J. Zool., Lond. (1992) **228,** 265–276

Population studies and reproduction of the feral cattle (*Bos taurus*) of Amsterdam Island, Indian Ocean

D. BERTEAUX* AND T. MICOL

Centre d'Etudes Biologiques de Chizé, 79360 Beauvoir sur Niort, France

(*Accepted 30 September 1991*)

(With 3 figures in the text)

Amsterdam Island has supported a population of feral cattle since 1871. In 1987 a fence was erected across the island, and in 1988 and 1989 the whole population ($n = 1059$) living south of the fence (study area) was removed. Nine hundred and sixty one culls were analysed. Age of calves indicated that reproduction was seasonal, as 78% of births occurred within four months. Age at first calving ranged from 2–4 years. An estimation of the fertility (rate of conception) was 0·73 foetuses per cow per year.

In the north part of the study area, 50–80 males have been killed for beef each year since 1951. The effect of hunting was analysed and a zone where cattle had been free from human interference was defined. In this zone sex ratio was biased towards males (252 M:201 F), owing to female biased mortality in individuals older than three years. The cause of the biased mortality might be a differential use of food resources between sexes.

Contents

Introduction

The feral cattle of Amsterdam Island (37° 40′ S, 77° 35′ E) have lived in the wild since 1871 (Lésel, 1969; Petit, 1977; Daycard, 1990). The herd initially numbered five individuals which had been imported from La Réunion by a settler, who released them after a few months (Lésel, 1969). They are descendants of French stocks present on La Réunion which at that time comprised the following breeds: Jersey, Tarentaise, Grey Alpine, Breton Black Pied. They are small-bodied and have horns of medium length, and many different patterns of colour are present including one reminiscent of the ancestral aurochs (Olson, 1980) which is common among males. They have neither predators nor competitors and the only human interference is the removal of 50–80 individuals each year, mainly adult and subadult males, in order to provide fresh meat for people living on Amsterdam Island. The cattle herd inhabited a total surface of 3000 ha and numbered

---

* Present address: Groupe de Recherche en Ecologie, Nutrition et Energétique, Département de Biologie, Université de Sherbrooke, Sherbrooke (Québec), Canada J1K 2R1

about 2000 at the beginning of 1988. There is no supplementary feeding, mineral supplementation, or routine or emergency veterinary care.

These cattle represent one of the very few feral herds of *Bos taurus* anywhere in the world. The only other herd to have been studied in any detail is that of Chillingham in northern England (Hall, 1986, 1989; Hall & Hall, 1988), which has inhabited a 134-ha park possibly since the 13th century. This herd numbered 46 in April 1991 (S. J. G. Hall, pers. comm.).

Prompted by evidence of pernicious influence of Amsterdam cattle on the unique flora and fauna of the island, a fence was erected across the isle in 1987 (Decante *et al.*, 1987), and all the cattle located to the south of it were removed. This provided the material required for defining demographic characteristics of the population. The present paper, which uses analysis of 961 culls, reports on herd size, density, age structure, sex ratio, mortality, fecundity and seasonality of reproduction. Furthermore, it compares the demographic characteristics of this population with what is known about *Bos taurus* and other polygynous ungulates. There are no plans for the elimination of the remaining cattle, which may represent a genetic resource worthy of conservation. This herd may possess unusual adaptations, particularly with regard to water economy (Petit, 1977).

Study area

Amsterdam Island is a 55 km^2 volcanic dome that rises to 881 m. It is one of the French Southern Indian Ocean Islands. The island is uninhabited, except for the transitory personnel of a scientific base which is manned by 35 men on average, relieved annually. It occupies a cool-temperate biogeographic realm characterized by mean air temperatures of 13·8 °C. The hottest month is February (17 °C) while the coldest is August (11 °C). One hundred and fifty days per year, wind speed exceeds 16 m.s^{-1}. The mean annual rainfall is 1120 mm and there are 239 rainy days per year (data from the Meteorological Office Recording Station located at Amsterdam Island).

The vegetation consists of four main communities (Jolinon, 1985; Decante *et al.*, 1987; Daycard, 1990; Frenot & Valleix, 1990):

(a) below 250 m, the vegetation cover is predominantly an overgrazed grassland often interrupted by rock outcrops. Original plant communities have been completely modified by cattle grazing and successive fires, and now most of the plant species are introduced ones (*Holcus lanatus*, *Leontodon taraxacoïdes*, *Cirsium vulgare*, *Poa annua*). In the south part of the island, *Scirpus nodosus* dominates a large area. *Phylica nitida* trees and ferns were formerly widespread but now occur only in sheltered areas free from grazing;

(b) from 250 to 350 m, 30–60% of the surface is occupied by *Juncus effusus* and *Scirpus nodosus*, while *Scirpus aucklandicus* and *Blechnum penna-marina* are also present;

(c) from 350 to 550 m, slopes are covered mainly by ferns and mosses. Both are endangered by cattle trampling;

(d) above this, vegetation comprises dwarf shrub (*Acaena magellanica*), sphagnum bogs and mosses (Clark & Dingwall, 1985). This is the only part of the island which has not been colonized by cattle.

Methods

All 1059 cattle south of the fence were removed, 932 being shot between 3 March and 18 April 1988, and the remaining 127 individuals from 20 January to 27 February 1989.

Nine hundred and sixty-five carcasses were classified as to sex and located on a 1:25000 map (500×500 m^2 grid). The distribution of the carcasses is believed to be representative of the distribution of individuals before the hunting period, as animals never moved far from their pasture when hunted.

The ages of 961 individuals were determined from the chronology of eruption of permanent incisors (Steenkamp, 1970), and from size and rate of attrition of milk teeth in individuals less than 2 years old. Six age classes were consequently distinguished, as follows: 0–1 years, 1–2 y, 2–3 y, 3–4 y, 4–5 y, $\geqslant 5$ y. No independent check of these ages was possible as dates of birth were not known. The relationship between age and dental development is not strict (Andrews, 1975), being influenced by many factors including breed and nutrition (Brookes & Hodges, 1979; Graham & Prise, 1982). None the less, for comparisons within a single population, this method is considered to be valid.

Age of juveniles was determined according to the relation between length of horns and age (Daycard, unpubl.): juveniles younger than 1 month do not have horns and the area where horns will grow is covered by hairs; at 1 month of age, hairs are replaced by horny skin; when 2 months old, juveniles have movable horns 1 cm long; at 3 months of age, horns are 2 cm long but still movable; then the horns become fixed and the length according to age is 3 cm (4 months); 4 cm (5 m); 5 cm (6 m); 6 cm (7 m); 7 cm (8 m); 8 cm (9 m); 9 cm (10 m); 10 cm (11 m). Published data on the relationship between age and length of horns are lacking. At Chillingham, a bull of 18 months old and 100 kg body weight may have horns 24 cm long (Hall, 1985), while a more general figure for horn length at this age is 16 cm (Habermehl, 1975).

Data recorded in 1988 and 1989 were gathered for analysis after 1 year had been subtracted from the ages of individuals killed in 1989.

Amsterdam Island cattle are believed (Petit, 1977) to stop growing by the age of 5 years. In order to assess the dimorphism of sexes, 19 individuals $\geqslant 5$ years old (14 males and 5 females) were weighed using a spring balance (max. 500 kg, precision 10 kg) suspended from a tripod.

Three hundred and ninety-four females more than 1 year old were scored as lactating or dry. In 76 of them, chosen at random, foetuses when present were sexed and weighed. For foetuses younger than 2 months, age was determined after Salisbury & Van Demark (1961) while the formula of Hugget & Widdas (1951) was used for those older than 2 months. The formulae were applied with the following gestation period and birth weight: 280 days (Asdell, 1964) and 20 kg (T. Micol, pers. obs. for 2 individuals). Conception and birth dates for each calf were calculated, respectively, as the sampling date minus foetal age and the conception date plus 280 days.

For data processing, 3 zones were defined with reference to the intensity of the hunting pressure during the years previous to the study, which had not been uniform over the whole area (Fig. 1). Zone I (767 ha) was located in the south part of the island, where cattle had never been hunted. Zone II (520 ha) was situated north of zone I, where hunting was rare as only 5–10 males (no females) were shot each year (J. P. Le Guillou, pers. comm.). Zone III (377 ha) was located north of zone II and was characterized by a very high hunting pressure during the years previous to study, as 30–50 animals (mainly males) were shot every year (J. P. Le Guillou, pers. comm.).

Statistical tests are described by Sokal & Rohlf (1981), means are accompanied when appropriate by the standard deviation.

Results

Herd size and spatial distribution

The 1059 individuals which were shot occupied a total surface of 1664 ha (density: 0·64 ind./ha). Of the 965 individuals whose location was known, 852 (88·3%) were found below an altitude of 250 m (Fig. 1). The mean altitude at which males were found ($155{\cdot}3$ m $\pm 83{\cdot}5$, $n = 497$) did not differ significantly ($t = 0{\cdot}079$, $P > 0{\cdot}05$, $d.f. = 963$) from the mean altitude at which females were found ($154{\cdot}9$ m $\pm 80{\cdot}9$, $n = 468$).

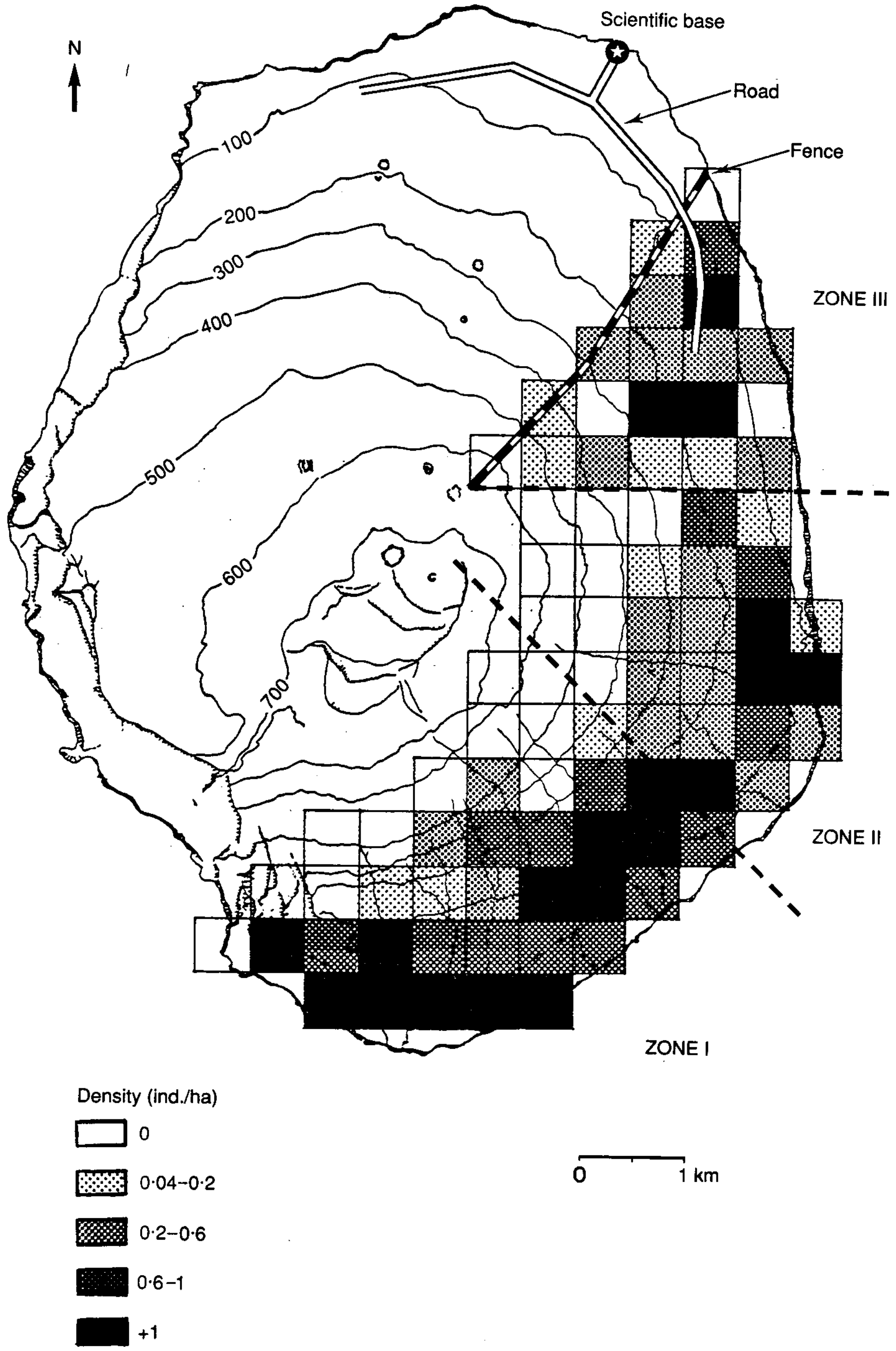

FIG. 1. Sketch map of Amsterdam Island showing spatial distribution of cattle removed. All cattle were removed from south of the fence. Zones I, II and III are separated by dotted lines.

TABLE I (a)

Age distribution of 468 male cattle (percentages in parentheses), classified according to the areas of Amsterdam Island where they were killed. A further age breakdown is available from the authors. Hunting pressures applied in the years previous to this study are indicated (see text for further details)

	Age (years)			
Area	0–2	2–5	>5	Totals
I (no hunting)	55 (21·8)	45 (17·9)	152 (60·3)	252 (100·0)
II (light hunting)	56 (41·5)	36 (26·7)	43 (31·9)	135 (100·0)
III (heavy hunting)	47 (58·0)	17 (21·0)	17 (21·0)	81 (100·0)

G test for homogeneity: $G = 59{\cdot}74$, $d.f. = 4$, $P < 0{\cdot}001$

TABLE I (b)

Age distribution of 493 female cattle. See caption for Table I (a)

	Age (years)			
Area	0–2	2–5	>5	Totals
I	65 (32·3)	63 (31·3)	73 (36·3)	201 (99·9)
II	40 (30·3)	37 (28·0)	55 (41·7)	132 (100·0)
III	50 (31·3)	47 (29·4)	63 (39·4)	160 (100·1)

G test for homogeneity: $G = 1{\cdot}764$, $d.f. = 4$, P N.S.

Age structure

In the case of male cattle, the age structures differed significantly among the three areas (Table Ia).

An unplanned test of homogeneity of replicates (Sokal & Rohlf, 1981) indicated that the populations of areas II and III did not differ (G = 2·8786, N.S.), indicating that the heterogeneity arose from the population of area I.

For females, age structure did not differ according to area (Table Ib).

A complete account of the age structure of this population would include life tables but these cannot be calculated because rates of increase of the population are not known.

Sex ratio

The sex ratio in zone I differed significantly from 1:1 (252 M:201 F, binomial test: $P < 0{\cdot}01$), while in zone III there were significantly fewer males than females (81 M:160 F, binomial test: $P < 0{\cdot}01$). In zone II, there was no significant difference between male and female numbers (135 M:132 F, binomial test: $P > 0{\cdot}05$).

In order to understand the contrast observed between the sex ratios of zones I and III, the sex ratio was analysed in each age-class of these two zones (Fig. 2). In each zone, the sex ratio did not

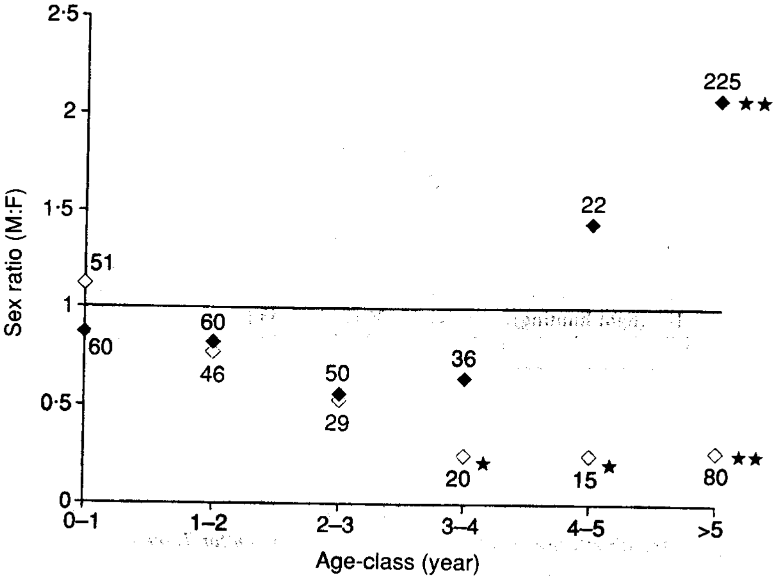

FIG. 2. Sex ratios observed in zone I (◆) and III (◇) for six age-classes. Sample sizes are given in the figure. Binomial test: observed sex ratio is compared to 50:50 ratio. ★: significance level 0·05; ★★: to 0·001.

differ significantly from parity in juveniles, but it tended to deviate towards females until age-class 2–3 years (though the deviation was not significant). This tendency was then maintained in older age-classes in zone III and led to a significant deviation of sex ratio towards females in individuals older than three years. In zone I the tendency was stabilized and led to a strong deviation of sex ratio in favour of males in individuals older than five years (see Fig. 2 for results of statistical analysis).

Thirty-eight foetuses were found in the 76 females which were autopsied. The sex of eight of them could not be determined because they were too young. The sex ratio of the 30 sexed foetuses was 16 M:14 F, and did not differ significantly from parity (binomial test: $P > 0{\cdot}5$).

Reproduction

Season of birth

Birth dates of calves sampled in 1988 ($n = 109$) were assessed from their age and are represented in Fig. 3a. The observed distribution at the birth dates is not significantly different from a normal distribution (χ^2 test of goodness of fit to an expected normal distribution of same mean and standard deviation: $\chi^2 = 9{\cdot}42$, $d.f. = 9$, $P > 0{\cdot}05$). Seventy-eight per cent of births occurred from mid-September to mid-January (50·5% occurred in October and November). The median birth date was 17 November (S.D. = 47 days).

Extrapolation of birth dates on the estimated ages of 15 foetuses collected in March 1988 (Fig. 3b) were consistent with the above results.

Extrapolation of birth dates on the estimated ages of 23 foetuses collected in January and February 1989 (Fig. 3c) showed a marked difference from the above-mentioned results, indicating earlier, and less synchronized conceptions.

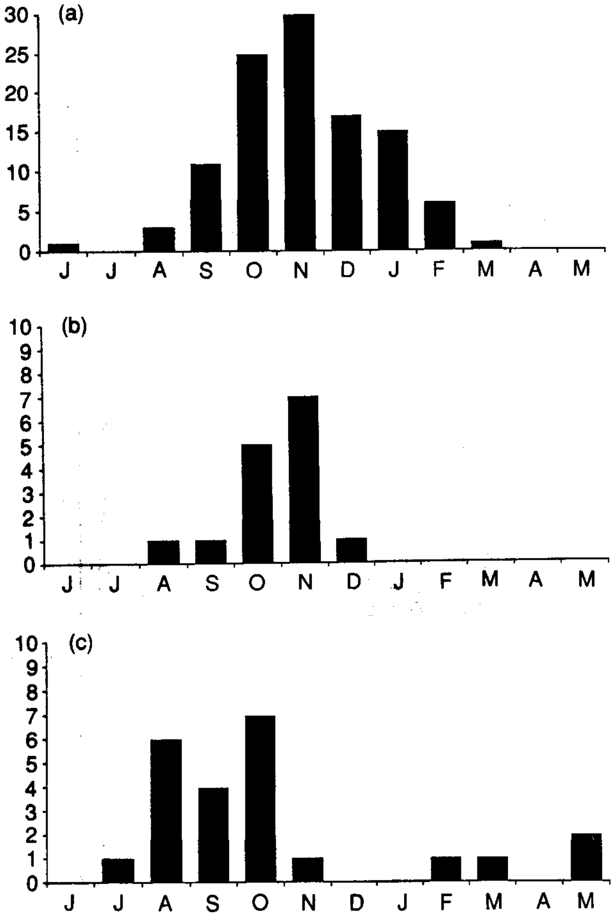

FIG. 3. Distribution of estimated dates of birth of: (a) calves sampled in 1988 ($n = 109$); (b) foetuses sampled in March 1988 ($n = 15$); and (c) foetuses sampled in January–February 1989 ($n = 23$).

Pregnancy and lactation rates of cows

Data on pregnancy come from the autopsied sample of 76 cows while lactation data come from the entire sample of 394 females.

In March 1988, 15 foetuses were found in post-mortem analysis of 30 cows, while in January–February 1989, 23 foetuses were found in post-mortem analysis of 46 cows. Thus 50% of females were pregnant in both investigations. Data of 1988 and 1989 have been gathered in Table II, where pregnancy and lactating rates of cows are presented according to their age.

Body mass

Males (389·6 kg ± 42·8, $n = 14$) were significantly heavier ($t = 4{\cdot}26$; $P < 0{\cdot}01$, $d.f. = 17$) than females (293·0 kg ± 45·8, $n = 5$).

TABLE II

Pregnancy and lactation in (a) 30 female cattle autopsied in March–April 1988, (b) 46 female cattle autopsied in January–February 1989, and (c) 318 female cattle whose lactation state, but not pregnancy, was recorded

Age-class (year)	Number		Number pregnant only		Number lactating only		Number pregnant and lactating		Number neither pregnant nor lactating		Lactation status only scored (c)		
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)	Number	Lactating	%
1–2	7	16	4	2	1	0	0	0	2	14	50	3	6
2–3	3	5	2	3	1	1	0	1	0	0	58	26	45
3–4	2	5	1	2	1	1	0	2	0	0	35	26	74
4–5	3	7	1	3	1	2	1	2	0	0	19	11	58
>5	15	13	3	3	8	5	3	5	1	0	156	109	70
Total	30 (100%	46 100%)	11 (37%	13 28%)	12 (40%	9 20%)	4 (13%	10 22%)	3 (10%	14 30%)	318	175	55

Discussion

Distribution and density

The calculated density (0·64 ind./ha) is calculated from the total surface occupied by cattle (Fig. 1). The area where cattle could feed was smaller than the whole area considered, because of rock outcrops and impenetrable zones of *Scirpus nodosus* (10–20% and 5–10% of the total surface, respectively; D. Berteaux & T. Micol, unpubl. data). The density of individuals per surface of available pasture might therefore be 0·75–0·91 ind./ha. These densities were very high compared to the resources, and overgrazing had been a consequence, observed by Lésel (1969), Petit (1977) and Decante *et al.* (1987). On Swona, Orkney Islands (Hall & Moore, 1986), there are 0·29 ind./ha and at Chillingham there are 0·39 cattle and 2·24 sheep per hectare (Hall, 1989).

Seasonality of breeding

Husbanded cattle, and the free-ranging herd at Chillingham, breed all year round (Hammond, 1927; Asdell, 1964; Hall & Hall, 1988). On Amsterdam Island, the present study confirms the findings of Lésel (1969) and of Daycard (1990), that there is a rut from January to March (the austral summer) with calvings concentrated in the period October–December. This is probably due to poor nutrition extending the post-partum anoestrus (Hansen, 1985) and it is predicted that improved nutrition would lead to year-round calving.

The finding that the conceptions of 1988 were earlier and not so synchronized as the conceptions of 1987 seems to confirm this prediction, as females remaining in 1988 were probably not affected by food shortage.

Age at first reproduction

Of the 73 females $\leqslant 2$ years old (Table II), four (6%) were lactating, indicating that they were rearing a calf. This implies that females could conceive before being 15 months old, but it was evidently rare. Alternatively, it is possible that dental development had been retarded by the demands of pregnancy and these ages may have been underestimated. Conception before two years old was more frequent. Of the 23 autopsied females $\leqslant 2$ years old, six (26%) were pregnant. This ratio was probably underestimated because the period of collection was before the end of the rutting period. This is confirmed by the observation that 29 of the 66 (44%) females 2–3 years old were lactating. It therefore appears that the earliest age of reproduction probably varies among cows but is only 2–3 years for most of them (all eight females 2–3 years old were pregnant, lactating or both). These results indicate that the first calf is usually born when the cow is between two and four years of age.

Age at first breeding varies widely among cattle. It is partly genetically determined (Toelle & Robison, 1985) but in practice, farmers may delay breeding for such reasons as avoidance of calving difficulties (Makarechian, Berg & Weingardt, 1982), or because, as has been found in Swiss cattle (Michel, 1988), the optimal first calving age may depend on whether cows are to be used for milk production (optimum 25·5–28 months) or for dual purpose, i.e. milk and beef production (27·5–30 months).

This is the first account of age at first calving in cattle free of human interference where this important reproductive parameter has been defined by autopsy. The only other account appears to be that relating to Chillingham cattle (Hall, 1979). These are believed to produce their first calf at the age of 3·5–5 years though when the herd was much smaller in numbers first calving was observed at ages as young as 1 year 10 months (average 2 years 7 months). However, these conclusions are not based on autopsies.

The prevalence of early calving in the Amsterdam Island cattle, in spite of the very obvious nutritional deficiencies, implies that factors other than food availability may be implicated in the onset of puberty in these female cattle. One such factor could be the presence of large numbers of bulls, which may prompt early puberty through a pheromonal effect (Izard & Vandenbergh, 1982).

The persistence of early puberty in this population may be reconciled with its current absence from the Chillingham herd, by postulating that the Amsterdam Island cattle are relicts of stocks which had undergone a much longer period of selective breeding. Such breeding could have fixed a propensity to early maturity.

Fecundity

Overall herd fertility can be estimated from pregnancy data. In March 1988, 50% of sampled cows were pregnant. As conceptions that would have occurred after March could not be taken into account, and as foetuses conceived in March were too small to be found during macroscopical inspection of female reproductive tracts, the observed distribution was truncated. Because the birth distribution is known (Fig. 3a), the distribution of conceptions can be reconstituted (possible foetal mortality is not taken into account). It should have the same standard deviation as the birth distribution, and the same median minus 280 days (gestation period; Asdell, 1964), i.e. 10 February. In 1988, 11 observed foetuses had been conceived before 10 February, and four after. Had the autopsies been effected at the end of the rutting period, 11 foetuses conceived after 10 February would theoretically have been observed. This leads to the conclusion that the 30 autopsied females would have conceived 22 foetuses (0·73 foetuses per cow per year). With a 1 : 1 sex ratio at birth, 0·37 female calves per cow year would be expected. Corresponding figures from Chillingham and from North American beef cattle are 0·29 and 0·42, respectively (Hall & Hall, 1988; Schons, Hohenboken & Hall, 1985).

Effect of hunting

In contrast to what we had anticipated, the comparison of the age and sex structures between the three zones showed great differences. The population in the severely hunted zone (III) was younger than that in the non-hunted zone (I). Moreover, the sex ratio was biased towards females in the hunted zone, whereas it was deviated towards males in the non-hunted zone. The analysis of age and sex structures of zone II, which was geographically intermediate, showed intermediate values.

These results are the consequence of the differences of hunting pressure among the three zones during the years previous to our study. Though zone I was free from hunting, did hunting pressure in zones II and III have any effect on the demographic structure of the herd living in zone I? Daycard (1990 and unpubl.) showed that marked individuals living in hunted areas had fixed home ranges. So it is unlikely that individuals would have moved from zones II or III towards zone I because of hunting. Conversely, could some males have migrated from zone I to zones II and III because of diminution of competition for females in the hunted zones? This hypothesis must not be excluded, but would not have changed the direction of the deviation of sex ratio observed in zone I. As a result, the demographic characteristics of the population of zone I are believed to be fully representative of the demographic characteristics of a population free from human interference.

Demographic structure of cattle free from interference

Nothing is known of the demographic structure of the aurochs, extinct ancestor of domestic cattle. This is why studies of feral cattle are very important in order to provide a basic understanding of the biology of this remarkably successful species. We compare here the structure of the herd located on the non-hunted area of Amsterdam Island (zone I) with the structure of the Chillingham cattle herd. After Hall & Moore (1986), at Chillingham 50% of males ($n = 20$) and 62% of females ($n = 39$) are $\geqslant 3$ years old. These proportions are different at Amsterdam Island, as 71% of males ($n = 252$) and 52% of females ($n = 201$) are $\geqslant 3$ years old. As far as sex ratio is concerned, females comprise 66% of the population at Chillingham (Hall & Moore, 1986), and only 44% on Amsterdam Island.

In cattle the sex ratio at birth is not significantly different from 50:50 (Hall & Hall, 1988, this study), so the predominance of males indicates that females survive less well than males on Amsterdam Island, thus contrasting with Chillingham cattle. According to the results of Fig. 2, we suggest that the deviation of sex ratio towards males is due to a differential mortality between the two sexes in individuals older than three years. This is surprising because Amsterdam Island cattle show pronounced sexual dimorphism (weight males/females = 1·33, this study). It has been observed in a large range of sexually dimorphic mammals (pinnipeds: Stirling, 1975; sperm whale: Ralls, Brownwell & Ballou, 1980; red deer: Clutton-Brock, Guinness & Albon, 1982) that, in adulthood, females survive better than males. So why should these cattle show the reverse effect, namely poorer survival of females? This may be due to the lack of any mechanism to cease breeding in anticipation of bad conditions. There may also be differences between the sexes in the nature of intrasexual competition for food. Hall (1986) suggested that cow-cow competition may be more severe than competition among bulls. The poor survival of cows on Amsterdam Island may be a consequence of such factors as these. Alternatively, Daycard (1990) showed that in winter adult males lived at higher altitude than adult females, and suggested that food was more abundant in the areas occupied by males, though of poor quality. Although we did not find such altitudinal difference as the study was done in summer, this might also be a possible explanation of the observed differential mortality.

It seems at least possible to speculate that the selection pressures exerted by man, which have probably made cows more reproductively precocious and bulls more behaviourally docile than the ancestral forms, may account for this situation which is at such variance with what is seen in wild sexually dimorphic mammals.

The Administration of 'Terres Australes et Antarctiques Françaises' provided financial and logistic support. We are indebted to P. Duncan for advice on sampling methods, and we thank J. P. Leguillou, F. Cavé and members of the 39th and 40th Amsterdam Island missions for their help in the field. The Meteorological Office Recording Station located on Amsterdam Island provided unpublished data.

We wish to thank especially S. J. G. Hall for useful advice and comments on earlier drafts of this manuscript. P. Duncan and P. Le Neindre suggested numerous improvements.

This paper is part of the programme 'Ecology of Birds and Mammals in T.A.A.F.' under the directorship of Dr P. Jouventin.

REFERENCES

Andrews, A. H. (1975). The relationship between age and development of anterior teeth in cattle as determined by the oral examination of 2900 animals between the ages of 12 and 60 months. *Br. Vet. J.* **131:** 152–159.

Asdell, S. A. (1964). *Patterns of mammalian reproduction.* 2nd edn. London: Constable & Co. Ltd.

Brookes, A. J. & Hodges, J. (1979). Breed, nutritional and heterotic effects on age of teeth emergence in cattle. *J. Agric. Sci.* **93:** 681.

Clark, M. R. & Dingwall, P. R. (1985). *Conservation of islands in the Southern Ocean. A review of the protected areas of Insulantarctica.* Cambridge: Cambridge University Press.

Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red deer. Behavior and ecology of two sexes.* Chicago: University of Chicago Press.

Daycard, L. (1990). Structure sociale de la population de bovins sauvages de l'île Amsterdam, sud de l'Océan Indien. *Rev. Ecol. (Terre Vie)* **45:** 35–53.

Decante, F., Jouventin, P., Roux, J. P. & Weimerskirch, H. (1987). *Projet d'aménagement de l'île Amsterdam.* Report S.R.E.T.I.E., T.A.A.F., C.E.B.A.S.

Frenot, Y. & Valleix, T. (1990). Carte des sols de l'île Amsterdam. *CNFRA Publs* **59.**

Graham, W. C. & Prise, M. A. (1982). Dentition as a measure of physiological age in cows of different breed types. *Can. J. Anim. Sci.* **62:** 745–750.

Habermehl, K. H. (1975). *Die Altersbestimmung bei Haus und Labortieren.* 2nd edn. Hamburg: Paul Parey.

Hall, S. J. G. (1979). Studying the Chillingham Wild Cattle. *The Ark* **6:** 72–79.

Hall, S. J. G. (1985). The Chillingham White Cattle. *Br. Cattle Breed. Club Dig.* **40:** 24–28.

Hall, S. J. G. (1986). Chillingham cattle: dominance and affinities and access to supplementary food. *Ethology* **91:** 201–215.

Hall, S. J. G. (1989). The White Herd of Chillingham. *J. R. Agric. Soc.* **150:** 112–119.

Hall, S. J. G. & Hall, J. G. (1988). Inbreeding and population dynamics of the Chillingham cattle (*Bos taurus*) *J. Zool., Lond.* **216:** 479–493.

Hall, S. J. G. & Moore, G. F. (1986). Feral cattle of Swona, Orkney Islands. *Mammal Rev.* **16:** 89–96.

Hammond, J. (1927). *The physiology of reproduction in the cow.* Cambridge: Cambridge University Press.

Hansen, P. J. (1985). Seasonal modulation of puberty and the postpartum anoestrus in cattle: a review. *Livestk Prod. Sci.* **12:** 309–327.

Hugget, A. S. & Widdas, W. F. (1951). The relationship between mammalian foetal weight and conception age. *J. Physiol., Lond.* **114:** 306.

Izard, M. K. & Vandenbergh, J. G. (1982). Priming pheromones from oestrous cows increase synchronization of oestrus in dairy heifers after PGF-2A injection. *J. Reprod. Fert.* **66:** 189–196.

Jolinon, J. C. (1985). *Rapport préliminaire de la Mission Botanique aux îles Saint-Paul et Nouvelle Amsterdam, Décembre 1984–Mars 1985.* Internal report, Terres Australes et Antarctiques Françaises.

Lésel, R. (1969). Étude d'un troupeau de bovins sauvages vivant sur l'île d'Amsterdam. *Revue Élev. Méd. vét. Pays trop.* **22** (I): 107–125.

Makarechian, M., Berg, R. T. & Weingardt, R. (1982). Factors affecting calving performance in range beef cattle. *Can. J. Anim. Sci.* **62:** 345–352.

Michel, A. (1988). *Influence of rearing intensity, first calving age and alpine pasturing on growth and milk performance of different cattle types.* Dissertation ETH 8533 of Eidgnoessischen Technischen Hochschule, Zurich.

Olson, T. A. (1980). Choice of a wild-type standard in color genetics of domestic cattle. *J. Hered.* **72:** 442–444.

Petit, J. P. (1977). Adaptation des bovins à l'écosystème constitué par l'île Amsterdam. In *Adaptation within Antarctic ecosystems*: 1181–1202. Llano, G. A. (Ed.). *Proc. 3rd S.C.A.R. Symp. Antarct. Biol.*

Ralls, K., Brownwell, R. L. & Ballou, J. (1980). Differential mortality by sex and age in mammals, with specific reference to the sperm whale. *Rep. Int. Commn Whal. (Spec. issue)* **2:** 223–243.

Salisbury, G. W. & Van Demark, N. L. (1961). *Physiology of reproduction and artificial insemination of cow.* San Francisco: W. H. Freeman & Co.

Schons, D., Hohenboken, W. D. & Hall, J. D. (1985). Population analysis of a commercial beef cattle herd. *J. Anim. Sci.* **61:** 44–54.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry.* 2nd edn. San Francisco: Freeman.

Steenkamp, J. D. G. (1970). The effect of breed and nutritional plane on the chronology of teeth eruption in cattle. *Rhod. J. agric. Res.* **8:** 3–13.

Stirling, I. (1975). Factors affecting the evolution of social behaviour in the Pinnipedia. *Rapp. P-v. Réun. Cons. perm. int. Explor. Mer* **169:** 205–212.

Toelle, V. D. & Robison, O. W. (1985). Estimates of genetic correlations between testicular measurements and female reproductive traits in cattle. *J. Anim. Sci.* **60:** 89–100.