, F.E., 1986: Great expectations: dominance, breeding success and offspring sex ratios in red deer. Anim. Behav. **34**, 460-471.

DAUPHINÉ, T., 1976: Biology of the Kaminuriak Population of Barren Ground Caribou. Part 4. Growth, Reproduction and Energy Reserves. Can. Wildl. Serv. Rep. Series, 71 pp.

FLUECK, W.T., 1994: Relationship between body weight, lipid reserves, and ovulation rate in non-equatorial cervids: a hypothesis. Z. Jagdwiss. **40**, 12-21.

FLUECK, W.T., 2001a: Body reserves and pregnancy rates of introduced red deer in Patagonia (Argentina) after a period of drought. Ecol. Austral **11**, 11-24.

FLUECK, W.T., 2001b: Offspring sex ratio of introduced red deer in Patagonia, Argentina after an intensive drought. J. Neotrop. Mammal.(Argent.) **8**, 139-147.

HARDY, I.C.W., 1997: Possible factors influencing vertebrate sex ratios: an introductory overview. Applied Animal Behaviour Science **51**, 217-241.

HEWISON, A.J.M., ANDERSEN, R., GAILLARD, J.M., LINNELL, J.D.C., DELORME, D., 1999: Contradictory findings in studies of sex ratio variation in roe deer (*Capreolus capreolus*). Behav. Ecol. Sociobiol. **45**, 339-348.

JONES, T.C., HUNT, R.D., 1983: Veterinary pathology. 5th Edition. Philadelphia: Lea & Febiger.

KISTNER, T.P., TRAINER, C.E., HARTMANN, N.A., 1980: A field technique for evaluating physical condition of deer. Wildlife Society Bulletin **8**, 11-17.

KOHLMANN, S.G., 1999: Adaptive fetal sex allocation in elk: evidence and implications. J. Wildl. Manage. **63**:1109-1117.

KRUUK, L.E., CLUTTON-BROCK, T.H., ALBON, S.D., PEMBERTON, J.M., GUINNESS, F.E., 1999: Population density affects sex ratio variation in red deer. Nature **399**, 459-461.

LANGVATN, R., 1992a: Seasonal and age related changes in size of reproductive structures of red deer hinds (*Cervus elaphus*). Rangifer **12**, 57-66.

LANGVATN, R., 1992b. Analysis of ovaries in studies of reproduction in red deer (*Cervus elaphus*): application and limitations. Rangifer **12**, 67-91.

MITCHEL, B., McCowan, D., Nicholson, I. A., 1976: Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. J. Zool., Lond. **180**, 107-127.

TRIVERS, R.L., WILLARD, D.E., 1973: Natural selection of parental ability to vary the sex ratio of offspring. Science **179**, 90-92.

VERME, L.J., 1983: Sex ratio variation in *Odocoileus*: a critical review. J. Wildl. Manage. **47**, 573-582.

VERME, L.J., 1985: Progeny sex ratio relationships in deer: theoretical vs. observed. J. Wildl. Manage. **49**, 134-136.

WOBESER, G.A., SPRAKER, T.R., 1980: Post-mortem examination. In: Schemnitz, S.D. (ed.) Wildlife management techniques manual. Washington, DC.: The Wildlife Society, pp. 89-98.

Zar, J.H., 1996: Biostatistical analysis. (Third edition). Prentice-Hall, Inc., New Jersey, USA

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