FEMALE-BIASED MORTALITY IN A SEXUALLY DIMORPHIC UNGULATE: FERAL CATTLE OF AMSTERDAM ISLAND

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I investigated the scale and pattern of mortality among feral cattle (*Bos taurus*) occurring on Amsterdam Island in 1988 to test hypotheses related to sexual dimorphism. Because cattle are sexually dimorphic ungulates and all deaths apparently were due to starvation, mortality was expected to be biased towards males. Mortality of juvenile males was higher than that of juvenile females (22.4 versus 11.7%), but mortality of adult males was lower than that of females (18.3 versus 47.7%). Causes for differential survival in adult age-classes are uncertain, but could involve sex differences in use of habitat, or consequences of previous selection during domestication.

Key words: *Bos taurus*, ungulate, sexual dimorphism, sex ratio, Amsterdam Island, Indian Ocean.

In mammals, the evolutionary consequences of polygyny commonly include sexual dimorphism in body size with males being larger than females (Clutton-Brock et al., 1977). The benefits of rapid growth and large size are great in males, and important implications for population dynamics are expected. For example, it has been suggested that males of sexually dimorphic species are more likely to die than females during periods of food shortage, both as juveniles and adults (Clutton-Brock and Albon, 1985). This is supported by evidence in many dimorphic mammals including wildebeest (*Connochaetes gnou*—Child, 1972; Talbot and Talbot, 1963); reindeer (*Rangifer tarandus*—Klein, 1968), Corsican mouflon (*Ovis ammon musimon*—Bousses et al., 1991), mule deer (*Odocoileus hemionus*—Robinette et al., 1957), wapiti (*Cervus elaphus*—Flook, 1970), and Soay sheep (*Ovis aries*—Grubb, 1974).

Sex differences in mortality probably have several causes. The reduced survival of juvenile males probably is a consequence of faster rates of growth, greater nutritional requirements, lower fat reserves, and higher metabolic rates (Clutton-Brock et al., 1985). In adults, the absolute requirements of males commonly exceed those of females (Coelho, 1974), and the larger individuals may be unable to subsist on sparse forage from which smaller individuals can collect adequate food (Illius and Gordon, 1987).

Differential mortality between sexes often was indicated solely by skewed sex-ratios (Bowyer, 1991; Ralls et al., 1980), because gathering accurate data on mortality usually is difficult in the field (Trivers, 1972). Moreover, testing effects of food shortage on survival is not feasible by manipulative experiments on large mammals (Millar and Hickling, 1990). Thus, data on mortality rates in response to environmental conditions are of interest. During 1988, 30% of a population of feral cattle (*Bos taurus*) died from starvation on Amsterdam Island (Indian Ocean). These cattle are polygynous, with marked sexual dimorphism (Berteaux and Micol, 1992; Lesel, 1969). In this paper, I describe juvenile, yearling, and adult mortality for each sex to test the prediction that mortality would be higher for males than for females and determine which processes are affecting sex ratios of feral cattle.

METHODS

Amsterdam Island (37°40'S, 77°35'E) is one of the French Islands of the Southern Indian Ocean. Topography, climate, and vegetation have been described by Daycard (1990) and Berteaux and Micol (1992). Briefly, the island is a 55-km^2 volcanic dome that rises to 881 m. It occupies a cool-temperate biogeographic realm characterized by mean air temperatures of 13.8°C. The hottest month is February (17°C) and the coldest is August (11°C). Wind speed exceeds 16 m/s 150 days/year. The mean annual rainfall is 1,120 mm and there are 239 rainy days per year (Meteorological Office Recording Station located on Amsterdam Island at 30 m above sea level).

The cattle population was described by Lesel (1969), Petit (1977), and Berteaux and Micol (1992). This population was introduced in 1871, and received neither supplemental food nor medical care; predators and interspecific competitors were absent. Cattle numbered 2,000 ± 100 (95% *C.I.*) at the beginning of 1988, but because of the considerable ecological burden of these animals on the unique flora and fauna of Amsterdam Island, a proposal to rehabilitate the island was accepted by the government in 1987, and the island was divided by a fence that year.

Cattle south of the fence ($n = 1{,}059$—Berteaux and Micol, 1992) were removed, whereas cattle located north of the fence (1,600 ha) remained and constituted the study population. The only interference with the study population was the removal of 50–80 individuals (mainly subadult and adult males) each year since 1950, to provide fresh meat for people living on Amsterdam Island (Daycard, 1990; Fiasson and Diallo, 1953).

The size and composition of the study population was determined by two observers who surveyed the area on foot during 3 consecutive days (23, 24, and 25 February 1988). The total counts of cattle involved a systematic search of the entire area. To prevent double counting due to movements of individuals during the night, cattle censused at the end of a day were identified on the basis of color patterns to ensure that herds did not move from a surveyed area to a nonsurveyed area between consecutive days. Herd location appeared to be stable overnight. Observations were made with binoculars and observers communicated with radios. Age classes included juveniles (< 1 year), yearlings (1–2 years), and adults (≥ 2 years) and were determined on the basis of body size and conformity, and horn size.

The study area was surveyed monthly for carcasses. Age class of dead individuals was determined from the chronology of eruption of permanent incisors (Steenkamp, 1970). For the purposes of this study, three age classes described previously were used. Carcasses remained undisturbed during several months (no predators) and were unlikely to be missed. Each carcass was tagged to avoid double counts.

Departure of sex ratios from parity were analysed by chi-square tests of goodness of fit. The expected 1:1 ratio at birth was derived from the sex ratio observed in a sample of 30 sexed fetuses (Berteaux and Micol, 1992). Comparisons of numbers among age classes, and comparisons of mortality rates between age or sex classes were analysed by chi-square tests of independence. All chi-squares were calculated by use of the SAS statistical package (SAS Institute Inc., 1985).

RESULTS

The population of cattle counted in surveys numbered 993 in February 1988. Among males there were 98 juveniles, 39 yearlings, and 241 adults, and among females there were 120 juveniles, 73 yearlings, and 422 adults. The sex ratio of juveniles did not differ from the expected 1:1 ratio ($\chi^2 = 2.22$, *d.f.* = 1, $P > 0.1$), but there were significantly fewer male than female yearlings ($\chi^2 = 5.28$, *d.f.* = 1, $P = 0.022$) and significantly fewer male than female adults ($\chi^2 = 25.18$, *d.f.* = 1, $P < 0.001$). Cattle died seasonally (Table 1); 90.8% of total deaths occurred from July to October, which is winter in the southern hemisphere.

Mortality did not differ significantly among the age classes of males (juveniles versus yearlings, $\chi^2 = 0.061$, *d.f.* = 1, $P = 0.805$; juveniles versus adults, $\chi^2 = 0.781$, *d.f.* = 1, $P = 0.377$; yearlings versus adults, $\chi^2 = 0.113$, *d.f.* = 1, $P = 0.737$). Mortality of adult females was higher than mortality of yearling females ($\chi^2 = 16.13$, *d.f.* = 1, $P < 0.001$) and juvenile females ($\chi^2 = 49.33$, *d.f.* = 1, $P < 0.001$). Mortality of juvenile

TABLE 1.—*Age and sex distribution of mortality in feral cattle on Amsterdam Island during 1988.*

Sex and age classes	J	F	M	A	M	J	J	A	S	O	N	D	Total
Males													
Juveniles								13	4	5			22
Yearlings								2	4	2			8
Adults		1		1	1	1	3	8	15	11	2	1	44
Females													
Juveniles							1	8	1	4			14
Yearlings					1		1	4	4	5	1		16
Adults		1		4	2	3	31	83	45	21	7	2	199

and yearling females did not differ significantly ($\chi^2 = 3.63$, *d.f.* = 1, $P = 0.057$).

Mortality of adult females (47.2% of 422) was significantly higher than for adult males (18.3% of 241; $\chi^2 = 55.18$, *d.f.* = 1, $P < 0.001$), while mortality of juvenile females was significantly lower than that of males (11.7% of 120 versus 22.4% of 98, $\chi^2 = 4.55$, *d.f.* = 1, $P = 0.033$). Mortality of female yearlings did not differ significantly from the mortality of male yearlings (21.9% of 73 versus 20.5% of 39; $\chi^2 = 0.03$. *d.f.* = 1, $P = 0.86$).

DISCUSSION

The female-biased sex ratio observed in February 1988 among yearlings and adults likely was due to selective hunting pressure before the study. The observed mortality probably was due to lack of food because no signs of disease were noted. Moreover cattle were emaciated and dying and appeared too weak to search for food. Harsh weather could have affected the extent of mortality, but Hall and Hall (1988) suggested that weather other than rain was unlikely to influence dynamics of cattle populations, and monthly rainfall figures in 1988 were not different from monthly means recorded since 1950. Similarly, wind and temperature patterns in 1988 were not different from monthly means recorded since 1950.

Winter corresponds with the period when physical condition of males was at its poorest in 1985 and 1986 (L. Daycard, pers. comm.). A winter decline in body condition of cattle on Amsterdam Island (males and females) also was observed qualitatively during winter 1987 (B. Leroy, pers. comm.). This decline might reflect an annual winter decrease in forage quantity or quality. Unfortunately, no data on annual variation in vegetation are available.

No difference was observed between age-classes of males. In contrast, mortality of adult females was higher than for yearlings and juveniles. Why would more adult females starve? Perhaps the census of carcasses underestimated juvenile mortality because of the difficulty to locate carcasses of small size. Such a bias, however, is unlikely because carcasses were easily found. Alternatively, adult females might have had much higher energetic needs than other age-classes because of reproductive costs. According to Berteaux and Micol (1992), 64% of females ≥ 2 years old are lactating in summer (6% for females <2 years old). Thus, at least 64% of females ≥ 2 years old are pregnant in winter. The primary reproductive costs to females are the high energetic demands of gestation and lactation that can occur simultaneously in cattle on Amsterdam Island, when a pregnant female is nursing the young of the previous year (Berteaux and Micol, 1992). As births mainly occurred from October to December (Berteaux and Micol, 1992), the observed period of high mortality corresponds with the last 3 months of pregnancy for many females, when the accelerated growth of the fetus increases the energy requirements of mothers (Moen, 1973).

The observed pattern of juvenile mortality is in agreement with the prediction of higher mortality of males. On Amsterdam Island, births mainly occur from October to February (Daycard, 1990; Lesel, 1969). Therefore, most juveniles were 5–9 months old at the beginning of the mortality period (July). According to field observations (D. Berteaux, pers. obs.), juveniles at this age satisfy their energy requirements both by nursing and grazing. Milk has a buffering effect against shortages of grass, but this effect diminishes with time (Baker and Baker, 1978). Further, juvenile males demand more milk than females, and this enhanced demand persists throughout the suckling period (Roy, 1980; Somerville et al., 1983). This implies two ways by which a period of food shortage may induce a higher mortality of juvenile males. First, when grass is scarce, mothers have less milk, and this may affect juvenile males more severely than females because of their greater needs. Second, lack of grass may have a direct effect on juvenile survival because of its importance in their diet, particularly later in the suckling period.

Sex differences in juvenile mortality might also be interpreted as a consequence of adaptative parental manipulation of the sex ratio. Where sons cost more to rear than daughters, parents might terminate investment prematurely if they cannot afford the expenditure necessary to rear them successfully. However, no study shows clear evidence of parental discrimination against offspring of one sex, in cattle or in any other species (Clutton-Brock, 1991).

In most well-studied mammal species (e.g., humans, rats, pigs), females are better able than males to withstand a shortage of food (Widdowson, 1976). This pattern often has been observed in the wild for dimorphic ungulates (Clutton-Brock and Albon, 1985), so the higher mortality of adult females in cattle on Amsterdam Island is in sharp contrast with what was expected. A similar pattern of adult mortality has been reported for the population of elephants *Loxodonta africana* of Tsavo National Park, Kenya, in which a female-biased mortality occurred during a prolonged drought (Corfield, 1973). This differential mortality apparently was related to a difference in habitat use between the sexes. Females that were rearing offspring had to stay near permanent water because their young were dependent on water sources, whereas adult males could move elsewhere. Competition for food was consequently higher among females than among males, and resulted in lower female survivorship. Sex differences in habitat use also have been shown on Amsterdam Island, where males occur at higher altitudes than females in winter (Daycard, 1990). For instance, in July only 14% of males were below 300 m, whereas 80% of females were in this zone. According to Petit (1977) and Daycard (1990), food might be more abundant but of poorer quality in higher altitudes. The observed difference in habitat use remains unexplained, but Daycard (1990) suggested that high-quality food is needed by females because of high energetic costs of reproduction. Therefore, they might be obliged to use habitat where food is scarce, whereas males could use areas where food is more abundant though of poorer quality. A consequence might be a difference between sexes in available food, that may lead to a more important food shortage in areas occupied by females. The temperature gradient from the wintering elevations of females with young to the higher elevations used by adult males may be of importance because of the lower surface-to-body mass ratio of adult males compared to juveniles, but this is uncertain.

The selective hunting of males during years previous to the study has reduced numbers of males. As a result, competition among males could have been artificially reduced, leading to less competition within male than female groups, thus to a differential mortality during a food shortage. Alternatively, the culling of males may have resulted in few males reaching old age, whereas females live longer. Thus, in times of exceptionally high mortality among adult animals, the bias apparently would be toward the female because there are more old females than old males. Although this may have reinforced the observed pattern of differential mortality between sexes, it cannot be the major cause of such mortality. Indeed, a male-biased sex ratio resulting from higher natural mortality of females was observed in nonhunted areas located in the southern part of Amsterdam Island (Berteaux and Micol, 1992), and also before hunting pressure could have been a source of differential mortality (in 1952 an estimation of the sex ratio of the population indicated five males for one female (Fiasson and Diallo, 1953).

It also seems possible to speculate (Berteaux and Micol, 1992) that the female-biased mortality might be a consequence of the selective pressures exerted by man during domestication. Domestication probably made females more reproductively precocious and males more behaviourally docile than the ancestral forms. As a consequence, costs of reproduction may have been artificially increased in females and diminished in males (less fights), contributing to a higher mortality of females than of males, which is at marked variance with what is seen in wild, sexually dimorphic mammals.

The relative contribution of different traits to differences in mortality is still far from clear. Are differences in mortality principally a consequence of sex differences in size or growth rate, space use, or energetic needs during reproduction, or previous selection exerted during domestication? Measures of energy requirements in both males and females, together with estimations of spatial and temporal variability in forage availability are needed to test these hypotheses.

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LITERATURE CITED

BAKER, R. D., AND J. M. BAKER. 1978. Milk-fed calves, 4. The effect of herbage allowance and milk intake upon herbage intake and performance of grazing calves. Journal of Agricultural Science (Cambridge), 90:31–38.

BERTEAUX, D., AND T. MICOL. 1992. Population studies and reproduction of feral cattle (*Bos taurus*) of Amsterdam Island. Journal of Zoology (London), 228:265–276.

BOUSSES, P., B. BARBANSON, AND J. L. CHAPPUIS. 1991. The Corsican mouflon (*Ovis ammon musimon*) on Kerguelen Archipelago: structure and dynamics of the population. Symposium "Ongulés/Ungulates 91," Société Française por l'Etude et la Protection des Mammifères et Institut de Recherche sur les Grands Mammifères, Toulouse, France, 661 pp.

BOWYER, R. T. 1991. Timing of parturition and lactation in southern mule deer. Journal of Mammalogy, 72:138–145.

CHILD, G. 1972. Observations on a wildebeest die-off in Botswana. Arnoldia, 31:1–13.

CLUTTON-BROCK, T. H. 1991. The evolution of parental care. Princeton University Press, Princeton, New Jersey, 352 pp.

CLUTTON-BROCK, T. H., AND S. D. ALBON. 1985. Competition and population regulation in social mammals. Pp. 557–575, *in* Behavioural ecology (R. M. Sibly and R. H. Smith, eds.). Blackwell Scientific Publications, Oxford, United Kingdom, 420 pp.

CLUTTON-BROCK, T. H., S. D. ALBON, AND F. E. GUINNESS. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature, 313:131–133.

CLUTTON-BROCK, T. H., P. H. HARVEY, AND B. RUDDER. 1977. Sexual dimorphism, socionomic sex ratio and body weight in primates. Nature, 269:797–800.

COELHO, A. M. 1974. Socio-bioenergetics and sexual dimorphism in primates. Primates, 15:263–269.

CORFIELD, T. 1973. Elephant mortality in Tsavo National Park, Kenya. East African Wildlife Journal, 11:339–368.

DAYCARD, L. 1990. Structure sociale de la population de bovins sauvages de l'ile Amsterdam, sud de l'Océan Indien. Terre Vie, 45:35–53.

FIASSON, R., AND R. DIALLO. 1953. Epizootie bovine à la nouvelle Amsterdam. Revue d'Elevage et de Médecine Vétérinaire des Pays Tropicaux, 6:1–18.

FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. Canadian Department of Indian Affairs and Northern Development, Wildlife Service Report Series, 11:1–71.

GRUBB, P. 1974. Population dynamics of the Soay sheep. Pp. 242–272, *in* Island survivors: the ecology of Soay sheep on St. Kilda (P. A. Jewell, C. Milner, and J. M. Boyd, eds.). Athlone Press, London, United Kingdom, 386 pp.

HALL, S. J. G., AND J. G. HALL. 1988. Inbreeding and population dynamics of the Chillingham cattle (*Bos taurus*). Journal of Zoology (London), 216:479–493.

ILLIUS, A. W., AND I. J. GORDON. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology, 56:989–999.

KLEIN, D. R. 1968. The introduction, increase and crash of reindeer on St. Mathew Island. The Journal of Wildlife Management, 32:350–367.

LESEL, R. 1969. Etude d'un troupeau de bovins sauvages vivant sur l'ile Amsterdam. Revue d'Elevage et de Médecine Vétérinaire des Pays Tropicaux, 22: 107–125.

MILLAR, J. S., AND G. J. HICKLING. 1990. Fasting endurance and the evolution of mammalian body size. Functional Ecology, 4:5–12.

MOEN, A. N. 1973. Wildlife ecology. W. H. Freeman and Company, San Francisco, 458 pp.

PETIT, J. P. 1977. Adaptation des bovins à l'écosystème constitué par l'île Amsterdam. Pp. 1181–1202, *in* Adaptation within Antarctic ecosystems, Third Scientific Committee for Antarctic Research. Symposium on Antarctic Biology (G.A. Llane ed.). Smithsonian Institution, Washington, D.C., 276 pp.

RALLS, K., R. L. BROWNELL, AND J. BALLOU. 1980. Differential mortality by sex and age in mammals, with specific reference to the sperm whale. Report of the International Whale Commission, Special Issue, 2:233–243.

ROBINETTE, W. L., J. S. GASHWILER, J. B. LOW, AND D. A. JONES. 1957. Differential mortality by sex and age among mule deer. The Journal of Wildlife Management, 21:1–16.

ROY, J. H. B. 1980. The calf. 4th ed. Butterworth, London, United Kingdom, 442 pp.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics. SAS Institute Inc., Cary, North Carolina, 956 pp.

SOMERVILLE, S. H., B. G. LOWMAN, R. A. EDWARDS, AND G. JOLLY. 1983. A study of the relationship between plane of nutrition during lactation and certain production characteristics in autumn-calving suckler cows. Animal Production, 37:353–363.

STEENKAMP, J. D. G. 1970. The effect of breed and nutritional plane on the chronology of teeth eruption in cattle. Rhodesian Journal of Agricultural Research, 8:3–13.

TALBOT, L. M., AND M. H. TALBOT. 1963. The wildbeest in western Masailand. East Africa Wildlife Monograph, 12:1–88.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179, *in* Sexual selection and the descent of man. Adline Publishing Company, Chicago, 388 pp.

WIDDOWSON, E. M. 1976. The response of the sexes to nutritional stress. Proceedings of the Nutritional Society, 35:175–179.

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